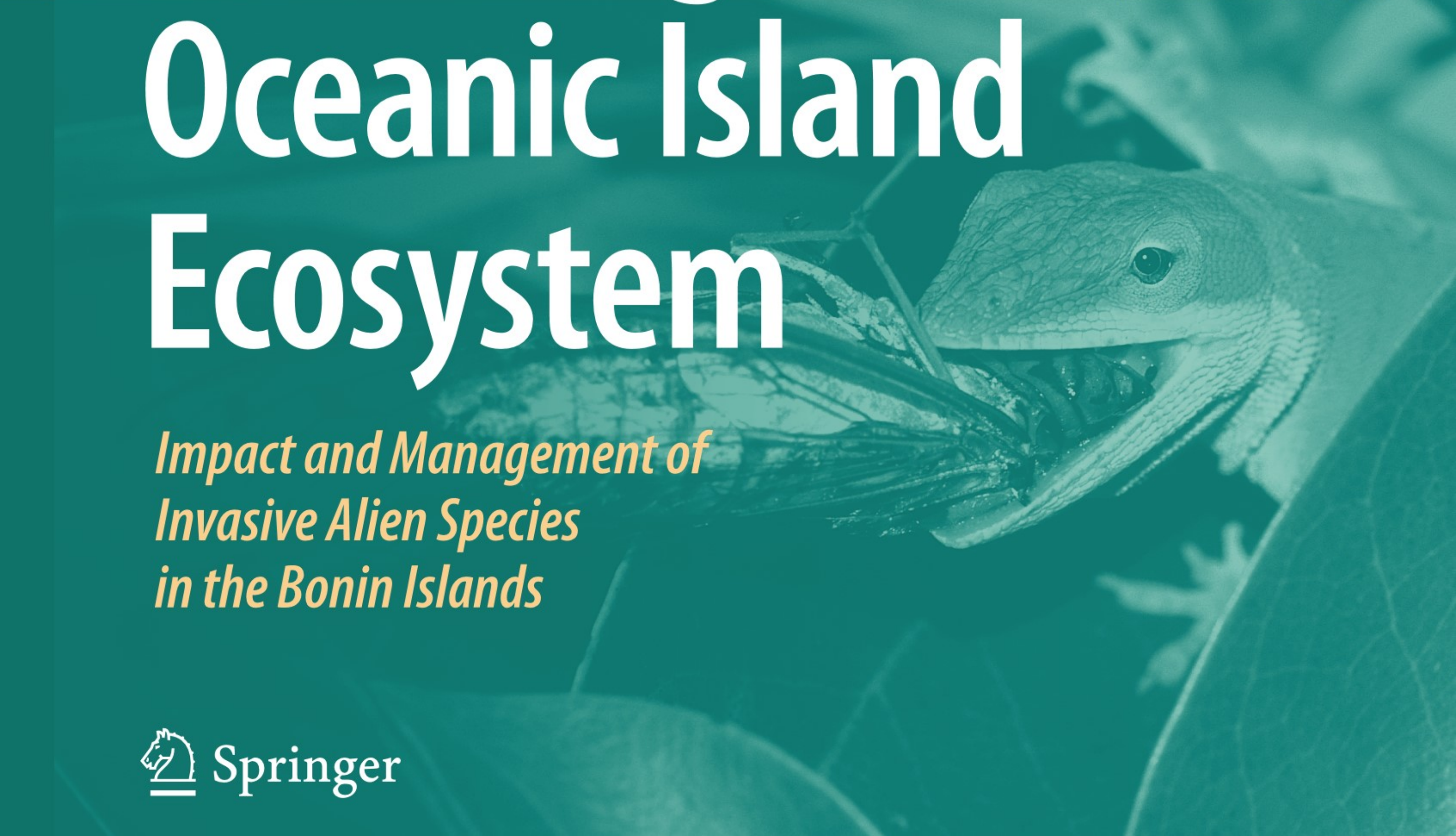
K. Kawakami · I. Okochi
Editors

Restoring the Oceanic Island Ecosystem

Impact and Management of Invasive Alien Species in the Bonin Islands



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Preface

Loss of biodiversity on tropical and subtropical oceanic islands is one of the most pressing conservation issues. These oceanic islands are well known for their unique fauna and flora, which evolved over long periods in isolation from external perturbation. However, the majority of these islands in the Pacific were eventually settled by Polynesians and then by Europeans; by about 200 years ago, only a few island groups remained untouched. The Bonin Islands are one of these groups.

The Bonin Island group is one of the most remote in the world. The islands are located 1,000 km south of Japan off the eastern fringe of Eurasia. They were first discovered by the Japanese in 1670, settled by Westerners from Hawaii in 1830, and finally recognized as a Japanese territory in 1862 on condition that previous settlers would be protected and allowed to remain with full rights. Because of this complicated history, the Bonins have two names. The Japanese refer to the archipelago as the Ogasawara Islands, after the name of the feudal lord Ogasawara, who insisted that he discovered these islands. The Western name for the island group is the Bonins, which originally came from the Japanese word *mounin*, meaning "uninhabited."

Before World War II, these islands were developed for crop farming, pasture land, and fuel wood production. During the war, almost all Japanese residents were evacuated from the islands to the mainland and were not allowed back until 1968, when the United States returned the Bonins to Japan. The forests appeared to recover during the postwar years, but researchers found that alien trees had come to dominate the secondary stands, and endemic insects and snails had declined rapidly. Although the researchers visited the islands mainly to seek new evidence of evolution or to search for new species, they found an island ecosystem in crisis. However, national and local government policy at that time was one of "sustainable development" for the local people, a concept based on the illusion that nature can tolerate increased development if it is carefully planned.

The government eventually changed its policy from one of sustainable development to "sustainable life with nature" after accumulating evidence revealed ongoing ecosystem destruction on the islands. Fortunately, this change was made in time to prevent irreversible damage to the island biota. When the new concept was first adopted, the distributions of destructive alien invaders, such as the green anole (*Anolis carolinensis*) and the predatory flatworm (*Platydemus manokwari*), were restricted to the two main inhabited islands. This allowed remaining endemic species to survive on the other islands. For example, the endemic land snail survives on Anijima Island.

Under the new policy, the role of academics changed. What government and residents of the islands need now from researchers is not just evidence of ecosystem destruction, but ways and means for restoration. Moreover, the actions of the government to restore ecosystems through eradication or management of invasive alien species are being accelerated by the fact that the Bonins have candidate status for UNESCO World Heritage Site listing. The expanded restoration programs have been running for about 15 years.

It is noteworthy that ecosystem problems on the Bonin Islands are common to the majority of Pacific islands, which share many members of a suite of problematic invasive alien species, including cats (*Felis catus*), black rats (*Rattus rattus*), goats (*Capra aegagrus*), pigs (*Sus scrofa domesticus*), cane toads (*Bufo marinus*), European honey bees (*Apis mellifera*), giant African land snails (*Achatina fulica*), predatory flatworms (*Platydemus manokwari*), and plants such as *Leucaena leucocephala*, *Casuarina cunninghamiana* and *Lantana camara*. Research and action investigating these invasive alien species on other islands has been of great assistance to our program, and our experience on the Bonins may be useful elsewhere.

Some invaders of the Bonins, such as bishopwood (*Bischofia javanica*), are currently being investigated, but previously unknown deleterious effects exist, such as the severe declines of endemic insects due to predation by the lizard *Anolis carolinensis*. Anoles are present in Hawaii and the Marianas, where deleterious effects on the insect fauna have not been reported. We are also facing emerging new problems whereby eradication of a dominant alien species may cause population expansion of other alien species previously suppressed by the dominant alien species.

Japanese academics have limited familiarity with oceanic islands because so few are included in the Japanese archipelago, and few workers are engaged in this area of research. Hence, international scientific cooperation among island nations is essential for increasing the conservation knowledge base of Pacific island ecosystems. Research resources available in single countries are insufficient. We have invited researchers from Hawaii, Australia, New Zealand, Spain, and the Galápagos Islands, enabling us to promote our studies and governmental action plans based partially on external advice. We also believe from these discussions that it is important to publish our research in order to share these experiences, which may help conservation on other oceanic island groups. This book was produced for that purpose.

Our research projects have been conducted with the cooperation of experts on a variety of taxa that are representative of the fauna and flora of the Bonins. The findings have been reported in scientific journals and have been applied in government restoration projects on Bonin ecosystems.

We selected 22 articles from among the published works to provide an overview of island conservation issues. Some were originally written in Japanese but have been translated into English for this book. We have also some newly written articles on latest issues. We introduce natural and historical backgrounds to Bonin Island ecosystems in Part I. The next two parts are major components of the book, in which we describe negative effects on island ecosystems of several important invasive species (Part II) and methods used to control these species (Part III). Conclusions from these research undertakings are discussed and summarized in Part IV.

I would like to sincerely thank all the researchers and many other people who participated in our projects. This book presents our common dream for restoring a Japanese oceanic island ecosystem, and we hope that this new synthesis will assist others who work toward conservation on their own islands.

Isamu Okochi, Editor

Acknowledgments

The chapters of this book are mainly the outcome of a series of research projects on the conservation and restoration of the Bonin Islands ecosystems since 1995. We would like to express our appreciation to a great number of researchers who participated in these projects. Discussion with them brought us the recent achievements. Although we could show only some of our outcomes in this book, there were many more results. We express our gratitude to Dr. Robert Cowie, Dr. Julie Denslow, Dr. Fred Kraus, Dr. Alan Tye, Dr. Anna Traveset, Dr. Mark Gardner, and Dr. Donald Drake for their participation in our meetings and for discussion on the management of invasive species in the Bonin Islands. We thank Dr. Koichi Goka, Dr. Hiroyoshi Higuchi, Ryuji Nakayama, Dr. Tadakuni Miyazaki, Dr. Yoshikazu Shimizu, and Kiyoshi Okutomi for their critical comments on our research planning. We express our sincerest gratitude to Dr. Noriko Iwai for her editorial assistance, which greatly supported the procedures. She always motivated us, managed our schedules, and patiently awaited the completion of our work. Without her help, we could not have finished this book on time. We are grateful to the staff of the Ogasawara Wildlife Research Society for their field assistance, and to Dr. Kenji Hata, Dr. Simon Lawson, Nodoka Nakamura and Yukiko Aoyama for providing invaluable assistance with the preparation of newly written or translated manuscripts. We are grateful to Yuko Matsumoto at Springer Japan, the publisher of the book, for her technical support. We also would like to thank the Ogasawara General Office (Ministry of Land, Infrastructure, Transport and Tourism), the Ogasawara Experimental Station, the Ogasawara National Park Ranger Office, the Ogasawara Islands Branch Office of the Tokyo Metropolitan Government, and Ogasawara Village for their receptive cooperation and legal support. Our research projects and the publication of this book were supported financially by the Ministry of the Environment of Japan (Global Environment Research Fund "F-051", Global Environment Research Coordination System Fund).

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Part I
The Bonin Islands

Chapter 1
What's the Bonin Islands?

Kazuto Kawakami

Abstract The Bonin Islands is comprised of oceanic islands located within the subtropical zone of the northwestern Pacific Ocean. Although species richness is low, high endemism is found on the islands due to physical isolation of the unique biota. However, human settlement began in 1830, causing extensive deforestation and the introduction of invasive species. At the height of prosperity, at least 14 islands were colonized and more than 7,000 people lived on them. The islands were under US occupation after World War II until 1968, when they were returned to Japan. Japanese people have since migrated to the islands, and various species have been introduced either intentionally or unintentionally. Insular populations are vulnerable to the devastating effects of introduced predators, competitors, and diseases because they have often evolved in the absence of these biotic factors. The species introduced to the Bonins by humans pose the greatest threat to the current ecosystem.

1.1 Location and Geography

The Bonin Islands are oceanic and arrayed across coordinates 26°33′–27°43′N and 142°05′–142°14′E in the northwestern Pacific Ocean (Fig. 1.1). More than 30 islands and rocks comprise three island groups, the Mukojima, Chichijima, and Hahajima groups. Although broad use of the term "Bonin Islands" sometimes includes the Volcano Islands and three isolated small islands (Nishinoshima, Minamitorishima, and Okinotorishima), we mostly use a narrower terminology here. We refer to the whole islands as the "Ogasawara Islands." Within this book, we include a selection of previously published works, among which island terminology may vary. As the Volcano Islands and the three other small isolated islands are closely related to the Bonins in biogeography and history, we have arbitrarily included information from these islands along with that from the Bonin Islands in the proper sense of the word.

The Bonin Islands are primarily volcanic, dating back to the Tertiary (Kuroda et al. 1981). They are located on the Philippine Sea Plate along its subduction zone at the interface with the Pacific Plate. Each island is relatively small; even the largest island, Chichijima, is only 24 km^2 in area, and the land mass of the whole islands covers just 70 km^2. The climate is subtropical, with monthly mean temperatures on Chichijima ranging from 18 to 28°C and an annual mean temperature of ca. 23°C (Japan Meteorological Agency 2001). Monthly precipitation ranges from 60 to 170 mm, with an annual rainfall of ca. 1,300 mm (Japan Meteorological Agency 2001).

1.2 Fauna and Flora

The biota of oceanic islands is distinct from that of continent because the resident species have never had contact with mainland communities (Carlquist 1974). The ancestors of island species arrived fortuitously after crossing open seas and establishing new populations. Wind dispersal, ocean currents, and bird vectors allowed only a limited number of species to reach the Bonin Islands. The biotas of islands are often species-poor and exist in ecosystem web structures that are simpler than are those in equivalent areas of mainland (Whittaker 1998). This tendency is particularly noticeable on smaller and more remote islands that typically lack indigenous land mammals and amphibians. On the Bonin Islands, no terrestrial vertebrates occur naturally other than the endemic Bonin flying fox *Pteropus pselaphon* and the endemic reptile *Cryptoblepharus nigropunctatus*; no native amphibians or snakes exist (Kuroda 1930; Momiyama 1930). Only 12 resident land bird species and 330 vascular plants are indigenous to the Bonin Islands (Momiyama 1930; Shimizu 2003).

Despite low species richness, the simple food webs of islands promote the evolution of endemism through adaptive radiation in the absence of competitors and/or predators.

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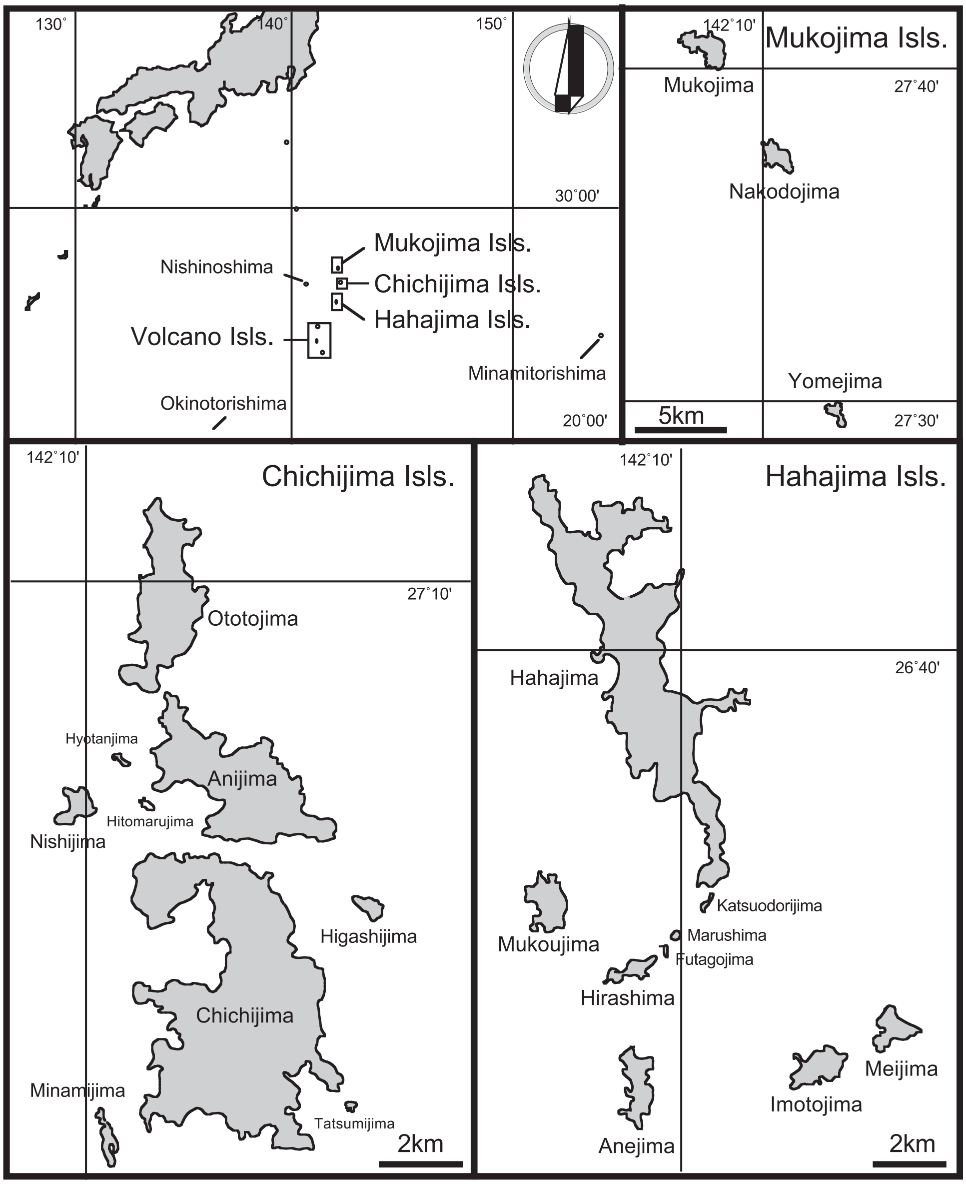

Fig. 1.1 Locations of the Bonin and Ogasawara Islands. The Bonin Islands include Mukojima, Chichijima and Hahajima Islands, whereas the Ogasawara Islands consist of the Bonins, Volcano Islands, and three small remote islands

The proportion of endemism on the Bonin Islands is 40% for all plants and 70% for arboreal species alone (Toyoda 2003); 80% of land birds are endemic species or subspecies (Ornithological Society of Japan 2000). Furthermore, more than 90% of native land snail species are endemic (Kurozumi 1988).

The flora of the Bonin Islands has a close relationship to those of Southeast Asia (e.g. Formosa, the Philippines, and Ryukyu Islands), although it also contains floristic elements found elsewhere, e.g., Japan, Hawaii, and the Polynesian Islands (Kobayashi and Ono 1987). The representative vegetation on Chichijima includes sclerophyllous scrubs dominated by *Distylium lepidotum* and *Rhaphiolepis wrightiana* whereas subtropical wet forests consisting of *Elaeocarpus photiniifolius* and *Schima mertensiana* characterize the vegetation on Hahajima (Okutomi et al. 1983).

1.3 History of Human Disturbances

Prehistoric remains (ca. 800–2000 years old) have been found on Kitaiwoto (Volcano Islands) and Chichijima (Oda 1998). Although the origin of these people is not clear, they may have arrived from the Izu Islands and/or the Marianas (Oda 1998). On many Pacific islands, some or many bird species survived until (but not through) the first contact with humans during prehistoric times (Olson and James 1982; Steadman 1995; Pimm et al. 2006). Although no direct evidence exists, the original fauna and flora may have been disturbed during this age. Prehistoric residents disappeared prior to the recent human repopulation of the Bonin Islands.

During recent history, the first human colonizers of the islands in 1830 were European and Polynesian. There was whaling in the sea around the islands, which served as whaling stations (Tsuji 1995a). The immigrants exploited forests, established farmlands for crops such as sugarcane, corns, and sweet potatoes (Tsuji 1995a), and introduced domestic animals such as pigs, goats, cows, ducks, chickens, cats, and rats, all of which eventually became feral. The Bonin thrush *Cichlopasser terrestris* has never been recorded since its discovery in 1828, and it likely became extinct during this era of human colonization (Greenway 1967).

The Ogasawara Islands were confirmed as Japanese territory in 1862, and Japanese people began extensive colonization in 1876. As a result, deforestation and animal introductions were accelerated. Primary forests were destroyed for wood, fuel, and farmland. *Morus boninensis*, an endangered mulberry species, was nearly eradicated for its valuable timber during this period (Shimizu 2003). On the main islands (Hahajima and Chichijima), all areas amenable to cultivation were converted to sugarcane fields until the value of this crop suddenly dropped in 1910 (Kurata 1983). Subsequently, the sugarcane fields were converted to farms producing vegetables and foliage plants for exportation to the Japanese mainland (Funakoshi 1992). At least 14 islands were successively colonized, and the maximum population of the islands reached approximately 7,711 people in 1944 (Tsuji 1995a). Two endemic species (Bonin pigeon *Columba versicolor* and Bonin grosbeak *Chaunoproctus ferreorostris*), and two endemic subspecies (rufous night-heron *Nycticorax caledonicus crassirostris*, and Bonin Islands white-eye *Apalopteron familiare familiare*) all became extinct during this period (Ministry of the Environment 2002). The non-endemic jungle crow *Corvus macrorhynchos* had also disappeared from the islands by 1920 (Momiyama 1930).

One of the strongest impacts of this age was overexploitation of seabirds for feathers, meat, and guano (Tickell 2000). The short-tailed albatross *Phoebastria albatrus*, for example, became locally extinct on the islands (Higuchi 1984). On Minamitorishima, the easternmost island of Japan, Laysan albatross *P. immutabilis* and black-footed albatross *P. nigripes*, whose numbers were described as "exceedingly abundant in former days," were nearly exterminated within only 6 years of the initial colonization in 1896 (Bryan 1903).

World War (WW) II also had a drastic impact on the biota of the islands. The Japanese government forced approximately 6,900 inhabitants to evacuate the Ogasawara Islands in 1944 (Funakoshi 1992), and the farmlands were left unmanaged. Intensive bombing destroyed the forests on at least Chichijima, Hahajima, and Iwoto (Funakoshi 1992). WWII was also the decisive event for many seabird species on Minamitorishima, where the physical topography was entirely altered during wartime (Kuroda 1954). Approximately 5,000 Japanese troops were garrisoned there, and the island was exposed to severe bombardment (Kuroda 1954). Together, exploitation for feathers and WWII caused the local extinction of nine seabird species on Minamitorishima (Bryan 1903; Kuroda 1954; Chiba et al. 2007).

The Ogasawara Islands were under United States occupation from the end of WWII until their return to Japan in 1968 (Kurata 1983). Only a few locals and the US army remained on Chichijima, Iwoto, and Minamitorishima during this post-war period (Kurata 1983; Tsuji 1995b; Okutomi and Iseki 2004). Secondary forests densely covered the cultivated lands and former residential areas, and introduced plants such as *Leucaena leucocephala* and *Bischofia javanica* expanded their distributions (Yoshida and Oka 2000, Shimizu 2003). The green anole *Anolis carolinensis*, an invasive lizard, was also introduced during this time (Hasegawa et al. 1988).

When the Ogasawara Islands were returned to Japan, they were recolonized by both former and new human inhabitants. Only Chichijima and Hahajima were inhabited by civilians, and the other islands were left unpopulated, with the exceptions of Iwoto and Minamitorishima, which were occupied by the Japan Self-Defense Forces, the Japan Meteorological Agency, and the Japan Coast Guard. The current population of Chichijima and Hahajima is approximately 2,400, and transportation from the mainland is by ship once a week (National Institute for Japanese Islands 2004). Since the return of inhabitants, the forests have again been used for residential construction, roadways, parks, and agriculture. Various introduced species have both intentionally and unintentionally accompanied this renewed human activity. The species introduced to the islands by humans pose the greatest threat to the native ecosystem. Typical effects include predation, competition, disease, hybridization, and grazing. Particularly important examples of the introduced species are listed in Table 1.1.

Table 1.1 Distribution of major invasive species and countermeasures against them

	Current distribution	Impact	Ongoing countermeasure	Related chapter
Mammalia				
Goat (*Capra aegagrus*)	CC, OT, ANI (MK, NK, YM, NS, HG, MN, HT, MKU, HR, FT, ANE, IM, MI: eradicated)	Habitat alteration; predation on plants; destruction of seabird nest	Nearly finished to eradicate on ANI eradicating on OT	14
Pig (*Sus scrofa domesticus*)	OT (CC)	Habitat alteration; predation on soil animals	Nearly finished to eradicate on OT	20
Cat (*Felis catus*)	CC, HH, OT, ANI (MKU: naturally disappeared)	Predation on birds	Locally removed on CC and HH Eradicating on OT	10, 11
Norway rat (*Rattus norvegicus*)	HH, HR (CC: naturally disappeared)	Disturbance of succession		23
Black rat (*Rattus rattus*)	Almost all islands	Disturbance of succession; predation on birds and small animals	Eradicating on NS, HG and MK	8, 9, 23
House mouse (*Mus musculus*)	CC, HH	Disturbance of succession		23
Reptilia				
Green anole (*Anolis carolinensis*)	CC, HH	Predation on invertebrates	Locally removed around harbor on CC and from exclosure on HH	12, 13, 20, 21, 22
Amphibia				
American bullfrog (*Rana catesbeiana*)	OT	Predation on aquatic invertebrates	Nearly finished to eradicate on OT	20
Cane toad (*Bufo marinus*)	CC, HH	Predation on soil animals	Developing eradication technique	20
Gastropoda				
Rosy wolfsnail (*Euglandina rosea*)	CC	Predation on land snails		3, 4, 18
Giant African snail (*Achatina fulica*)	CC, HH (OT, ANI, HG, HR: naturally disappeared)	Predation on plants		18
Turbellaria				
Platydemus manokwari	CC	Predation on land snails	Preventing range expansion from CC	3, 4, 5, 6, 7, 18, 19
Magnoliopsida				
Bischofia javanica	CC, HH (OT, HR: nearly eradicated)	Forming uniform forest; competitive exclusion	Eradicating on CC and HH	15, 24, 25, 26
Casuarina equisetifolia	CC, HH, OT, ANI, NS, MKU, ANE	Forming uniform forest; competitive exclusion	Eradicating on ANI and MKU	20
Leucaena leucocephala	Almost all islands	Forming uniform forest; competitive exclusion	Eradicating on MK and NK	16
Lantana camara	CC, HH, MK, OT, ANI	Disrupting succession	Developing eradication technique	
Ficus microcarpa	CC, HH, MK, OT, ANI, HR	Strangling surrounding plants	Developing eradication technique	

CC Chichijima, *HH* Hahajima, *MK* Mukojima, *NK* Nakodojima, *YM* Yomejima, *OT* Ototojima, *ANI* Anijima, *NS* Nishijima, *HG* Higashijima, *MN* Minamijima, *HT* Hitomarujima, *HT* Hyotanjima, *MKU* Mukoujima, *HR* Hirashima, *FT* Futagojima, *ANE* Anejima, *IM* Imotojima, *MI* Meijima
Brackets show former distributions

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Part II
Impacts of Invasive Alien Species

Chapter 2
Impacts of Invasive Alien Species on Native Ecosystems on the Bonin Islands

Naoki Kachi

Abstract This part introduces quantitative studies on the impacts of invasive alien animals and plants on native ecosystems on the Bonin Islands. Predation by alien predatory flatworms such as *Platydemus manokwari* has caused the rapid decline or extinction of many endemic land snails. In addition, predation by black rats can cause microevolutionary changes in shell morphology and habitat use of endemic land snails. Feral cats prey upon land birds as well as seabirds characteristic to the Bonin Islands. An introduced lizard, the green anole (*Anolis carolinensis*), has caused serious damage to many insect populations, resulting in changes in the pollination systems of many native plants. Grazing and trampling by feral goats has caused destruction of vegetation, leading to accelerated soil erosion on some islands. An alien tree, *Bischofia javanica*, has replaced native trees due to its greater survival and seedling growth than those of native tree species. Invasion and dominance of an exotic shrub, *Leucaena leucocephala*, have prevented the establishment of some native woody species. Scientific understanding of the impacts of invasive species and their interactions with native species is essential for conservation and restoration of the native Bonin Island ecosystems.

2.1 Background

Invasive alien species often have strong impacts on native ecosystems through a variety of interspecific interactions (Parker et al. 1999). Ecosystems on oceanic islands are particularly vulnerable to invasions of these species (Loope et al. 1988). On the Bonin Islands, many alien species have invaded since human settlement began (Chap. 1), and some of these invaders have affected native ecosystems on the islands, in some cases causing degradation of ecosystem functioning and loss of biodiversity (Shimizu 2003). Eradication and control of invasive species are essential for the conservation and restoration of native ecosystems. To identify the target species for effective eradication and control programs and to develop conservation strategies for native ecosystems, it is essential to use scientific and quantitative data to evaluate the ongoing and potential future impacts of alien species on native ecosystems and to clarify the mechanisms underlying these impacts.

The impacts of invasive alien species include direct effects, such as prey–predator relationships and competition between plants for limited resources such as light, as well as indirect effects through complex interactions, such as ecosystem engineering and trophic cascades (Richardson et al. 2000). Therefore, invasion of alien species not only can affect the population dynamics of certain native species, but it can also disrupt community structures and ecosystem functioning.

Once an alien species invades and becomes established in a habitat, the alien species is incorporated into the invaded ecosystem, creating new interactions between the alien and native species. These new interactions must be considered when impacts of alien species are evaluated. For instance, some of these interactions may facilitate invasions of other alien species, a process called "invasional meltdown" (Simberloff and Von Holle 1999). In addition, eradication of an alien species incorporated into an ecosystem can cause unexpected changes (Zavaleta et al. 2001).

This part introduces some quantitative studies of the impacts of invasive alien animals and plants on native ecosystems on the Bonin Islands.

2.2 Flatworms

Land snails are a major and highly endemic component of the biotas of Pacific islands, and their dramatic decline has been reported from islands throughout the Pacific (Hadfield and Miller 1989; Cowie and Cook 2001). The decline or extinction of endemic land snails on the Bonin Islands may be caused by predation by several alien predatory flatworms, which were introduced into the islands accidentally and incidentally. Okochi et al. (Chap. 3) described the cause of the

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decline of endemic land snails. Some small endemic snails, such as *Hirasea* spp. and *Ogasawarana* spp., are already rare, and more common endemic snails, such as *Mandarina* spp., are also declining in the northern mountains of Hahajima, one of two human-populated islands. The snail decline cannot be explained by deforestation and subsequent regeneration. Three species of flatworms were found to eat small snails under captive conditions. The distribution of these flatworms is restricted to the northern mountains of Hahajima, where *Mandarina* is declining and its survival is poor. Thus, these predators are plausible candidates as a cause of the decline of the endemic snails.

Ohbayashi et al. (Chap. 4) examined the distribution of *Mandarina* spp., endemic land snails of the Bonin Islands, from 1986 to 2003 on Chichijima and Hahajima, the first and second largest of the Bonin Islands. Many *Mandarina* spp. have declined since the 1990s, and their decline corresponded to the expansion of flatworm populations. Moreover, Chichijima and Hahajima differ in the pace of their respective *Mandarina* declines, perhaps because of differences in the abundance of a predatory flatworm, *Platydemus manokwari*. The flatworm only invaded Chichijima in the 1990s.

Although the ecological impacts of *P. manokwari* on endemic snails have been clarified, the flatworm's feeding habits were poorly understood. Ohbayashi et al. (Chap. 5) examined the distribution and feeding habits of *P. manokwari* on Chichijima. *P. manokwari* was distributed over a large area of the island, and few live land snails were found in the area where *P. manokwari* was distributed. Furthermore, *P. manokwari* fed on live land snails, including predatory species, as well as other food resources such as live flatworms, a land nemertean species, and the carcasses of slugs and earthworms.

To clarify the effect of *P. manokwari* on land snail survival in the field, Sugiura et al. (Chap. 6) examined survival rates of snails placed experimentally in areas where snails were absent (i.e., *P. manokwari* was present) on Chichijima. They found that over 50 and 90% of the snails were dead after 3 and 11 days, respectively, and the main cause of mortality was predation by *P. manokwari*. Sugiura and Yamaura (Chap. 7) evaluated the deteriorative impacts of *P. manokwari* on arboreal snails by examining survival rates of land snails placed experimentally on tree trunks (0.5–2.0 m above the ground) in a forest on Chichijima. Over 40% of the snails placed on tree trunks with snail scent trails were eaten by *P. manokwari* within 7 days.

2.3 Black Rats

Introduced predators can cause extinction of island endemics. With human settlement, alien rats have colonized many oceanic islands and dramatically affected the endemic ecosystems (Courchamp et al. 2003). Black rats, *Rattus rattus*, frequently cause fatal damage to seabird populations through direct predation. Particularly with small-sized petrels, the impacts are devastating. Kawakami et al. (Chap. 8) described the massive die-off of Bulwer's petrels, *Bulweria bulwerii,* on Higashijima due to rat predation on adult individuals as well as eggs.

The black rats also may cause micro-evolutionary changes in populations of native species. Chiba (Chap. 9) showed that predation by black rats, has resulted in ecological and morphological changes in the land snail *Mandarina anijimana* from Anijima, one of the most well preserved of the Bonin Islands. The close association between shell morphology and habitat use of *Mandarina* spp. suggests that the habitat shift induced by the predation of *R. rattus* has caused changes in the shell morphology of *M. anijimana* over an evolutionarily short period of only 17–19 years.

2.4 Feral Cats

Domestic cats, *Felis catus*, were introduced to the Bonin Islands by settlers and became feral (Obana 1877), and feral cats are now considered to have an adverse impact on the islands' native wild birds. Kawakami and Higuchi (Chap. 10) investigated the extent of predation on native Bonin Island passerines by collecting and identifying the feathers of birds eaten by a domestic cat. The number of passerines predated was particularly high during the breeding season probably because of the greater vulnerability of fledglings. The cat took Japanese white-eye, *Zosterops japonicus*, in proportion to their availability. Predation by cats is a serious problem for two endangered passerines: the endemic Bonin Islands white-eye, *Apalopteron familiare*, and the endemic subspecies of the oriental greenfinch, *Carduelis sinica kittlitzi*.

Feral cats also target seabirds frequently because seabirds cannot move quickly once they have landed. Kawakami and Fujita (Chap. 11) examined the remains of birds to investigate which species are most frequently preyed upon by feral cats in the Minamizaki area of Hahajima. Most remains were those of wedge-tailed shearwaters, *Puffinus pacificus*, a dominant seabird species on the Bonin Islands (Hasuo 1970), which had been killed by feral cats after the birds had landed. Although brown boobies, *Sula leucogaster*, breed in the Minamizaki area (Ministry of the Environment 1980), few remains were found in the sample. These observations support the possibility that cat predation has prevented them from breeding.

2.5 Green Anoles

Green anoles, *Anolis carolinensis*, were introduced into the Bonin Islands in the early 1960s and have the potential to cause mass extinctions of endemic insects on the islands.

The population density of *A. carolinensis* found on Chichijima was much higher than that reported on Saipan and the Bahamas. The higher density may explain why insect populations have declined on some of the Bonin Islands but not on Saipan.

Some male lizards were also observed to have pollen of endemic rosewood, *Schima mertensiana*, on their heads. The pollen may have become attached to their heads when *A. carolinensis* was sucking nectar, as is the case for other known lizard pollinators (Okochi et al. Chap. 12). In addition to serving as potential pollinators, green anoles could also decrease the population sizes of flower visitors, resulting in changes in native pollination systems on islands. Abe et al. (Chap. 13) identified the main cause of the population decline of native pollinating insects by testing four potential causal factors: (1) honeybee competition, (2) forest decline, (3) agricultural insecticides, and (4) anole predation. The results of the predation experiment explained well the composition of flower visitors on the main islands of Chichijima and Hahajima. They concluded that the invasive predatory green anole has changed the pollination systems on the Bonin Islands.

2.6 Feral Goats

Feral goats graze and trample vegetation on many oceanic islands, which often causes destruction of vegetation and accelerates soil erosion (Coblentz 1978; Coblentz and Van Vuren 1987). Therefore, feral goats have been eradicated from many islands. After the eradication, vegetation has recovered on some oceanic islands (Hamann 1975), but it has not on others. Hata et al. (Chap. 14) quantified changes in vegetation on Nakodojima in the Mukojima group, which had been greatly disturbed by feral goats, by comparing aerial photographs taken in 1978, 1991, and 2003. An eradication effort began in 1997, and goats were completely eradicated from the island by 1999. Between 1978 and 1991, some grassland changed to bare ground, which resulted in a decrease in the area of grassland and an increase in the area of bare ground during this period. On the other hand, some bare ground changed to grasslands between 1991 and 2003. A considerable area of forest changed to grassland or bare ground even after the eradication of feral goats.

2.7 Bischofia javanica

The invasion of alien woody species has seriously affected many natural forest ecosystems (Richardson 1998). *Bischofia javanica* is an invasive alien tree on the Bonin Islands. This species shows aggressive growth and competitively replaces native tree species in the natural forests of the islands (Shimizu 1988). Yamashita et al. (Chap. 15) examined the survival and growth of seeds and seedlings, two demographic parameters that might confer an advantage to the establishment of *B. javanica* over native trees, by analyzing these parameters during the early life history of *B. javanica* and *Elaeocarpus photiniaefolius*, a native canopy dominant, in actively invaded forests. Compared with *E. photiniaefolius*, greater seed longevity, less seed predation by introduced rodents, longer fruiting periods, and the ability to form seedling banks under a closed canopy appear to have contributed to the invasive success of *B. javanica* on the Bonin Islands.

2.8 Leucaena leucocephala

The shrub *Leucaena leucocephala* has invaded and formed dense monotypic thickets in disturbed areas on many oceanic islands (e.g., Decker 1992; Yamamura et al. 1999). The dense thickets may prevent seedlings of woody species and understory herbaceous species from germinating or growing under canopies of *L. leucocephala*. In a field experiment, Hata et al. (Chap. 16) investigated the effects of *L. leucocephala* invasion on subsequent establishment of a native mid-successional wooden species, *Schima mertensiana*, at the early-successional stages after disturbance. Germination of seeds and growth of seedlings of *S. mertensiana* were inhibited by *L. leucocephala* at the disturbed site, suggesting that the presence of this invasive alien species changes the early-successional pathway of the plant community.

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Chapter 3

The cause of mollusk decline on the Ogasawara Islands

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Key words: Decline, Flatworm, Island, Land snail, *Mandarina*, Mollusk, Ogasawara Islands, Predator

Abstract. Decline of land snails on the Ogasawara Islands was studied. In Hahajima, major alien predators such as *Euglandina rosea* and *Platydemus manokwari* are not present, but some small endemic snails, for example, *Hirasea* spp. and *Ogasawarana* spp., are already rare and more common endemic snails, for example, *Mandarina* spp., are also declining in the northern mountains. The decline cannot be directly explained by forest deforestation and by its subsequent regeneration. Three species of flatworms were found to eat small snails under captive conditions. The distribution of these flatworms is restricted to the northern mountains of Hahajima where *Mandarina* is declining and its survival is low. These predators are plausible candidates as a cause of the decline of the endemic snails.

Introduction

Land snails are a major and highly endemic component of the biotas of Pacific islands. Their dramatic decline has been reported from islands throughout the Pacific (Clarke et al. 1984; Hadfield 1986; Murray et al. 1988; Hadfield and Miller 1989; Cowie 1992, 2001; Hadfield et al. 1993; Cowie and Cook 2001). The Ogasawaras are subtropical islands belonging to Japan, lying about 1000 km south of the main Japanese islands. Their land snail fauna is highly endemic but has been subject to significant decline and extinction (Tomiyama and Kurozumi 1992; Tomiyama 1994). The islands were almost entirely deforested prior to World War II, which led to the decline and extinction of many species. However, subsequent secondary regrowth appeared to provide the opportunity for those species remaining to increase again. Why this has not happened and many species continue to decline is the subject of this paper. As such, it is of great interest from the perspective of conservation of island snail faunas in the Pacific.

The snail declines in the Pacific have been mainly caused by two alien predators, a predatory snail, *Euglandina rosea*, and a flatworm, *Platydemus manokwari* (Clarke et al. 1984; Murray et al. 1988; Hopper and Smith 1992; Hadfield et al. 1993; Eldredge and Smith 1995; Cowie and Cook 2001). However, these are only found on Chichijima among the Ogasawara Islands, but the decline also occurs on Hahajima (Tomiyama 1992; Tomiyama and Kurozumi 1992). We suspected that

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several flatworms were the causal agents, because they are often found where the endemic snails are declining. The conclusion drawn is that these predatory flatworms are the cause of the continuing decline of these species.

Methods and study area

Study island and snails

All studies were done on Hahajima, the second largest island in the Ogasawara Islands (Figure 1). It is one of only two islands that are allowed to be populated, and people are restricted to one port, Oki-kou. A large part of the island is covered by natural secondary forest. There are also two old-growth forest stands, Mt. Kuwanokiyama and Sekimon (Figure 1, E and F), that were protected even before World War II. These are *Elaeocarpus* mesic forests (Ono and Okutomi 1985), which once covered a large part of the islands before human arrival (Shimizu and Tabata 1991). Some areas of former farms still remain as grassland or scrub dominated by the alien *Leucaena leucocephala* (Ono and Okutomi 1985).

The two serious alien predators of snails in the Pacific islands, *P. manokwari* and *E. rosea*, have not been found on the island. Introduced pigs (*Sus scrofa*) and goats (*Capra hircus*) are also absent, but invasive rats (*Rattus rattus*) are present.

We examined primarily the forest floor snail species, *Mandarina aureola*, *Mandarina polita*, *Mandarina ponderosa*, *Achatina fulica* and *Bradybaena similaris*. The first three species are endemic to the islands, and the latter two alien. They are relatively large species and are easy to find in the field. We also included *Mandarina hahajimana* and *Mandarina exoptata* in a comparison of population density throughout Hahajima. These are endemic arboreal species, but are occasionally found on the forest floor. *Ogasawarana* spp., small endemic snails, were also used in experiments to evaluate mortality and predation by flatworms. Since all endemic species are protected by national legislation, the study was done with the permission of the Japanese Ministry of Education. Because of ministerial requirements, the number of snails used in experiments was restricted.

Population density

Each research plot was established as an area of ground surrounded by 3–4 trees. The size of the plots was calculated from the distances between the perimeter trees. Larger land snails in the litter and on the surface of the soil were searched by hand and counted.

In order to compare densities of *Mandarina* spp. between secondary broadleaf forest and *Leucana* scrub, we surveyed nine plots in each habitat type, all in the Minamizaki area (Figure 1, between A and B). Plot size varied from 3.4 to 11.8 m^2 (average 6.3 m^2) because of the site's condition. Live snails and dead shells were counted separately. The survey was conducted from 1–4 March 1996.

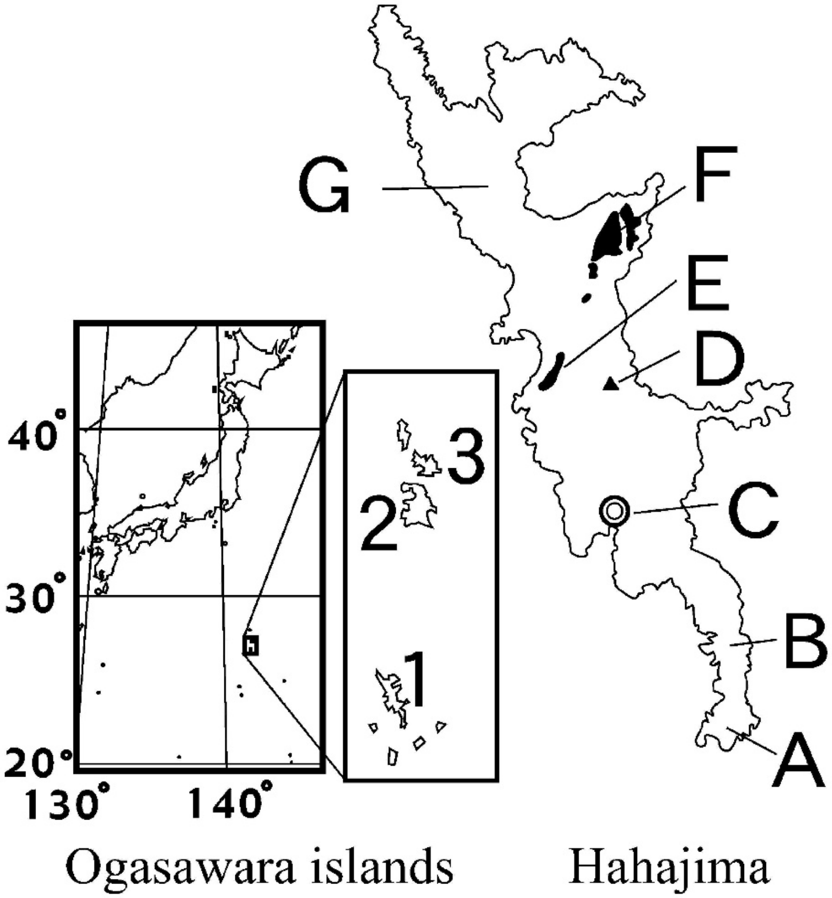

Figure 1. Location of the Ogasawara islands and study sites in Hahajima. Black areas indicate remnant old growth forests. 1: Hahajima, 2: Chichijima, 3: Anijima. A–B: Minamizaki area, A: Mt. Kofuji, B: Omotohama, C: Oki-kou port, D: Mt. Chibusayama, E: Mt. Kuwanokiyama, F: Sekimon, G: Nijucho-toge.

To investigate densities of live *Mandarina* spp. and alien mollusks throughout Hahajima, 27 sites were surveyed. Each site included 1–8 plots. Only live snails were counted. Densities from several plots at the same site were combined. The surveyed area varied from 1.3 to 52.6 m^2, average 9.3 m^2. Larger sites combined data from several plots in the same locality. Data from the Minamizaki area from the above comparison were included. The surveys were done on 1–4 March 1996, 15 September 1997, and 27 February–1 March 1998.

Mortality

Ogasawarana spp. and adults and young of *M. aureola* were collected from the Minamizaki area (Figure 1, A and B). They were put in mesh bags (50 cm × 50 cm at the bottom) together with some litter that had been collected from their habitat and which was steam-sterilized. Leaves of a mulberry, *Morus australis*, were also put in the bags as food. Bags were made of 4 mm nylon mesh for adult *M. aureola* or 1.5 mm glass wool mesh for young *M. aureola* and *Ogasawarana* spp.

Bags containing *Ogasawarana* spp. were put out on 9 September 1998 at four sites: Nijucho-toge, a shrub forest on the ridge of the mountains in the north of the island (Figure 1, G), Mt. Kuwanokiyama, a primary forest in mountains near the middle of the island (Figure 1, E), and Omotohama (Figure 1, B) and Mt. Kofuji (Figure 1, A), which are secondary forests in the Minamizaki area in the southern hills. Mt. Kofuji is the only site where *Ogasawarana* is still found on Hahajima. Bags were collected on 17 October 1998.

Bags containing adult *M. aureola* were set out at two sites: Mt. Kuwanokiyama (Figure 1, E) and Omotohama (Figure 1, B). *M. aureola* is found in Omotohama but is extinct on Mt. Kuwanokiyama. The bags were put out and collected on the same dates as those for *Ogasawarana* spp.

Bags containing young *M. aureola* were set out at three sites: Nijucho-toge (Figure 1, G), Mt. Kuwanokiyama (Figure 1, E), and Omotohama (Figure 1, B), on 15 September 1999 (Figure 1, B, E, and G) and collected on 16 October 1999.

After collection of bags, snails were located in the litter and mortality was determined.

Predators

We tested five species of flatworms, *Bipalium* sp., *Bipalium kewense*, *Platydemus*? sp. 1, *Australopacifica* sp., from Hahajima, and *P. manokwari* from Chichijima. A land nemertine, *Geonemertis palaensis*, was not tested because it did not eat snails in a preliminary test. Flatworms from the forest floor were brought to the laboratory and kept in plastic boxes with a small amount of soil. Identification of flatworms followed Kawakatsu et al. (1999). *Ogasawarana* spp. and young *M. aureola* were put in the boxes to test if the flatworms ate them. The boxes were kept at 25 °C and were observed almost every day for 10 days following commencement during September and October 1998.

Distribution of predators

If predacious flatworms act as an important agent in the decline of endemic snails, they should be most abundant where decline is most severe. We used several collection methods to assess flatworm density. They are often found under stones, rotten logs and plastic bags in the daytime, but appeared on the ground surface at night. Therefore, we used three methods; placing plastic mats on the forest floor, searching under stones and logs, and direct observation on the forest floor in the middle of the night. Plastic mats were placed near roads or paths in locations from the northern to the southern ends of the island on 8–11 September 1998, and were checked on 16 October 1998 and 12–15 September 1999. Searches for flatworms were done when the mats were placed and when snail research was being conducted in these locations. We also searched for flatworms several times in the mountain area, at Sekimon primary forest and at Mt. Chibusayama, by looking under stones,

Table 1. Densities of *Mandarina* species in the Minamizaki area.

	Evergreen forest (no./m^2)	*Leucaena* scrub (no./m^2)
M. aureola		
Live	0.28 ± 0.31	0.35 ± 0.23
Dead	2.41 ± 2.53	1.93 ± 1.04
M. ponderosa		
Live*	0.43 ± 0.75	0.00 ± 0.00
Dead**	7.94 ± 8.83	0.14 ± 0.26

Means ± S.D. of the data from nine plots are given.
Mann–Whitney *U*-tests were used for the difference between evergreen forest and *Leucaena*.
*$P < 0.05$; **$P < 0.01$.

logs, etc. Night observations were mainly done at Mt. Kuwanokiyama and Omotohama (Figure 1, E and B).

Results

Population density

M. aureola and *M. ponderosa* were the dominant land snails in the Minamizaki area, with a few of an arboreal species, *M. hahajimana*, also found. Table 1 shows the densities of the two land species in the area. Densities of live and dead *M. aureola* did not differ between natural secondary forest and *Leucaena* scrub (Mann–Whitney *U*-test). No live *M. ponderosa* were found in the *Leucaena* scrub, and there was a significant difference in the densities of live *M. ponderosa* between the two habitats ($p = 0.0291$). Densities of dead *M. ponderosa* were significantly higher in secondary natural forest ($p = 0.0003$).

Densities of live *Mandarina* spp. throughout Hahajima are shown in Figure 2a. They were very low in the northern part of Hahajima, even in the primary forest on Mt. Kuwanokiyama. Live *M. aureola* were found at Sekimon, another primary forest, but no live *Mandarina* were found at Mt. Kuwanokiyama. We found live *M. polita* and *M. exoptata* near the top of Mt. Chibusayama, the highest mountain, where there were no tall trees. Near Oki-kou port, we found many live *M. polita* at one site, while no live *Mandarina* were found at another site 300 m away. Many populations of *M. aureola*, *M. ponderosa* and *M. hahajimana* were surviving well in the southern part of Hahajima.

Old, discolored dead shells of *Mandarina* spp. were found frequently at many sites in the northern mountain area including Mt. Kuwanokiyama, though no live *Mandarina* were found.

B. similaris, an alien snail from mainland Japan, was abundant in the northern area, especially along roadsides. *A. fulica*, another alien snail, originally from Africa, also occurred in the northern area. These species were generally found

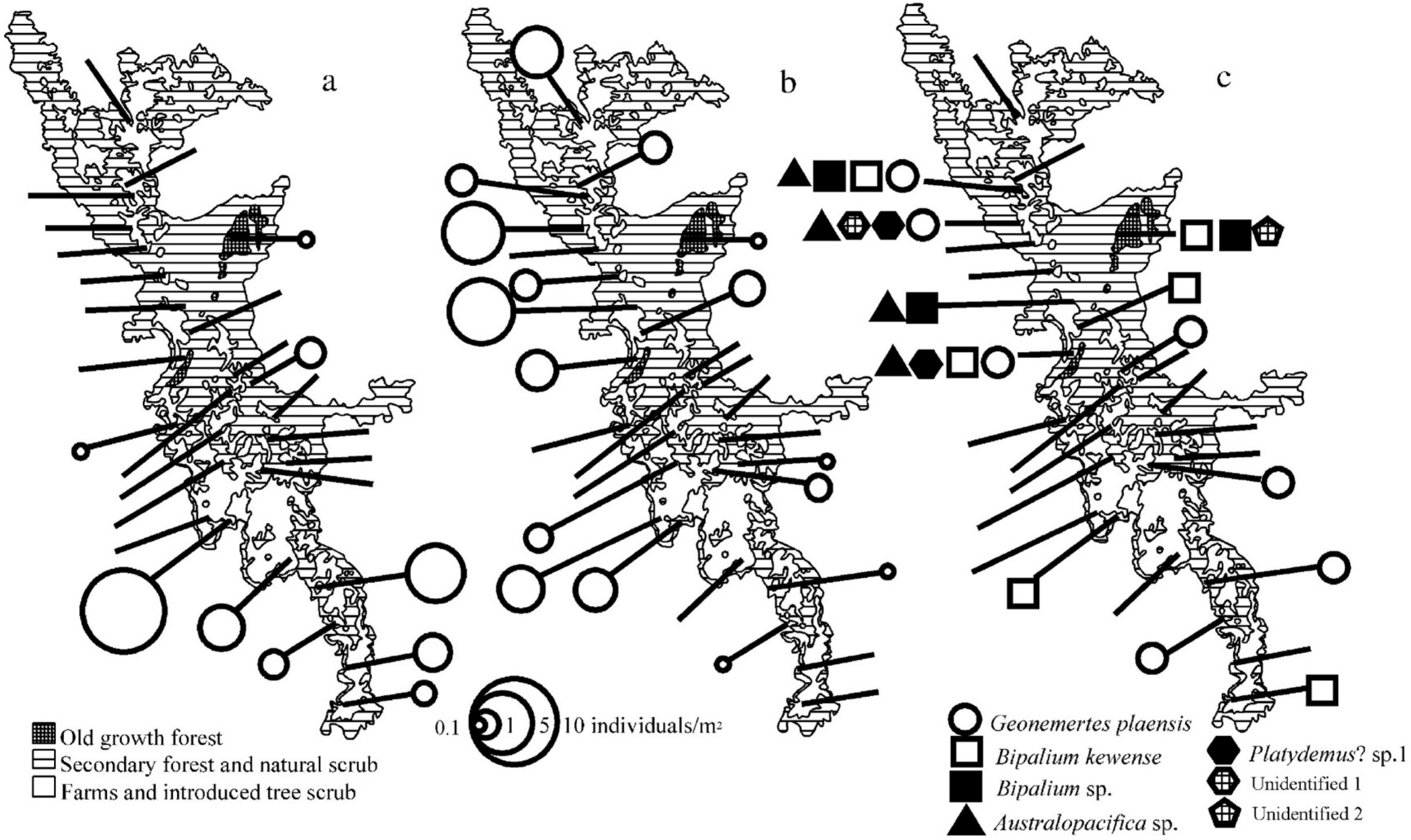

Figure 2. Densities of *Mandarina* spp. (a), exotic mollusks (b), and distribution of land planarians and land nemertine (c). Open circles in (a) and (b) indicate snail densities $0 < x \leq 0.1$, $0.1 < x \leq 1$, $1 < x \leq 5$, $5 < x \leq 10$ individuals/m^2, respectively. Lines without circle show that no live snails were found. Symbols in (c) indicate planarian species. Solid and open symbols in (c) show predators of snails and non-predators of snails, respectively. Hatched symbols show that their food type is unknown, and they are not listed in Kawakatsu et al. (1999).

Table 2. Survivorship of endemic snails kept in mesh bags that allowed entry of flatworms.

	Ogasawarana spp.	*M. aureola*	
		Young	Adults
Northern mountains			
G (Nijucho-toge)	5/9[1,2]	11/17[1,3,*]	–
E (Mt. Kuwanokiyama)	6/9[1]	5/11*	5/5
(G + E)	(11/18)**	(16/28)*	
Southern hills			
B (Omotohama)	9/9	18/18	4/5
A (Mt. Kofuji)	8/9	–	–
(B + A)	(17/18)		

First number indicates surviving and second number indicates number of individuals. *Ogasawarana* spp. and young *M. aureola* were examined from 10 September to 17 October 1998. Adult *M. aureola* were examined from 15 September to 16 October 1999.

[1] *Australopacifica* sp. found in bag.

[2] *G. plaensis* found in bag.

[3] *Platydemus*? sp. 1 found in bag.

*Survivorship is significantly lower than that of B (Fisher's exact probability test, $P < 0.01$).

**Survivorship of (G + E) is significantly lower than that of (B + A) ($P < 0.05$).

where no *Mandarina* species occurred, with one exception (Figure 2b). Because of this one exception, an inverse correlation between the densities of *Mandarina* spp. and alien species was not significant.

Mortality

The survivorship of young *M. aureola* in the northern mountain area was significantly lower than that in the southern hills area (Table 2, Fisher's exact probability test, $P < 0.01$). This appears to correspond to the distribution of the living population, since live snails were not found in the high mortality sites in the northern mountains, but were found in the southern hills. However, survival of adult *M. aureola* was as high in the northern mountains as in the southern hills.

The survivorship of *Ogasawarana* spp. was also lower in the northern mountains (Table 2). Since the number of individuals used in this study was limited, the data were combined to evaluate the difference in survival between the northern mountains and southern hills. This difference was significant (Fisher's exact probability test, $P < 0.05$).

Predators

P. manokwari began to eat snails within a day of their placement in an experimental box. No predation by *B. kewense* was observed. Other flatworms, *Bipalium* sp., *Platydemus*? sp. 1 and *Australopacifica* sp., ate the snails in some cases, but the

Table 3. Predation on endemic snails in plastic containers by flatworms.

Species of flatworms	Number of young *M. aureola*		*N*[1]	Number of *Ogasawarana* spp.		*N*[1]
	No. dead	No. available		No. dead	No. available	
P. manokwari	2	2	1	–	–	–
Platydemus? sp. 1	4	4	1	1	2	1
Platydemus? sp. 1	0	2	4	1	2	4
Platydemus? sp. 2	0	1	1	0	1	1
B. kewense	0	3	1	0	2	1
Bipalium sp.	1	3	1	1	3	1
Bipalium sp.	4	5	3	–	–	–
Australopacifica sp.	2	2	2	0	3	2
Australopacifica sp.	0	2	7	0	2	7
Control	0	4	0	0	4	0

Results are for 10 days after introduction of flatworms and snails to a container.
[1] Number of flatworms introduced into each container.

results were not consistent (Table 3). They may therefore be able to prey on snails only under suitable conditions, or the observation period (10 days) was not long enough for them to be able to attack.

Distribution of predators

We found six species of flatworms, and one nemertine (Figure 2c) Among the flatworms, *Bipalium* sp., *Platydemus*? sp. 1 and *Australopacifica* sp. were predators of snails but *B. kewense* is not. The land nemertine, *Geonemertes plaensis* is not a predator of snails. Another two unidentified species, shown as unidentified 1, 2 in Figure 2, were not listed in Kawakatsu et al. (1999). Since there were only a few individuals present, we could not check their diet. All the predacious flatworms were found only in the northern mountain area, where decline of snails is severe. The two unidentified species were also found in the northern mountains. In the southern hills, where *Mandarina* spp. were still surviving well, we only found *B. kewense* and *G. plaensis*, non-predacious flatworm and nemertine.

Discussion

The presence of discolored dead shells of *Mandarina* on the forest floor throughout the island and the limited distribution of living populations indicate that *Mandarina* has decreased in abundance in the northern area recently. These results are similar to those of previous studies on the island (Kurozumi 1988; Tomiyama and Kurozumi 1992).

Comparison of the population densities of *Mandarina* spp. between broadleaf stands and *Leucaena* stands showed that *M. ponderosa* may avoid *Leucaena* stands while *M. aureola* does not. Kurozumi (1988) and Tomiyama (1992) suggested that the islands' native snail species may seldom invade and re-colonize secondary forests that grow on severely disturbed land such as farms. This hypothesis is supported by the results reported here for *M. ponderosa*, but not by the results for *M. aureola*. Since the floor of a native evergreen broadleaf forest is darker than that of a *Leucaena* stand, it may be that *M. ponderosa* prefers dark, moist stands. Chiba (1999) also reported that *M. ponderosa* did not occur in shrubby vegetation while *M. aureola* and *M. polita* did. *M. ponderosa* can thus be thought of as species of forest interiors. *M. aureola* and *M. polita* may be able to increase in regenerating forest if their decline has only been caused by past deforestation. However, no such recovery was observed in the northern area, even though this area is covered with dense forest, in contrast to the southern hills where populations of *Mandarina* spp. are not in decline. This contradicts the predictions of previous researchers that deforestation is a major factor in the decline of these snails. Past deforestation might therefore have caused snail decline at the time of its occurrence, but it is not a dominant cause of the recent decline.

The area in which *Mandarina* occurs in high densities appears to be distinct from the area where alien species are abundant. Therefore competition has been suspected as one of the major agents of decline (Kurozumi 1988; Tomiyama 1992; Tomiyama and Kurozumi 1992). However, there is one exception. This is a shrine at Oki-kou port, where both *M. polita* and *A. fulica* occur at high densities. This case is difficult to explain using the competition hypothesis.

Since some species of flatworms attack small snails, they are potential agents in the decline of small species. However, adults of *M. aureola* seem not to be affected by flatworms, so only survival of juveniles may be affected. Totani (personal communication) found that the flatworm *Australopacifica* sp. ate hatchlings of *A. fulica*. He also found that *Bipalium* sp. ate small snails and slugs, such as juvenile *A. fulica* (about 500 mg weight), *B. similaris* (about 500 mg), *Allopeas kyotoense* (about 200 mg), and *Meghimatium bilineatum* (about 200 mg) in captivity. The Ogasawara Subtropical Branch of Tokyo Metropolitan Agricultural Experiment Station (2001) also reported that *Bipalium* sp. ate young *A. fulica* in captivity. These results support our findings that *Bipalium* sp., *Austropacifica* sp. and *Platydemus*? sp. 1 are predators of small snails. Since their distribution is restricted to the northern mountains, they are the most likely candidates as agents of snail decline.

Extinction of endemic species on islands caused by alien predators has frequently been observed (e.g., Greenway 1967; Savidge 1987; Cowie 1992; Primack 1993). In the context of the present study it is therefore essential to know whether the predatory flatworms on the Ogasawara Islands are endemic or alien. Unfortunately, since flatworms have been poorly studied, their former distributions are not well known. Kawakatsu and Organ (1994) listed *Australopacifica* sp. and *Platydemus*? sp. 1 as occurring on the northern Mariana Islands. They could be alien both to the Marianas and the Ogasawaras.

It is also possible that a native prey species can be driven to extinction by a native predator in the presence of an alien prey species. Alien snails can be a food resource of predators (Cowie 2001). In this instance, assume that the alien prey species is much more fecund than the native prey species and that the population of the native predator depends largely on the alien prey population and is not affected by decline or extinction of the native prey species. In this case the origin of the predator is not important. Endemic prey species will only be able to survive where the alien prey species does not occur. Thus, the final distribution pattern of the native and alien prey will be similar to that predicted by direct competition. The distribution of alien and endemic species here is almost as distinct as would be expected from the above mechanism of extinction. Mead (1963) also presented a similar mechanism between Hawaiian endemic flatworms and snails. Additionally, on the Ogasawara Islands *Mandarina* only lay one or two eggs at a time (Tomiyama 1997; Sato and Okochi 1999) while *A. fulica* lays about 50 eggs at a time (Ogasawara Subtropical Branch of Tokyo Metropolitan Agricultural Experiment Station 1994). Predation by the small flatworms may therefore explain the decline of the endemic snails, which occurred before arrival of the major alien predators, *E. rosea* and *P. manokwari*.

A disappointing conclusion from this study is that populations of *Mandarina* are not recovering, even though the natural forest is regenerating and even if we can prevent invasion of *P. manokwari* and *E. rosea* from Chichijima. Protection activity must be considered to influence both predatory flatworms and alien snails. The island snails may only be able to be conserved through a combination of captive breeding for the declining species and isolation of the smaller islands to prevent further decline, as in the case of *Partula* in the central Pacific islands (Tonge and Bloxam 1991). These can readily be transported by soil on boots, construction machines, or on plant seed material used in the restoration of vegetation. It is therefore desirable to restrict landing of people on all the uninhabited small islands. The 'Bonin' Islands, another name for the Ogasawara Islands, originally means 'uninhabited' islands. For conservation purposes perhaps they should be left as they were 200 years ago, as their name indicates.

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Chapter 4

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Rapid decline of endemic snails in the Ogasawara Islands, Western Pacific Ocean

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Abstract

The distribution of *Mandarina* spp., endemic land snails (ground-dowelling ecotype species) of the Ogasawara (Bonin) Islands (Japan), was examined from the 1980's to the present in Chichijima and Hahajima islands. In Chichijima Island, *M. mandarina* has been rapidly declining since the 1990's in the northeastern area of the island. On the other hand, *M. chichijimana* has only slightly declined since the 1990's in the southern area of the island. In Hahajima Island since the 1990's, *M. polita* has slightly declined in the central area while *M. ponderosa* has been rapidly declining, and *M. aureola* has shown almost no decline in the southern area of the island. These circumstances offer evidence of the expansion of land snail predators (flatworms). Moreover, Chichijima and Hahajima islands differ in the pace of their respective decline, perhaps because of a predatory flatworm, *Platydemus manokwari*, used previously as a biological control agent abroad for the giant African snail, *Achatina fulica*, which only invaded Chichijima Island in the 1990's.

Key words: *Mandarina* spp.; land snail decline; island biology; *Platydemus manokwari*; Ogasawara (Bonin) Islands

INTRODUCTION

In tropical oceanic islands, it has been found that many endemic land snails have already become extinct as a result of exotic predators such as the predatory snail, *Euglandina rosea* or the predatory flatworm, *Platydemus manokwari* introduced for biological control of the giant African snail, *Achatina fulica*, or through accidental invasion (Muniappan, 1983, 1987, 1990; Clarke et al., 1984; Muniappan et al., 1986; Takeuchi et al., 1991; Hopper and Smith, 1992; IUCN/SSC Mollusc Specialist Group, 1995; Cowie, 2001a, b; Tomiyama, 2002a; Ohbayashi et al., 2005; Sugiura et al., 2006); however, the process by which extinction occurs is relatively unknown.

The Ogasawara (Bonin) Islands are located in the western Pacific Ocean about 1,000 km south of the mainland of Japan. More than 100 species of land molluscs have been recorded on the islands, of which 94% are endemic (Tomiyama and Kurozumi, 1992; Tomiyama, 1994); however, about 40% of the endemic species are already extinct (Kurozumi, 1988; Tomiyama and Kurozumi, 1992).

The following may be possible reasons for this decline: introduction of exotic snails such as *A. fulica* (Kurozumi, 1988; Tomiyama, 2002a); introduction of the predatory snail *E. rosea* for the control of *A. fulica* in 1965 in Chichijima Island (Takeuchi et al., 1991); predation by predatory flatworms distributed before *P. manokwari* invasion (Kawakatsu et al., 1999; Okochi et al., 2004); invasion of the alien predatory flatworm *P. manokwari* in Chichijima Island in the 1990's (Kawakatsu et al., 1999; Tomiyama, 2002a; Ohbayashi et al., 2005); predation by alien rats (Tomiyama, 2002a); and forest destruction (Tomiyama, 2002a). In Chichijima Island, the most likely cause of the decline of land snails is thought to be the invasion of

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P. manokwari in the 1990's (Kawakatsu et al., 1999; Tomiyama, 2002a; Ohbayashi et al., 2005; Sugiura et al., 2006).

One of the endemic genus *Mandarina* has diversified into taxa occupying many habitats (e.g. arboreal, semi-arboreal, terrestrial, dry, and wet habitats), and shows remarkable diversity in shell and genital morphology (Minato, 1978; Chiba, 1996, 2003); however, *Mandarina* spp. also has suffered serious destruction due to predation by introduced species such as *P. manokwari* (Chiba, 2003). Thus, understanding the process of the decline of *Mandarina* spp. and the impact of *P. manokwari* on *Mandarina* spp. might useful for the conservation of *Mandarina* spp. in future.

This study was undertaken to clarify the process of extinction of *Mandarina* spp. from the 1980's to the present through distribution research, and how *P. manokwari*, which invaded Chichijima Island in the 1990's, relates to the decline of *Mandarina* spp. by comparing the process of decline in Chichijima and Hahajima islands.

MATERIALS AND METHODS

Study areas. All studies were conducted in Chichijima and Hahajima islands, which are part of the Ogasawara (Bonin) Islands (Fig. 1).

Distribution of *Mandarina* spp. From 1986 to 2003 (covering spring to winter, with search areas and months differing with the year), we searched under fallen leaves, logs and stones in the daytime, and recorded the sites where live ground-dwelling ecotypes *Mandarina* spp. (*M. mandarina*, *M. chichijimana*, *M. polita*, *M. aureola* and *M. ponderosa*) were detected every 1 to 5 years. Each site was about 1 m^2 in area. Species of *Mandarina* spp. were identified according to Chiba (1989, 2003, 2004).

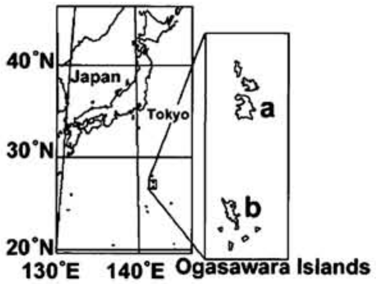

Fig. 1. Location of the Ogasawara Islands. a: Chichijima Island; b: Hahajima Island.

There were 26 research sites in Chichijima Island and 73 sites in Hahajima Island.

Changes in the distribution area of *Mandarina* spp. According to Tomiyama (2002a), the mobility of *Mandarina* spp. is very low, so we assumed that the restoration of extinct populations by re-invasion would not occur during the research years. Therefore, we regarded populations at sites where live snails were confirmed to have been in the same location and not migrants from elsewhere. If a population was not confirmed at a site one year but was discovered at the site in a later year, we assumed that its density had been too low to have been detected in the earlier year. According to these assumptions, we made distribution maps for the years 1986, 1995 and 2003.

Distribution of *Platydemus manokwari*. We searched under stones and logs in the daytime in the years 1995, 1998, 2002, 2003 and 2004 (29 times in total) in Chichijima Island and in the years 1998 and 1999 (5 times in total) in Hahajima Island (covering spring to winter, with search areas and months differing with the year). We also conducted nighttime observations of the forest floor (once in December 1998 and once a month from January to July, 2004 in Chichijima Island and once in January 1999 in Hahajima Island), and recorded the sites where *Platydemus manokwari* was detected.

We also used 20 cm×20 cm mesh bags made of 5 mm nylon mesh as attractant traps into which one live *A. fulca* (shell height: over 40 mm) was put in Chichijima Island. The traps were set on the forest floor near a road (45 sites) from March to May 1998, checked every few weeks, and the sites where *P. manokwari* was detected were recorded.

RESULTS

Distribution of *Mandarina mandarina* (Chichijima Is.)

Mandarina mandarina was distributed over the northern and northeastern areas of Chichijima Island in 1986 (Fig. 2a). In 1995, the first local extinction occurred at one point in the northern area of Chichijima Island (Fig. 2b). After that, extinction advanced rapidly to the year 2003 in Chichijima Island, so that *M. mandarina* now only occurs

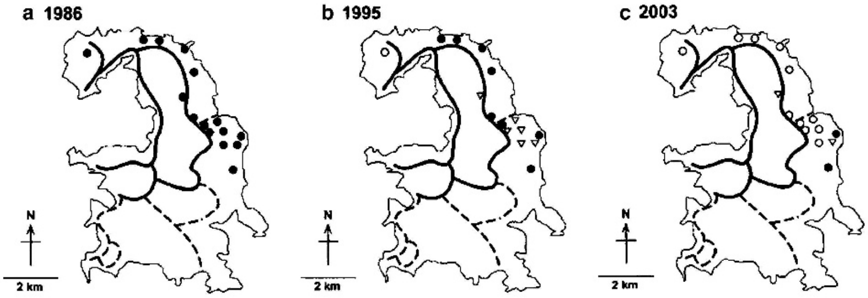

Fig. 2. Distributions of *Mandarina mandarina* in Chichijima Island in the years 1986 (a), 1995 (b) and 2003 (c). ●: Live *M. mandarina* was recorded; ○: Live *M. mandarina* was not recorded; ▽: Research was not conducted. Solid lines in the maps indicate surfaced roads and broken lines indicate mountain trails.

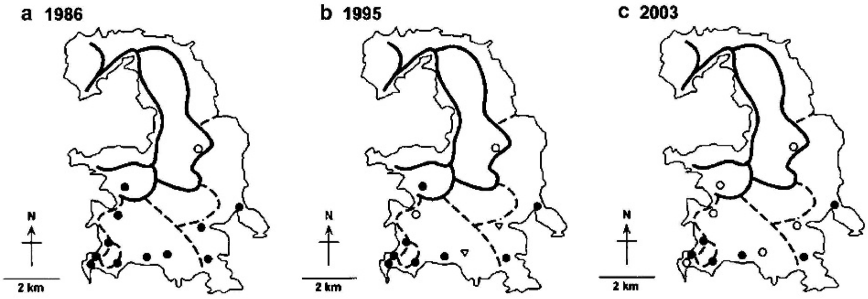

Fig. 3. Distributions of *Mandarina chichijimana* in Chichijima Island in the years 1986 (a), 1995 (b) and 2003 (c). ●: Live *M. chichijimana* was recorded; ○: Live *M. chichijimana* was not recorded; ▽: Research was not conducted. Solid lines in the maps indicate surfaced roads and broken lines indicate mountain trails.

in the northeastern area (Fig. 2c).

Distribution of *Mandarina chichijimana* (Chichijima Is.)

In 1986, *Mandarina chichijimana* was distributed over the southern area of Chichijima Island, but there was already no live *M. chichijimana* in the central area of the island (Fig. 3a). In 1995, the first local extinction occurred at one point in the southwestern area of Chichijima Island (Fig. 3b). Subsequently, extinction advanced slightly so that by 2003 in Chichijima Island, the distribution area of *M. chichijimana* was limited to the southeastern and southwestern areas (Fig. 3c). The extinction areas of *M. chichijimana* and *M. mandarina* were sequenced.

Distribution of *Mandarina polita* (Hahajima Is.)

In 1986, *Mandarina polita* was distributed over the northern and central areas of Hahajima Island (Fig. 4a). By 1995, extinctions had occurred at two points of the central area (Fig. 4b). After that, further extinction advanced in the central area to the year 2003 (Fig. 4c). Moreover, another extinction occurred in the northern area, but it was not clear when it had started (Fig. 4c).

Distribution of *Mandarina aureola* (Hahajima Is.)

Mandarina aureola is an allopatric species whose distribution area is adjacent to the area of *M. polita*. This species was distributed over the southern area and one point of the northern area of Hahajima Island in 1986 (Fig. 5a), and no obvious extinction was observed in either 1995 or 2003 (Fig. 5b, c).

Distribution of *Mandarina ponderosa* (Hahajima Is.)

Mandarina ponderosa is a sympatric species whose distribution area overlapped the area of *M. aureola* and *M. polita*. In 1986, this species occurred sporadically over the northern, central and

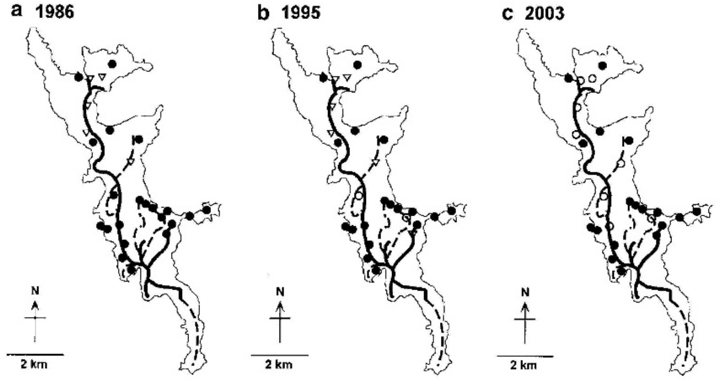

Fig. 4. Distributions of *Mandarina polita* in Hahajima Island in the years 1986 (a), 1995 (b) and 2003 (c). ●: Live *M. polita* was recorded; ○: Live *M. polita* was not recorded; ▽: Research was not conducted. Solid lines in the maps indicate surfaced roads and broken lines indicate mountain trails.

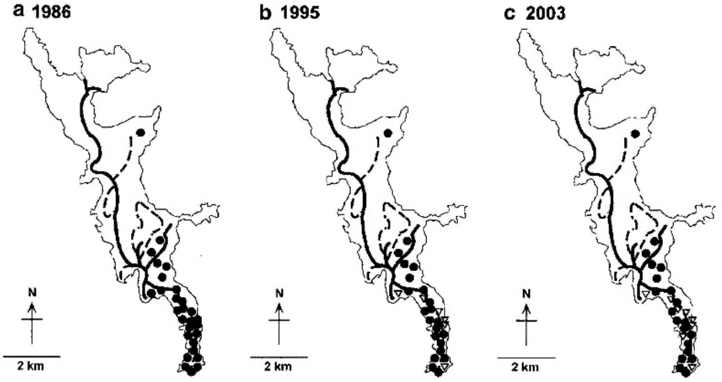

Fig. 5. Distributions of *Mandarina aureola* in Hahajima Island in the years 1986 (a), 1995 (b) and 2003 (c). ●: Live *M. aureola* was recorded; ○: Live *M. aureola* was not recorded; ▽: Research was not conducted. Solid lines in the maps indicate surfaced roads and broken lines indicate mountain trails.

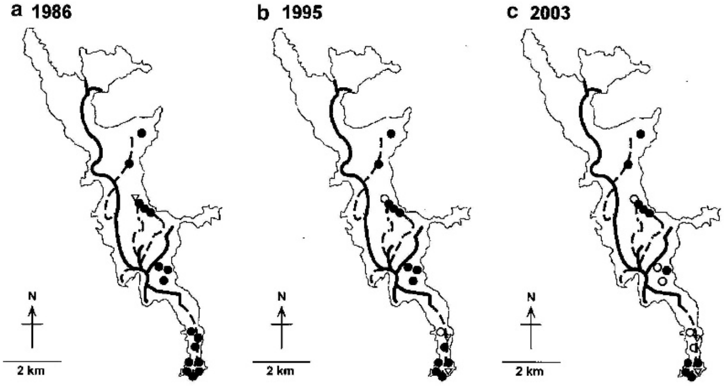

Fig. 6. Distributions of *Mandarina ponderosa* in Hahajima Island in the years 1986 (a), 1995 (b) and 2003 (c). ●: Live *M. ponderosa* was recorded; ○: Live *M. ponderosa* was not recorded; ▽: Research was not conducted. Solid lines in the maps indicate surfaced roads and broken lines indicate mountain trails.

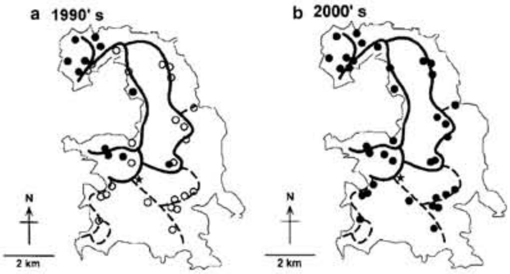

Fig. 7. Distributions of *Platydemus manokwari* on Chichijima Island in the 1990's (a) and 2000's (b). ●: *P. manokwari* was recorded; ○: *P. manokwari* was not recorded; ★: The point where one of the attractant traps was set. Solid lines in the maps indicate surfaced roads and broken lines indicate mountain trails.

southern areas of Hahajima Island (Fig. 6a), but by 1995, there had been a decline in the central and southern areas (Fig. 6b). Further decline had occurred in the southern area by the year 2003 (Fig. 6c).

Distribution of *Platydemus manokwari*

In Chichijima Island, *Platydemus manokwari* was detected near the town (northwest) and farmland (central) areas, and along the road linking these areas in the 1990's (Fig. 7a). In the present decade, *P. manokwari* has been detected over a wide area of the island (such as the central mountain areas), except for the eastern and southern coastal areas (Fig. 7b).

In nine of the 37 sites where *P. manokwari* was recorded, land snails and *P. manokwari* coexisted, but at the other 28 sites, only *P. manokwari* was recorded, and only one of the 45 traps attracted *P. manokwari* (★ of Fig. 7).

On the other hand, in Hahajima Island, no *P. manokwari* was detected in any area.

DISCUSSION

Until the mid 1980's, before *Platydemus manokwari* invaded Chichijima Island, there were many *Mandarina* spp. populations in Chichijima (and Hahajima) Island(s) (Kurozumi, 1988 and Figs. 2-6). This suggests that the impact of predators such as *Euglandina rosea*, introduced in the 1960's to Chichijima Island (Takeuchi et al., 1991) distributed in limited area, was not so serious in those days (Kurozumi, 1988).

However, around 1986 in Chichijima Island, there was already no *Mandarina* spp. from the northwest coastal area to the south-central area (Figs. 2 and 3). There are many farmlands and roads in these areas which were home to many exotic snails (such as *Achatina fulica* and *Bradybaena similaris*), as well as the predatory snail, *E. rosea* (Kurozumi, 1988; Takeuchi et al., 1991; Tomiyama, 1991, 1994). *E. rosea* is not distributed in Hahajima Island, but except for this point, the conditions on Chichijima Island in the 1980's were similar to those on Hahajima Island at present (Okochi et al., 2004).

In the 1980's, there were several species of predatory flatworms (but not *P. manokwari*) in Chichijima Island (Kawakatsu et al., 1999), so a similar decline caused by alien species and predators may have occurred there, similar to the current situation in Hahajima Island.

In 1995, *M. mandarina* was extinct in one of the northern areas of Chichijima Island (Fig. 2b). There were already *E. rosea* (Kurozumi, 1988) and several predatory flatworms (but not *P. manokwari*) in this area (Kawakatsu et al., 1999), so these predators affected *M. mandarina* in the 1980's, and subsequently in the 1990's, the invasion of *P. manokwari* might have been the final blow for *M. mandarina*. Incidentally, this point is thought to be where *P. manokwari* began its invasion (Fig. 7).

On the other hand, one extinct area of *M. chichijimana* population in the southwestern area of Chichijima Island in 1995 (Fig. 3b) was far from the first area invaded by *P. manokwari*, but recently, *P. manokwari* has been recorded in the vicinity (Fig. 7b). Consequently, this extinction is thought to have been caused by *P. manokwari*.

The expansion of extinct areas during the eight years from 1995 to 2003 has been startling (Figs. 2 and 3). *P. manokwari* occurred in those areas (Fig. 7b), so it is believed to be the cause of decline. This sudden expansion might have been caused by artificial transmission by human activities, and the abundant supply of exotic land snails as food sources. So it is likely that *M. chichijimana*, as the endemic species of Chichijima Island, might become extinct some time in the future.

In Hahajima Island, *M. polita* has slightly declined (Fig. 4). This decline was thought to have been caused by predation by flatworms (Kawakatsu et al., 1999) which have increased their population by preying upon, and winning competition against, exotic land snails such as *A. fulica* (Okochi et al., 2004). The extinction areas were concentrated along surfaced roads from north to south on Hahajima Island and the mountain trail in the central part of the island. According to Numazawa et al. (1988), the exotic land snail *A. fulica* preferred disturbed areas affected by human impact. Furthermore, Okochi et al. (2004) described that predators such as *P. manokwari* can readily be transported by human activities, so disturbance caused by the construction of these roads has led to the invasion of exotic land snails and predators and, as a result, extinction areas might be increasing.

Meanwhile, *M. aureola*, which is distributed in the southern area of Hahajima Island, was thought to be safe from extinction (Fig. 5); however, a surfaced road was constructed in the southern area of Hahajima Island recently, but exotic land snails are still rare there (Okochi et al., 2004), so *M. aureola* is surviving.

M. ponderosa has declined in the central and, especially, southern areas of Hahajima Island (Fig. 6), but the reason for its decline is thought to be different from that of *M. polita*. They are all ground-dwelling ecotypes (Chiba, 2003), so they compete against each other; therefore, extinction may occur if their populations are decreased by environmental deterioration. Except for one northern area where *M. ponderosa* has survived and *M. polita* is extinct, *M. ponderosa* is competitively inferior to *M. polita* and *M. aureola*.

These findings reveal that the respective processes of extinction of *Mandarina* spp. in Chichijima and Hahajima islands are very different (Figs. 2–6), as is the distribution of *P. manokwari* in the two islands (Fig. 7). In other words, the invasion of *P. manokwari* has caused a rapid decline in land snails; if the invasion of *P. manokwari* had not occurred, the decline might have been slow. Indeed, Sugiura et al. (2006) confirmed that *P. manokwari* puts high predation pressure on land snails in Chichijima Island.

The invasion of *P. manokwari* is rapidly bringing about the extinction of *Mandarina* spp. in the oceanic Ogasawara Islands because ecological resistance against the invasion of *P. manokwari* there might be weak. Moreover, the expansion of *P. manokwari* might be very rapid in disturbed areas (Fig. 7). It thus might be very difficult to eradicate *P. manokwari* that has already invaded Chichijima Island (Tomiyama, 2002b), so it is necessary to take immediate steps to preserve the populations of endemic species, *M. chichijimana*. For this purpose, populations must be isolated from predators, or introduced (or re-introduced) to outlying islands where no *Mandarina* spp. occur (if possible, to islands where land snails were distributed previously).

Moreover, it is necessary to make all possible efforts to prevent *P. manokwari* from invading Hahajima Island as well as uninhabited islands surrounding Chichijima and Hahajima islands. However, since a large amount of materials are moved between Chichijima Island and Hahajima Island, it will be necessary to restrict the transfer of plant seedlings and cars that have soil adhering to them. In addition, efforts should be made to keep uninhabited islands such as Anijima Island isolated.

P. manokwari is vulnerable to low temperature (Kaneda et al., 1992) and seawater (Ohbayashi, unpublished), so to prevent it from invading these uninhabited islands, shoes ought to be sterilized using refrigeration or seawater.

Incidentally, in Hahajima Island, which has currently not been invaded by *P. manokwari*, extinction by alien species and predatory flatworms has occurred in disturbed areas such as road construction sites; however, it is notable that extinction has also occurred at Mt. Chibusa in the central area, where only mountain trails have been constructed (Figs. 4 and 6). So in areas where many endemic land snails still survive, the construction of mountain trails should be reconsidered, and if possible, these areas should be managed to avoid disturbing endemic snail habitats.

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Chapter 5

Food habit of *Platydemus manokwari* De Beauchamp, 1962 (Tricladida: Terricola: Rhynchodemidae), known as a predatory flatworm of land snails in the Ogasawara (Bonin) Islands, Japan

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Abstract

The distribution and food habit of the flatworm species *Platydemus manokwari*, which is known to be a predator of land snails, were examined on Chichijima Island of the Ogasawara (Bonin) Islands, Japan. *P. manokwari* was distributed over a wide area of the island. Few live land snails were found in the area where *P. manokwari* was distributed. Further, it was revealed that *P. manokwari* fed not only on live land snails including predatory species, but also on other food resources such as live flatworms or a land nemertean species and the carcasses of slugs and earthworms. Therefore, *P. manokwari* is expected to survive even if the populations of land snails are almost lost on Chichijima Island in the future, and so will affect the biodiversity of Chichijima Island.

Key words: *Platydemus manokwari*; *Euglandina rosea*; *Achatina fulica*; decline of land snails; Ogasawara (Bonin) Islands

INTRODUCTION

The Ogasawara (Bonin) Islands are located in the northern Pacific Ocean about 1,000 km south of the mainland of Japan. More than 100 species of land mollusks have been recorded on the islands, of which 94% are endemic to the islands (Tomiyama and Kurozumi, 1992; Tomiyama, 1994).

However, about 70% of the endemic species have already become extinct (Tomiyama, 2002). The decline and extinction of endemic land snails in tropical oceanic islands is a major concern for conservation biology (Clarke et al., 1984; Hopper and Smith, 1992; IUCN/SSC Mollusc Specialist Group, 1995). Furthermore, the population of introduced species such as the giant African snail *Achatina fulica* has also declined in recent years on Chichijima Island (Tomiyama, 1991; Ohbayashi, 2002).

The following possible reasons for this decline on Chichijima Island have been pointed out: introduction of the predatory snail *Euglandina rosea* for the control of *A. fulica* in 1965 (Takeuchi et al., 1991); predation by a predatory flatworm (Okochi et al., 2004); invasion of the alien predatory flatworm *Platydemus manokwari* since the 1990s (Kawakatsu et al., 1999; Tomiyama, 2002); predation by alien rats (Tomiyama, 2002); and forest destruction (Tomiyama, 2002).

Among them, two invasive aliens, *E. rosea* and *P. manokwari*, could be major reasons because they invaded only Chichijima Island, which would explain the sharp decline of both endemic and exotic snails on Chichijima Island. The most likely cause of the decline of land snails on Chichijima Island is thought to be the invasion of *P. manokwari* in the 1990s (Tomiyama, 2002).

Although land snails have already become extinct in most areas on Chichijima Island (Tomiyama and Kurozumi, 1992; Tomiyama, 1994), *P. manokwari* remains distributed over these areas (Ohbayashi, 2002). Furthermore, there used to be other land planarians (including snail predators) and land nemertean worms distributed on Chichijima Island (Kawakatsu et al., 1999), but in

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recent years there are few in areas where *P. manokwari* has already invaded, suggesting that these land planarians and land nemerteans have been defeated by interspecific competition with *P. manokwari* (Ohbayashi, 2002).

The food habit of *P. manokwari* has not been investigated previously in sufficient detail. Waterhouse and Norris (1987) noted, as a personal communication from Winsor (1985), that *P. manokwari* feed on anything other than live land snails, while Kaneda et al. (1990) reported that *P. manokwari* preyed only on live land snails. Furthermore, Hopper and Smith (1992) suggested that *P. manokwari* also feeds on another alien predatory snail, *E. rosea*, but this has not been verified. It is important to clarify the food habit of *P. manokwari* and interspecific relationships among *P. manokwari* and other predators for the conservation of endemic land snails.

This study was undertaken to clarify the food habit of *P. manokwari*, and to confirm the interactions between other predators of land snails.

MATERIALS AND METHODS

Distribution and field observation of the food habit of *P. manokwari*. All studies were conducted on Chichijima Island, the largest island in the Ogasawara (Bonin) Islands.

We searched under stones and logs in the daytime of the years 1995, 1998, 2002, 2003, and 2004 (29 times in total, covering spring to winter, and search areas and months differed with years). The sites where both land snails and flatworms were recorded (whether at the same time or not) were regarded as areas of coexistence at the time of the search. We also conducted nighttime observations of the forest floor (once in the month in December 1998 and once every month from January to July, 2004), and recorded the sites where *P. manokwari* and live land snails were detected. During the survey of the distribution of *P. manokwari*, we recorded the species predated by the animal.

We also used 20 cm×20 cm mesh bags made of 5 mm nylon mesh as attractant traps in which one live *A. fulca* (shell height: over 40 mm) was put. The traps were set on the forest floor near a road (45 sites) from March to May 1998, checked every few weeks, and the sites where *P. manokwari* was detected were recorded.

Feeding tests. Five species of live flatworms (*Bipalium kewense* (adults), *Bipalium* sp. (adults), *Platydemus* sp. -1 (adults), *Platydemus* sp. -2 (adults), and *Australopacifica* sp. (adults)), one species of live land nemertean (*Geonemertes pelaensis* (adults)), six species of live land snails and slugs (*Achatina fulica* (juveniles and adults), *Limax marginatus* (adults), *Deroceras laebe* (adults), *Euglandina rosea* (juveniles and adults), *Bradybaena similaris* (adults), and *Acusta despecta sieboldiana* (juveniles and adults)), and earthworms (*Haplotaxida* spp. (adults), dead or alive) were tested as the prey of *P. manokwari* (Table 1). Species of flatworms and land nemerteans were identified according to Kawakatsu et al. (1999).

One specimen of *P. manokwari* (body length: over 30 mm) and one specimen of a test animal species were put together in a plastic cup (ϕ90 mm, 40 mm height) in which a paper towel moistened with distilled water was laid. They were kept at 25°C under room light conditions, and predation was checked every day for 10 d.

Predation was detected by direct observation during the daytime (every hour from 07:00–23:00), and by video camera (SONY CCD-TRV86PK) recording during the night (23:00–07:00).

Cannibalism of *P. manokwari* was also tested. One, three or five specimens of mature *P. manokwari* (collected at different sites of Chichijima Island, body length: over 30 mm) were put in a plastic cup (ϕ80 mm, 25 mm height) in which a paper towel moistened with distilled water was laid, and were checked every day for 10 d (25°C, room light conditions).

RESULTS

Distribution and field observation of the food habit of *P. manokwari*

P. manokwari is distributed over a wide area of Chichijima Island, except for the east and south coast areas (Fig. 1). In contrast, endemic snails are distributed only in the east and south coast areas (Fig. 1).

In nine sites of the 37 sites where *P. manokwari* was recorded, land snails and *P. manokwari* coexisted, but at the other 28 sites, only *P. manokwari* was recorded. Therefore, it was difficult to find live land snails in the area where *P. manokwari* was detected (Fig. 1), and only one trap (set at Kita-

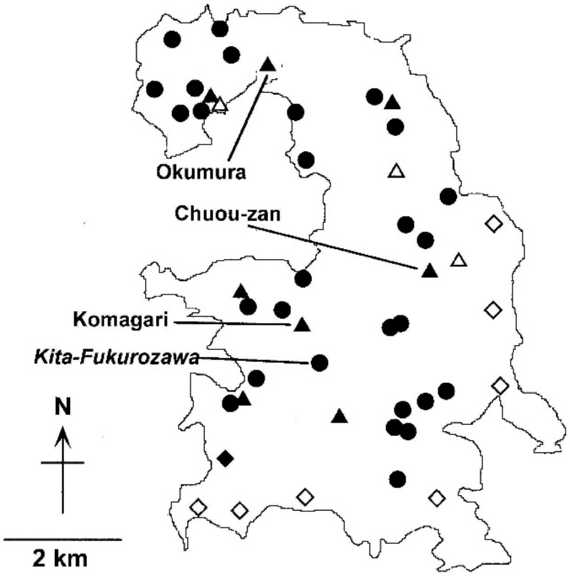

Fig. 1. Distributions of *Platydemus manokwari* and land snails (endemic/exotic) in Chichijima Island (1995–2004). Solid (●/◆/▲) and open (◇/△) symbols show whether *P. manokwari* was recorded or not, respectively. Patterns of symbols are as follows: ●: no snails (both endemic and exotic) were recorded; ◆/◇: endemic snails were recorded; ▲/△: exotic snails were recorded. Points indicated by lines are where predation of *P. manokwari* was recorded. The point "*Kita-Fukurozawa*" is the point where one of the attractant traps was set).

Fukurozawa) of the 45 traps attracted *P. manokwari* (Fig. 2b).

In the field research, it was observed that *P. manokwari* preyed on live land nemertean (*G. pelaensis*) at Chuou-zan (14 Nov. 2002: Figs. 1 and 2a), attacked live *A. fulica* put in the mesh bag at Kita-Fukurozawa (11 Mar. 1998: Figs. 1 and 2b), fed on the carcass of slug (*Incilaria* sp.) at Chuou-zan (19 Aug. 2002: Figs. 1 and 2c), attacked live *E. rosea* at Okumura (23 Apr. 2002: Figs. 1 and 2d), and fed on the carcass of earthworms (*Haplotaxida* spp.) at Komagari (4 Dec. 1998: Figs. 1 and 2e).

In the case of *E. rosea*, three *P. manokwari* attacked one *E. rosea* at the same time ("gang-attack": Mead, 1963). The shell height of the *E. rosea* was 57.6 mm, and the wet body weights of the *P. manokwari* were 0.37, 0.27 and 0.21 g, respectively.

Feeding tests

P. manokwari preyed on live land planarians (except *P. manokwari*), live land nemerteans, and live land snails (including *E. rosea*) tested within 10 d (Table 1). Further, *P. manokwari* fed on the carcass of earthworms within 10 d, but did not prey on live earthworms at all for more than 10 d (Table 1). Cannibalism was not observed at all for more than 10 d.

When *P. manokwari* attacked snails, other planarians and a land nemertean, it followed their trails. When *P. manokwari* fed on land snails, it bent its mid-abdomen and inserted it into the aperture of the prey, then digested the flesh of the snail and sucked (Fig. 3a). Meanwhile, when *P. manokwari* fed on land planarians and land nemerteans, it extruded a proportionately long, white proboscis near the mid-ventral surface of the body, and sucked directly (Fig. 3b).

DISCUSSION

We confirmed that *P. manokwari* feeds not only on live land snails, but also on other species of live flatworms or land nemerteans, and on the carcasses of slugs and earthworms, both in the field and in captivity.

There used to be other land planarians (such as *Bipalium* sp.) and a land nemertean (*G. pelaensis*) distributed widely on Chichijima Island, but in recent years there are few in areas where *P. manokwari* has already invaded (Kawakatsu et al., 1999; Ohbayashi, 2002). This is in contrast to the abundance of these land planarians and a land nemerteans on Hahajima Island, which has not been invaded by *P. manokwari* (Kawakatsu et al., 1999; Okochi et al., 2004). Therefore, these land planarians and land nemerteans may have been consumed by *P. manokwari* on Chichijima Island.

The food habit of *P. manokwari* suggests that the reason why *P. manokwari* still exist in areas where both the number of endemic and exotic land snails has already been reduced may be that *P. manokwari* can use food resources other than live land snails.

On the other hand, on Hahajima Island, other species of predatory flatworms (such as *Bipalium* sp., *Platydemus* sp. -1, and *Australopacifica* sp.) eradicated endemic snails but are coexisting with exotic snails because they need live snails as food (Okochi et al., 2004).

We also confirmed that *P. manokwari* feeds on *E. rosea*, a predatory land snail, both in the field and in captivity, suggesting that *P. manokwari* may be a major reason why *E. rosea* populations have de-

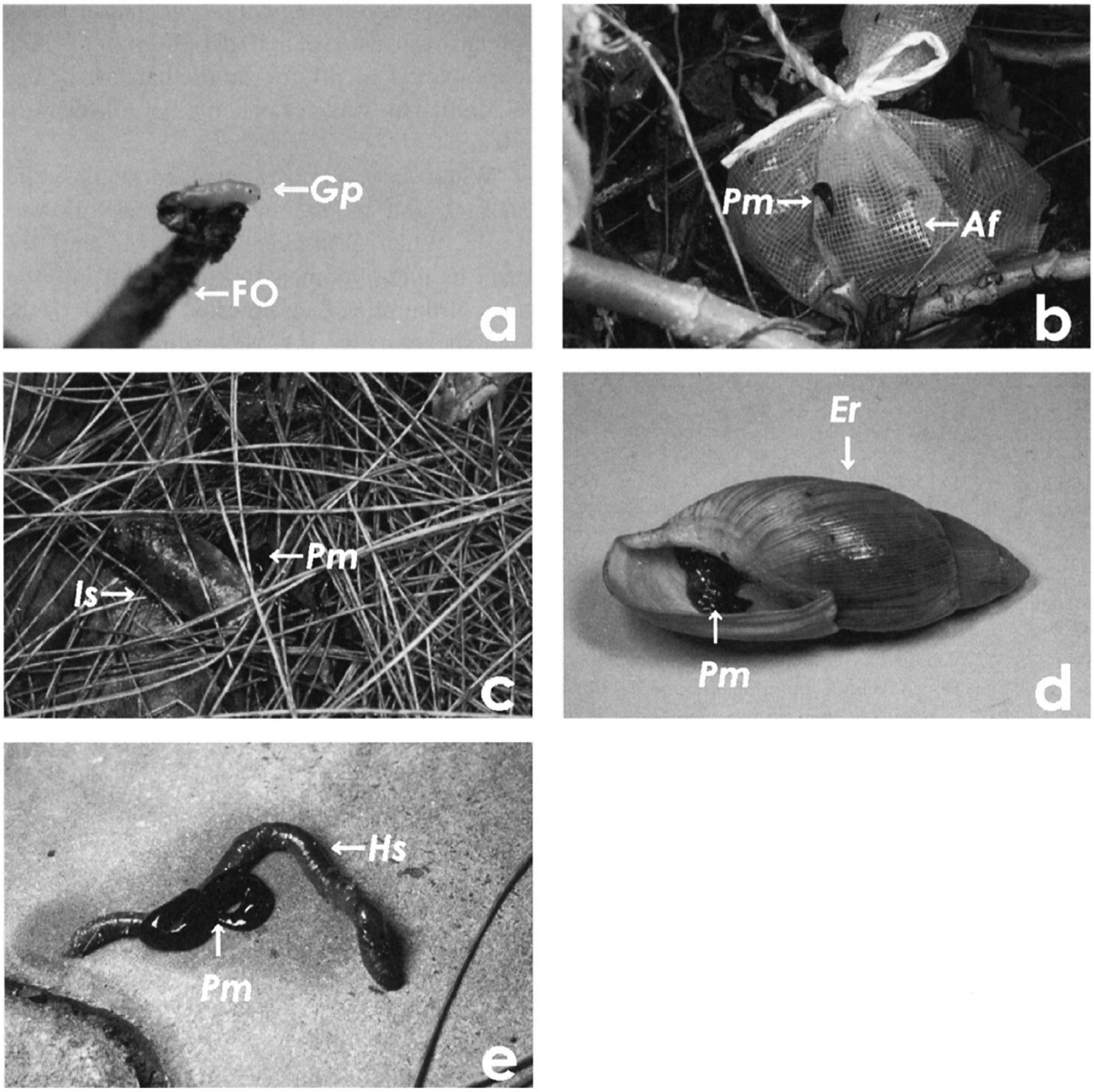

Fig. 2. Feeding on various food resources by *Platydemus manokwari* (*Pm*) on Chichijima Island. a: Head region of land nemertine (*Geonemertes pelaensis*: *Gp*, photograph in the laboratory, FO: forceps holding the head region); b: live *Achatina fulica* (*Af*) put in mesh bag; c: carcass of slug (*Incilaria* sp.: *Is*); d: live *Euglandina rosea* (*Er*, photograph in the laboratory); e: carcass of earthworm (*Haplotaxida* sp.: *Hs*).

creased on Chichijima Island, as well as those in other tropical oceanic islands such as Guam (Hopper and Smith, 1992).

Therefore, as *P. manokwari* can use various food resources, this flatworm is expected to survive in the future and make it difficult for the land snails of Chichijima Island to survive.

Furthermore, adults of *P. manokwari* were not observed to cannibalize each other. This suggests that there may be no chance of population limitation by cannibalism.

In conclusion, it has been confirmed that the introduced predatory flatworm *P. manokwari* presently poses a major threat to the survival of both the endemic and exotic land snails, including *E. rosea* on Chichijima Island at present. This animal may also cause a reduction of other land snail predators such as other flatworms. Therefore, *P. manokwari* threatens the biodiversity of Chichijima Island.

It is important to take measures to prevent the further invasion of *P. manokwari* to other islands for the conservation of endemic land snails, land planarians, and land nemertine. Such action is also

Table 1. Predation on various food resources in captivity by *Platydemus manokwari*

Food resources	Size (mm)[a]	*N*[b]	Number of prey	Days to start of preying
Live land planarians				
Bipalium kewense	>60	2	1[c]	1
Bipalium sp.	>25	6	5[d]	1–6
Platydemus manokwari	>30	4	0	—
Platydemus sp. -1	>15	1	1	1
Platydemus sp. -2	>35	4	4	1–10
Australopacifica sp.	>15	1	1	1
Live land nemertine				
Geonemertes pelaensis	>25	3	3	2–6
Live land snails and slugs				
Achatina fulica	<5, >50	4	4[e]	6–7
Limax marginatus	>25	2	2	1
Deroceras laebe	>15	7	7	1–3
Euglandina rosea	<5, >50	2	2[e]	1–5
Bradybaena similaris	>10	1	1	2
Acusta despecta sieboldiana	<5, >20	5	5[e]	1–7
Earthworm				
Haplotaxida spp. (live)	>50	5	0	—
Haplotaxida spp. (dead)	>50	5	5	1

[a] Body length (planarians, nemertine, slugs, and earthworm) or shell heights (snails).

[b] Number of trials.

[c] During experiment, one *Bipalium kewense* dead (not by predation).

[d] During experiment, one *Bipalium* sp. dead (not by predation).

[e] Both young and adult snails were preyed upon.

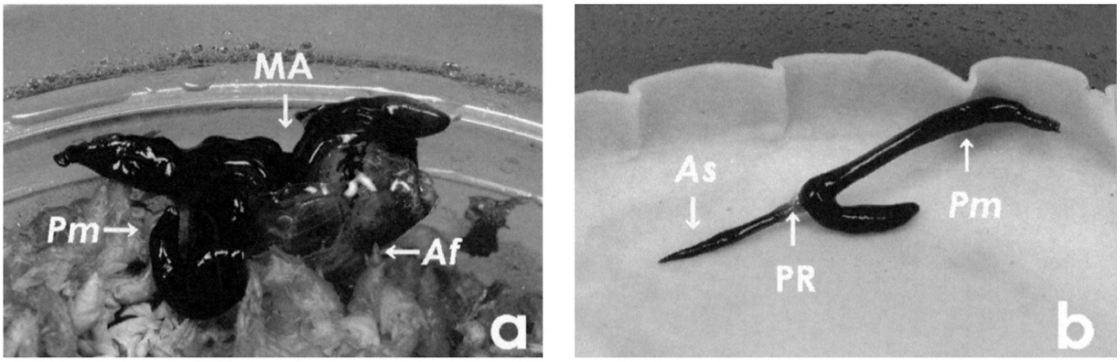

Fig. 3. Styles of predation by *Platydemus manokwari* (*Pm*). a: live snail, *Achatina fulica* (*Af*);. b: live land planarians, *Australopacifica* sp. (*As*). MA: mid-abdomen; PR: proboscis.

required on other tropical oceanic islands of the world.

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Chapter 6

High Predation Pressure by an Introduced Flatworm on Land Snails on the Oceanic Ogasawara Islands[1]

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ABSTRACT

The introduction of a predatory flatworm, *Platydemus manokwari*, has been considered a cause of the decline of endemic land snails on the tropical oceanic islands. To clarify the effect of *P. manokwari* on land snail survival in the field, we examined survival rates of snails experimentally placed in areas where snails are absent (*i.e.*, *P. manokwari* is present) on Chichijima, Ogasawara (Bonin) Islands. We found that over 50 and 90 percent of the snails were dead after 3 and 11 d, respectively, and that the main cause of mortality was predation by *P. manokwari*.

Key words: conservation; invasive species; *Platydemus manokwari;* snail predators.

TROPICAL OCEANIC ISLANDS SUPPORT UNIQUE LAND SNAIL FAUNAS with high endemism. Most of these endemic species, however, have declined dramatically since human colonization of the islands, as a result of various factors, including habitat destruction and the impacts of introduced species (Lydeard *et al.* 2004), in particular, rats, the predatory snail *Euglandina rosea* (Férussac) (Gastropoda: Spiraxidae), and the flatworm *Platydemus manokwari* De Beauchamp (Tricladida: Rhynchodemidae) (Clarke *et al.* 1984, Hopper & Smith 1992, Hadfield *et al.* 1993, Eldredge & Smith 1995, Civeyrel & Simberloff 1996, Cowie 2001, Cowie & Cook 2001). *Euglandina rosea* and *P. manokwari* have been introduced to several areas of the Pacific as biological control agents against the giant African snail *Achatina fulica* (Férussac) (*e.g.*, Muniappan 1987, 1990; Eldredge & Smith 1995; Civeyrel & Simberloff 1996; Cowie 2001). These species pose a serious threat to endemic land snails because both species feed on live snails of any species, including *A. fulica* (Kaneda *et al.* 1990, Hopper & Smith 1992, Civeyrel & Simberloff 1996, Cowie 2001, Cowie & Robinson 2003). Such nontarget effects of biological control have been recently discussed (Follett & Duan 1999). Although nontarget effects of *E. rosea* have been examined in the field (Hadfield & Mountain 1980, Hadfield *et al.* 1993), the effect of *P. manokwari* on land snails has been little examined.

The Ogasawara (Bonin) Islands are located in the northwestern Pacific Ocean, about 1000 km south of the mainland of Japan (Fig. 1a). More than 100 species of land snails have been recorded from these islands, of which about 90 percent are endemic to the islands (Kurozumi 1988). Most of the endemic species, however, have already become extinct or endangered (Tomiyama 2002). Furthermore, both introduced and endemic land snails have been declining on the largest of the Ogasawara Islands, Chichijima (Ohbayashi *et al.* 2005). Ohabayashi *et al.* (2005) examined the distribution of *P. manokwari* and land snails and suggested that the predatory flatworm *P. manokwari* had expanded its distribution over a wide area of Chichijima, eradicating the land snail fauna. The effects of *P. manokwari* on the survival of land snails have not been quantitatively examined in the field, although snail predation by *P. manokwari* has been studied in the laboratory (Kaneda *et al.* 1990, Ohbayashi *et al.* 2005). Therefore, we examined the survival rate of snails experimentally placed in areas where snails are present and absent on Chichijima to determine the contribution of *P. manokwari* to the absence of snails.

The study was conducted in an urban area and its surroundings on Chichijima, Ogasawara Village, Tokyo Metropolitan, southeast Japan (Fig. 1b; 27°05′N, 142°12′E). The mean annual temperature was 23.2°C and the annual precipitation was 1292 mm in 1987–1998 on Chichijima (Toyoda 2003). The climate is subtropical.

We surveyed the presence/absence of land snails and *P. manokwari* in September–October 2005 and found land snails of introduced species [*A. fulica*, *Acusta despecta* (Sowerby), and *Bradybaena similaris* (Férussac)] surviving in the coastal area, probably because of the absence of *P. manokwari* (Fig. 1c). *Platydemus manokwari* does not occur in the urban coastal area, perhaps because of environmental factors such as lack of adequate vegetation (S. Sugiura *et al.*, pers. comm.).

To clarify the factors affecting the distribution and survival of land snails, we examined the survival rate of land snails experimentally placed at sites where snails were present and absent: snails present, Okumura Ground (Okumura; 27°05′N, 142°12′E; Fig. 1c); snails absent, Kiyose Experimental Station of the Forestry and Forest Products Research Institute (FFPRI) (Kiyose; 27°06′N, 142°11′E; Fig. 1c). Palms and broad-leaved trees had been planted

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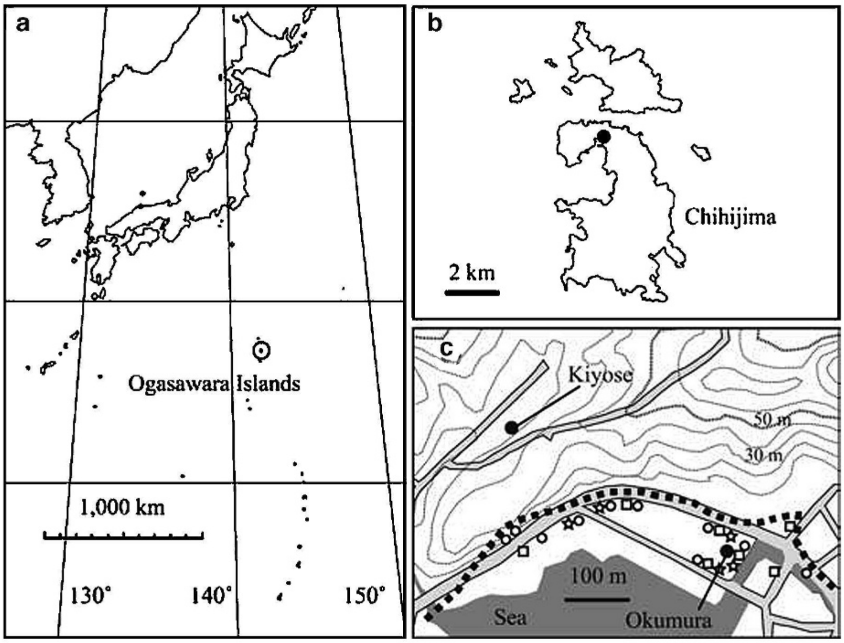

FIGURE 1. (a) Location and map of Ogasawara Islands (an open circle). (b) Study site (a closed circle) on Chichijima. (c) The experimental sites (closed circles) and the distribution of land snails: *Achatina fulica* (open stars), *Acusta despecta* (open circles), and *Bradybaena similaris* (open squares). The dashed line indicates the boundary between the areas where snails were present and absent.

on both sites, although the tree density was higher at Kiyose than at Okumura. At Okumura, the mean ± SE densities (individuals/m^2, $N = 3$) of *A. fulica, A. despecta,* and *B. similaris* were 4.7 ± 2.7, 22.3 ± 6.3, and 9.7 ± 3.7, respectively, on 14 October 2005. *Platydemus manokwari* has been observed at Kiyose, although it was difficult to find at common scales of density (*e.g.*, individuals/m^2).

We investigated snail survival by placing bags of snails on the ground in vegetation at each site. We used juveniles and adults of the introduced species *A. despecta* and *B. similaris* (shell diameter: <20 mm) collected at Okumura. To determine the effects of *P. manokwari* on snail survival, we placed snails in two types of bags (*ca* 30 × 25 cm): 2 mm mesh nylon bags that allowed the entry of *P. manokwari* (control bags) and <0.5 mm mesh unwoven fabric bags that excluded *P. manokwari* (treatment bags). Fleshy mulberry leaves and pieces of rigid plastic were also placed in the bags as food and resting sites for snails, respectively. Five snails of the same species were placed in each bag. We used eight bags of *A. despecta* and three bags of *B. similaris* per bag type at each site. The bags were placed >1 m apart. The experiment was conducted on 14–25 October 2005. We checked the survival of land snails on 17 and 25 October. The mean temperature was 26.5°C, the mean relative humidity was 79.4 percent, and the mean daily precipitation was 1.6 mm (total precipitation, 17.5 mm) during the experiment (Chichijima Meteorological Observation Station, 27°05′N, 142°11′E).

We used two-way ANOVA to examine the effects of site and bag type on snail survival of each species for 3 d. Survival rates were calculated as the proportion of living snails per bag and the values were arcsine-transformed prior to statistical analysis.

The survival rates of *A. despecta* and *B. similaris* in the control bags placed at the site where snails were absent (Kiyose) were 7.5 and 0.0 percent, respectively, after 11 d (Table 1). In contrast, their survival rates in the treatment bags at Kiyose and in both types of bags at the site where snails were present (Okumura) ranged from 93.3 to 100.0 percent (Table 1). The survival of snails in the control bags at Kiyose rapidly decreased after the bags were deployed: more

TABLE 1. *Survival rates of the snails* Acusta despecta *and* Bradybaena similaris *at sites with and without snails.*

				Cumulative survival rate (%) (mean ± SE)	
Snail species	Site	Bag type	No. of bags	17 October (Day 3)	25 October (Day 11)
A. despecta					
	Kiyose	Control	8	47.5 ± 12.5	7.5 ± 3.7
		Treatment	8	100.0 ± 0.0	97.5 ± 2.5
	Okumura	Control	8	100.0 ± 0.0	100.0 ± 0.0
		Treatment	8	97.5 ± 2.5	95.0 ± 3.3
B. similaris					
	Kiyose	Control	3	26.7 ± 26.7	0.0 ± 0.0
		Treatment	3	100.0 ± 0.0	100.0 ± 0.0
	Okumura	Control	3	100.0 ± 0.0	100.0[a]
		Treatment	3	100.0 ± 0.0	93.3 ± 6.7

[a] One bag was missing because of an artificial disturbance.

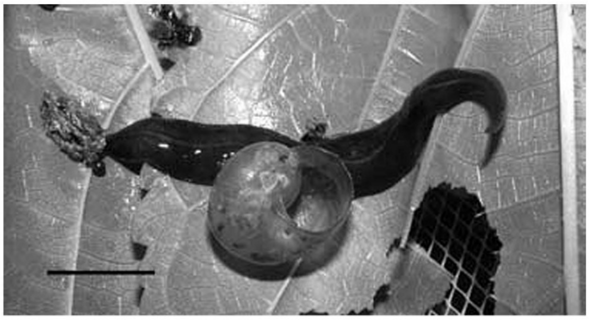

FIGURE 2. The introduced flatworm *Platydemus manokwari* and a dead snail, of which the soft-bodied part was completely consumed, from a control bag at the site where snails were absent (Kiyose). Scale bar: 10 mm.

than 50 percent of the snails were dead after 3 d (Table 1). Therefore, the site and bag type significantly affected the survival rate of snails, even after only 3 d (two-way ANOVA; *A. despecta*: site, $F_{1,28} = 14.4$, $P < 0.0001$, bag type, $F_{1,28} = 14.4$, $P < 0.0001$, site × bag type, $F_{1,28} = 20.2$, $P < 0.0001$; *B. similaris*: $F_{1,8} = 16.7$, $P < 0.001$, bag type, $F_{1,8} = 16.7$, $P < 0.001$, site × bag type, $F_{1,8} = 16.7$, $P < 0.001$).

On day 3 (17 October), we found *P. manokwari* (Fig. 2) in 37.5 and 66.7 percent of control bags of *A. despecta* and *B. similaris*, respectively, at Kiyose; there was approximately one individual of *P. manokwari* per bag. In contrast, we found no *P. manokwari* in the treatment bags at Kiyose or in either type of bags at Okumura. We observed *P. manokwari* attacking snails in the control bags at Kiyose on 17 October. Soft parts of most dead snails at Kiyose were completely consumed by *P. manokwari,* and only empty shells remained (Fig. 2). Although we found no *P. manokwari* in the control bags at Kiyose on day 11 (25 October), empty shells remained in all of the control bags, indicating predation by *P. manokwari*. Therefore, at Kiyose, *P. manokwari* invaded the control bags, consumed the snails, and left. Small insects (<3.0 mm), such as ants and staphylinid beetles, were frequently found in the control bags at both Kiyose and Okumura on 25 October; however, they were not observed attacking snails, but rather scavenging dead snails.

On Chichijima, *P. manokwari* is thought to have been introduced accidentally, and it became established in the early 1990s (Kawakatsu *et al.* 1999). In areas where snails were absent, we found that more than 50 and 90 percent of snails were preyed upon by *P. manokwari* after only 3 and 11 d, respectively. Therefore, it is likely that high predation pressure by *P. manokwari* resulted in the general absence of snails from this area. Our estimates of mortality may have been too high because the snails were kept in closed bags where their movement was limited. However, the snail mortality rate caused by *P. manokwari* predation was much more rapid than that of endemic snails caused by other flatworm species on Hahajima Island (*ca* 50 km south of Chichijima), where *P. manokwari* has not been introduced (mortality rate in mesh bags in the field was 33.3–54.5 percent after 1 mo from mid-September to mid-October; Okochi *et al.* 2004). This is the first demonstration of the rapid decrease in land snail survival caused by *P. manokwari* predation in the field.

In the laboratory, *P. manokwari* feeds on juveniles of the endemic snail genus *Mandarina* (Okochi *et al.* 2004), which is thought to have declined because of *P. manokwari* predation on Chichijima (Chiba 2003, Ohbayashi *et al.* 2005). The snails we used (shell diameter, <20mm) were as large as *Mandarina* juveniles. As pointed out by Ohbayashi *et al.* (2005), the effect of *P. manokwari* on *Mandarina* survival could be great. *Platydemus manokwari* feed on dead earthworms, as well as live snails, and thus have survived in areas where snails have been absent since their invasion (Ohbayashi *et al.* 2005). Since *P. manokwari* can readily be transported by soil on boots, construction machines, or on plant seed material used in the restoration of vegetation, it is desirable to restrict transporting of materials with soils to other islands (Okochi *et al.* 2004). Our results confirm that the introduction of *P. manokwari* is a serious concern in the conservation of the unique land snail faunas of tropical islands.

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Chapter 7

Potential impacts of the invasive flatworm *Platydemus manokwari* on arboreal snails

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Abstract The introduction of the snail-eating flatworm *Platydemus manokwari* (Tricladida: Rhynchodemidae) has been considered a cause of the extinction of native land snails on several Pacific islands. Although *P. manokwari* is known to attack land snails on the ground, whether *P. manokwari* attacks snails on trees remains unclear. To clarify the effect of *P. manokwari* on arboreal snails, we examined survival rates of land snails experimentally placed on tree trunks (0.5–2.0 m above the ground) in a forest on Chichijima, Ogasawara (Bonin) Islands, in the northwestern Pacific Ocean. The survival of snails experimentally placed on tree trunks with artificially created snail scent trails rapidly decreased for 7 days, and the mortality was caused by *P. manokwari* predation. However, snails placed on tree trunks without snail scent trails were not attacked by *P. manokwari*. Therefore, *P. manokwari* climbed tree trunks, likely tracking the snail scent. We found that over 40% of the snails placed on tree trunks with snail scent trails were eaten by *P. manokwari* within 7 days. This experiment supports the hypothesis that *P. manokwari* predation is an important cause of the rapid decline or extinction of native arboreal snails on Pacific islands.

Keywords Conservation · Invasive alien species · Land molluscans · Land planarians · Oceanic islands · Pacific islands · Predation · Snail predators · Tree-dwelling species

Introduction

Terrestrial mollusks have the highest number of documented extinctions of any major taxonomic group (Lydeard et al. 2004). Pacific islands support unique land snail faunas with high endemism. However, most endemic species have become extinct or have dramatically declined since human colonization of the islands because of habitat destruction and the impacts of introduced species (reviewed in Lydeard et al. 2004). The predatory snail *Euglandina rosea* (Férussac) (Gastropoda: Spiraxidae) and the snail-eating flatworm *Platydemus manokwari* De Beauchamp (Tricladida: Rhynchodemidae) have been introduced to several areas of the Pacific as biological control agents against the giant African snail *Achatina fulica* (Férussac) (e.g., Muniappan 1990; Eldredge and Smith 1995; Civeyrel and Simberloff 1996; Cowie 2001). However, these species pose a serious threat to endemic land snails because both *E. rosea* and *P. manokwari* feed on live snails of any species, including *A. fulica* (Kaneda et al. 1990; Hopper and Smith 1992; Civeyrel and Simberloff 1996; Cowie 2001; Cowie and Robinson 2003).

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Island land snails live in various types of habitats such as terrestrial, semiarboreal, and arboreal surroundings (Chiba 1999). The diversity and endemism of arboreal snails such as tree snails of the genera *Achatinella* and *Partula* characterize the Pacific land snail fauna (Cowie 1992; Lydeard et al. 2004). It is well documented that the predatory snail *E. rosea* impacts tree snails of the genera *Achatinella* (Hadfield et al. 1993) and *Partula* (Clarke et al. 1984; Murray et al. 1988). Like *E. rosea*, *P. manokwari* is considered to impact arboreal snails, and the extinction and decline of tree snails of the genus *Partula* on Guam are considered to have been caused by *P. manokwari* predation (Hopper and Smith 1992). However, the arboreal behavior of *P. manokwari* has rarely been observed. Therefore, the impact of *P. manokwari* on arboreal snails remains unclear.

Here, we examined the survival rates of snails experimentally placed on tree trunks on an island of the Ogasawara (Bonin) Islands, which *P. manokwari* has already invaded, in order to address the following questions: (1) to what extent are arboreal snails attacked by *P. manokwari*? and (2) how does *P. manokwari* locate arboreal snails to attack?

Materials and methods

Study site and species

The Ogasawara Islands are oceanic islands located in the northwestern Pacific Ocean, about 1,000 km south of the mainland of Japan (Shimizu 2003). The climate is subtropical; the mean annual temperature was 23.2°C and the annual precipitation was 1,292 mm during 1987–1998 on Chichijima (Toyoda 2003).

Ninety-five species of land snails have been recorded from the Ogasawara Islands, of which about 90% are endemic to the islands (Tomiyama and Kurozumi 1992; Chiba et al. 2007). However, over 70% of native land snail species on the largest of the Ogasawara Islands, Chichijima, have become extinct (Chiba et al. 2007). Furthermore, endemic land snails have been rapidly declining on Chichijima since the early 1990s (Ohbayashi et al. 2005, 2007). *Platydemus manokwari* (Fig. 1a) is thought to have been introduced to Chichijima accidentally and became established in the early 1990s (Ohbayashi et al. 2005). *Platydemus manokwari* predation is considered an important cause of the rapid decline of land snails on Chichijima (Ohbayashi et al. 2005, 2007; Sugiura et al. 2006). *Platydemus manokwari* feeds on dead animals (e.g., earthworms), as well as live snails, and has thus survived in areas where snails have been absent since its invasion (Ohbayashi et al. 2005).

Field experiment

To estimate potential impacts of *P. manokwari* on arboreal snails, we examined the survival of snails experimentally placed on tree trunks in a forest of the Kiyose Experimental Station of the Forestry and Forest Products Research Institute on Chichijima (Kiyose; 27°06′ N, 142°11′ E). The forest was composed of palms, pines, and broad-leaved tree species. *Platydemus manokwari* was observed to hide under stones during the day, and crawl along the forest floor at night. In this forest, the predation pressure by *P. manokwari* on ground-dwelling snails was extremely high, and therefore few snails survived (Sugiura et al. 2006). The experiment was conducted in early November 2007. The mean temperature, mean relative humidity, and mean daily precipitation during the experiment was 24.2°C, 78.3%, and 3.9 mm, respectively (Chichijima Meteorological Observation Station, 27°05′ N, 142°11′ E).

To compare the survival rates of land snails on the ground and on tree trunks, we placed nylon bags containing land snails on the ground, on tree trunks 0.5 m above the ground, and on tree trunks 1.0 m above the ground. We used juveniles and adults of the introduced species *Acusta despecta* (Sowerby) (shell diameter <20 mm) collected from coastal areas of Chichijima where many introduced snails survive because of the absence of *P. manokwari* (Sugiura et al. 2006). We placed land snails in 2-mm mesh nylon bags (approximately 30 × 25 cm) that allowed the entry of *P. manokwari* but not the escape of the snails. Fleshy mulberry leaves and pieces of rigid plastic were also placed in the bags as food and resting sites for snails, respectively. Five *A. despecta* individuals were placed in each bag. In an earlier study (Sugiura et al. 2006), we also used bags that excluded *P. manokwari* to clarify the effects of *P. manokwari* on land snails in bags that do allow the flatworm to enter. *Platydemus manokwari* did not

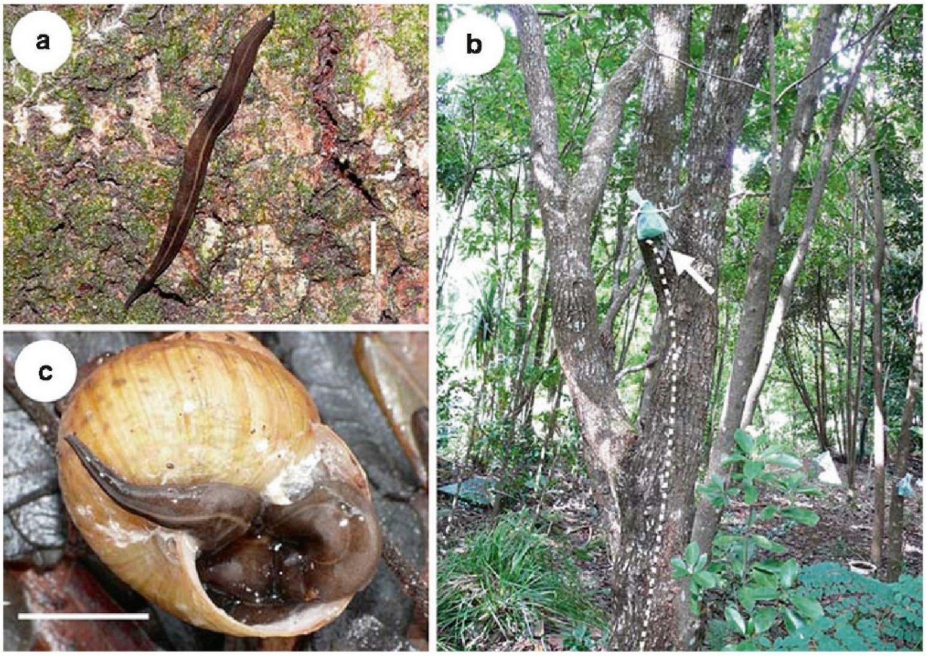

Fig. 1 (**a**) *Platydemus manokwari*. (**b**) A 2-mm mesh nylon bag (containing five snails) tied to a tree trunk 2 m above the ground. The arrow indicates the bag. The dashed line indicates the tree trunk to which a 10-mm wide snail scent trail was applied. (**c**) *Platydemus manokwari* feeding on a snail. Bars: 10 mm

kill land snails placed in <0.5-mm mesh fabric bags that excluded *P. manokwari* at this study site; therefore, this treatment was not repeated in the present study. We randomly selected 14 trees (diameter at breast height (DBH) 67–191 mm) and tied single bags (containing five snails each) to each tree using plastic ropes (Fig. 1b). We placed one bag per tree trunk. Because *P. manokwari* uses chemical senses to locate prey under laboratory conditions (Kaneda et al. 1990), *P. manokwari* may follow the scent of snails on trees to track and find arboreal snails in the field. Therefore, we used live individuals of *A. despecta* to apply their scent along a 10-mm-wide trail to tree trunks from the ground to each bag (Fig. 1b). We used seven bags per height treatment: 0 m (on the ground), 0.5 m (on tree trunks), and 1.0 m (on tree trunks). Tree DBH did not differ among height treatments (Welch's *t*-test, $t_9 = -1.06$, $P = 0.32$). Bags were placed >1 m apart. We checked the survival of land snails and counted the number of *P. manokwari* invading each bag 1, 2, 3, and 7 days after placement.

Another experiment was conducted to test whether *P. manokwari* climb trees while tracking the snail scent applied to tree trunks. We randomly selected 28 trees (DBH 64–354 mm) and tied a single bag (containing five snails) to each tree using plastic ropes (Fig. 1b). Twenty-one and seven bags were tied to tree trunks 1.0 and 2.0 m above the ground, respectively. We compared the number of bags invaded by *P. manokwari* among the different treatments. The first treatment consisted of a snail scent trail applied to tree trunks from the ground to the bags (Fig. 1b; height 1.0 m, $N = 7$; height 2.0 m, $N = 7$). We used live individuals of *A. despecta* to apply their scent along a 10-mm-wide trail to tree trunks from the ground to each bag (Fig. 1b). The alternative treatment included water applied to tree trunks from the ground to the bags (height 1.0 m, $N = 7$). As the control, nothing was applied to tree trunks (height 1.0 m, $N = 7$). Tree DBH did not differ among treatments (one-way ANOVA, $F_{3,24} = 0.08$, $P = 0.97$). We checked the survival of snails and counted the number of *P. manokwari* invading each bag 1, 5, and 7 days after the placement. When *P. manokwari* escaped from the bags after predation, we measured the invasion of *P. manokwari* into each bag by checking land snails killed by *P. manokwari* in the bags.

Data analysis

To examine the effects of snail bag position (i.e., on the ground and on trunks at 0.5 and 1.0 m height) on the number of live snails per bag, we used generalized linear models (GLMs) with Poisson error distribution and log link (i.e., Poisson regression).

We also examined the effects of snail bag position on the number of *P. manokwari* invading each snail bag using Poisson regression. We examined these effects at 1, 2, 3, and 7 days separately. To clarify what *P. manokwari* used to climb tree trunks, we also examined the effects of tree trunk treatments (control, water, snail scent trails at 1.0 m, and snail scent at 2.0 m) on invasion or non-invasion (1/0) of *P. manokwari* into each bag using GLMs with binomial error distribution and logit link (i.e., logistic regression). When residual deviance was larger than residual degrees of freedom (i.e., overdispersion), we used quasi-Poisson or quasi-binomial error distribution instead of Poisson or binomial error distribution, respectively (Crawley 2007). Then we tested these effects using *F*-tests or chi-square tests (Crawley 2007). We used R Ver. 2.4.1 for these statistical analyses (R Development Core Team 2006).

Results

Survival of the snails experimentally placed on tree trunks as well as on the ground rapidly decreased over only 3 days (Table 1). *Platydemus manokwari* was frequently observed feeding on snails in bags for 2 days after bag placement (Fig. 1c; Table 2). Although the number of *P. manokwari* per bag differed significantly with bag position, its significance disappeared after considering overdispersion (Table 2). Soft parts of most dead snails were completely consumed by *P. manokwari*, and only empty shells remained. All mortalities of land snails were caused by *P. manokwari* predation. We found that 91.4% (32/35), 40.0% (14/35), and 45.7% (16/35) of the snails placed on the ground, on tree trunks at 0.5 m height, and on tree trunks at 1.0 m height, respectively, were eaten by *P. manokwari* within 7 days. Therefore, survival of land snails differed significantly with snail bag position (Table 1).

Bags placed on tree trunks with snail scent trails were invaded by *P. manokwari*, whereas bags placed on tree trunks without snail scent were rarely invaded (Table 3; GLM, bimodal distribution, $\chi^2_3 = 8.64$, $P = 0.03$; quasi-bimodal error distribution, $F_{3,24} = 3.29$, $P = 0.04$). Some snails (one or two per bag) were killed in the bags invaded by *P. manokwari*. Therefore, *P. manokwari* probably located bagged snails by tracking the snail scent on tree trunks.

Table 1 Effects of different bag positions on survival of snails in bags

	Numbers[a] of live snails per bag			Test[b]		
	On the ground	Tree trunk (0.5 m)	Tree trunk (1.0 m)	d.f.	χ^2	*P*
Set (Day 0)	5 (5–5)	5 (5–5)	5 (5–5)			
Day 1	3 (1–5)	4 (2–4)	3 (3–4)	2	0.21	0.90
Day 2	1 (0–3)	3 (2–4)	3 (2–4)	2	6.40	0.04
Day 3	1 (0–2)	3 (2–4)	3 (2–4)	2	8.97	0.01
Day 7	0 (0–1)	3 (2–4)	3 (2–4)	2	17.37	0.0002

[a] Median (min–max)

[b] GLM using Poisson error distribution

Table 2 Effects of different bag positions on *Platydemus manokwari* invasions into bags

Bag positions	Numbers[a] of *P. manokwari* per bag			Chi-squared test[b]			*F*-test[c]		
	On the ground	Tree trunk (0.5 m)	Tree trunk (1.0 m)	d.f.	χ^2	*P*	d.f.	*F*	*P*
Day 1	2 (1–16)	1 (1–3)	2 (1–3)	2	8.85	0.01	2,18	1.61	0.23
Day 2	3 (0–10)	1 (0–5)	1 (0–5)	2	10.01	0.01	2,18	2.17	0.14
Day 3	0 (0–6)	0 (0–0)	0 (0–1)	2	9.64	0.01	2,18	2.07	0.16
Day 7	0 (0–0)	0 (0–0)	0 (0–0)	2	0.00	1.00			

[a] Median (min–max)

[b] Poisson error distribution

[c] Quasi-Poisson error distribution

Table 3 Effects of different treatments on invasions by *Platydemus manokwari* into bags

Tree trunk treatment	Tree trunk height (m)	No. bags	No. bags invaded by *P. manokwari* (%)*
None (control)	1.0	7	0 (0.0)
Water	1.0	7	1 (14.3)
Snail scent	1.0	7	4 (57.1)
Snail scent	2.0	7	3 (42.9)

* Significant difference among treatments; GLM, bimodal distribution, $\chi_3^2 = 8.64$, $P = 0.03$; quasi-bimodal error distribution, $F_{3,24} = 3.29$, $P = 0.04$. The values did not differ with number of days (1, 5, or 7) after placement

Discussion

Platydemus manokwari is an important mortality factor for arboreal snails (Table 1). Furthermore, our findings suggest that snail scent is an important cue to *P. manokwari* for locating arboreal snails in the field (Table 3). Locating prey using chemical cues has been found previously under laboratory conditions (Kaneda et al. 1990). This study is (1) the first demonstration of the rapid decrease in arboreal snail survival caused by *P. manokwari* predation and (2) the first field evidence of *P. manokwari* locating prey using chemical cues.

Some arboreal snail species do not descend from trees to the ground (e.g., Hadfield and Mountain 1980). Thus, how would the ground-dwelling *P. manokwari* locate such arboreal snails? Heavy rains may result in the scent of tree snails being carried down tree trunks to the ground, thereby enabling *P. manokwari* to locate tree snails using the snail scent trails on tree trunks. Our experiment also indicated that an individual *P. manokwari* could climb a tree trunk subjected only to the water treatment (Table 3), suggesting that conditions of heavy rain, which make tree trunks wet, enable *P. manokwari* to be able to search for prey on tree trunks. Furthermore, some species of arboreal snails that descend from and move among trees (Cowie 1992; Chiba 1999) may leave trails (i.e., chemical cues) for *P. manokwari* to follow up tree trunks.

Mortality in this experiment may have been overestimated because the snails were kept in closed bags in which their movement was limited. However, even if arboreal snails can escape from *P. manokwari* attacks by falling to the ground, they may experience higher *P. manokwari* predation pressure on the ground. Therefore, our results support the hypothesis that the introduction of *P. manokwari* is an important cause of the rapid decline or extinction of native arboreal snails as well as ground-dwelling snails on Pacific islands.

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Chapter 8

Impacts of Predation by the Invasive Black Rat *Rattus rattus* on the Bulwer's Petrel *Bulweria bulwerii* in the Bonin Islands, Japan

Kazuto Kawakami, Kazuo Horikoshi, Hajime Suzuki, and Tetsuro Sasaki

Abstract The black rat *Rattus rattus* is one of the most invasive alien species in the Bonin Islands and has been recorded on at least 16 of the islands. Higashijima, an uninhabited satellite island of Chichijima, provides breeding sites for thousands of Bulwer's petrels (*Bulweria bulwerii*), and a massive die-off of this small petrel caused by rat predation was detected there in 2006. In total, 237 adult carcasses and 61 broken eggs were found in small plots totaling 0.035 ha in area during the year; this predation was estimated to have had devastating impacts on the population. Rat eradication was conducted in 2008, and although the petrel population was small, chicks were observed in 2009. The prompt eradication efforts during the early stages of rat predation prevented local extinction of the Bulwer's petrel. Broken eggs, a sign of rat predation, have also been found on other islands, and rats have been detected on most islands >2 ha in size. Eradication programs should be promoted on islands that currently support both small petrel populations and introduced rat populations before a crisis occurs.

8.1 Introduction

Invasive mammals have caused numerous extinctions of insular species over the past 1,000 years (Howald et al. 2007). Introduced rodents are one of the greatest threats to island ecosystems because they can affect plants, reptiles, mammals, and birds (Atkinson 1985; Towns et al. 2006). Previous studies have illustrated that introduced rodents have been responsible for a great number of extirpations and population declines of seabirds through predation on eggs, chicks, and adults (Atkinson 1985; Jones et al. 2008).

The Bonin Islands are oceanic islands located within 26°33′–27°43′N and 142°05′–142°14′E in the northwestern Pacific Ocean and consist of two inhabited islands (Chichijima and Hahajima) and more than 30 uninhabited islands. Due to their biogeographical isolation, the biota of the islands is depauperate and disharmonic (Shimizu 2003; Kawakami 2008). For instance, no land mammals naturally occur except for the Bonin flying fox *Pteropus pselaphon*, and no native snakes exist (Kuroda 1930). Because of the lack of terrestrial predators, the islands have provided secure breeding grounds for ten seabird species (Chiba et al. 2007).

Rats and mice, often unintentionally introduced to islands via ships, were likely introduced to the Bonin Islands during the early stages of human colonization. The islands were first colonized by western and Polynesian people in 1830. The presence of many rodents throughout the Bonin Islands had been already reported in 1877 (Obana 1877), and three rodent species have since been documented on the islands: the house mouse *Mus musculus*, the Norway rat *Rattus norvegicus*, and the black rat *Rattus rattus* (Kuroda 1930; Yabe and Matsumoto 1982).

Black rats have been reported on at least 16 of the Bonin Islands (Mukojima, Torishima next to Mukojima, Nakodojima, Yomejima, Ototojima, Anijima, Nishijima, Chichijima, Higashijima, Minamijima, Hahajima, Hirashima, Mukoujima, Anejima, Imotojima, and Meijima), whereas the ranges of the other two rodents are limited to a few islands (Chap. 23). Black rats are considered to have a greater impact on seabirds than do Norway rats (Jones et al. 2008). In particular, small and burrow-nesting seabirds such as those in the family Hydrobatidae are vulnerable to black rat predation (Jones et al. 2008). In the Bonin Islands, Tristram's storm-petrels, *Oceanodroma tristrami* (small burrow-nesters), have been preyed on in their colony on Mukotorishima (Chiba et al. 2007).

Higashijima (28 ha, 27°05′40″N–142°14′10″E), a satellite uninhabited island of Chichijima, provides breeding sites for thousands of the Bulwer's petrel *Bulweria bulwerii* (Fig. 8.1; Chiba et al. 2007). The Bulwer's petrel is the most common small-sized petrel in the Bonin Islands, and the colony on Higashijima is one of the largest in the islands, along with that on Minamijima (Chiba et al. 2007). This species nests in burrows and rock piles and under vegetation in general (Harrison 1990).

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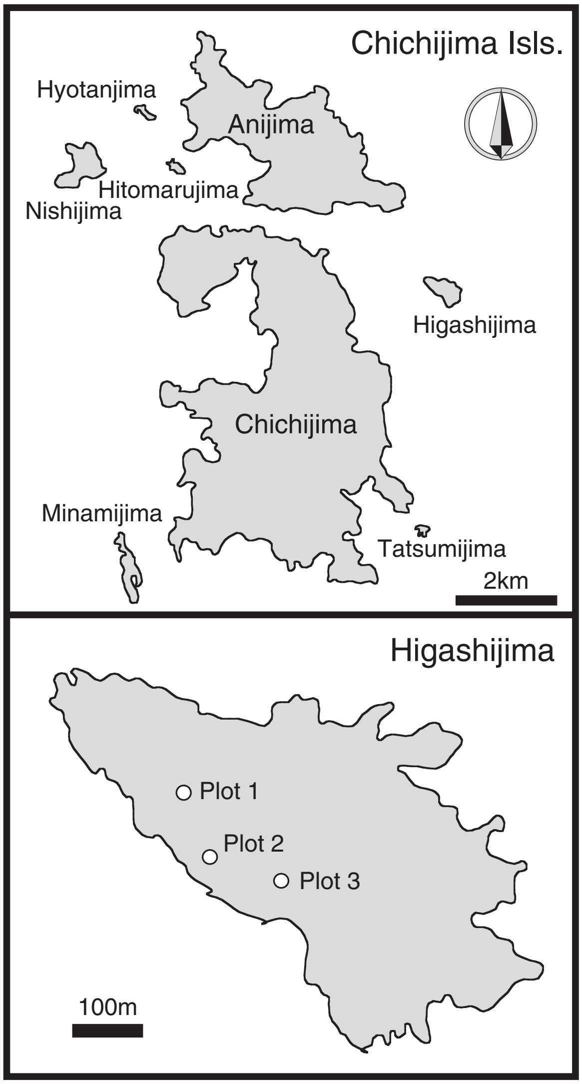

Fig. 8.1 Locations of the studied islands. *Open circles* indicate locations of survey plots on Higashijima

Dozens of adult Bulwer's petrel carcasses were detected on Higashijima in July 2005 and later, apparently killed by rats. Using a camera trap, we confirmed that black rats entered the burrow nests of the Bulwer's petrel in 2006 (Fig. 8.2); this evidence was the first confirmation of predation on adult petrels by rats in the Bonin Islands. Rat eradication by poison was subsequently conducted by the Japanese Ministry of the Environment in August 2008. In this report, we describe the damage to and the current status of the petrel population and the rat distribution in the Bonin Islands.

Fig. 8.2 Photographs of a Bulwer's petrel entering its own nest and a black rat subsequently following it

8.2 Mortality on Higashijima

To estimate the impact of the rats on the Bulwer's petrel, the numbers of carcasses and broken eggs eaten by rats were counted at three survey plots, Plots 1 (200 m^2), 2 (100 m^2), and 3 (50 m^2), located on Higashijima (Fig. 8.1). Surveys were conducted in 2006, 2008, and 2009 (14 and 22 June, 19, 23, and 28 July, 20 and 29 August, 13 and 28 September, and 25 October 2006; 26 July, 3 and 26 August, 7 and 21 September, and 2 November 2008; and 25 June and 26 August 2009). Detected carcasses and broken eggs were removed from each plot to avoid repeat counting. Two predators inhabit the islands, the endemic subspecies of common buzzard *Buteo buteo toyosimai* and the rats. If masses of scattered feathers were found with unbroken quills, the deaths were attributed to raptors, because feathers are frequently bitten and broken when birds are preyed on by carnivorous mammals (Brown et al. 2003). If rat teeth marks were detected on carcasses or if feather quills were broken, deaths were attributed to rats. All broken eggs were attributed to rat predation, because raptors seemed unlikely to prey on eggs located in burrows or under vegetation. Incidentally, the incubating period of the petrels in the Bonin Islands is June and July and the chick-rearing period is August and September.

In total, 201 carcasses and 9 broken eggs, 21 carcasses and 26 broken eggs, and 15 carcasses and 26 broken eggs were detected at Plots 1, 2 and 3, respectively in 2006 (Fig. 8.3). Numerous victims were also identified in 2007, although no quantitative records were available for that year. The total area of the survey plots was only 0.035 ha, and the extent of the breeding sites on Higashijima was at least five times that great. Given that we also found carcasses outsides the plots at a rate similar to that inside the plots, we estimate that more than 1,000 individuals may have been killed in 2006. The number of detected carcasses increased in August and September (Fig. 8.3), probably because many non-breeding individuals come to breeding sites on Higashijima at this time of year. In 2008, only three carcasses were found at Plot 1, and only a few broken eggs were detected in total at the three plots, suggesting that rat predation had already had a dramatic impact on the population.

8.3 Post Eradication Status

Rat eradication was conducted in August 2008, and no rats have been found since that time (Chap. 23), suggesting that the rat population has become very small or extinct on Higashijima. No carcasses or eggs preyed on by rats were detected at the three plots in the 2009 breeding season (Fig. 8.3). Some chicks were observed in Plots 2 and 3 in late August 2009 (chick rearing season), whereas no chicks had been found during the same season in 2006 and 2008 (Fig. 8.4). However, no chicks were detected in 2009 in Plot 1, where the predation damage was the most intense.

The rat eradication program was conducted 2 years after the detection of rat predation on petrels on Higashijima. This prompt action had a successful outcome. The few surviving petrels continued to reproduce, despite the severe damage to their population. As damages from rat predation are not homogeneous across the islands, it is difficult to estimate the number of surviving petrel individuals. However, we suspect that more than 100 breeding pairs are alive and that the population may be able to recover.

8.4 Situation on the Other Islands

Although the distribution of rats on the relatively large islands of the Bonin Islands has been reported (Chap. 23), the distributions on the smaller islands, where seabirds frequently breed (Chiba et al. 2007), are unknown. To confirm the presence of rats on seabird breeding islands, we set up traps and/or motion-sensing cameras and/or searched for field signs such as feces and tooth marks on food remains. Surveys were conducted on Horaijima (0.7 ha, 26°36′58″N, 142°10′31″E), Katsuodorijima (4 ha, 26°36′15″N, 142°10′40″E), Nakakatsuodorijima (1 ha, 26°36′00″N, 142°10′30″E), Kokatsuodorijima (0.8 ha, 26°36′03″N, 142°10′24″E), Marushima (6 ha, 26°35′40″N, 142°10′05″E), Futagojima (9 ha, 26°35′30″N, 142°09′55″E), Sanboniwa (1.4 ha, 26°32′50″N, 142°09′00″E), Minamitorishima (2.3 ha, 26°32′25″N, 142°09′18″E), Torishima (next to Imotojima; 2.4 ha, 26°33′07″N, 142°12′27″E), Yagishima (0.8 ha, 26°33′57″N, 142°12′45″E), unnamed island next to Meijima (0.4 ha, 26°34′21″N, 142°13′34″E), Tatsumijima (4.2 ha, 27°02′50″N, 142°14′20″E), Hyotanjima (9 ha,

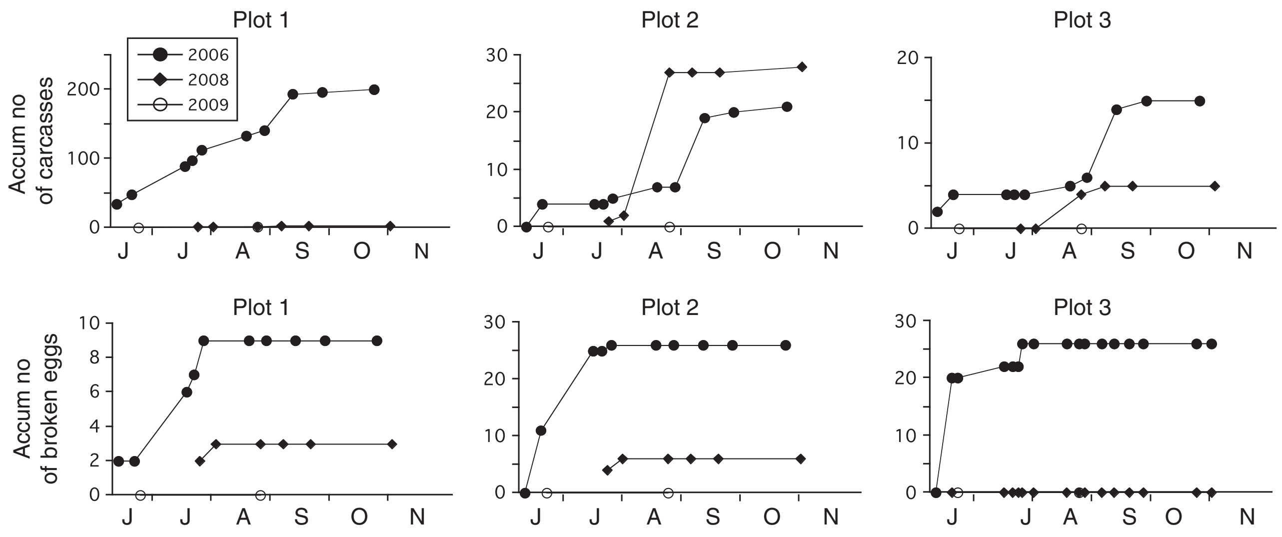

Fig. 8.3 Accumulated number of detected carcasses and broken eggs of the Bulwer's petrel at the three survey plots on Higashijima during June–November 2006, 2008, and 2009

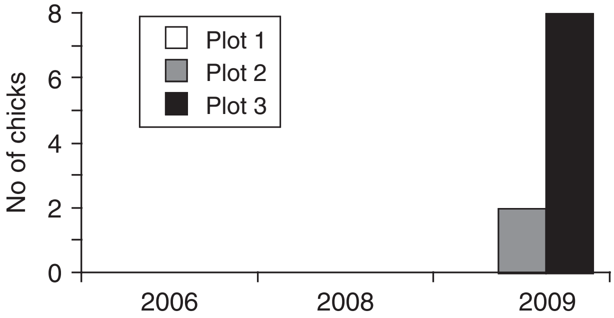

Fig. 8.4 Number of Bulwer's petrel chicks found at the three plots on Higashijima in late August 2006, 2008, and 2009

27°07′40″N, 142°10′50″E), Hitomarujima (6 ha, 27°07′00″N, 142°11′10″E), Kannukijima (0.8 ha, 27°02′36″N, 142°10′38″E), Tatejima (0.9 ha, 27°02′44″N, 142°10′56″E), two unnamed islands next to Tatejima (0.05 ha, 27°02′48″N, 142°10′58″E and 0.4 ha, 27°02′37″N, 142°10′55″E), Torishima next to Nakodojima (3 ha, 27°38′15″N, 142°10′06″E), and Kitanoshima (19 ha, 27°43′10″N, 142°05′50″E) from August to October 2007.

Rats were recorded on Horaijima, Katsuodorijima, Marushima, Futagojima, Minamitorishima, Torishima, Tatsumijima, Hyotanjima, and Hitomarujima, and they were not observed on the other islands. All larger islands (>2 ha) were invaded by rats except for Kitanoshima (19 ha), and smaller islands (<2 ha) were free of rats except for Horaijima (0.7 ha). The vegetation on the smaller islands is relatively poor; thus, the food availability on these islands may be lower. The low carrying capacities of these smaller islands may have limited the success of invasions.

To confirm the current status of rat predation on Bulwer's petrels on islands besides Higashijima, the number of active breeding nests, the numbers of carcasses and eggs eaten by rats, and the number of carcasses attributable to raptor predation were counted on Hitomarujima (Fig. 8.1; 3 July 2007 and 23 June 2009), Hyotanjima (3 July 2007 and 23 June 2009), and Tatsumijima (4 July 2007 and 25 June 2009).

The sizes of the petrel breeding populations were very small (<10) on Hitomarujima and Hyotanjima. We could not find active nests there, and broken eggs were detected on both islands (Table 8.1). On Tatsumijima, a few broken eggs were also detected in addition to many active nests. These results suggest that, although egg predation is occurring, intense predation on adult petrels has not yet started on these islands. Raptor predation was detected on all three islands. Although introduced animals such as the black rat have replaced native animals as a major food source of the common buzzard (Kato and Suzuki 2005), the Bulwer's petrel might be one of the original major food items.

8.5 Conclusions

The situation on Higashijima was the first recorded massive bird die-off attributed to rat predation in the Bonin Islands; seabird mortality on Hahajima caused by cat predation has been previously reported (Kawakami and Fujita 2004). Although the damage was very severe on Higashijima, the prompt eradication of the rat population during the early impact stage prevented the extinction of the local Bulwer's petrel population. Urgent early rat eradication was shown to be of benefit to seabird conservation. Although such intense predation on adult petrels has not occurred on the other breeding populations in the Bonin Islands, egg predation has already occurred on some islands. Rats might suddenly switch their food habit on these islands where seabirds and rats currently coexist. Thus, rat eradication programs should be promoted on these islands before a crisis develops.

Rat eradications were recently conducted on Nishijima and Mukojima (Chap. 23), and eradication programs are expected to proceed on many more islands. Such prompt countermeasures would likely save the endangered petrel populations on Hitomarujima and Hyotanjima. Because Minamijima and Tatsumijima maintain colonies of small seabirds such as the Bulwer's petrel and Tristram's storm-petrel (Chiba et al. 2007), rats should also be eradicated on these islands as soon as possible.

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Table 8.1 Total numbers of active nests, broken eggs and carcasses found on three satellite islands of Chichijima

	Hitomarujima		Hyotanjima		Tatsumijima	
	Jul 2007	Jun 2009	Jul 2007	Jun 2009	Jul 2007	Jun 2009
Active nests	0	0	0	0	>20	>20
Broken eggs	2	3	1	0	0	2
Carcasses preyed by rats	0	0	0	0	0	0
Carcasses preyed by raptors	1	0	2	0	5	5

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Chapter 9

SPECIAL ISSUE

Evolution in biological invasion

Satoshi Chiba

Morphological and ecological shifts in a land snail caused by the impact of an introduced predator

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Abstract Introduced predators have become major threats to native animal species in oceanic islands. A number of studies have shown that alien predators have caused serious extinctions of island endemics. However, little attention has been paid to the evolutionary impacts of alien predators on native species. The present study shows that predation by black rats, *Rattus rattus*, has resulted in ecological and morphological changes in the land snail *Mandarina anijimana* from the island of Anijima in the Ogasawara archipelago. The frequency of empty predated shells has increased over the past 17–19 years in southern areas of the island. The shells of these snails were found to be significantly higher, smaller and darker in the survey in 2006 than in the survey in 1987–1989 performed in central and southern parts of Anijima, where predation by *Rattus* was serious. *M. anijimana* were formerly restricted to shallow broad-leaved litter, whereas they are currently found in deep palm litter, where predation pressure from *Rattus* may be lower. This suggests that increased predation pressure by *Rattus* has changed the habitat use of *M. anijimana*. The close association between shell morphology and habitat use of *Mandarina* species suggests that the habitat shift induced by the predation of *Rattus* has caused these changes in the shell morphology of *M. anijimana* over a period of 17–19 years.

Keywords Biological invasion · Evolution · Land snails · Mandarina · Ogasawara · *Rattus*

Introduction

The introduction and spread of alien species has become a global ecological and conservation crisis: invasive organisms are increasingly altering terrestrial and aquatic communities (Van Driesche and Van Driesche 2000; Mack et al 2000; Pimentel 2002). Ecologists and conservation biologists widely believe that invasions by non-native predators are a leading cause of recent species extinctions. The most serious examples of extinctions of native species as a result of the introduction of alien predators are the endemic land snails of the Pacific islands (Lydeard et al. 2004). Many of the native land snails of the Hawaiian, Tahitian, Mariana and other Pacific islands have gone extinct as a result of predation by introduced carnivorous snails, rats (particularly *Rattus rattus*), ants and flatworms (Gagné et al. 1985; Murray et al. 1988; Cowie 1992; Hadfield et al. 1993; Lydeard et al. 2004; Okochi et al. 2004). However, very little is known about the evolutionary responses of native land snails to alien predators.

There has recently been a strong focus on studying the evolutions of alien species introduced into new habitats and the evolutions of native species in response to introduced species (Mooney and Cleland 2001; Lee 2002; Strauss et al. 2006; see a review by Cox 2004). For example, niche shift has occurred and feeding traits or life history traits have evolved in response to introduced hosts (Zimmerman 1960; Singer et al. 1993; Carroll and Dingle 1996; Carroll et al. 2005; Graves and Shapiro 2003). Native prey species exhibit behavioral and morphological responses to the presence of introduced predators (McIntosh and Townsend 1994; Kiesecker and Blaustein 1997; Moore et al. 2004). In Mollusca, *Nucella lapillus* showed an adaptive phenotypic change—increased shell thickness—after a crab invasion (Vermeij 1982). Shells of *Littorina obtusata* became markedly flatter and thicker within a period of 100 years due to the impact of predation by alien crabs (Seeley 1986).

The present study examines phenotypic changes in the land snail *Mandarina anijimana* in response to predation by *R. rattus*. *Mandarina* is an endemic genus from the Ogasawara Islands in the northwestern Pacific, and it has undergone adaptive radiation within the islands (Chiba 1996, 1999a, 2004). Although many endemic

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species from Ogasawara are extinct or have seriously declined as a result of habitat destruction and the impact of predatory flatworms (Tomiyama and Kurozumi 1992; Tomiyama 1994, 1998; Okochi et al. 2004), all of the native land snail species on the island of Anijima have survived, because their native habitat has been preserved in excellent condition (Tomiyama and Kurozumi 1992). However, as shown in the present study, predation pressure by *R. rattus* on these native land snails has increased markedly over the past 17–19 years on Anijima. Studies of *M. anijimana* on Anijima have been performed over the past 17 years, and data on its population density, habitat use and shell morphology are available (Chiba 1988, 1999b). In this work, the past and present ecologies and morphologies of this species are compared, and the evolutionary impacts of predation by *R. rattus* on the native land snails are assessed.

Materials and methods

Estimation of predation pressure by *Rattus rattus*

Attacks on land snails by *Rattus* produce characteristic shell damage (Elton 1958; Brook 1999) (Fig. 1). *Mandarina* shells preyed on by rats typically have the periphery or base of the body whorl bitten back from the outer lip, leaving the edges of the broken area jagged and irregular. The percentage of empty shells with predation scars exhibiting *Rattus* damage is therefore easily determined and provides a relative measure of the prevalence of *Rattus* attacks on snails.

Presence or absence of *Rattus* damage on empty shells was examined at six localities on Anijima (Fig. 2) in March 2006. A 30 m × 30 m quadrat was placed at each locality and all of the empty shells of adult and semi-adult snails found within the quadrat were examined. The frequency of broken shells was also examined in shells collected from the same areas in 1987–1989 in order to examine the relationship between predation and level of color polymorphism. The past and present conditions of the vegetation and forest floor at these localities were mostly the same. In some cases it was difficult to assess whether the shells were broken by rats or birds. However, the only bird in Ogasawara that eats snails is *Turdus dauma*. This species is fairly rare in Anijima, and no increase in this species over the past 17–19 years has been documented. Thus, any change in the frequency of broken shells is regarded as being due to changing levels of predation by *Rattus*. The frequency of broken shells in the 2006 survey was statistically compared to the frequencies seen in previous surveys performed at the same locality using the χ^2-test.

Morphological analysis

Empty shells collected at the above five localities (locs. 1–5) (Fig. 2) were measured and compared with those collected in 1987–1989 at the same localities. The sample from loc. 6 was not used for the analysis because of the insufficient number of shells found at this locality due to a decrease in population size. Shell height, diameter and thickness of the outer lip were measured and three characters, relative shell height (shell height/diameter), size (shell height + diameter) and relative shell thickness (thickness of outer lip/diameter), were calculated. Sample means of these characters were compared between the present and the past using ANOVA. Shell color was assigned to one of the following six morphs—type B: no band with bright background color; type BL: a single black line at the periphery with bright background color; type BF: four black bands with bright background color; type D: no band with dark brown background color; type DL: a single black line at the periphery with bright background color; type DF: four black bands with dark brown background color. Frequencies of these color morphs were compared statistically with those in obtained in 1987–1989 using the

Fig. 1a–b **a** A cluster of *Mandarina* shells broken by *Rattus*. **b** An empty *Mandarina anijimana* shell after predation by *Rattus*

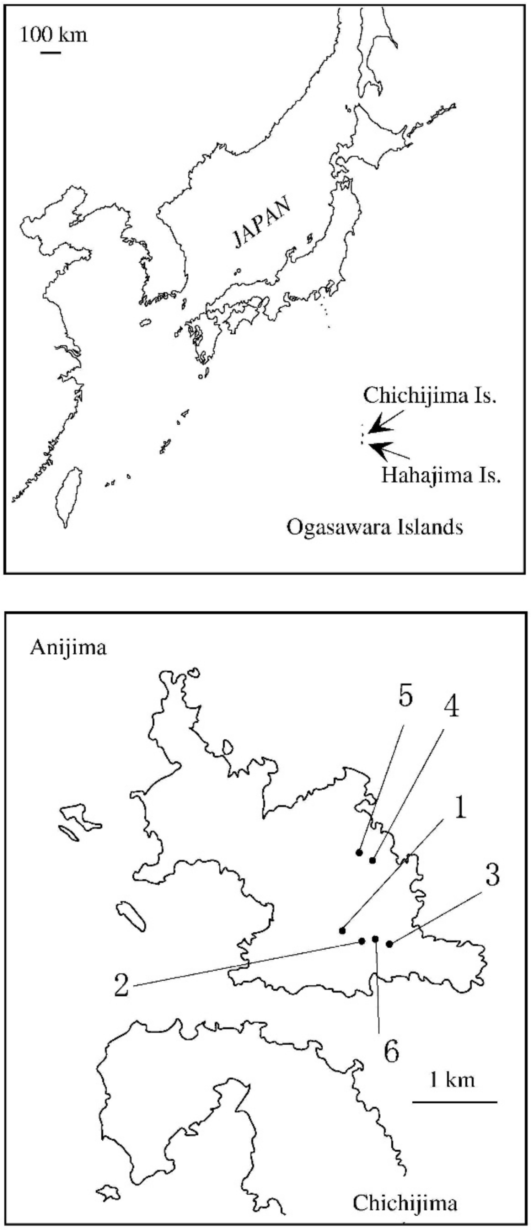

Fig. 2 Maps of the Ogasawara Islands and Anijima showing the locations of the study sites

χ^2-test. The probabilities were adjusted by the Bonferroni method, which provides protection against the possibility of a false rejection of the null hypothesis for multiple tests carried out simultaneously.

Analysis of habitat use

The analysis of habitat use is based on the microsites of living snails. Habitat use by *M. anijimana* was previously examined in only loc. 1 among the five localities in 1992 (Chiba 1999b). Each time a living snail was found in the 30 m × 30 m quadrat, the types of litter that occurred at the point where the snail was found were recorded. The litter was divided into three types based on the dominant type of leaves: palm (*Livistona chinensis*), pandanus (*Pandanus boninensis*) and broad-leaved trees. The palm leaves were very large (more than 50 cm in width and 50 cm in length). The pandanus leaves were long (more than 50 cm) but narrow (width of the leaf is approximately 1/10 of its length). The leaves of most species of the broad-leaved trees were less than 10 cm in both length and width. Litter dominated by palm leaves was the thickest and wettest, and that of pandanus was moderately thick and wet. The litter dominated by leaves of broad-leaved trees was usually the thinnest and driest.

The numbers of snails found at a site did not provide information on the absolute density; however, they probably reflect the true proportions of the species at each site. The area of each litter type at the quadrat, roughly estimated, was mostly the same between the present and the past.

Results

Change in predation pressure

There was no significant difference in the frequency of broken shells (6–10%) among the six localities in 1987–1989 ($\chi^2_5 = 2.39$, $p > 0.05$). However, the frequency differed among localities for the samples obtained in 2006. Frequency of broken shells was significantly higher in samples obtained in 2006 (35–92%) than in samples obtained in 1987–1989 at the four sites (locs. 1, 2, 3, 6) in the central and southern parts of Anijima, but no significant difference was found at the other two sites (locs. 4 and 5) in the northern parts of Anijima (Fig. 3). At localities 1 and 2, the frequency of broken shells was more than 50%, and approximately five times greater than it was 17–19 years ago. In addition, nearly all of the empty shells found at loc. 6 were broken.

Morphological change

Relative shell height was significantly greater in the present samples than obtained 17–19 years ago at two localities, loc. 1 ($F_{(1,228)} = 8.32$, $p < 0.05$) and loc. 2 ($F_{(1,192)} = 6.40$, $p < 0.05$) (Fig. 4). At loc. 1, shells became significantly smaller over the 17–19 years ($F_{(1,228)} = 7.48$, $p < 0.05$) (Fig. 5). When the three samples in the central and southern parts of Anijima were combined, a significant increase in the relative shell height (nested ANOVA, $F_{(1,656)} = 3.90$, $p < 0.05$) and a decrease in the shell size (nested ANOVA, $F_{(1,656)} = 4.97$, $p < 0.05$) was observed after 20 years. However, no significant difference was found in relative shell height (nested ANOVA, $F_{(1,468)} = 2.42$, $p > 0.05$) or shell size (nested ANOVA, $F_{(1,468)} = 0.46$, $p > 0.05$) between the present and the past when the samples from the northern parts of the island were combined (locs. 4 and 5). No significant difference was found in shell

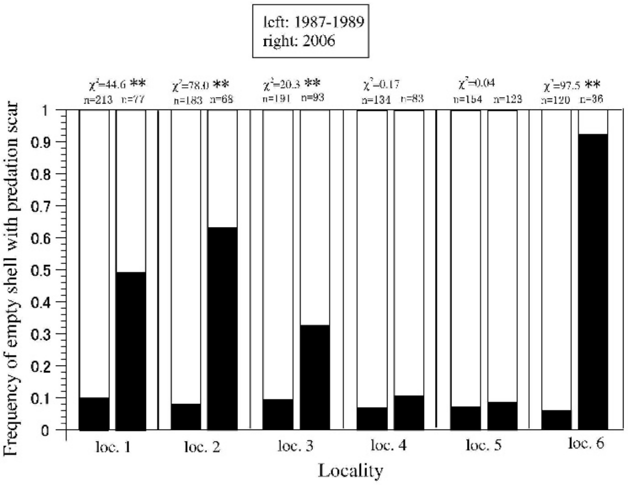

Fig. 3 Difference between the frequency of empty shells predated by *Rattus* between 1987–1989 (*left*) and the frequency in 2006 (*right*) (**$P < 0.01$)

thickness between the present and the past at any localities.

At locs. 1, 2 and 3, the frequency of dark color morphs (types D, DL, DF and BF) was greater in the samples obtained in 2006 (in total 43–63%) than in the earlier samples (24–40%), and the difference was significant at loc. 1 ($\chi^2_1 = 7.05$, $p < 0.05$) and loc. 3 ($\chi^2_1 = 6.70$, $p < 0.05$). Although the difference was not significant, the frequency of the dark morph also increased at loc. 2. No clear change in the frequency of the dark morph over time was found at other localities.

Thus, the shells became smaller, higher and darker over the 17–19 years in the localities in central and southern Anijima.

Shift in habitat use

In 1992, *M. anijimana* snails were absent from the palm litter at loc. 1. The frequency of snails found in the pandanus litter was 39% among the snails found at loc. 1 ($N = 31$). However, in the samples obtained in 2006, the frequency of snails found in the palm litter was 25%, and in the pandanus litter it was 50% ($N = 16$). The frequency of the snails found in the broad-leaved litter decreased from 61% in 1992 to 25% (present). This decrease in the frequency of snails inhabiting broad-leaved litter over 15 years is significant ($\chi^2_1 = 4.20$, $p < 0.05$). Thus, microhabitat use by the snails shifted to the thicker and wetter litter at loc. 1.

Discussion

The increase in the frequency of broken shells at the three localities studied in Anijima during the past 17–19 years reflects an increase in predation by *R. rattus* in the central and southern parts of Anijima, as no other mammal predators of land snails inhabit Anijima, and *Turdus dauma*, another predator that can break shells, is rare in Anijima. The increase in predation by *Rattus* suggests that the population density of *Rattus* may have increased during the past 17–19 years on Anijima. Lots of products and materials were imported to Anijima from other islands in the late 1980s, and this may have directly or indirectly increased the number of *Rattus* in Anijima. An alternative hypothesis is, however, that *Rattus* may have changed its diet to land snails from other diets such as plant seeds and insects. In arid regions, small mammals eat land snails to obtain water (Broza and Nevo 1994). Ogasawara has become drier since the 1980s (Shimizu 1988), and this climatic change may have resulted in a shift in the diet of *Rattus*. In either case, the above results suggest that predation by *Rattus* has rapidly become serious and is a major threat to *M. anijimana*.

In the central and southern parts of Anijima, where predation by *Rattus* on *M. anijimana* is serious, the shells have become smaller, higher and darker during the past 17–19 years. The absence of morphological changes in *M. anijima* in other localities where predation by *Rattus* is not serious suggests that the morphological changes in *M. anijimana* have occurred as a response to increased predation by *Rattus*.

Although details of the life history of *M. anijimana* are not clear, mark and recapture experiments suggest that this species matures after approximately 1.5 years. Although this species lays only two eggs for single oviposition, it reproduces more than three times in a year. Based on the length of the generation time of this species, the changes observed in this study are very rapid.

Shell size and morphology are interpretable as anti-predator adaptations (Vermeij, 1987, 1993). Decrease in shell size as a result of the impact of predators is common amongst Gastropoda (Oosterhoff 1977). The shell of the native gastropod species *L. obtusata* rapidly became thick and flat following invasion by effective predators (Seeley 1986). This rapid morphological change in *L. obtusata* has been explained as an ecologically plastic response to predation (Trussell 1996; Trussell and Smith 2000; Trussell and Nicklin 2002). Although morphological changes induced by predation include changes that may result from ecological plasticity, evolutionary change may also be possible. A high heritability is reported for relative shell heights of land snails, and variation in this character has been suggested as being highly reflective of genetic variation (Murray and Clarke 1968; Welter-Schultes 2000). Although breeding experiments would be required to demonstrate the genetic control of shell shape conclusively, the temporal change in relative shell height of *M. anijimana* is likely to be an evolutionary change in response to predation by *Rattus*. However, the relationship between predation by rats and relative shell heights of snail shells is unclear. The direction of change in shell height observed in the present study is contradictory to that reported in *Littorina* as a response to predation by crabs.

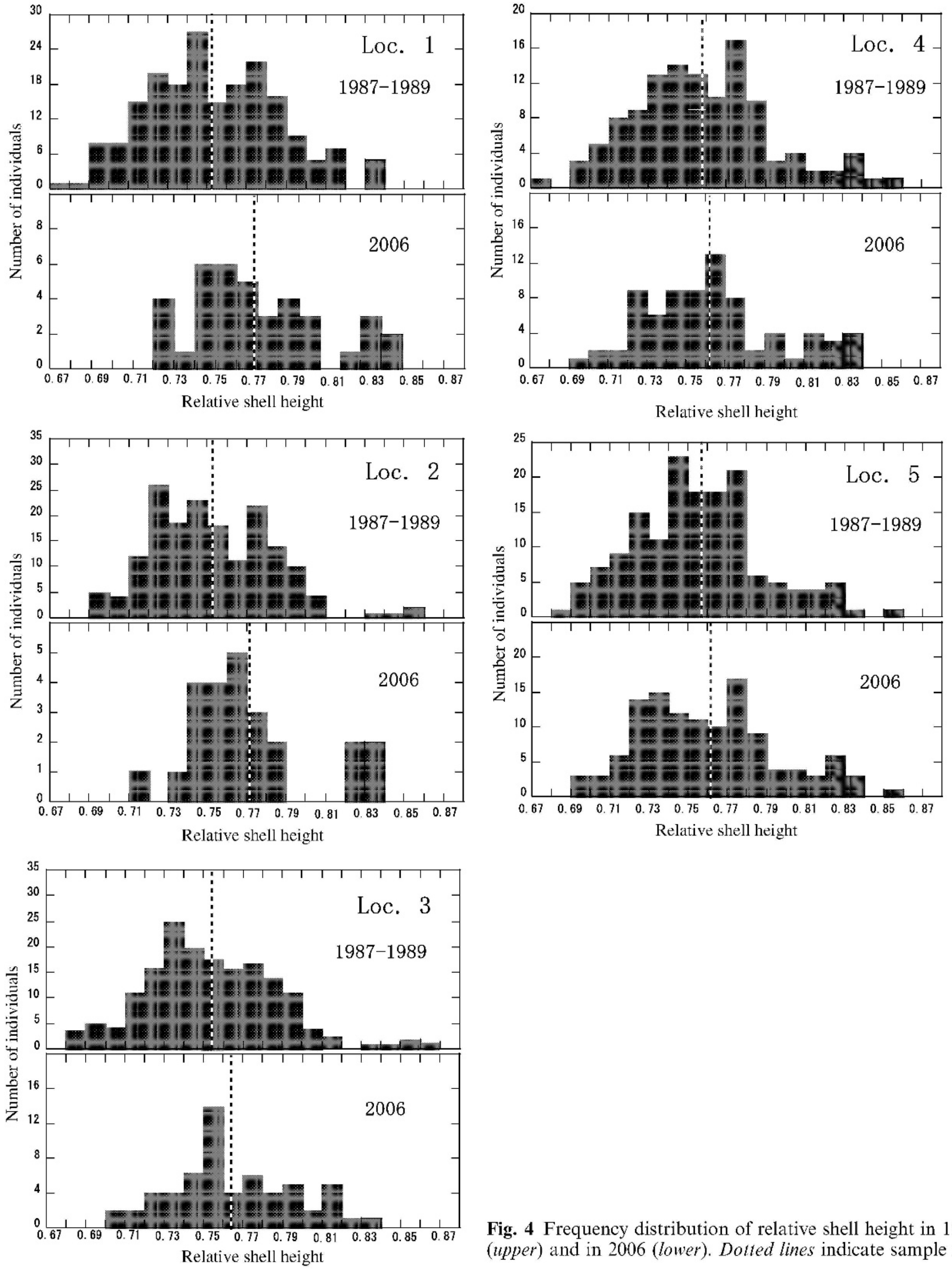

Fig. 4 Frequency distribution of relative shell height in 1987–1989 (*upper*) and in 2006 (*lower*). *Dotted lines* indicate sample means

The change from a flat shell to a high shell observed in *M. anijimana* may not be caused directly by predation, but may be an indirect response to predation. This assumption is supported by the findings that no change has occurred in shell thickness in spite of increasing predation. It is well known that a thickened shell provides the most effective protection from predation (West et al 1991; Quensen and Woodruff 1997). The lack of increase in shell thickness in the snails in the 2006 samples suggests that selection pressure to increase shell strength was weak and insufficient to promote evolution of a predator-resistant shell. The power of *Rattus* to

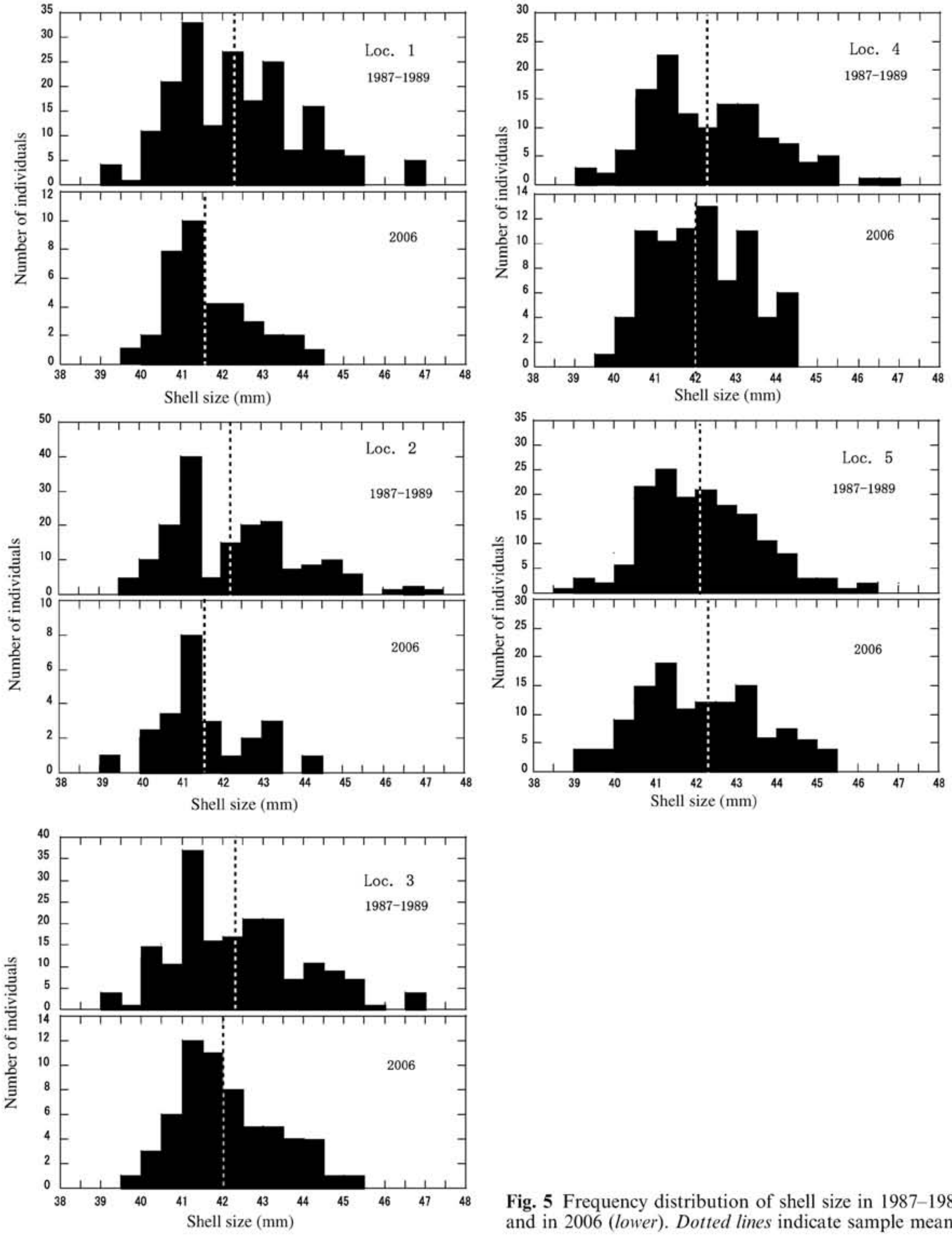

Fig. 5 Frequency distribution of shell size in 1987–1989 (*upper*) and in 2006 (*lower*). *Dotted lines* indicate sample means

break shells is so strong that the differences in shell traits that appeared in the snail populations might provide no difference in terms of increased protection against the predation behavior of *Rattus*.

The temporal change of shell color is most likely to be an evolutionary change as a result of increased predation, because breeding experiments have shown that background color and number of color bands are genetically determined, though the details of the genetic control of color patterns in *Mandarina* are unknown (Chiba and Davison, unpublished). However, it is unlikely that predation by *Rattus* affects shell color directly. The change in shell color is possibly caused by the change in habitat use in *M. anijimana* that resulted from predation by *Rattus*. *M. anijimana* was formerly restricted to the thin broad-leaved litter, whereas a greater number of individuals of this species are now found in the thick palm and pandanus litter rather than in the broad-leaved litter. Snails from the broad-leaved litter may be more heavily predated than those in the palm and pandanus litter, because the thick litter layer and large leaves of the palm and pandanus litter provide refuge for snails against attack by rats. Unfortunately, the hypothesis that predation is more serious in broad-leaved litter than in palm litter could not be tested, because *Rattus* do not eat the snails where they find them but carry them to particular places to eat them (Fig. 1). Further analyses of foraging behavior and the diet of *Rattus* in Anijima are needed to test this hypothesis.

The increase in numbers of shells with dark coloration is likely to be an evolutionary response to the habitat shift of *M. anijimana* to palm litter, because the shell coloration of *Mandarina* is closely associated with habitat use (Chiba 1999b). Species possessing a shell with bright coloration are found in broad-leaved litter, whereas those with dark coloration are found in palm litter. Dark colors release heat from the shell faster than bright colors under dark conditions and prevent the shell from heating up. In contrast, bright colors reflect heat and prevent overheating under light conditions. Presumably, bright colors are advantageous for snails in the exposed habitats of broad-leaved litter, whereas dark coloration is advantageous for snails in the sheltered habitats of palm litter (Chiba 1999b). The increased shell height in the 2006 samples would also have resulted from the habitat shift to thicker litter, because *Mandarina* species inhabiting palm litter tend to have a higher shell than the species inhabiting broad-leaved litter (Chiba 2004).

These facts suggest that rapid morphological and ecological changes occur as a result of either plasticity or evolutionary processes in response to predation by alien predators. Introduced predators cause not only the extinction of native species but also phenotypic and ecological changes in native species, and even alter interactions among native species. Ecological shifts caused by the impact of alien predators may alter interactions among native species. These findings suggest that it is crucial to consider the evolutionary impacts of alien species when developing conservation programs.

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Chapter 10

SHORT COMMUNICATION

Bird predation by domestic cats on Hahajima Island, Bonin Islands, Japan

ORNITHOLOGICAL SCIENCE

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The Bonin Islands are oceanic islands situated in the northwest Pacific Ocean 1,000 km south of the Japanese main island of Honshu. These islands lacked terrestrial mammalian carnivores until human colonization in 1830. Early immigrants introduced domestic cats *Felis catus* to the islands, some of which escaped from the island's residential area. Even by 1877 there were already reports of there being many feral cats on the island (Obana 1877). Cat predation is known to impact native bird populations on various islands around the world, such as the offshore islands of New Zealand and the Canary Islands in the eastern Atlantic Ocean (Fitzgerald & Veitch 1985, Nogales et al. 1992, Powlesland et al. 1995). In the Bonin Islands also, many studies have highlighted the impact of cat predation on native birds (e.g. Tokyo Regional Forest Office 1994, Tokyo Regional Forest Office 1996, Kawakami 2000). Yamashita (1934) supposed that the extinction of endemic birds (such as the Ogasawara Islands Thrush *Turdus terrestris* and the Ogasawara Islands Grosbeak *Chaunoproctus ferreorostris*) in the Bonin Islands was partly caused by predation of increased feral cats. But, no detailed study has been conducted on the diet of feral cats. Cat predation on small birds is considered to be underestimated, because such prey are eaten whole by cats and few visible remains are left after predation (Kawakami 2000).

In order to elucidate the extent of predation on native Bonin Island passerines, we collected, and identified, the feathers of birds eaten by a domestic cat. The cat involved was a free-roaming neutered tabby female about eight years old. The cat brought prey remains, including feathers, to the cat-owner's house in the Okimura area of Hahajima (Haha Island). The owner collected feathers, at our request, whenever he found them. The collection was conducted from September 1998 to November 1999. The owner was not absent for any prolonged periods during the survey, nor was the collection effort biased seasonally. The remains included not only feathers but also a few torn legs, wings and heads, which were available for species identification. We referred to feather specimens, photos and measurement data to identify the feathers. As the samples included characteristic pieces of various body parts, we were easily able to identify the species concerned. The minimum number of each species estimated from feather samples was recorded. English names and classification follow the Ornithological Society of Japan (2000).

The feathers were identified as belonging to 39 individuals of four species: thirty-one Japanese White-eyes *Zosterops japonicus*, five Bonin Islands Honeyeaters *Apalopteron familiare*, two Siberian Meadow Buntings *Emberiza cioides*, and one Oriental Greenfinch *Carduelis sinica*. The number predated was particularly high during the breeding season probably because of the greater vulnerability of fledglings. Though Brown-eared Bulbuls *Hypsipetes amaurotis* and Blue Rock Thrushes *Monticola solitarius* also occurred on the island they were not found among the remains. As these species are larger than the other four species, the cat may either prey on them less frequently than the other species, or did not bring them to the house. Kawakami (2000) reported that these species and other larger birds were preyed upon by cats. Therefore, it is considered that bulbuls and rock-thrushes are within the normal prey range, but for some reason were not recorded in this survey. The white-eye is an introduced species, now the dominant species in the study area. The honeyeater is endemic to the islands and is classed as a vulnerable species by Birdlife International (2001). The sub-

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species of the greenfinch on the Bonin Islands, *C. s. kittlitzi*, is endemic to the islands and its population is considered to be at most 200 individuals (Tokyo Regional Forest Office 1996). These three species are residents, whereas the bunting is a winter visitor to the islands.

On Hahajima, feral cats have been observed widely in various kinds of habitats, including primary forests. There is no appropriate estimate of their population, however judging by the frequency of detection, there are likely to be more than 100 feral or half-feral cats on the island. The cat we studied was a free-roaming domestic individual fed regularly by its owner, thus its hunting was supplementary to its basic dietary needs. Feral cats are presumed to prey on even more birds. We are unable to estimate the frequency of predation on birds by the study cat, because it did not bring all its prey to the house.

The Japanese White-eye is the dominant species in the study area and was the commonest species represented among the prey remains, indicating that the cat took them in proportion to their availability. As the population density of this species has increased over the last 20 years (Kawakami, K. unpublished data), the impact of cat predation on it is not deemed critical. Predation by cats is a serious problem, however, for the two endangered native passerines—the endemic Bonin Islands Honeyeater, and the endemic subspecies of the Oriental Greenfinch. Since both of these species frequently forage on the ground, they make easy prey for cats. As the total number of the latter is particularly small, the urgent eradication of feral cats is essential as a conservation measure.

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Chapter 11

SHORT COMMUNICATION

Feral cat predation on seabirds on Hahajima, the Bonin Islands, Southern Japan

ORNITHOLOGICAL SCIENCE

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The Bonin Islands are oceanic islands that have never been connected with the Japanese mainland, as such they remained free of terrestrial mammalian carnivores until human settlement began in 1830. Shortly thereafter, however, the domestic cat *Felis catus* was introduced to the islands by settlers and became feral (Obana 1877). The number of feral cats has increased to the point where they are now considered to have an adverse impact on the native wild birds (Kawakami 2002; Kawakami & Higuchi 2002). On Hahajima, one of the islands of the Bonin group, there are now considered to be more than 100 feral or half-feral cats ranging throughout the island (Kawakami & Higuchi 2002). Kawakami (2000) has already reported that many native birds, especially seabirds, are preyed upon by feral cats, and has speculated that seabirds are frequently targeted because they can not move quickly once they have landed.

In the Minamizaki area of Hahajima, many dead seabirds were found to show signs of being killed by feral cats. Since there is no prior information on such bird mortality from the islands, we report here on species composition, and on which parts of birds most frequently remain after predation. Since predated individuals often decompose and some parts are lost, it is not easy to assess the number of individuals involved. We propose, therefore, a convenient method for estimating the minimal number.

METHODS

The Minamizaki area (26°36′N, 142°10′E) is the southernmost cape of Hahajima (Fig. 1), and provides nesting habitat for the Brown Booby *Sula leucogaster*, which breeds there at an altitude of 10–20 m (Ministry of the Environment 1980). The area consists of open grassland with small thickets of *Pandanus boninensis* and *Scaevola frutesches*, and there are no human settlements in the area. On small islands nearby (e.g. Katsuodori Island and Maru Island), Brown Boobies and Wedge-tailed Shearwaters *Puffinus pacificus* have been reported as breeding (Ministry of the Environment 1980; Chiba & Funatsu 1991).

Seabird carcasses were sought in the grassland areas of the study area once each year (Fig. 1). Surveys were conducted on 6 December 1996, 6 November 2001, 4 July 2002, 9 February 2003 and 4 February 2004, and each time carcasses were removed so as to avoid to redundant counting.

Firstly, in order to propose a convenient method for estimating the minimal number, we counted the number of main bones that were included in the dead bodies of Wedge-tailed Shearwaters, which were by far the most numerous. We selected only bones of right or left side at which more bones were found, for counting minimal number of individuals from bones of wings, legs, and shoulder girdle. This survey was conducted on the samples from 1996, 2001 and 2002.

Secondly, we counted the minimal number of dead individuals for each species for each year using the above method. Thirdly, we collected cat feces from the area and ascertained whether they included seabird feathers or not.

RESULTS

In the case of Wedge-tailed Shearwaters, wing bones, especially humeri, were found most frequently each year (Fig. 2), whereas legs were most easily lost after predation. Therefore, in order to estimate the minimal number of dead bodies, it is convenient to count the number of humerus bones.

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A total of 159 seabird remains were found: 144 Wedge-tailed Shearwaters, 9 Bulwer's Petrels *Bulweria bulwerii*, three Brown Boodies, two Tristram's Storm-petrels *Oceanodroma trestrami* and one Brown Noddy *Anous stolidus* (see Table 1). All individuals included in the samples were adults except for one immature Brown Booby found in 2001. Many bones carried tooth marks of animals, in particular almost all of the sternums examined had such marks, however, we were unable to distinguish between the marks of cats and rats, thus the identity of the predator involved was not certain. However, 45 feces of cats were found, of which 49% included seabird contour feathers identified on the basis of their morphological characters. Because of the difficulties in identifying contour feathers to species, the exact identity of the seabirds eaten by cats was not clear. Rats, insects, and crabs were also found in the feces.

DISCUSSION

A convenient method for estimating the minimum number of dead seabirds involves counting the number of wings, especially the humeri. Using this method, it was shown that many seabirds, chiefly Wedge-tailed Shearwaters, had died at Minamizaki. Furthermore, many cat feces containing seabird feathers were found in the same area. It is unreasonable to consider that so many individual seabirds had

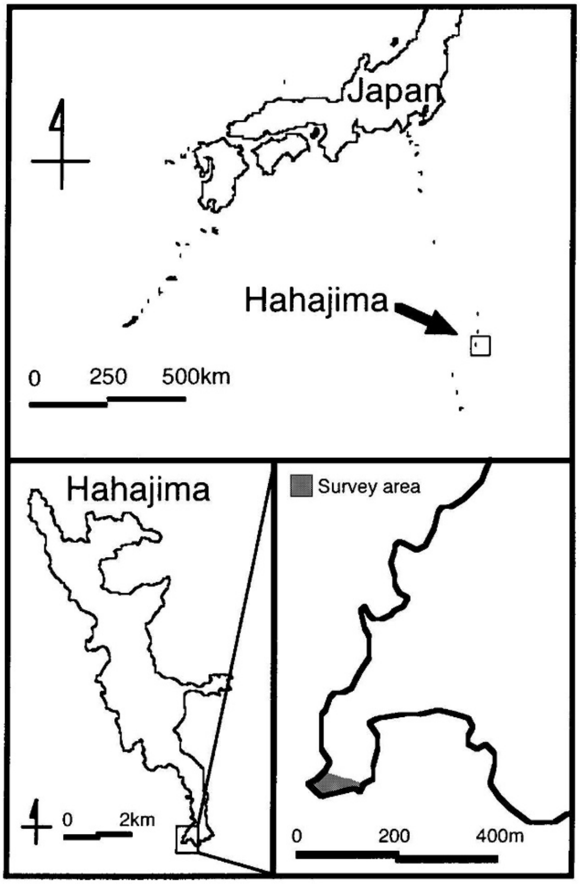

Fig. 1. The location of Minamizaki, Hahajima, the Bonin Islands, Japan. The gray area is the survey area.

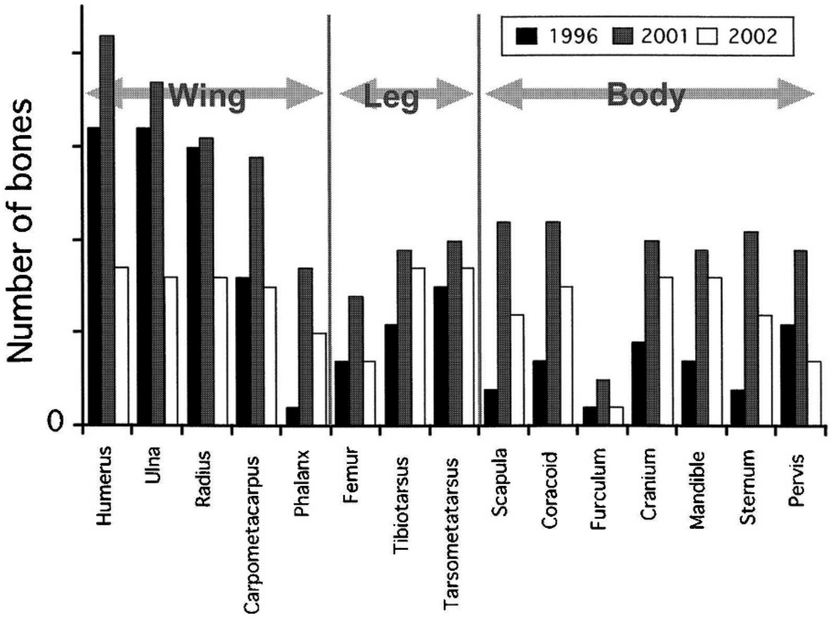

Fig. 2. The number of Wedge-tailed Shearwater bones of each type found in the Minamizaki area of Hahajima in 1996, 2001 and 2002.

Table 1. The species composition of dead birds found in the Minamizaki area of Hahajima Island.

	1996	2001	2002	2003	2004	Total
Brown Booby	0	1	1	1	0	3
Wedge-tailed Shearwater	32	42	17	28	25	144
Bulwer's Petrel	0	0	5	4	6	9
Tristram's Storm-Petrel	0	1	1	0	0	2
Brown Noddy	0	0	1	0	0	1

been eaten by cats after they had died from other causes. It seems most likely that a proportion of them at least had been killed by feral cats, after the birds had landed for some reason (such as for breeding, or to escape from bad weather). Kawakami (2000) suggested that more than half of the seabirds found dead on Hahajima had been killed by feral cats, and our results are consistent with previous data.

Hasegawa (1991) mentioned that Wedge-tailed Shearwaters, Bulwer's Petrels, Brown Boobies and Brown Noddies are observed frequently near Hahajima, with the shearwater occurring most often (about two-thirds of all seabirds observed). The species composition in our samples was roughly consistent with Hasegawa's (1991) observations. Though Brown Boodies breed in the Minamizaki area (Ministry of the Environment 1980), few remains were found in the sample. This was thought to be either because of the larger body size, or the smaller population size, of the species.

The Wedge-tailed Shearwater is the dominant seabird species in the Bonin Islands (Hasuo 1970). It was recorded to be breeding in the Minamizaki area in 1996 (H. Chiba pers. comm.), but there have been no breeding records there since, and no immature individuals were found in the samples, either. Though the relationship between the breeding failure of this species and cat predation is not proven, there is the possibility that cat predation has prevented them from breeding.

Neither Bulwer's Petrels, Tristram's Storm-petrels nor Brown Noddies have been recorded as breeding on Hahajima (Hasegawa 1991), thus the reasons for them landing in the Minamizaki area are not clear. These may have landed either because they prospected for breeding sites or because of bad weather. Seabirds sometimes land on Hahajima during bad weather (H. Chiba pers. comm.).

The feral cats in the Bonin Islands are the cause of great concern in relation to the conservation of native birds (Tokyo Regional Forest Office 1996; Kawakami & Higuchi 2002). Among the species found dead during this study, Tristram's Storm-Petrel is listed as 'Vulnerable' in the Japanese Red Data Book, so it is especially urgent to take measures to conserve them (Ministry of the Environment 2002). Many other threatened seabirds such as Matsudaira's Storm-Petrel *O. matsudairae* and Audubon's Shearwater *P. lherminieri bannermani* also breed in the Bonin Islands and they sometimes accidentally land on the ground in bad weather making them vulnerable to cat attacks (H. Chiba pers. comm.). Thus, it is necessary to clarify the extent of feral cat predation in the islands and to control the cat population.

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Chapter 12

High population densities of an exotic lizard, *Anolis carolinensis* and its possible role as a pollinator in the Ogasawara Islands.

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and SUZUKI Hajime4)

Abstract

It has been postulated that an ongoing decline of endemic insects in the Ogasawara Islands since the 1970's may be mainly due to predation by an exotic lizard, *Anolis carolinensis* from North America. Population density of *A. carolinensis* found on Chichijima Island in the Ogasawaras was much higher than that reported in Saipan and the Bahamas. This may explain why insect populations have declined in the Ogasawaras but not in Saipan. Some males were observed to have pollen of Rosewood, *Schima mertensiana,* an endemic tree to the islands on their heads. This pollen may be attached to their heads when *A. carolinensis* is sucking nectar, as is the case for other known lizard pollinators.

Key words : Ogasawara, exotic *Anolis*, endemic insect, decline, density, pollinator

Photo. 1. A male green anole, *Anolis carolinensis* showing attached yellow pollen on the nose

Introduction

Invasion of alien predators to oceanic islands sometimes cause mass extinctions of endemic species (Blackburn et al., 2004; Cowie & Cook, 2001; Elton, 1958; Hopper & Smith, 1992), and this can be the case even if the alien species is a reptile (Savidge, 1987). The green anole, *Anolis carolinensis*, originally distributed in North America, and Caribbean Islands (Conant, 1958), is such an alien species on Pacific Islands. Recently, the Caribbean populations of the *A. carolinensis* were treated as several different species, but we treat them here as '*A. carolinensis*' in terms of an '*A. carolinensis* subgroup' since they are closely related allopatric species (Glor et al., 2005). *A. carolinensis* was introduced into the Ogasawara Islands in the early 1960's via Guam (Hasegawa et al., 1988). Recently, it has been postulated that an ongoing decline of endemic insects such as dragonflies, butterflies, bees and longicorn beetles in the Ogasawara's since the 1970's may be mainly due to lizard predation, because this decline has only occurred since the invasion and the increase in population density of the lizards, and the declining insects are limited to diurnal species (Karube and Suda, 2004; Makihara et al., 2004; Yoshimura & Okochi, 2005). Since these declining insects include major pollinators, this decline may change the ecological and evolutionary processes of the island ecosystems. However, *A. carolinensis* has also invaded other Pacific islands such as Guam, Saipan and Hawaii, where severe declines of endemic insects have not been reported. We hypothesized that the decline of the insects in the Ogasawara islands may have occurred because of the very high population density of lizards observed in the island compared to that in the other islands. Therefore, we estimated the population density of the lizard and the observation rate per unit time to

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compare with the available data in other islands where the lizard is present. We also discuss the possibility of *A. carolinensis* acting as a pollinator in relation to a hypothesis that pollination by lizard evolve when its density is high in an island.

Methods and study area

Densities of lizard populations were estimated from June 7 to 12, 2004 at 11 sites in Chichijima Island, the largest island in the Ogasawara Islands. Tree height at the study sites varied from 1.3 m to 8 m. Three sites were located in *Leucaena* forest stands dominated by an introduced tree species, *Leucaena leucocephara*. The other sites were in native evergreen broadleaf forest, mainly dominated by native trees. Size of study sites ranged from 63 m^2 to 150 m^2 depending on site condition, which was mainly related to tree height. *A. carolinensis* individuals were captured using a fishing rod and hook and using a mealworm as bait. The rate of new captures decreased as time passed, so after three hours collecting at each site we moved to another. We measured lizard Snout Vent Length (SVL) and verified their sex as determined by observation of post-anal scales, and then marked them with a number written on the body with white marker. Recapture was done the next day using the same method. Density at each site was estimated by the Chapman modification of the Petersen method (Ito & Murai, 1977; Young & Young, 1998).

To enable us to compare densities in the Ogasawara Islands with data from Saipan (Wiles & Guerrero, 1996), we also calculated the observation frequency from 06:00 to 17:00 on September 14, 2003 at Hatsuneura on Chichijima Island. Observations were made by slowly walking along a forest pathway (Wiles & Guerrero 1996). Using this observation method, sex could be determined only from body size, though we were able to distinguish between adult males and hatchlings, but not between females and young males.

In five native forest sites along Tasumi road and two *Leucaena* scrub sites in Kominato we also verified if the heads of lizards were yellow in appearance while we marked and recaptured them. Samples of this yellow material were taken by soft paper and brought back to the mainland to be examined under a microscope.

Results

Estimated densities of individuals of both sexes varied from 600 to 2570 individuals per ha in Chichijima (Table. 1). Density estimates were not correlated with tree height. Densities of *A. carolinensis* in *Leucaena* stands did not differ from those in native forest stands. Estimated densities of each sex are also shown in Table 1. Male densities varied from 440 per ha to 1920 per ha with no significant correlation to tree height. Female density and its 95% confidence limit was only able to calculated for one stand, with an estimate of 640 ± 220 females per ha.

Observation frequencies at the Hatsuneura site were 5.8 large males per hour, 5.0 females and young males per hour, and 0.8 hatchlings per hour. In total, 11.6 individuals were observed per hour.

Yellow-headed individuals were observed only in native forest stands in Tatsumi road and all of them were males. The heads of nine out of 27 males at Tatsumi road were yellow in color, while four females observed at these sites did not show yellow colouring. The 19 males and five females observed at the *Leucaena* sites in Kominato were not yellow-headed. The

Table 1. Estimated densities in 11 populations of *Anolis carolinensis* in Chichijima Island

			All individuals			Males			Females		
Location	Vegetation	Tree height (m)	Density (nos./ha)	95% C. L.*	n**	Density (nos./ha)	95% C. L.*	n**	Density (nos./ha)	95% C. L.*	n**
Asahi-daira	Native forest	1.3	1360	510	9	1000	290	7	-	-	-
Asahi-daira	Native forest	2.5	2570	950	22	1920	830	16	640	220	6
Tasumi road	Native forest	4	1190	270	6	1190	270	6	-	-	-
Tasumi road	Native forest	4	930	160	7	830	190	6	-	-	-
Mt. Mikazuki	*Leucana* shrub	4	1780	530	10	1220	310	7	-	-	-
Tasumi road	Native forest	6	1000	720	8	670	410	6	-	-	
Tasumi road	Native forest	6	670	290	7	440	140	5	-	-	-
Tasumi road	Native forest	6	930	410	7	930	570	6	-	-	-
Kominato	*Leucana* shrub	6	1120	450	10	840	280	8	-	-	
Kominato	*Leucana* shrub	6	600	140	6	600	140	6	-	-	-
Tasumi road	Native forest	8	1800	1470	12	1600	1280	11	-	-	-
Average			1270			1020					

Estimated densities were calculated using the Chapman modification of the Petersen method.
Female density could not be calculated because of there were no or few recaptures except at a single site.
*: 95% confidence limit
**: Number of captured individuals

most conspicuous flowers in the native forest stands in June were of the Rosewood, *Schima mertensiana*, an endemic tree to the islands which mainly flowers during this season (Abe et al., 2004).

We found our observation note on sucking behavior of *A. carolinensis* in which an individual of *A. carolinensis* with a yellow head was observed at 8:30 am on June 13, 1998 pushing its head into an androecium of a *S. mertensiana* flower and seemed to be sucking the nectar. After sucking it did not move for a few minutes.

Discussion

Density of *A. carolinensis* in island populations is generally higher than those in mainland populations (Schoener & Schoener, 1980). Therefore, we compared the density of the lizard in the Ogasawaras to those in the Bahama Islands, which have a similar latitude and where *A. carolinensis* is endemic. Schoener & Schoener (1980) showed that the densities of *A. carolinensis* at many sites on several Bahamian islands ranged from 0 to 1420 individuals per ha, with an average of 480 individuals per ha. The density of *A. carolinensis* in the Ogasawaras was much higher, with an average of 1,270 per ha. However, *A. carolinensis* is not the only species of *Anolis* that occurs on the Bahama Islands. The most frequently observed species in the Bahamas is *A. sagrei*, with an average density of 3600 per ha (Schoener & Schoener, 1980). The density of *A. carolinensis* in the Ogasawaras is therefore only about half of the density of *A. sagrei* in the Bahamas. However, it can also be considered that the body size of *A. segrei* is much smaller than that of *A. carolinensis*. Hence, the density of *A. carolinensis* in the Ogasawaras can be thought to be of a similar level in terms of ecological impact with that in the Bahamas. The density in the Ogasawaras is also similar to those of tropical Caribbean species (Bennett & Gorman, 1979; Heckel & Roughgarden, 1979; Roughgarden, 1995), which are some of the highest densities of lizards known (Schoener & Schoener, 1980).

Frequency of observation of *A. carolinensis* on Chichijima Island in this study was very similar to that recorded at Hahajima Island from 1995 to 1997 (range 3 to 13 individuals per hour, Suzuki, 2000). However, this density is much higher than those recorded in Saipan, where observation frequencies range from 0.0 to 0.7 per hour (Wiles & Guerrero, 1996). If the density of *A. carolinensis* in the other Mariana Islands is similar to those in Saipan, this difference in densities between the Marianas and the Ogasawaras may explain why *A. carolinensis* has caused a severe decline of endemic insects only in the Ogasawara Islands. On the other hand, the density of *A. carolinensis* in the Ogasawaras does not appear to be greatly higher than that in the Bahama Islands. Therefore, the rapid decline of endemic insects in the Ogasawaras can not only be due to the lizard density. Before the invasion of *A. carolinensis* into the Ogasawaras 40 years ago, only one species of small skink, *Cryptoblepharus boutonii*, was native as a diurnally active lizard (Suzuki, 1999). Since this skink is small and not adapted to arboreal life compared with *A. carolinensis*, it is suggested that the inexperience of endemic insects in relation to specialist arboreal lizard predation may also be an important reason for the rapid decline of these insects in the Ogasawara Islands.

Nectar consumption and pollination by lizards has been reported previously (Eifler, 1995; Pérez-Mellado & Casas, 1997; Nyhagen et al., 2001; Traveser & Sáez, 1997). High population density and lower availability of prey on islands is thought to be the reason for the evolution of fruit and nectar consumption by lizards and which leads to pollination and seed dispersion by them (Olesen and Valido, 2003). The observations here of pollen-carrying by *A. carolinensis* in the Ogasawara islands seems to fit this hypothesis since the population density has become very high. However, there is a major difference between this case and previous reports. All previous reports have been of pollination of native flowers by native lizards, but in this case we observed pollination of a native flower by an alien lizard. The flowers of *S. mertensiana* are known to be ornithophilous and entomophilous, but the main pollinator is the Japanese white eye, *Zesterops japonica* (Tanaka 1993). This implies that the pollen of *S. mertensiana* easily attaches to the bird's bill and the quantity of nectar is enough to satisfy a bird, a much larger and more voracious feeder than an insect. Thus the adaptation of *S. mertensiana* to ornithophily may enable *A. carolinensis* to become a pollinator. In this case, the substantial amount of floral nectar attracts the lizard (which faces a food shortage due to its high population density), and the pollen, which is adapted to attaching to bird beaks also easily attaches to the lizard's face. Therefore, this may be a new step for an alien lizard to become a pollinator in a new ecosystem where much of the endemic insect pollinator fauna has been destroyed by the lizard itself. However, this may not necessarily benefit *S. mertensiana* since male *A. carolinensis* are territorial and so may seldom carry pollen to other trees and *S. mertensiana* can be pollinated by birds. Female does not carry pollen in our observation, probably because of male's activity to monopolize a nectar resource. Further investigations to elucidate the possible role of *A. carolinensis* as a new pollinator in the Ogasawara Islands ecosystems are required.

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Chapter 13
Why have endemic pollinators declined on the Ogasawara Islands?

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Abstract Flower visitors recently decreased in the Ogasawara Islands which are subtropical Pacific oceanic islands located 1,000 km south from Japan mainland. The aim of this study was to determine the main cause of this pollinator decline. We assumed four hypothesis, (i) honeybee competition hypothesis, (ii) forest decline hypothesis, (iii) agricultural insecticides hypothesis, and (iv) anole predation hypothesis. They were tested by distribution survey in the field, historical survey using literature, and predation experiment using mesh cages. As a result, the factors affecting the distribution among the islands and the timing of observed declines of native pollinators supported the anole predation hypothesis rather than other hypotheses. In addition, result of experimental predation test well explained the composition of flower visitors in the main islands (Chichi-jima and Haha-jima). So, we concluded that one invasive predator (the anole) has changed the pollination network in the Ogasawara Islands. To conserve the native pollination network, eradication of this invasive predator should take priority over the eradication of honeybees.

Keywords Alien predator · *Anolis carolinensis* · Biological invasions · Distributional pattern · Introduced honeybee · Oceanic islands · Pollination disruption

Introduction

Biological invasions have caused catastrophic shifts in ecosystem function in the world's oceanic islands (Cole et al. 1992; Fritts and Rodda 1998; Coote and Loève 2003; Mack and D'Antonio 2003). The ecosystem of the Ogasawara Islands (Fig. 1) has also been disturbed by various alien species (Shimizu 2003; Yamashita et al. 2003; Kawakami and Fujita 2004; Okochi et al. 2004). Recently, a decline in the pollination network attracted the attention of researchers in these islands (Kato et al. 1999; Abe 2006b). Endemic small bees had existed until the 1970s on Chichi-jima Island and until 1990s on Haha-jima Island (Yasumatsu 1955; Hasuo 1970; Kato et al. 1999). However, these endemic small bees and other native

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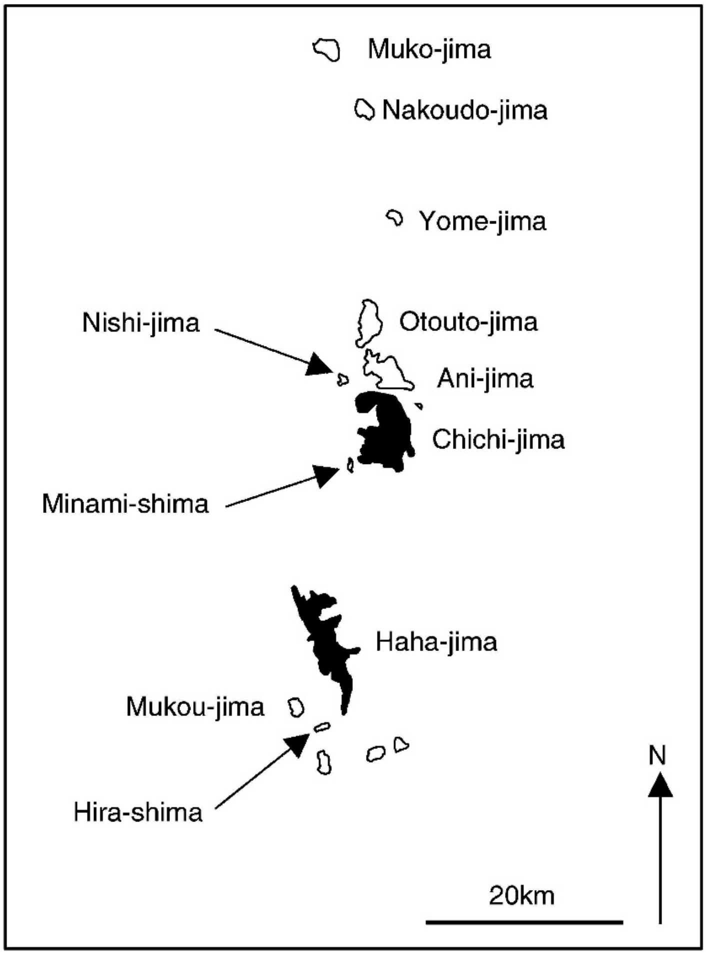

Fig. 1 Surveys of the Ogasawara Islands in the present study. Black represents the main islands on which the green anole can be found; white represents islands on which endemic bees are frequently found. Honeybees are found on Ani-jima, Otouto-jima, Minami-shima, and Nishi-jima as well as the main islands

visitor insects have become nearly extinct on Chichi-jima and Haha-jima (Abe 2006b). Such a dramatic change in the pollinator fauna appears to be unique. In addition, this event may have affected the reproduction of native plants adapted to native flower visitors (Abe 2006b). Currently, there are four hypotheses to explain why the pollinator fauna changed in the Ogasawara Islands: honeybee competition, forest decline, agricultural chemicals, and anole predation. In this paper, we consider these hypotheses based on empirical evidence and a controlled experimentation.

Methods

Four hypotheses

Honeybee competition hypothesis

The honeybee (*Apis mellifera* L.) was first introduced to Chichi-jima Island for apicultural purposes in 1880 (Funakoshi 1990; Hara 1996). Introduced honeybees spread rapidly because they lacked any natural enemies such as wasps (Kato et al. 1999). In general, social insect including honeybees requires relatively huge amounts of resources to maintain its large nests (Seeley 1985). This suggests the possibility that the native floral resources within the Ogasawara, which coevolved with opportunistic solitary pollinators, may be exhausted by intense visitation by honeybees. In other studies, native pollinators have sometimes declined because *A. mellifera* was able to collect available resources more quickly and thus won the resource competition (Roubik 1978, 1980; Donovan 1980; Schaffer et al. 1983; Buchmann 1996; Butz Huryn 1997; Goulson 2003; Paini 2004). Indeed, the honeybee has been shown to reduce the fecundity of a solitary bee in Australia (Paini and Robert 2005), and in another study, the eradication of honeybee nests increased native bee populations on Santa Cruz Island (Wenner and Thorp 1994).

Forest decline hypothesis

The primary forests of Chichi-jima and Haha-jima were extensively destroyed by forestry and agricultural development during the late nineteenth and early twentieth centuries (Takeuchi 1989; Shimizu 2003; Toyoda 2003). Secondary forest succession began after World War II because developments of the islands stopped under the U.S. administration that governed of the islands until 1968, after which the islands reverted to Japan. During this process, it was possible that populations of endemic bees, which nest on dead tree trunks and branches (Goubara 2002), declined as a result of decreased forest cover or local extinction of specific tree species used as nest substrates. Habitat fragmentation decreased the amount and diversity of pollinators in other studies (Rathcke and Jules 1993; Kearns et al. 1998; Steffan-Dewenter and Tscharntke 1999).

Agricultural insecticides hypothesis

Most insect pollinators are sensitive to agricultural insecticides (Thomson and Plowright 1985; Nabhan and Buchmann 1996; Kearns et al. 1998; Richards 2001). Since the Ogasawara Islands became Japanese territory in 1876, agriculture developed in the surrounding islands to increase the food supply and to promote industry in the islands (Kurata 1983; Shimizu 2003; Toyoda 2003). After reversion of the islands to Japan in 1968, agriculture began once more on Chichi-jima and Haha-jima Islands.

Anole predation hypothesis

The green anole, *Anolis carolinensis*, was introduced to the Ogasawara Islands by at least the late 1960s (Hasegawa et al. 1988), probably as a pet or by accidental inclusion in freight shipments by the U.S. Army (Miyashita 1980; Karube and Suda 2004). Afterwards, the anole spread rapidly on Chichi-jima and Haha-jima, and the populations showed exclusive distribution from that of a native lizard, *Cryptoblepharus boutonii nigropunctatus* (Hasegawa et al. 1988). Populations of diurnal longicorn beetles have decreased for the past two decades in Ogasawara Islands, whereas populations of nocturnal longicorn beetles have not decreased. This faunal decline is consistent with the diurnal activity of the green anole (Makihara et al. 2004). Green anoles have been frequently observed seeking prey insects around inflorescences on Chichi-jima and Haha-jima. Alien predators sometimes quickly destroy the native fauna on islands (Savidge 1987; Fritts and Rodda 1998; Courchamp et al. 2003; O'dowd et al. 2003; Nogales et al. 2004; Croll et al. 2005). Several studies have shown that predation of flower visitors affected both the pollinator visitation rate and the fruit set of the affecting plants (Dukas and Morse 2003; Suttle 2003; Muñoz and Arroyo 2004; Dukas 2005).

Test of hypotheses

To clarify the relationship between visitation rate and factors, we observed flower visitor on 12 islands from 2001 to 2005. Flower visitors were observed by directly observation and using digital video camera, and the amount of survey reached totally 982 observation periods for 228 days and 459 h 20 min on 143 plant species. Observed visitation rate was converted to the value of per time per inflorescence. Census routes and observation range were described in detail by Abe (2006b). In these route censuses, we also investigated the presence/absence of green anole in each island. In addition, historical records of factors being likely to affect pollination network were surveyed by literatures.

Surveyed 12 islands were classified into five groups by geographical and ecological aspects. Main islands (Chichi-jima and Haha-jima) was human inhabiting and there are green anoles and introduced honeybees. Muko-jima Islands (Muko-jima, Nakoudo-jima and Yome-jima) are covered mostly by grassland vegetation with several small forest fragments (Shimizu 1993). Green anole and honeybee are not in these islands. Chichi-jima Satellite Islands (Ani-jima, Minami-shima, Nishi-jima and Otouto-jima) are not invaded by green anole but honeybees distribute in all islands. Haha-jima Satellite Islands (Hira-shima and Mukou-jima) are lacking in both green anole and honeybee. Nishino-shima Island is erupted in 1973 and biota was poor and there is no alien species (Abe 2006a). Visitation rate of each island group was the average of component plant species.

To test the honeybee competition hypothesis, visitation rates were compared between the main islands and Chichi-jima Satellites Islands (57 h for 34 plant species). In addition, flower visitors on Chichi-jima and Haha-jima were observed during nighttime when green anoles are not active. Visitation rate of nighttime (80 h 50 min for 36 plant species) was compared with that of daytime in 132 species (339 h 50 min). Comparison of visitation rate between islands or daytime/nighttime was tested by ANOVA using JMP software (Sall et al. 2004).

To test the preference of food material for green anole, we performed a predation experiment using mesh cages ($30 \times 30 \times 30\ \mathrm{cm}^3$) in the Ogasawara Islands. In a trial of this experiment, an anole and 2–6 insects were put into a cage and recorded the predation time for 60 min. This trial was replicated 29 times using five anoles (three females and two males). Before the trial, anole was fasted at least 2 days. Insects supplied as prey were 25 honeybees, 22 endemic small bees (2 *Ceratina boninensis* and 20 *Hylaeus* spp.), 65 flies (29 *Ophyra chalcogaster* and 36 Calliphoridae spp.) and 9 moths (Noctuoidea spp.). One or two species of these insects were supplied in a trial.

Results and discussion

Flower visitation by endemic bees was frequent on all satellite islands except for Nishino-shima (Table 1), where they were absent probably because this volcanic island erupted recently rather than because of anthropogenic disturbance (Abe 2006a). But endemic bees disappeared almost entirely from the two main islands (Chichi-jima and Haha-jima). Introduced honeybees were observed on the Chichi-jima Satellite Islands (2.7 ± 1.2 (SE) visits) as well as on the main islands (3.4 ± 0.5). However, visitors other than honeybees were observed frequently on the Chichi-jima Satellite Islands (15.0 ± 6.6 visits) while the

Table 1 Distribution of pollinators and of factors that affect them in the Ogasawara Islands

Island groups	Endemic small bees	Carpenter bees	Honey bees	Forests	Insecticide	Anole
Main	–	C	A	A	C	A
Chichi Satellite	A	C	C	A	–	–
Muko	A	C	–	–	–	–
Haha Satellite	A	C	–	A	–	–
Nishino	–	–	–	–	–	–

A = Abundant, C = Common, – = None or rare

Table 2 Chronology of key events related to the Ogasawara pollination system

Year	Endemic bees on Chichi jima and Haha jima Islands	Events	Reference
1870s–1980s		Introduction of various alien plants	Toyoshima (1938)
1880s		Introduction of honeybees Forest cutting Agricultural development	Funakoshi (1990), Hara (1996) Toyoda (2003)
1930s	Yes	Typelocalities of endemic small bees were recorded	Yasumatsu (1955)
1960s		Introduction of anoles on Chichi-jima	Hasegawa et al. (1988)
1968, 1969	Yes	Insect fauna research	Hasuo (1970)
1991	Yes but rare	Decline of endemic small bees	Kato (1992), Kato et al. (1999), Miyano (1998)
2003	No	Endemic small bees almost extinct	Abe (2006b)

number of visits by these visitors decreased dramatically on the main islands (1.7 ± 0.4 visits, $F_{1,164} = 15.3$, $P < 0.001$). In particular, endemic small bees disappeared from the main islands (0.0 ± 0.0 visits) but remained dominant on these satellite islands (7.4 ± 3.4 visits, $F_{1,164} = 18.1$, $P < 0.001$). Thus, native flower visitors on these satellite islands retained a rich species diversity and high abundance. Honeybee competition hypothesis cannot explain the difference of visitor fauna between the main islands and Chichi-jima Satellite Islands. In addition, a historical timetable of the related events exhibited a critical time lag between honeybee introduction and pollinator decline; pollinator decline in the main islands were reported in the 1990s but the honeybee was introduced in the 1880s (Table 2). Moreover, various insect taxa such as beetles and dragonflies that do not depend on the floral resource have also declined since the first list of Ogasawara fauna was published (Ohbayashi et al. 2003). Although the resource competition hypothesis has been supported in various regions, it is not always a significant factor in determining populations of native bees (Steffan-Dewenter and Tscharntke 2000; Roubik and Wolda 2001). Field evidences suggests that the resource competition hypothesis is unlikely to be the primary reason for the dramatic observed decline in native pollinators in the Ogasawara Islands.

We also rejected the forest decline hypothesis. Endemic bees were observed even on Muko-jima, Yome-jima and Nakoudo-jima, where the forests were limited to very small remnants because of goat grazing after clear-cutting of the primary forests (Fig. 2). This finding probably results from the fact that endemic small bees such as those in genus *Hylaeus* may use burrow in soil as nesting substrate (Daly and Magnacca 2003). In contrast, large forests are still remaining on Chichi-jima and Haha-jima, where native pollinators

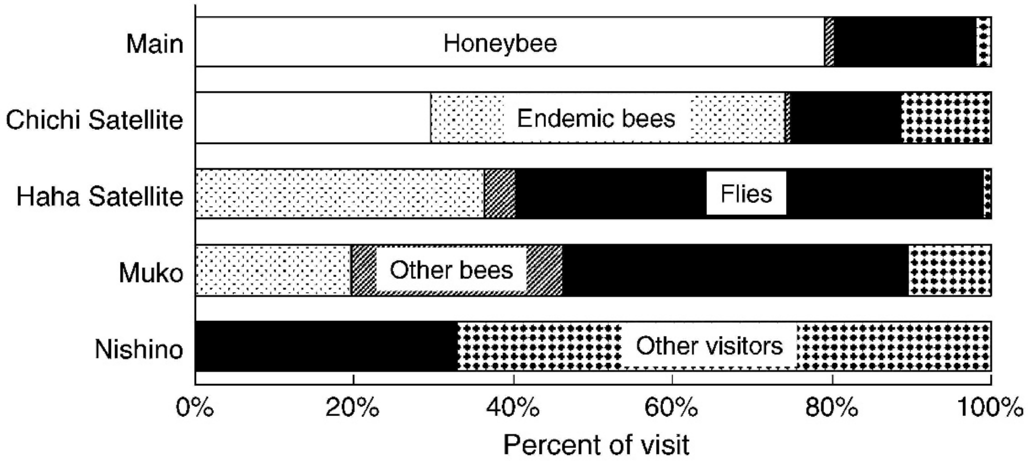

Fig. 2 Composition of primary floral visitors in five island groups

Table 3 Result of the anole feeding experiment

Insects	Predation	Alive	Test by honeybee		
			χ^2	df	P
Honeybee	0	25			
Endemic small bee	11	1		1	<0.001
Fly	49	0		1	<0.001
Moth	5	4	16.3	1	<0.001

have declined. Thus, the forest decline hypothesis does not provide a satisfactory explanation for the pollinator decline on Chichi-jima and Haha-jima.

Today, the insecticides and other agricultural chemicals are used on Chichi-jima and Haha-jima. If the insecticide use destroyed endemic bee populations, honeybees and endemic *Xylocopa ogasawarensis* would both have been damaged on the main islands. However, they remain common flower visitors (Abe 2006b). In addition, although much of the land on the two main islands was converted into sugar cane fields before the war, the native insect fauna was maintained after reversion of these islands to Japan (Yasumatsu 1955; Hasuo 1970).

It seems possible to explain the distribution of endemic small bees based on the anole predation hypothesis (Table 1, Fig. 1). Field observations of anole predation are now difficult because most flower visitors have already disappeared on the main islands. Instead, predation experiment showed that the anole preferred native flower visitors to introduced honeybees (Table 3). All attacks on honeybees resulted in the anole being stung by the bee's powerful stinger; thereafter, once stung, individual anoles never again attacked the bees. This probably explains why the endemic carpenter bee, *X. ogasawarensis* continue to survive on Chichi-jima and Haha-jima. The timing of the anole introduction and of the decline in insect fauna also supports the anole predation hypothesis (Table 2). Visitation rate on the main islands was 5.1 ± 1.5 in daytime and 15.8 ± 3.0 in nighttime (ANOVA, $F_{1,164} = 9.9$, $P = 0.002$). This suggests that there is no predation pressure by green anole in nighttime while daytime activity of green anole would depress the reproductive success of plants without nocturnal pollination syndrome.

These four hypotheses are not mutually exclusive. In reality, they may act together to explain the decline in native visitors. However, the differences in the relative magnitudes of these factors among islands and in the historical background of individual islands suggest that anole predation is the most critical cause of the observed decline.

Perspectives for Conservation

Acts to restore the endemic pollination network is needed on the Ogasawara Islands. Based on our study results, predation by the alien anole has had a serious impact not only on insect fauna but also on the network of mutualistic interactions. In addition, the distribution of introduced honeybees has extended to satellite islands near Chichi-jima. However, eradication of honeybees is not a suitable plan for restoration of pollination network because recover of endemic bee fauna like on Santa Cruz island (Wenner and Thorp 1994) would be prevented by anole predation. The honeybee is one of the most strongly linked pollinators in these islands (Abe 2006b), and the removal of this species poses a great risk for the conservation of plant species diversity (Memmott et al. 2004). In addition, beekeeping operations on Chichi-jima and Haha-jima would make it difficult to eradicate honeybees completely without economic impacts for farmers. The best plan for the restoration thus appear to require eradication of the green anoles, followed by reintroduction of native insects from the satellite islands if their populations do not recover naturally.

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Chapter 14

Vegetation changes between 1978, 1991 and 2003 in the Nakoudojima island that had been disturbed by feral goats

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Key words: aerial photographs, bare ground, Bonin Islands, forest, grassland, oceanic island, recovery of vegetation

Abstract

Changes in vegetation of the Nakoudojima island between 1978, 1991 and 2003 were quantified with aerial photographs. The island was divided into 9200 plots (10 m x 10 m) on the aerial photographs and the plots were categorized into forest, grassland, bare ground or others. Percentages of the grassland increased 66.3% to 69.0% and those of the bare ground increased from 7.0% to 15.5% for 23 years. Some grasslands became bare ground between 1978 and 1991, which resulted in a decrease in the area of the grassland and an increase in the area of the bare ground during this period. On the other hand, some bare ground changed to grasslands between 1991 and 2003, which meant an increase of grasslands. These changes in vegetation would be due mainly to grazing and trampling, and their termination caused by feral goats. Percentages of the forest decreased from 16.2% to 6.0% for 23 years. Many forests changed into grasslands or bare ground even after the eradication of feral goats, which suggests that canopy trees in the forest died by natural disturbances in addition to the lack of seedlings by the grazing of feral goats.

Introduction

Feral goats graze and/or trample vegetation in many oceanic islands, which often causes destruction of vegetation and acceleration of soil erosion (Coblentz, 1978; Coblentz and van Vuren, 1987; Stone and Loope, 1987; Loope et al., 1988; de la Luz et al., 2003). The feral goats were, therefore, eradicated in many islands for native conservation (a review, Campbell and Donlan, 2005). After the eradication, vegetation recovers in some oceanic islands (Hamann, 1975, 1979; Mueller-Dombois and Spatz, 1975; Bullock et al., 2002; Kessler, 2002; Shimizu, 2003a), but it does not in others. One of the reasons why the vegetation did not recover would be shortage of dispersed seeds because of the mortality of reproducing trees.

Vegetation of the Nakoudojima island, one of the Bonin islands in the north-eastern Pacific (27°37'-27°38'N, 142°10'-142°11'E) had been severely disturbed by feral goats and the goats were completely eradicated by 1999. The goats reduced

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the vegetation cover of forests and grasslands by grazing and/or trampling, which accelerated erosion of the soil by 1999 (Japan Wildlife Research Center, 1992; Shimizu, 1993). After the eradication, herbaceous species reestablished at some sites in the island (Japan Wildlife Research Center, 2002; Shimizu, 2003b), but there were few saplings and seedlings of tree species except for *Trema orientalis*, *Callicarpa subpubescens* and *Leucaena leucocephala* (Shimizu, 2003b). The above-mentioned changes in vegetation were described only qualitatively by Shimizu (2003b) but not quantitatively. In this study, we quantified areas of forests, grasslands and bare ground, and clarified their spatial distribution in the island with aerial photographs in order to describe how the vegetation of the Nakoudojima island was disturbed and recovered.

Methods

Three successive sets of aerial photographs in 1978 (1:10000, Japan Geographical Survey Institute), 1991 and 2003 (1:10000, Japan Ministry of the Environment) were used to quantify the spatial and temporal changes of vegetation in the Nakoudojima island. Peripheral areas of the island were not included in this analysis because they were coasts or cliffs without vegetation. The island except for coasts and cliffs was divided into 9200 plots (10 m x 10 m) on the aerial photographs (Fig. 1). The plots were categorized into forest, grassland, bare ground or others based on the largest area in each plot of the aerial photographs. The bare ground meant sites at which surface soil was exposed, and sites at which surface soil was completely lost were categorized into others. The others were mainly consisted of cliffs or rocks.

It is difficult to determine exactly when goats were introduced to the island, but over 60 goats were kept as livestock in the island in 1883 (Ogasawara-Touchoh, 1888). The naturalized goats after World War II increased their numbers and they reached about 500 in 1991 (Japan Wildlife Research Center, 1992). Their eradication was begun in 1997 and completed in 1999 by the Tokyo local government (Japanese Wildlife Research Center, 2002).

Results

Over twenty plots belonging to the bare ground aggregated in the section B3, C3 and D4 in 1978 in Fig. 2a. Less than ten plots of the bare ground aggregated throughout the island in 1978. In 1991, Over one-hundred plots of the bare ground aggregated in the section A4, B2, B3, B4, C3 and D4 in Fig. 2b. Most of the plots of the bare ground had been those of the grassland in 1978. A part of the plots of the bare ground in 1991 changed into those of the grassland between 1991 and 2003 (Fig. 2c).

There was an area of the forest consisted of over two-hundred plots at D3 and the forest area composed of ca. one-hundred plots in the section B4 in 1978 (Fig. 2a). Forest patches consisted of less than thirty plots scattered in the island in 1978. Between 1978 and 1991, 62.1% of the plots of a forest changed into the grassland

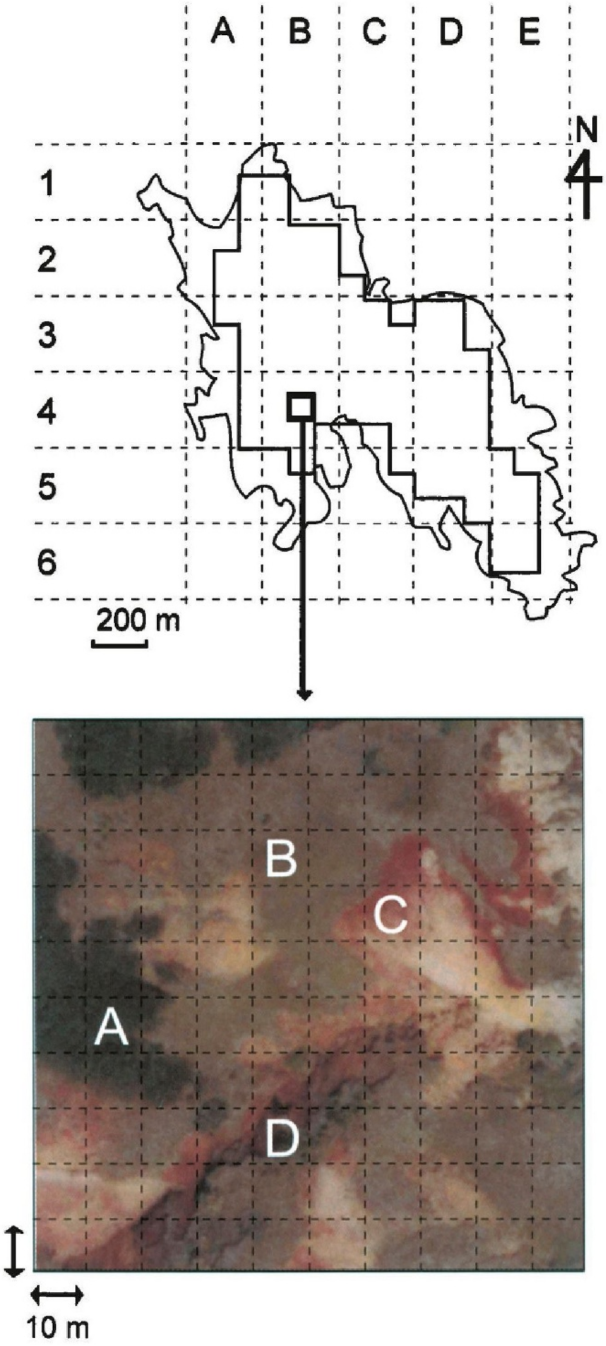

Figure 1 Locations of 10 m x 10 m plots on the Nakoudojima island. The inner area of the solid line was divided into nine-thousand-two-hundred 10 m x 10 m plots. The photograph shows forest (A), grassland (B), bare ground (C) and others(D) .

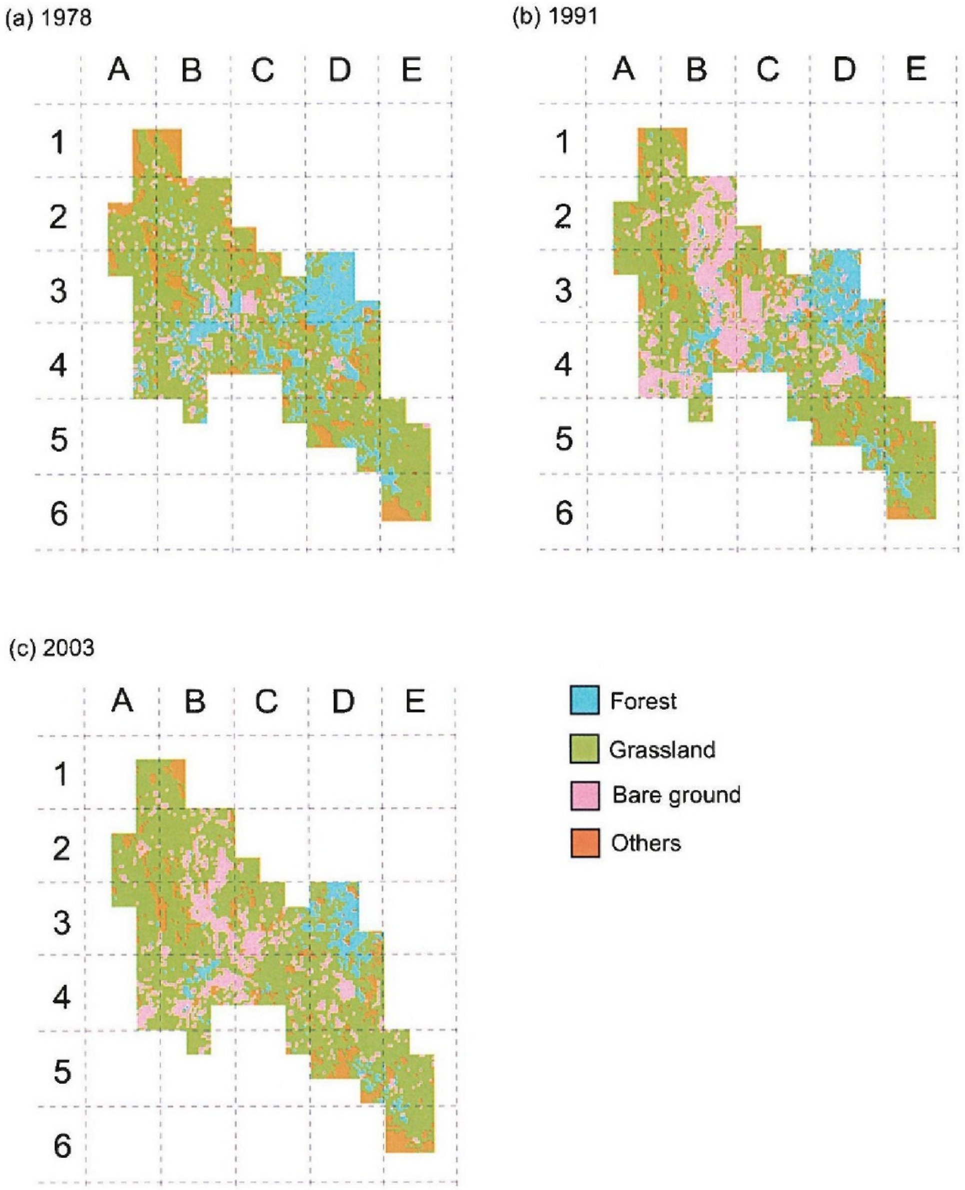

Figure 2 Spatial distribution patterns of forest, grassland, bare ground and others in (a) 1978, (b) 1991, and (c) 2003.

or the bare ground and 59.0% of the plots of the forest into the grassland or the bare ground between 1991 and 2003. As a result, numbers of plots of the forest in the section D3 and B4 in 2003 decreased by 50% of the numbers in 1978. Most forests patches in 1978 disappeared by 2003 (Fig. 2b, c).

Number of the 10 m x 10 m plots belonging to the bare ground was the smallest of those of four categories in the Nakoudojima island in 1978 (Fig. 3). The number drastically increased between 1978 and 1991, and the percentage of the plots of the bare ground against 9200 plots increased from 7.0% to 21.9%. The number of the plots, however, decreased from 1991 to 2003, and its percentage in 2003 was 15.5%. The number of the plots belonging to the grassland decreased from 1978 to 1991, while it increased from 1991 to 2003. Its percentage was 66.3% in 1978 and 58.8% in 1991, while it increased to 69.0% in 2003. The number of the plots belonging to the forest decreased for 23 years. Its percentage was 16.2% in 1978, 11.0% in 1991 and 6.0% in 2003. There were few changes in numbers of the plots belonging to others for 23 years.

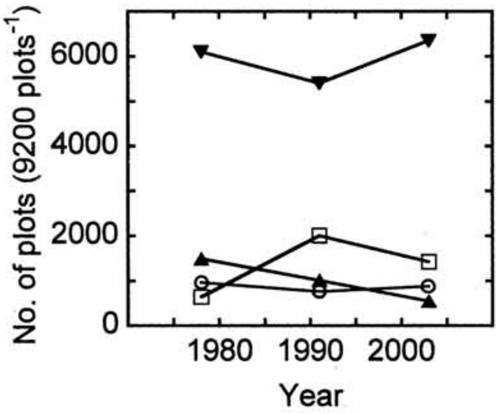

Figure 3 Changes in numbers of the 10 m x 10 m plots of forest, grassland, bare ground and others during the 23 years.
▲ : forest, ▼ : grassland, □ : bare ground, ○ : others

Discussion

Decreases in the grassland and increases in the bare ground between 1978 and 1991 suggests that large biomass of herbaceous plants were lost by grazing and trampling of feral goats. These results were similar to the tendency observed between 1968 and 1991 in this island (Japan Wildlife Research Center, 1992). On the other hand, increases in the grassland and decreases in the bare ground between 1991 and 2003 suggest that herbaceous plants reestablished in some areas of bare ground after release from grazing and trampling of feral goats by the eradication of the goats, which is consistent with the results of the field experiment conducted in the Nakoudojima island. In the experiment, rapid growth of herbaceous plants were observed at sites from which feral goats were experimentally excluded

(Japan Wildlife Research Center, 2002). The results obtained by this study are also consistent with previous studies in other oceanic islands (Hamann, 1979; Mueller-Dombois and Spatz, 1975; Bullock et al., 2002; Kessler, 2002).

Decreases in the forest between 1978 and 1991 would be caused by mortality of canopy trees due to natural disturbances and by the grazing of seedlings of trees (Shimizu, 1993). There were, indeed, few seedlings on the forest floor in the Nakoudojima islands before the eradication of feral goats (Shimizu, 1993), which was also observed in other oceanic islands (Schofield, 1989).

After the eradication of feral goats, the lack of dispersed seeds due to death of reproducing trees and, thus, the lack of seedlings result in decreases in the forest between 1991 and 2003. In fact, densities of seeds of tree species in the soil of the grassland and bare ground were very low after the eradication of feral goats (Weerasinghe, per. com.). Therefore, it would need long for recovery of forests in the Nakoudojima island after the eradication.

Recovery of vegetation would depend on seed rain. The seed rain would be affected by feral goats in the grassland as well as the forest. The grassland was recovered after the eradication in the Nakoudojima island while the forest was not. The seed rain of the forest would not be sufficient probably because of effects of feral goats and physical disturbances such as typhoons or severe droughts. Therefore, it would need more time for recovery of the forest than that of the grassland.

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Chapter 15

Seed and seedling demography of invasive and native trees of subtropical Pacific islands

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Abstract. *Bischofia javanica* is an invasive tree of the Bonin Islands in the western Pacific, Japan. This species has aggressive growth, competitively replacing native trees in the natural forest of the islands. The aim of this study was to examine seed and seedling factors which might confer an advantage to the establishment of *Bischofia* over native trees. During a 5-yr period we compared the demographic parameters of early life history of *Bischofia* and *Elaeocarpus photiniaefolius*, a native canopy dominant, in actively invaded forests. Predation of *Elaeocarpus* seeds by in troduced rodents was much higher before (27.9-32.9%) and after (41.3-100%) dispersal of seeds than that of *B. javanica*. Most *Elaeocarpus* seeds lost viability ca. 6 mo after burial in forest soil while some seeds of *Bischofia* remained viable for more than 2 yr. Seedling survival in the first 2 yr was much higher in *Bischofia* (16%) than in *Elaeocarpus* (1.3%). The high persistence of *Bischofia* in the shade, coupled to its rapid acclimation to high light levels, is an unusual combination because in forest tree species there is generally a trade-off between seedling survival in the shade and response to canopy opening. Compared with a native canopy dominant, greater seed longevity, lower seed predation by introduced rodents, longer fruiting periods and the ability to form seedling banks under closed canopy appear to have contributed to the invasive success of *Bischofia* on the Bonin Islands.

Keywords: *Bischofia javanica*; Bishopwood tree; *Elaeocarpus photiniaefolius*; Japan; Seed bank; Shade tolerance.

Nomenclature: Satake et al. (1989).

Introduction

The invasion of alien tree species has seriously affected many natural forest ecosystems in the world (Reichard & Hamilton 1997; Richardson 1998). *Bischofia javanica* (*Euphorbiaceae*), bishopwood tree, indigenous to southeast Asia, tropical Australia and Polynesia, has successfully invaded several disparate locations including southern Florida (Horvitz et al. 1998; Morton 1984), mid-Pacific islands such as Hawaii (Gerrish & Mueller-Dombois 1980) and the west Pacific Bonin Islands (Shimizu 1988). *Bischofia* was introduced into the Bonin Islands, a group of remote oceanic islands in the western Pacific of Japan, in the early 1900s as a timber tree because of its vigorous growth rate. In its native range, this species occurs in evergreen, dry mixed deciduous, mesic, or swamp forest but never as a weedy species. In the Bonin Islands *Bischofia*, with pulpy seeds attractive to birds, has escaped from plantations and spread widely in the natural forest, competitively replacing native tree species. It is now a canopy dominant in ca. 11% of the natural forest on Hahajima-island (the most strongly invaded island) (N.Tanaka et al. unpubl.). The threats to native species and forest biodiversity by *Bischofia* are made more acute given the high number (75%) of endemic tree species (Kobayashi 1978). Furthermore, in other invaded areas such as Florida, this species is reported to have become the prime host for several foliage diseases and pests affecting adjacent cultivated areas and subtropical forests (Horvitz et al. 1998; Morton 1984).

Oceanic islands, such as the Bonins, are thought to be more susceptible to plant invasion than continents because long periods of isolation have led to a native island flora that is poor in some functional plant groups, low in species diversity and low in competitive ability due to a weaker selective environment (e.g. Loope et al. 1988; Vitousek 1988). However, since invasion by *Bischofia* is observed in both oceanic islands and on continents, the

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invasive success may depend more on the site-specific differences between invasive and native species in life history and demographic characteristics (Mack & Pyke 1983; Rongers & Hartemink 2000), and in their response to resource variations related to habitat disturbance (Simberloff 1995; Stohlgren et al. 1999; Mack et al. 2000). While the process of plant invasion is often difficult to evaluate, it appears that some successful invasive species can either use limiting resources more efficiently or use them at times when they are unavailable to native species (Vitousek 1986). Studies on the comparison of invasive and native species have provided valuable insight into the proximal mechanisms underlying the success of invasive species. While some qualitative and quantitative observations have revealed better competitive ability of invasive over native species (Kitayama & Mueller-Dombois 1995; Rejmánek & Richardson 1996; Pattison et al. 1998; Yamashita et al. 2000), others failed to identify any such differences (Thompson et al. 1995; Blaney & Kotanen 2001).

Some studies have found certain attributes associated with invasiveness by comparing life history traits of invasive and non-invasive species of close phylogeny (Pantone et al. 1995; Rejmánek & Richardson 1996), but others found no clear life history distinctions among species (Radford & Cousens 2000). It may be that a successful invasive alien possesses a combination of physiological and demographic attributes that are pre-adapted to the local habitat (Thébaud et al. 1996; Levine & D'Antonio 1999; Naeem et al. 2000). In this study, we attempted to quantify the demographic attributes conferring the success of *Bischofia* at locations where active invasion has taken place. The approach taken here is to contrast the invasive species with a native canopy dominant species that appears to have been the most effective in resource use before the invasion. We know of no previous studies on invasiveness taking this comparative approach.

In the natural forests of the Bonins, *Elaeocarpus* is an endemic late-successional canopy dominant in the mesic forest most affected by *Bischofia* (Shimizu 1988; Tanimoto & Toyoda 1996). Given its high acclimation response to changes in light compared to native species (Yamashita et al. 2000, 2002), *Bischofia* has aggressive growth in canopy gaps (Shimizu 1988). For *Bischofia* to excel in a canopy gap, it must also possess an ability to survive under an intact canopy until a gap event. In comparison, native late-successional trees such as *Elaeocarpus* are known to persist for a long time in an undisturbed understorey but at low densities. The total number of tree seedlings (> 20 cm tall and < 5 cm DBH) under a closed canopy sampled in 2000 was 17 090.ha^{-1}, of which 49% was *Bischofia* and 11% *Elaeocarpus* (N. Yamashita et al. unpubl.). At these seedling densities, it is more likely for *Bischofia* to first occupy and pre-empt undisturbed sites before canopy gaps occur which may otherwise be available to native seedlings. Since the ultimate abundance and spatial distribution of a species is initially determined at the stage of germination and seedling establishment when mortality is greatest (Harcombe 1987; Silvertown & Doust 1993), we hypothesize that the more advantageous early life history traits of *Bischofia* in pre-empting shaded understorey sites will contribute to the exclusion of native species.

To quantify the factors in early life history that may confer such an advantage, we conducted a 5-yr field study in a mesic forest in the Bonin Islands comparing seed dispersal, seed germination and seedling establishment of *Bischofia* with *Elaeocarpus*. This study addressed the importance of site-specific characteristics that influence invasion success by contrasting demographic traits between the invasive and native canopy dominant species, considering functional roles of species in the forest ecosystem.

Methods

Study site

The study was conducted in a permanent plot of 60 m × 60 m located in the Mt. Kuwanoki Forest Reserve, a natural mesic forest on Hahajima Island (in the Bonin Island group) situated in the western Pacific Ocean ca. 1000 km south of Tokyo (26°39' N, 142°9' E, 256 m a.s.l.). The climate is subtropical and maritime. The annual mean temperature is 22.9 °C and mean precipitation is 1261 mm (1969-1990, Hahajima Municipal Office). There are over 20 native woody species in the mesic forest including the evergreen canopy dominant *Elaeocarpus* and the understorey shrub *Ardisia sieboldii* (Shimizu 1988; Shimizu & Tabata 1991). Reproductive *Bischofia* represents ca. 11% of the forest canopy at this site. *Bischofia* fruit is ca. 1 cm diameter borne as a cluster on terminal inflorescences. Fruit requires 9 -10 mo to mature on the tree. The seeds (mean 4-6 seeds per pulp) are surrounded by fleshy pulp favoured and dispersed by birds. The main seed predator in the study area has been identified as an introduced tree climbing rodent (*Rattus rattus*) (H. Takano unpubl.).

Seed fall and seedling emergence census

In 1995, we placed 16 sets of seed traps (two 0.5-m^2 traps per location) and an adjacent 1 m^2 quadrat on the forest floor under the canopy of *Bischofia* (five sets), *Elaeocarpus* (six sets) and other native canopy trees (five sets). The seed traps were made of 2 mm mesh nylon cloth and placed 1 m above the ground. We collected seeds from the traps once every month. Seeds were identified to species, sorted according to their condition (i.e. sound, immature, decayed, damaged by insects or damaged by *R. rattus*) and counted. Newly emerged seedlings in the adjacent quadrats were individually marked and counted every two months. The fate of each seedling was followed for 5 yr. To monitor the state of developing seedlings in more detail we tagged 50 newly emerged seedlings each of *Bischofia* and *Elaeocarpus* at three locations with similar daily total photosynthetic photon flux density of ca. 3% of full sun in May 1998. The number and visible condition of leaves (e.g. extent of herbivory, abnormal coloration or other symptoms suggesting disease) were recorded once every two weeks. Causes of seedling mortality were assigned to five categories: (1) damping-off, (2) herbivory, (3) physical damage, (4) wilting and (5) unknown. Damping-off is defined as dead seedlings with symptoms such as decomposing or brownish stem. Dead seedlings with one of the following causes of damage recorded in the preceding census were classified as herbivory: hypocotyls or epicotyls eaten or severed, or > 50% of the total leaves eaten. Seedlings killed physically were either buried by fallen litter or had roots entirely exposed by soil erosion. Wilted seedlings had visible wilting of cotyledons or true leaves (with no damping-off symptom). Seedlings that had disappeared since the previous census were classified as unknown.

Seed removal experiments

To estimate relative intensity of seed predation of invasive *Bischofia* and native *Elaeocarpus* on the forest floor, field assays were conducted following the method described in Diaz et al. (1999). A large number of fresh seeds were collected from four individuals each of *Bischofia* and *Elaeocarpus* in the autumns of 1999 and 2000. Plastic trays (10 cm diameter, 5 cm deep and perforated to allow drainage) were placed on the forest floor and anchored to the ground to prevent tipping over by animals. Twenty seeds per tray were placed on top of paper towel and covered by a thin layer of sieved soil. For each species, one tray with and one without leaf litter cover were placed at four replicate sites under both intact canopy and canopy gap, to see the effect of leaf litter on seed predation. A tray without seeds was also placed at each site as a control for additional seed fall into the trays. Experiments were run for five consecutive days and repeated twice in April and December 2000, coinciding with just after seed fall and peak seed fall for the study area, respectively. After five days, all trays were collected and the number of remaining sound seeds counted.

Seed bank experiment

To assess seed longevity of the two species in the forest soil, seeds of each species were packed in stainless steel bags (2 mm mesh) and buried in three replicate forest locations. Seeds used in this experiment were collected from mother trees near the permanent plot in November 1996 for *Elaeocarpus* and January 1997 for *Bischofia.* Because *Elaeocarpus* seeds are relatively large (dry weight ca. 630 mg), the viability of *Elaeocarpus* seeds was easily determined by cutting the seeds to examine the condition of the albumen. It is more difficult to determine the viability of the smaller *Bischofia* seeds (dry weight ca. 15 mg) through visual examination. Instead, they were incubated at 20/30 °C (12 h / 12 h) for 40 days. The optimum temperature for *Bischofia* germination was previously found to be 15-30 °C (N. Yamashita unpubl.). Viability was high for both species: *Bischofia* (98.0%) and *Elaeocarpus* (99.0%). At each location, we buried 14 bags each of *Bischofia* and *Elaeocarpus* seeds. For *Bischofia* there were seven bags each containing 100 pulpless seeds and seven with 50 intact fruits containing ca. 230 seeds in each bag. For *Elaeocarpus*, all bags contained 30 seeds, seven bags with and seven without pulp. All bags were buried at a depth of 2 cm. Two bags (one with and one without pulp) for each species were recovered from each location at 8, 19, 26, 40, 64, 78 and 104 wk after burial for *Bischofia* and at 19, 26, 40 wk for *Elaeocarpus*. The number and viability of seeds remaining in each bag were checked and counted.

Estimation of soil seed bank

To estimate the number of seeds in the soil seed bank, a seedling emergence method was used (Gross 1990). In March 1998, we collected soil samples from the forest understorey at the 16 sites adjacent to the quadrats and seed traps. A 20 cm × 20 cm × 20 cm volume of forest substrate was removed and separated into six layers: loose litter, 0-2, 2-4, 4-6, 6-10, and 10-20 cm. Substrate samples were spread in trays to a depth of ca. 1 cm on a bed of vermiculite. Trays were placed in a greenhouse (50% full sun) and watered 2 to 3 times per week to maintain near field capacity. For the following 15 weeks (after which no further seedling emergence was observed), emerged seedlings were tagged and counted at ca. five day intervals; seedlings were removed as soon as they had been identified to species.

Data analyses

Degree of seed predation was compared among species, seasons, locations and presence of litter cover with four-way ANOVA on arcsine-transformed data. Repeated-measure ANOVA using arcsine-transformed data were used to test for differences in seedling survival patterns between *Bischofia* and *Elaeocarpus*.

Results

Annual variation in seed production

The amount and yearly variation of seed fall was greater for *Bischofia* than for *Elaeocarpus* (Fig. 1, Table 1). Both species produced the largest seed crop during the study period in 1995-1996 (Table 1). *Bischofia* had mast production on alternate years. The fruiting period lasted for 2-3 mo.yr^{-1} for *Elaeocarpus* but 2-5 mo.yr^{-1} for *Bischofia* (Table 1). The peak period of seed dispersal was October to November for *Elaeocarpus* and November to January for *Bischofia*. In 1997, most *Bischofia* fruits contained immature seeds because they were dropped prematurely due to several typhoons. Overall, most of the dispersed mature seeds of *Bischofia* were sound (88.3-95.9%), of these 35.9-59.3% were seeds with pulp while the remainder were found with damaged or no pulp. The total number of sound seeds dispersed during the 5 yr period by *Bischofia* (3082 seed.m^{-2}) was ca. 16 × higher than that by *Elaeocarpus* (191 seed.m^{-2}). *Elaeocarpus* seeds suffered heavy predation (27.9-32.9%) compared to *Bischofia* (4.1-11.7%) by *R. rattus* before dispersal (Fig. 1).

Table 1. Seed fall, germination and seedling emergence ratio of *Bischofia javanica* and *Elaeocarpus photiniaefolius* derived from seed trap data and emerged seedling density in 16 pairs of seed traps and 1-m^2 quadrats. Fruiting (fr) period is defined as the month when sound seeds were found in the traps. Seedling emergence ratio (the probability of successful germination of viable seeds) is the ratio of seedlings observed in each non-fruiting (–fr) period and sound seed fall in the previous fruiting period. Data are shown as mean ± 1 s.d.

	Period (month)	Sound seed fall (m^{-2})	Seedlings obs (m^{-2})	Emergence ratio (%)
B. javanica				
1995-1996	fr (5)	2370 ± 5607	-	
	–fr (9)	-	209 ± 338	8.8
1996-1997	fr (2)	63 ± 174	4 ± 12	
	–fr (6)	-	50 ± 1093	79.6
1997-1998	fr (5)	194 ± 317	17 ± 39	
	–fr (7)	-	563 ± 103	29.0
1998-1999	fr (3)	1 ± 3	16 ± 38	
	–fr (6)	-	1 ± 3	109.9
1999-2000	fr (5)	455 ± 849	21 ± 44	
	–fr (7)	-	46 ± 60	10.2
E. photiniaefolius				
1995-1996	fr (2)	124 ± 161	-	
	–fr (10)	-	< 1	0.3
1996-1997	fr (2)	46 ± 579	0	
	–fr (10)	-	< 1	0.1
1997-1998	fr (2)	17 ± 29	0	
	–fr (9)	-	< 1	1.1
1998-1999	fr (3)	1 ± 2	0	
	–fr (8)	-	0	0
1999-2000	fr (2)	3 ± 5	0	
	–fr (10)	-	0	0

- : no data available.

Seed predation

The number of seeds lost through predation was significantly different between species, seasons, locations and the presence or absence of litter cover (four-way ANOVA, Table 3). There was a significant interaction among the three parameters (species, locations and seasons) and the two parameters (species and seasons). The number of sound *Elaeocarpus* seeds remaining in the trays presented to seed predators was significantly lower than that of *Bischofia* (Fig. 2). Predation was higher for both species post seed fall (April 2000), in gaps and without the litter cover. No additional seed fall of either species was found in the control trays in either year. Almost all *Elaeocarpus* seeds were predated by *R. rattus* in the April 2000 experiment, after the season of seed fall (Fig. 2a).

Distribution of seed bank in the soil profile

By incubating soil samples collected from the 16 sites adjacent to the seedling quadrats and seed traps, we observed germination of 16 herbaceous and nine woody species (six tall tree and three shrub species). Among the six tall tree species (Fig. 3), two were native pioneers (*Trema orientalis*, *Fagara boninsimae*), one was a native canopy tree (*Celtis boninensis*) and the remaining three were non-indigenous (*Bischofia javanica*, *Carica papaya*, *Morus australis*). Relative to other species, *Bischofia* seeds were distributed nearer to the soil sur-

Table 2. Total number of viable seeds in seed traps (no.m^{-2}), emerged seedlings (no.m^{-2}) and seedling emergence ratio (%; total number of seedlings in quadrats adjusted to the seed traps per total number of sound seeds in seed traps) pooled over a 5 yr period for *Bischofia javanica* and *Elaeocarpus photiniaefolius* under three different types of canopy. Data are shown as mean ± 1 s.d.

	Canopy type		
Species	*B. javanica*	*E. photiniaefolius*	Others
B. javanica			
Viable seed fall	9771 ± 10143	189 ± 118	321 ± 345
Seedlings observed	1130 ± 692	41 ± 10	174 ± 251
Emergence ratio	11.6	21.7	54.1
E. photiniaefolius			
Viable seed fall	62 ± 75	432 ± 220	44 ± 31
Seedlings observed	< 1	2 ± 4	< 1
Emergence ratio	0.6	0.4	0.9

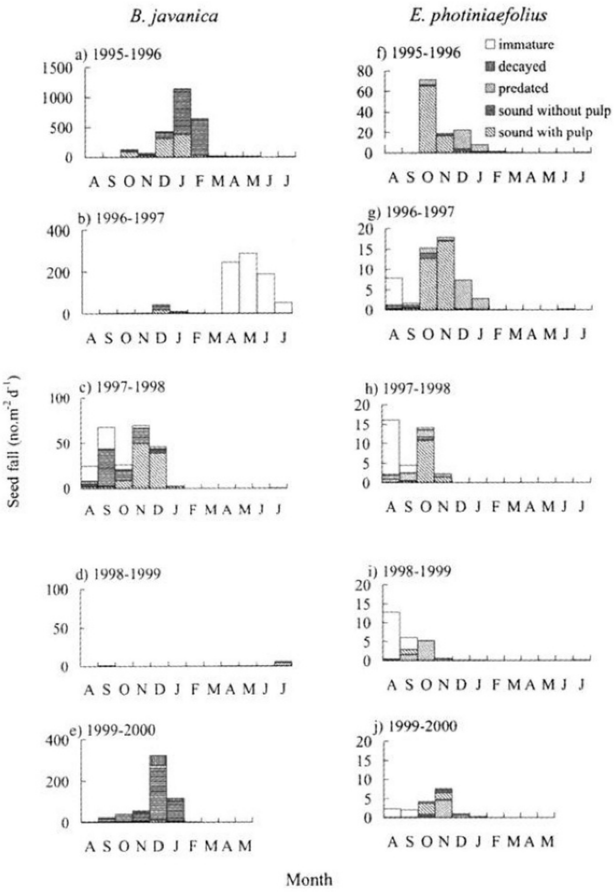

Fig. 1. Patterns of seed rain and pre-dispersal mortality for *Bischofia javanica* (**a-e**) and *Elaeocarpus photiniaefolius* (**f-j**) over a 5-yr period on Hahajima Island.

face. The combined number of seedlings emerged from all soil depths was largest in *F. boninsimae* (165.6 ind.m^{-2}), smallest in *C. boninensis* (7.8 ind.m^{-2}) and intermediate in *Bischofia* (126.6 ind.m^{-2}). No germination was observed for *Elaeocarpus* even though samples were taken from the vicinity of four seed bearing trees.

Seed longevity in forest soil

For seeds buried with and without pulp, seed longevity of *Bischofia* exceeded that of *Elaeocarpus* (Fig. 4). After burial in soil for 2 yr, 7.1% of *Bischofia* seeds with pulp and 2.3% without pulp were still viable (Fig. 4a). In contrast, *Elaeocarpus* seeds lost viability quickly with 0 and 3.3% of seeds with and without pulp, respectively, remaining viable after being buried for only 180 d (Fig. 4b).

Seedling emergence and survival

Seedling density of both species generally corresponded to the density of seeds dispersed in the previous

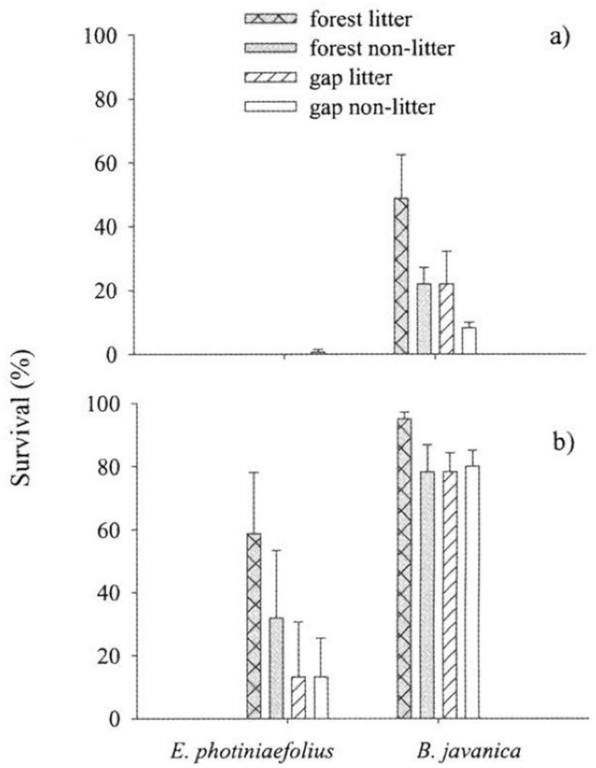

Fig. 2. Mean percentage + 1 s.d. of sound seeds remaining in trays after being left in forest understorey and under canopy gaps. Experiments were repeated twice in (**a**) April and (**b**) December 2000, coinciding with just after seed fall and at peak seed fall for the study area, respectively.

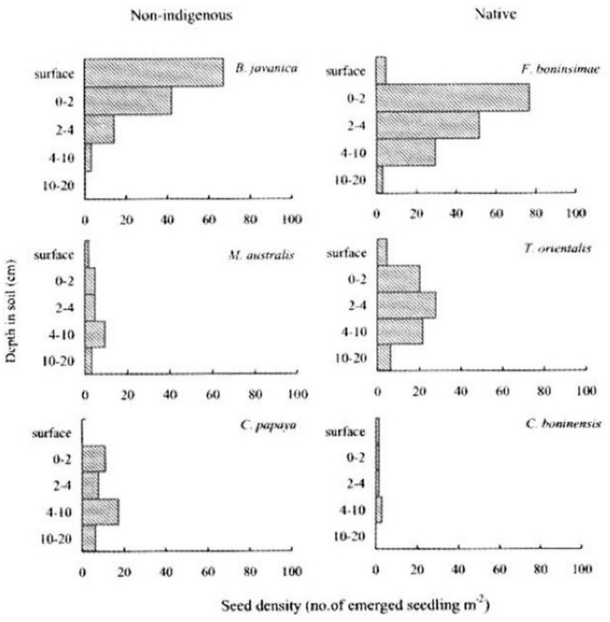

Fig. 3. Vertical distribution of viable seeds in the forest soil of Hahajima Island. Data show mean numbers of emerged seedlings of six tall tree species which had more than one seedling emerged during the 15 week observation period. Density of viable seeds in the soil was calculated from the cumulative number of germinated seedlings from 16 sample plots.

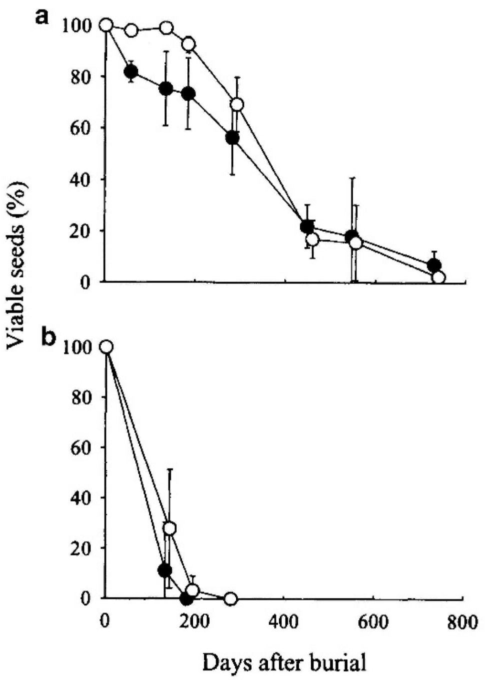

Fig. 4. Changes in seed viability in forest soil for (**a**) *Bischofia javanica* and (**b**) *Elaeocarpus photiniaefolius* measured by periodic recovery and germination test of seeds with pulp (●) and without pulp (○) in packets buried in three forest plots on Hahajima Island. Data are means ± 1 s.d.

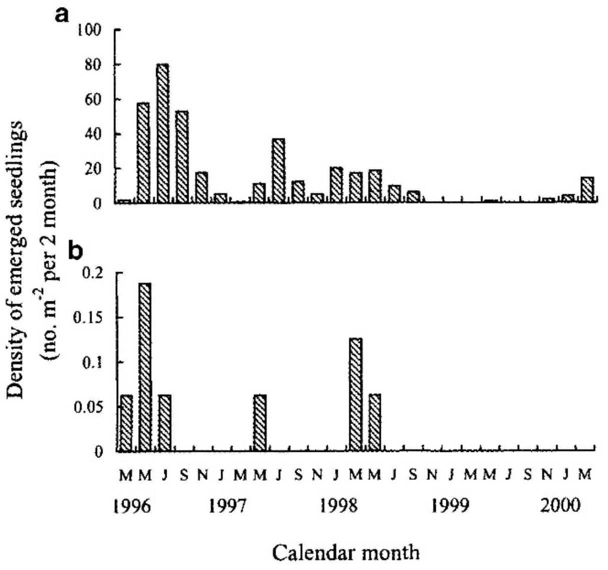

Fig. 5. Seasonal changes in the density of emerged seedlings for (**a**) *Bischofia javanica* and (**b**) *Elaeocarpus photiniaefolius* estimated from seedling censuses taken at 2-mo intervals in 16 plots.

year (Table 1). Emergence of *Bischofia* seedlings peaked in April to July, just after the end of the rainy season, but a few seedlings continued to emerge throughout the year (Fig. 5a). In contrast, the emergence of *Elaeocarpus* seedlings was restricted to the period from February to May (Fig. 5b). Seedling emergence ratio, an indicator of the probability of successful germination of viable seeds, was estimated from the ratio of emerged seedling density during a non-fruiting period (when no sound seeds were found in the traps) to the density of seeds dispersed in the previous fruiting period. The seedling emergence ratio (Table 1) of *Bischofia* was relatively low (8.8 and 29.0%) the year following the mast seed years of 1995-1996 and 1997-1998, respectively, but was high (79.6 and 109.9%) in years following the poor seed years of 1996-1997 and 1998-1999, respectively. Compared to *Bischofia*, the percentage germination of viable *Elaeocarpus* seeds in all years was very low at 0 -1.1%.

Table 3. Results of four-way ANOVA for the effects on seed removal by predator of species (*Bischofia javanica* or *Elaeocarpus photiniaefolius*), locations (forest or gap), seasons (after seed fall; April or peak; December) and litter (covered or not). Significant effects were only shown because all other combined effects were not significant.

Source of variation	df	MS	*F*	*P*
Species	1	7.449	64.505	0.0001
Locations	1	1.359	11.771	0.0008
Seasons	1	10.732	92.932	0.0001
Litter	1	0.786	6.806	0.0103
Species × Seasons 1	1.314	11.3821	0.001	
Species × Seasons × Locations	1	0.468	4.055	0.0464
Error	112	0.115		

To determine whether different canopy types affected the percentage germination, we compared seed fall and seedling emergence under the canopy of *Bischofia*, *Elaeocarpus* and other native species with data collected from seed traps and adjacent quadrats. The total number of viable fallen seeds and observed seedlings of each species during a 5 yr period were, as expected, high under the canopy of its own parent trees (Table 2). However, under non-parent canopy trees, the seedling emergence ratio during the five years was considerably higher in *Bischofia* (11.6-54.1%) than in *Elaeocarpus* (0.4-0.9%). Notably, the seedling emergence ratio of *Bischofia* was highest under the canopy of other native trees (54.1%) than under parental canopy (11.6%). Difference in seedling survival between two species was significant (Fig. 6, Repeated-measure ANOVA, $F_{44,\,44} = 5.225$, $P < 0.0001$). *Elaeocarpus* seedlings had a rapid decline with only 5.2% surviving to 200 days after germination. On the other hand, *Bischofia* seedlings maintained a much higher initial survival rate than *Elaeocarpus* where 96.0% of tagged seedlings remained after 200 days and 16.7% nearly two years after germination. In both species, damping-off was the main cause of seedling mortality with minor contributions from herbivory and other factors (Fig. 7).

Discussion

Seeds of the native dominant *Elaeocarpus* suffered heavy pre- and post-dispersal predation by the introduced *R. rattus* (Fig. 1), contributing to the low number of viable seeds relative to the invasive *Bischofia*. In contrast, most of the pre-dispersed seeds of *Bischofia* were unaffected by rodents and the intensity of post-dispersed seed predation was also lower than for *Elaeocarpus* (Fig. 2). Such differential seed predation has been recognized as a key factor in demographic and evolutionary changes in plant populations (Janzen 1971; Louda 1989). This is especially important in places such as the Bonin Islands where rodent seed predators were absent until their recent introduction. Serious impact by introduced rodents on the native ecosystem of the formerly rodent free Seychelle Islands has also been reported (Thorsen et al. 2000). Therefore, predation by small mammals could be a crucial factor in mortality for pre- or post-dispersed seeds (Tanaka 1995; Masaki et al. 1998; Diaz et al. 1999). While the degree of seed predation among tree species may depend on predator preference, in general, larger seeds are chosen by rodents (Louda 1989; Westoby et al. 1992; Reader 1993; Osunkoya 1994). Since *Elaeocarpus* seed size (mean seed dry weight 631 mg) and other native canopy trees (e.g. *Planchonella obovata*; 39 mg, *Celtis boninensis*; 56 mg, *Machilus boninensis*; 113 mg, *Melia azedarach*; 286 mg, *Sapinsus mukorossi*; 1018 mg and *Ochrosia nakaiana*; 5906 mg) in this forest are all considerably larger than that of *Bischofia* (15 mg), the small seed of the latter could have contributed to its lower predation and higher seed survival.

In general, larger seeds have also been correlated with reduced seed longevity and lower growth rates in forest gaps but greater early seedling survival in the forest understorey (e.g. Foster & Janson 1985; Osunkoya et al. 1994; Kitajima 1996; Bekker et al. 1998). Consistent with this, seed longevity of *Bischofia* was greater than that of *Elaeocarpus*. However, the inverse relationship between seed size and seedling survival under shade did not hold as seedling survival was lower in *Elaeocarpus* than *Bischofia* in an intact forest (Fig. 4, 6). These results suggest that seedling survival of *Elaeocarpus* may be more dependent on gap formation in the early stage of emergence than that of *Bischofia*. Shade grown seedlings of *Bischofia* have been found to exhibit a greater photosynthetic acclimation ability and higher growth rate in response to increased light compared with native seedlings of both pioneer and late successional species including *Elaeocarpus* (Yamashita et al. 2000). Thus, the small seeded *Bischofia* is capable of rapid growth when available light has increased, as well as greater survival in the shade.

Bischofia had considerably higher seed production and longer fruiting periods than the native *Elaeocarpus* (Table 1). This would lead to a large seedling population with longer periods of seedling emergence if factors affecting seed viability were similar. Differences in seed production and the length of flowering and fruiting periods between invasive and non-invasive species can be a determining factor of invasiveness (Rejmánek 1996; Reichard & Hamilton 1997). While most *Bischofia* seedlings developed from seed dispersed in the previous year (Table 1) in poor seed years, older seeds make a greater contribution to the emerging seedling population. This suggests the presence of a soil seed bank in *Bischofia* which modulated the yearly number of emerging seedlings against fluctuations in seed production. The large and widely dispersed seedling population (Table 2) could allow *Bischofia* to pre-empt safe sites under a closed canopy, and increase its probability of encountering a gap essential for further growth compared to native seedlings. The advantage associated with this early life history trait is more effective in the Bonin Islands where typhoon disturbances are frequent. In addition, emergence of *Bischofia* seedlings was not limited to the vicinity of its parent trees but was also

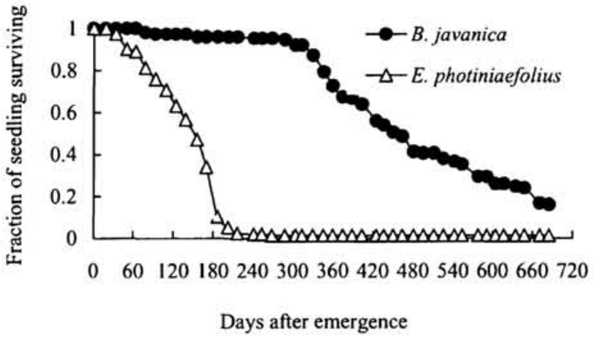

Fig. 6. Seedling survivorship curves of *Bischofia javanica* and *Elaeocarpus photiniaefolius*. Each curve shows the survivorship of a 150 seedling cohort germinated and tagged in early May 1998.

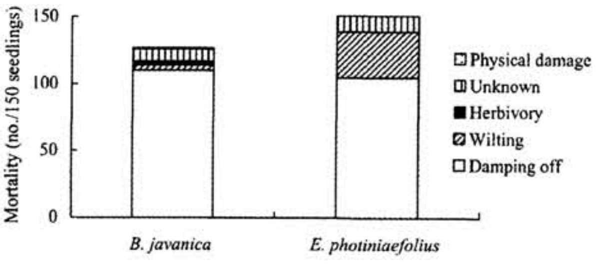

Fig. 7. Mortality factors of seedlings of the two species. Data were obtained from the same seedlings used in Fig. 6 monitored over a 22-mo period.

high under the canopy of *Elaeocarpus* and other native trees. The higher seedling emergence ratio of *Bischofia* under non-parental canopies (Table 2) is consistent with the many studies which reported high mortality near conspecific adults or at places of high density (Janzen 1970; Howe & Smallwood 1982; Shibata & Nakashizuka 1995; Packer & Clay 2000). In comparison, *Elaeocarpus* seedling emergence was considerably lower than that of *Bischofia* under all canopy types. This observation indicates that *Bischofia* can successfully establish and invade forest understorey previously occupied by native species, and with a greater probability of replacing the native canopy trees when they are disturbed.

Changes in plant communities by an invasive species can be accelerated when life history or physiological traits of the invader are optimally coupled with a frequently or intensely disturbed environment (Hobbs & Huenneke 1992; Horvitz et al. 1998). In our case, the large seedling population and high acclimation potential of *Bischofia* may enable it to respond aggressively to gap events created by the typhoons. Its high persistence in the shade and rapid acclimation to high light levels is an unusual combination since there is generally a trade-off between seedling survival in the shade and response to canopy opening in forest tree species (e.g. Bazzaz 1996; Kitajima 1996). A similar response was also found in *Sapium sebiferum* (Chinese tallow tree), another invasive species in the southeastern US which is both shade tolerant and capable of growing rapidly in full sunlight (Jones & McLeod 1990; Wall & Darwin 1999). The persistence of *Bischofia* is further enhanced by a higher rate of seed predation of its native competitor *Elaeocarpus* by an invasive rodent. It may be the unique combined effects of these two invasive species in Bonin Islands that accelerated the decline of native trees. This may well be a case where the synergistic interactions among invaders has exacerbated the impact on a native ecosystem (Simberloff & Holle 1999).

Understanding the life history traits conferring an advantage to invasive species could have wider implications. Those traits associated with the success of invasive species may be used to forecast ecosystem changes by comparing the phenotypic expression of these traits among species within a community. The overall superior performance of *Bischofia* over native *Elaeocarpus* in terms of early life history traits is consistent with the general trend found between invasive species and their congeneric native counterparts (Rejmánek 1996; Rejmánek & Richardson 1996; Reichard & Hamilton 1997). *Bischofia* possessed those same demographic traits related to invasiveness, such as small seed size, short interval between major seed crops and longer fruiting periods. We found, in addition to the general trends, greater seed longevity, less susceptibility than native seeds to novel rodent predation and hence the ability to form a seedling bank under a closed canopy that could further enhance invasiveness. Because forest trees may require several gaps to reach maturity (Canham 1985), shade tolerance in the seedling or sapling stage may be essential for survival. The replacement of native canopy dominants by *Bischofia* could be significantly enhanced if seeds and seedlings of *Bischofia* are more persistent in the forest understorey.

We suggest that a better understanding of invasiveness requires an approach where the coupling of early life history traits and the actively invaded environment is explicitly quantified, taking into consideration the functional roles of each species in the ecosystem. By taking this approach where growth and survival are dependent on the interactions among life history traits, resource availability and susceptibility to predation, potential impacts of invaders can be better predicted. In the case of the Bonin Islands, the success of the invasive tree species facilitated by an invasive rodent further emphasizes the importance of accounting for the broader interactions at play in the environment.

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Chapter 16

Effects of an alien shrub species, *Leucaena leucocephala*, on establishment of native mid-successional tree species after disturbance in the national park in the Chichijima island, a subtropical oceanic island

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ABSTRACT Effects of an invasion of an alien shrub species, *Leucaena leucocephala*, were investigated on subsequent establishment of a native mid-successional wooden species, *Schima mertensiana* at early-successional stages after disturbance in a subtropical oceanic island, Chichijima in Japan. Changes in basal areas, densities and size distribution of forests at a site dominated by *L. leucocephala* were compared with those at a site dominated by native shrub species, *Trema orientalis* at early-successional stages. Effects of *L. leucocephala* on germination of seeds and growth of seedlings of *S. mertensiana* were quantified at the sites. There were few recruited seedlings of *S. mertensiana* and they did not grow at the site dominated by *L. leucocephala*. On the other hand, there were a few recruited seedlings within a 1 m x 1 m area and they positively grew at the site dominated by *T. orientalis*. Germination rates of seeds and growth rates of seedlings of *S. mertensiana* at the site dominated by *L. leucocephala* were lower than those at the site dominated by *T. orientalis*. Germination of seeds and growth of seedlings of *S. mertensiana* were inhibited by *L. leucocephala* at the disturbed site, which potentially changed an early successional pathway of the plant community.

Key words: invasive plants, *Schima mertensiana*, Bonin Islands, seed germination, seedling growth, *Trema orientalis*

INTRODUCTION

Invasion of an alien plant species often prevents native plant species (Myers & Bazely, 2003) from establishment due to shading (Weihe & Neely, 1997), litter accumulation (Walker & Vitousek, 1991) and allelopathy (Gentle & Duggin, 1997), which would change successional pathways of native plants in an invaded habitat. The successional pathways of native species in some tropical and subtropical oceanic islands were affected by an alien shrub species, *Leucaena leucocephala* (L.) de Wit (Leguminosae). The species invaded and formed dense monotypic thickets in disturbed areas in many oceanic islands, which should have prevented seedlings of woody species and understory herbaceous species from germination and/or growth under canopies of *L. leucocephala* (e.g. Decker 1992, Mueller-Dombois and Fosberg 1998, Yamamura et al. 1999).

Germination or growth of some plant species in a subtropical region were inhibited by aqueous extracts of plant tissues of *L. leucocephala* under experimental conditions (Chou & Kuo, 1986). These allelopathic effects of *L. leucocephala* could prevent seedlings of endemic and other native plants from establishment in oceanic islands, which inevitably influences the native successional pathway. This process should be quantitatively described for conservation of endemic plants in oceanic islands.

Effects of invasion of *L. leucocephala* on native successional pathways were described by comparison of structure of the secondary forests between forests dominated by *L. leucocephala* and those by native species in the Bonin Islands. In addition, histories of vegetation types of the forests were also analyzed based on aerial photographs (Yoshida & Oka, 2000). There were differences in the structures and successional pathways of the forests (Yoshida & Oka, 2000). However, we still do not know quantitative effects of the invasion of *L. leucocephala* on establishment of native plants at mid- or late-successional stages. For this purpose, it is necessary to compare establishment and growth of native plants at sites at which *L. leucocephala* invaded or not.

It is hypothesized that native plants of mid- or late-successional species in subtropical oceanic islands would be prevented from establishment in a forest dominated

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by *L. leucocephala* at early successional stages because of allelopathic effects of *L. leucocephala* (Chou & Kuo, 1986). Based on the hypothesis, we tested the prediction that germination of seeds and growth of seedlings of native mid-successional species under plants of *L. leucocephala* are lower than those under plants of native species.

In order to test the prediction, firstly, we compared changes in biomass, densities and size distribution of dominant species in a forest dominated by *L. leucocephala* with those in a forest dominated by native species at early-successional stages for three years in the Bonin (Ogasawara) Islands, subtropical islands in the northern Pacific. Secondly, we compared germination rates of a mid-successional species of a native tree and growth rates of its seedlings in the forest dominated by *L. leucocephala* with those in the forest dominated by a native species appeared at early-successional stages by field experiments.

MATERIALS AND METHODS

Plant species

A shrub species, *L. leucocephala*, was introduced to the Bonin Islands in 1862 (Funakoshi, 1989) and spread into abandoned areas (Shimizu, 1989). A native shrub species, *Trema orientalis* Blume (Ulmaceae) appears at early stages in a secondary succession in the Bonin Islands (Shimizu, 1989). A wooden species, *Schima mertensiana* (Sieb. et Zucc.) Koidez (Theaceae), is endemic to the Bonin Islands, and dominates at middle stages in secondary succession (Shimizu, 1989).

Study site

This study was conducted at two sites in secondary forests at Yoakedaira (27°05′N, 142°12′E, 220 m above sea level) in the national park in the largest island of the Bonin Islands, Chichijima. The ground at the study sites (ca. 400 m^2) were bared by the removal of broadcasting towers in 1999. Surface soils and vegetation around the towers were cleared. One of the study sites was invaded and dominated by an alien species, *L. leucocephala*, and another site by a native species, *T. orientalis* after 1999. The study sites were surrounded by the secondary forest dominated by *S. mertensiana* (Appendix 1). Many mature trees of *S. mertensiana* could be homogeneously dispersed in the secondary forests. Indeed, dispersed seeds of *S. mertensiana* were often observed at the study sites (personal observation). Therefore, sufficient numbers of seeds of *S. mertensiana* could be dispersed at the both sites. Forest floors of the study sites were covered with herbaceous species, and the most dominant species was *Stachytarpheta jamaicensis* (L.) Vahl (Verbenaceae).

Measurements of forests dominated by *L. leucocephala* or *T. orientalis*

A 10 m × 10 m plot was established at each site in July 2001. The areas from which the broadcasting towers were removed were so limited that only one plot was established at the site. All the individuals of woody species in the plots were tagged, and their diameters at ground level were measured. Subsequent measurements were carried out in July 2002 and September 2003.

Field experiments

A field experiment was carried out in order to test whether established plants of *L. leucocephala* prevented plants of *S. mertensiana* from germination and growth. Five 1 m × 1 m plots were established under canopies of *L. leucocephala* outside of the 10 m × 10 m plot at the site dominated by *L. leucocephala* and other five 1 m × 1 m plots under canopies of *T. orientalis* outside of the 10 m × 10 m plot at the site dominated by *T. orientalis*. Each 1 m × 1 m plot was located at least 1 m away each other.

These five 1 m × 1 m plots were divided into three categories: three 1 m × 1 m plots of the five 1 m × 1 m plots were allocated to a seedling transplant experiment. In one of the rest two 1 m × 1 m plots, germinated seedlings were counted. Total canopy openness was measured in the rest 1 m × 1 m plots.

In May 2002, the seedling transplant experiment was conducted. Sixty seedlings of *S. mertensiana* with ca. 10 cm in height and ca. 0.2 cm in diameter at ground level were collected near the 10 m × 10 m plots but outside of the 1 m × 1 m plots. Ten of the seedlings were transplanted into each of the 1 m × 1 m plots after their diameters at ground level and heights were measured. Each of the seedlings was planted 20 cm away from the others. All transplanted seedlings were harvested and dried at 70 °C for 72 h for weighting at the end of the transplant experiment in May 2003.

The initial biomass of the transplanted seedlings was estimated based on the relationship between diameters at ground level, heights, and dry weights. The relationship was determined by the 24 seedlings of *S. mertensiana* collected near the 10 m × 10 m plots but outside of the 1 m × 1 m plots. The regression equation was;

the initial dry weight (g) = 0.23116 + 1.2608 (diameter at ground level (cm))^2 x height (cm), $r^2 = 0.667$, $p < 0.0001$.

One of the six 1 m × 1 m plots was abandoned because nine transplanted seedlings died by June 2002. A 1 m × 1 m plot, therefore, was newly established and ten seedlings of *S. mertensiana* were transplanted in the plot in June 2002.

Two hundred seeds that were collected in a secondary forest around the study sites were sown in November 2002 into a pot with 21 cm in diameter and 17 cm in depth. Three of the pots with seeds were set in the 1 m × 1 m plot at each of the study sites. Soil for the germination experiment was taken at the site at which the pots were set and seeds in the soil were eliminated before the experiment. Numbers of seedlings were counted in May 2003. The ungerminated seeds were collected and checked whether they were alive or dead in May 2003. The seed germination experiment was conducted in pots because there could be seeds of *S. mertensiana* in the soil at the sites.

Total canopy openness was determined based on hemispherical photographs in order to estimate light exposure in a 1 m × 1 m plot. Hemispherical photographs were taken at 0.1 m above ground in the 1 m × 1 m plot. The photographs were taken in five points in each plot at around noon on cloudy days in July 2004 (Fisheye Converter FC-E8 0.21x, Nikon, Tokyo, Japan and Nikon Coolpix 880, Nikon, Tokyo, Japan). HemiView 2.1 Canopy Analysis Software (Delta-T Devices, Burwell, Cambridge, UK) was used to calculate the values of total canopy openness of each point.

Data analysis

Effects of existences of *S. jamaicensis* on germination of seeds and growth of seedlings of *S. mertensiana* were not detected (data not shown). Therefore, the effects were not considered in the further analyses.

All statistical analyses were carried out using the software, R 2.0.1 (http://www.r-project.org/). Differences in size increments of the seedlings in the transplant experiment were analyzed by a nested one-way analysis of variance (ANOVA) (Zar, 1999). The independent variables were sites (*L. leucocephala*-dominated site and *T. orientalis*-dominated site) and blocks (three replicates of a 1 m × 1 m plot). The sites were fixed factors. The blocks were random factors and nested with the fixed factors. Differences in the results of the germination experiment were analyzed by t-test. The germination rates of seeds were arcsine transformed. T-test was also conducted to detect differences in values of the total canopy openness after arcsine-transformed.

RESULTS

Changes in basal areas and densities of forests dominated by *L. leucocephala* or *T. orientalis*

Basal areas of all woody species increased at the two sites during three years of this study (Table 1). The basal area

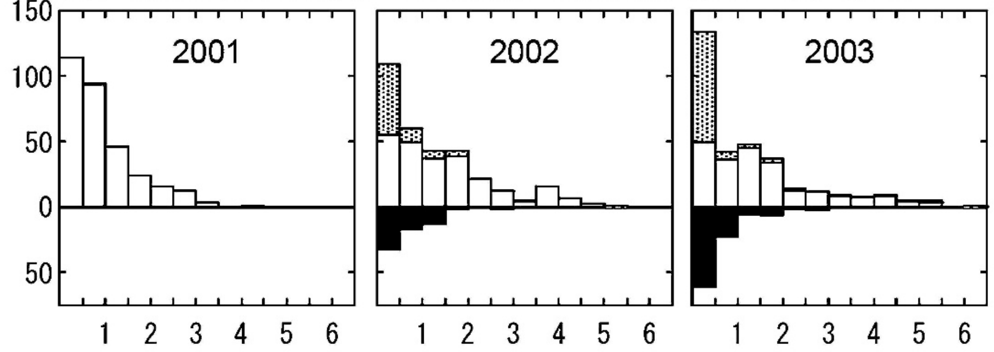
Table 1. (a) Basal areas (cm^2 100 m^{-2}) and (b) numbers (100 m^{-2}) of woody species in the 10 m x 10 m plots.

(a) Basal areas*	Site dominated by *Leucaena leucocephala*			Site dominated by *Trema orientalis*		
Species	2001	2002	2003	2001	2002	2003
Leucaena lecocephala	352.3	746.3	815.0	3.7	6.7	10.4
Trema orientalis	82.1	197.3	316.0	140.0	239.0	208.6
Schima mertensiana	< 0.1	0.1	0.4	21.1	85.0	268.7
Other species	5.5	27.9	98.5	6.7	43.9	316.2
Total	439.9	971.6	1229.9	171.5	374.6	803.9

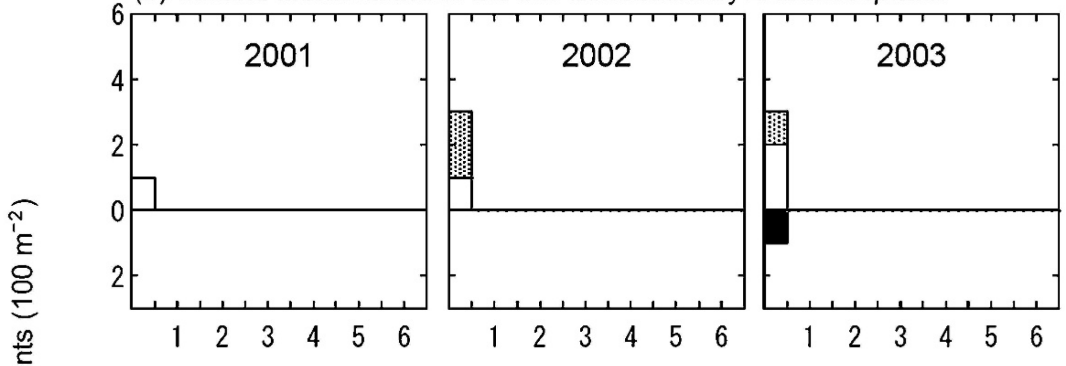
(b) Numbers	Site dominated by *Leucaena leucocephala*			Site dominated by *Trema orientalis*		
Species	2001	2002	2003	2001	2002	2003
Leucaena lecocephala	312	322	324	4	13	24
Trema orientalis	28	14	10	108	72	43
Schima mertensiana	1	3	3	381	767	822
Other speices	21	19	21	37	91	114
Total	362	358	358	530	943	1003

*Basal areas of woody species were calculated from diameters at above ground of woody species.

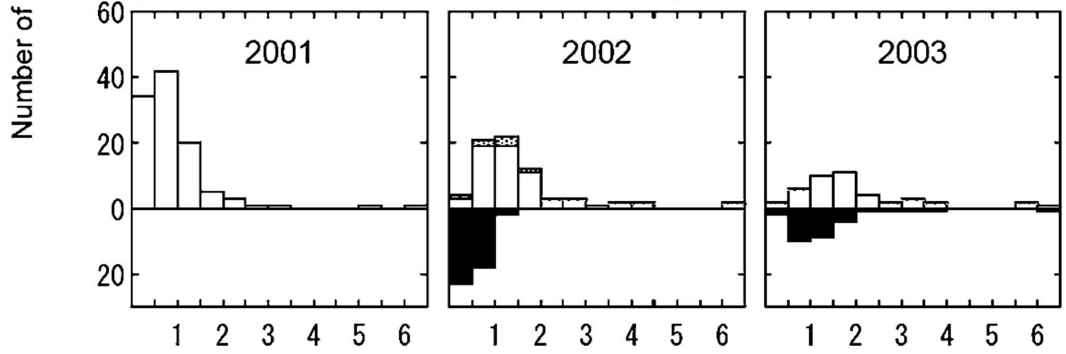
(a) *Leucaena leucocephala* at the site dominated by *L. leucocephala*



(b) *Schima mertansiana* at the site dominated by *L. leucocephala*



(c) *Trema orientalis* at the site dominaetd by *T. orientalis*



(d) *Schima mertensiana* at the site dominated by *T. orientalis*

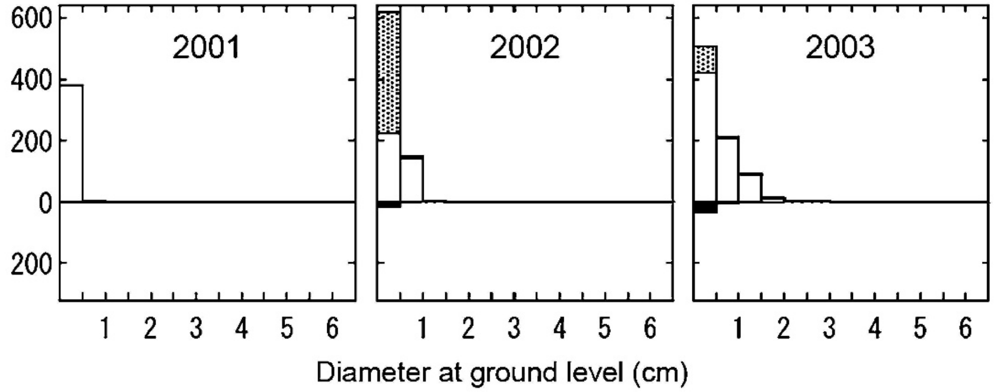


Fig. 1. **Frequency distributions of diameters at ground level in the 10 m × 10 m plots for (a) *Leucaena leucocephala*, (b) *Schima mertensiana*, (c) *Trema orientalis* and (d) *S. mertensiana* for three years. (a), (b): the site dominated by *L. leucocephala*; (c), (d): the site dominated by *T. orientalis*. Open bars indicated alive plants in the current year. Shaded bars indicated recruited plants in the current year. Closed bars indicated that plants died in the current year.**

of *L. leucocephala* at the site dominated by *L. leucocephala* in 2003 was about 2.8 times as large as that in 2001, while percentages of relative dominance of *L. leucocephala* decreased from 80.0% to 66.3% in three years. Densities of all woody species hardly changed for three years at the site dominated by *L. leucocephala* (Table 1). The percentages of number of plants of *L. leucocephala* against number of all woody species at the site were approximately 90% throughout three years. Few plants of *S. mertensiana* were observed at the site for three years.

Basal area of *T. orientalis* increased between 2001 and 2002 and slightly decreased from 2002 to 2003 at the site dominated by *T. orientalis* (Table 1). Percentages of basal areas of *T. orientalis* decreased from 81.6% to 26.0% in three years. Number of all woody species increased for three years at the site dominated by *T. orientalis* (Table 1), while number of plants of *T. orientalis* decreased for three years. The percentages of relative dominance of *T. orientalis* also decreased from 20.4% to 4.3% in the same period. In spite of the decrease of *T. orientalis*, substantial increases in basal areas and in number of trees of *S. mertensiana* were observed and percentages of basal area and relative dominance of *S. mertensiana* increased from 12.3% to 33.4% and from 71.9% to 82.0% at the site dominated by *T. orientalis* in three years.

Changes in size distributions of forests dominated by *L. leucocephala* or *T. orientalis*

Size distribution of *L. leucocephala* always exhibited L-shaped distribution at the site dominated by *L. leucocephala*. Shape of the size distribution changed for three years (Two-sample Kolmogorov-Smirnov test, $D = 0.16$, $p < 0.001$) due to frequent recruitment and high mortality of small-sized plants (Fig. 1a). Few plants of *S. mertensiana* recruited and grew at the site dominated by *L. leucocephala* for three years (Fig. 1b).

Size distribution of *T. orientalis* was weakly skewed in 2001, and it was bell-shaped one in 2003 at the site dominated by *T. orientalis* (Two-sample Kolmogorov-Smirnov test, $D = 0.56$, $p < 0.0001$) due to few recruited plants of *T. orientalis* for three years (Fig. 1c). Diameters at ground level of all plants of *S. mertensiana* were smaller than 0.5 cm in 2001 (Fig. 1d). In 2002, diameters at ground level of 147 plants of *S. mertensiana* were larger than 0.5 cm and there were 401 recruited plants. Diameters at ground level of 103 plants were larger than 1 cm and there were 94 recruited plants in 2003. As the results, shape of size distribution of *S. mertensiana* was weakly L-shaped one in 2003 (Two-sample Kolmogorov-Smirnov test, $D = 0.47$, $p < 0.0001$).

Field experiments

In total, 20 transplanted seedlings of *S. mertensiana* under canopies of *L. leucocephala* survived and 26 transplanted seedlings under canopies of *T. orientalis* survived at the end of the experiment. There was a significant difference in size increments of the transplanted seedlings of *S. mertensiana* between two sites (nested One-way ANOVA, $F_{(1, 2)} = 9.39$, $p < 0.001$). A mean of size increments of the seedlings at the site dominated by *L. leucocephala* was 0.08 g year^{-1} (± 0.07 s.e.) and that at the site dominated by *T. orientalis* 0.87 g year^{-1} (± 0.19 s.e.). There were no significant effects of blocks ($F_{(2, 42)} = 1.41$, $p = 0.25$).

There was a marginal difference in germination of seeds of *S. mertensiana* between sites (t-test, $p = 0.057$) and ungerminated seeds in the experimental period had died in May 2003. The rate of germination at the site dominated by *L. leucocephala* was 1.3% (± 0.9 s.e.) and that at the site dominated by *T. orientalis* 20.9% (± 5.2 s.e).

A mean of total canopy openness in the 1 m x 1 m plots under canopies of *L. leucocephala* was 0.24 (± 0.003 s.e.) and that under canopies of *T. orientalis* was 0.22 (± 0.015 s.e.). There was not significant difference in the total canopy openness between the sites (t-test, $p = 0.18$).

DISCUSSION

Lack of replacement by middle- or late-successional native woody species after invasion of *L. leucocephala* (Yoshida & Oka, 2000) could be due to the prevention of establishment of seedlings of native species. Actually, establishment of seedlings of *S. mertensiana* hardly occurred at the sites dominated by *L. leucocephala* and there were, therefore, a very few plants of *S. mertensiana* at the site.

Establishment and growth of the seedlings of *S. mertensiana* were observed at the site dominated by *T. orientalis*. Basal areas and densities of *S. mertensiana* increased at the site dominated by *T. orientalis*, which indicated that the *T. orientalis* could be replaced by *S. mertensiana*. Changes in size distribution of *T. orientalis* at the site dominated by *T. orientalis* also suggested the replacement. This result was consistent with the results of secondary succession in the Chichijima island (Shimizu, 2005).

There were differences in establishment and growth of *S. mertensiana* between the two sites although there could be sufficient seed rains of *S. mertensiana* at the sites. The lack of establishment and growth of *S. mertensiana* at the site dominated by *L. leucocephala* might change the successional pathways in the forests because *S. mertensiana* is one of the most dominant species in secondary forests at mid- or late-successional stages in the Chichijima island (Shimizu & Tabata, 1991).

The lack of establishment of *S. mertensiana* would be caused by inhibition of seed germination and seedling growth of *S. mertensiana* by existence of *L. leucocephala*. There were no differences in the total canopy openness of understory between two sites, which suggested that light conditions of the two sites were comparable. At the both sites, the amounts of available light in the 1 m x 1 m plots would be large enough for germination of seeds and growth of seedlings of *S. mertensiana*, because values of the total canopy openness in the 1 m x 1 m plots dominated by plants of *L. leucocephala* were equivalent to those under forest gaps (e.g. Silbernagel & Moeur, 2001).

Seed germination and seedling growth of *S. mertensiana* would be inhibited by the allelopathic effects of *L leucocephala*. Indeed, there are few understorey plants under *L. leucocephala*, which is caused by phytotoxic chemicals including fresh leaves, litter and seeds of *L. leucocephala* (Chou & Kuo, 1986). The allelopathic effects of *L. leucocephala* may play an important role to prevent plants of native species from a subsequent establishment.

Our results demonstrated that invasions of alien plants at early successional stages after disturbance by human activities could prevent from establishment of native plants of mid- or late-successional species. Forests in the Ogasawara National Park in the Chichijima island are often subject to disturbances, which would bring about an invasion of *L. leucocephala*. The invasion of *L. leucocephala* could be crucial problems for conservation of endemic species in the island. Unfortunately, there were no replications of our study because the forests including the study sites were situated within the protected area in the Ogasawara National Park. Therefore, we could not disturb the forests in order to create additional bare ground. The results, however, can provide useful information to restore native forests of the Bonin Islands after disturbances.

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Appendix 1. Plant species composition of secondary forests around the study sites in which the 10 m x 10 m plots were established.

	Secondary forest around the site dominated by *Leucaena leucocephala*					Secondary forest around the site dominated by *Trema orientalis*				
Species	No. of trees (0.12 ha^{-1})	Density (ha^{-1})	(%)	Basal area* (m^2 ha^{-1})	(%)	No. of trees (0.12 ha^{-1})	Density (ha^{-1})	(%)	Basal area* (m^2 ha^{-1})	(%)
Ardesia sieboldii	107.0	891.7	13.6	3.3	5.0	47.0	391.7	5.5	0.2	0.3
Bischofia javanica	8.0	66.7	1.0	0.2	0.3					
Callicarpa subpubescens	1.0	8.3	0.1	<0.1	<0.1					
Casuarina equisetifolia	1.0	8.3	0.1	1.6	2.4	1.0	8.3	0.1	0.5	0.8
Cinnamomum japonicum	19.0	158.3	2.4	0.1	0.2					
Cinnamomum pseudo-pedunculatum	3.0	25.0	0.4	<0.1	<0.1					
Cyathea mertensiana	4.0	33.3	0.5	1.6	2.4					
Drypetes integerrima						6.0	50.0	0.7	<0.1	<0.1
Elaeocarpus photiniifolius	8.0	66.7	1.0	1.8	2.7	32.0	266.7	3.7	4.4	6.7
Ficus nishimurae	3.0	25.0	0.4	<0.1	0.1					
Ficus spp.	1.0	8.3	0.1	<0.1	<0.1					
Freycinetia boninensis	4.0	33.3	0.5	<0.1	<0.1	7.0	58.3	0.8	<0.1	<0.1
Hernandia nympheaeifolia						1.0	8.3	0.1	<0.1	<0.1
Hibiscus glaber	20.0	166.7	2.5	0.8	1.3	44.0	366.7	5.1	2.8	4.2
Ilex mertensii	9.0	75.0	1.1	0.3	0.5					
Ligustrum micranthum	18.0	150.0	2.3	0.1	0.1	16.0	133.3	1.9	0.1	0.1
Livistona chinensis	15.0	125.0	1.9	6.3	9.7	23.0	191.7	2.7	6.6	9.9
Machilus kobu	58.0	483.3	7.4	2.4	3.7	86.0	716.7	10.0	2.3	3.4
Neolitsea aurata	58.0	483.3	7.4	0.8	1.2	116.0	966.7	13.5	2.2	3.2
Ochrosia nakaiana	4.0	33.3	0.5	0.1	0.2	9.0	75.0	1.0	0.1	0.2
Osmanthus insularis	31.0	258.3	3.9	0.3	0.4	21.0	175.0	2.4	0.2	0.3
Pandanus boninensis	7.0	58.3	0.9	0.7	1.1	19.0	158.3	2.2	1.5	2.2
Photinia wrightiana						10.0	83.3	1.2	0.1	0.1
Pinus luchuensis	3.0	25.0	0.4	1.7	2.6	4.0	33.3	0.5	5.2	7.8
Porteria obovata	28.0	233.3	3.6	2.2	3.4	35.0	291.7	4.1	2.5	3.8
Psidium cattleianum	4.0	33.3	0.5	<0.1	<0.1	12.0	100.0	1.4	<0.1	<0.1
Rhaphiolepis wrightiana	39.0	325.0	5.0	1.5	2.3	46.0	383.3	5.4	1.7	2.5
Schima mertensiana	**320.0**	**2666.7**	**40.7**	**38.7**	**59.1**	**321.0**	**2675.0**	**37.4**	**36.3**	**54.5**
Syzygium cleyeraefolium	4.0	33.3	0.5	<0.1	<0.1					
Trema orienrtalis	6.0	50.0	0.8	0.2	0.2					
Zanthoxylum ailanthoides	4.0	33.3	0.5	0.7	1.0	1.0	8.3	0.1	<0.1	<0.1
unknown						1.0	8.3	0.1	<0.1	<0.1
total	787.0	6558.3		65.5		858.0	7150.0		66.6	

*Basal areas were calculated from diameters at breast height.

Part III
Countermeasure Against Invasive Species

Chapter 17
Management of Invasive Alien Species in the Bonin Islands

Shun'ichi Makino

Abstract The remote Bonin Islands, a unique theater of evolutionary plays, are in danger of ecosystem degradation, and many endemic species are threatened with extinction because of various invasive aliens. To stop and reverse, if possible, the process of degradation, scientists have been attempting to control the impacts and spread of aliens. Our aim is to mitigate ecosystem degradation in such a way that native species can thrive without constant care or human management. In most cases, eradication of aliens is an effective way to achieve this goal. Whatever the strategy, however, it should be adaptable so that tactics can be switched or modified in case of unpredicted side effects of these interventions. This is particularly important in the Bonin Islands, where alien species are frequently deeply embedded in the native ecosystem. In this part, nine chapters explore strategies and tactics for controlling four major invaders in the Bonin Islands: the flatworm *Platydemus manokwari*, the green anole *Anolis carolinensis*, the black rat *Rattus rattus*, and the bishopwood *Bischofia javanica*.

17.1 Management of Invasive Alien Species in the Bonin Islands

As described in the previous part, invasive alien species have had a grave impact on the ecosystem of the Bonin Islands, as in many other oceanic islands around the world. Indeed, some native species are in peril of extinction. Not only are individual species at risk, but their ecological interactions (e.g., pollination systems) are also affected (e.g. Kawakami 2008). Unless effective countermeasures are taken as soon as possible, the Bonin Islands, known as the "Oriental Galapagos Islands" for their unique evolutionary history producing innumerable endemic species, will likely experience further ecosystem deterioration. What strategy should we adopt to manage an ecosystem that is so severely damaged by alien species?

The ideal solution would be to reproduce the complete "original" ecosystem that had existed before the alien species were introduced. Unfortunately, this would be impossible in most cases. Many of the aliens have not only degraded the original interactions among native species and placed them at risk, but they have also become deeply embedded in the ecosystem, creating complex networks with native or other invasive species. In addition, the records on original fauna or flora, which are essential for their artificial reconstruction, are usually incomplete due to fragmentary scientific surveys. Therefore, even if we were to remove as many alien species as possible and reintroduce locally extinct species, we could not expect a complete reproduction of the original ecosystem state.

Our goal is not a complete reproduction of the original ecosystem, but a mitigation to create a sustainable ecosystem where existent native species can thrive without constant care and intervention through intensive human management. Although we should pay attention to the assumed original state as a "reference," we direct our efforts toward setting a stage where native species can survive into the future. More specifically, we assign priority to the eradication of invasive alien species. If total eradication is technically or economically impossible at present, aliens should be extinguished from selected areas (local extinction) that have a high priority, or, at the very least, should be prevented from further expansion. We thus promote recolonization and reproduction of the native species in those alien-eradicated areas.

In most cases, it is accepted that eradication is the most effective countermeasure against invasive alien species, because otherwise we would have to continue to control those aliens with much larger amount of chemicals in total than eradication (Clout and Veitch 2002). However, short-term eradication of an invader is often practically impossible because of limited financial or other resources. In that case, we should apply "local eradication" to selected areas, and increase the area of eradication step by step to finally achieve total eradication. To carry out this procedure, we need information of various fields to decide where and how to set the priorities for local eradication.

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The control of invasive alien species should always be "adaptive." It is often difficult or simply impossible to predict the cascade effect of artificial removal of alien species, since in most cases those species are deeply involved in the local ecosystem and interact with native species, as mentioned above. Therefore, in the course of control, we must always be prepared to modify or switch our tactics by watching the effects of control and monitoring what occurs in other species following alien eradication. This is particularly important for those invaders whose disappearance is expected to cause large-scale changes to habitats.

17.2 Strategy and Tactics Toward Eradication of Selected Alien Species

In the Bonin Islands, trial eradication of important introduced species has been made in uninhabited small islands, and proved successful in some cases. For example, wild goats were eradicated from Nakodojima, Yomejima and Mukojima, and eradication operations are now under way in the largest uninhabited island, Anijima (Kawakami 2008). In addition, almost all individuals of the invasive tree *Bischofia javanica* were killed on Ototojima by means of herbicide injection, as described below (Chap. 24).

In this part, we explore strategies and tactics to eradicate or control the following four invasive alien species: flatworm (*Platydemus manokwari*), green anole (*Anolis carolinensis*), black rat (*Rattus rattus*), and *Bischofia javanica* tree. Although these organisms are taxonomically and ecologically very different, all were introduced by humans intentionally or unintentionally, and have had a very large impact on the native organisms and ecosystem of the Bonin Islands.

17.2.1 Flatworm

The flatworm *P. manokwari* is included in the IUCN's "100 of the World's Worst Invasive Alien Species." This organism was possibly introduced accidentally and became established in Chichijima in the early 1990s. It is preferentially predacious on land snails, thus presenting a great threat to the fauna of the Bonin Islands where many endemic land snail species have evolved. Chiba (Chap. 18) shows us how the evolution of land snails (*Mandarina*) in the Bonin Islands has produced a great variety of endemic species, which diversified into arboreal, semi-arboreal and ground-dwelling types. In this respect, the genus *Mandarina* is a typical and excellent example of evolution in geographically isolated habitats of oceanic islands. He also shows that, contrary to morphological and ecological differences, genetic diversification between species is quite small within the genus. These endemic land snails have been severely affected by various agents, particularly the flatworm (Chap. 3).

Eradication of *P. manokwari* is impossible at present because of its ubiquity and abundance in Chichijima. Prevention of its unintentional introduction to other islands is one of several countermeasures that we can take right now. The Ministry of the Environment and Ogasawara local authority require people to dip their shoe soles in seawater to kill attached flatworms before embarking on a ship from Chichijima to other islands. Another possible invasion route of the flatworm is transportation with various goods, such as potted plants. Sugiura (Chap. 19) experimentally discovered that immersion in hot water (≥43°C) effectively kills flatworms present in the soil. Hot water treatment of plant pots or other materials thus seems a promising way to prevent unintentional introduction of flatworms from Chichijma to other islands. Besides control of flatworms, Chiba proposes captive breeding and extensive research on the genetic structure of *Mandarina* for their future reintroduction.

17.2.2 Green Anole

Many diurnal insect species on Chichijima and Hahajima have greatly declined in population over the past 20–30 years. Until recently, this phenomenon was attributed to destruction of forests by a huge typhoon, use of insecticides, or other anthropogenic causes. However, it is now believed that the green anole is responsible for the decline (Chap. 20). Karube (2005) was the first to strongly point out the hypothesis that predation by green anoles is responsible for decline or disappearance of many diurnal insect species. All conditional evidence suggests that the green anole *A. carolinensis* was either accidentally introduced along with goods, or intentionally as a pet, in Chichijima in the mid-1960s, and became established before the mid-1970s. It was also introduced in Hahajima, about 50 km from Chichijima, in the early 1980s. These periods agree well with the decline in number of many insect species.

Yoshimura and Okochi (Chap. 21) found that assemblages of aquatic invertebrates in ponds were markedly different between Chichijima, which is inhabited by the green anole, and Anijima or Ototojima, which are free of this lizard. In particular, odonate larvae were completely absent from Chichijima. Considering that green anoles feed on odonate adults, it is probable that the lizard is responsible for the decline in odonates as well as for many other diurnal insects.

Yoshimura and Okochi emphasize the urgent need to control *A. carolinensis* in order to conserve odonates of the Bonins, which include many endemic species. The control of green anole populations, however, is very difficult. Toda et al.

(Chap. 22) show that the population density of the green anole is over 1,000 individuals/ha, which seems much higher than the density observed in any other part of the world. Again, total eradication is impossible for the time being, because of the high population density and ubiquity of this species.

Toda et al. (Chap. 22) have practiced two different countermeasures against green anoles. One is an adhesive trap, which is attached to tree trunks or on structures in environments with high lizard density. For application of the trap, priority is given to areas in or around the port to prevent accidental transportation from Chichijima to other, anole-free islands by ship. Another countermeasure is a stainless-steel mesh fence that lizards are unable to climb. By enclosing a relatively small area with the fence, we can kill all green anoles in it by hand or traps; the fence system effectively protects the area from reinvasion by the anole. In Hahajima, a greater number of endemic insect species survive than in Chichijima, presumably because the green anole invaded there later than in Chichijima. An experimental fence system with a perimeter of 900 m has been constructed in an area of Hahajima where endangered endemic insects are confirmed.

17.2.3 Black Rat

The black rat is a cosmopolitan species, and, like the flatworm, is designated as 1 of the 100 of the World's Worst Invasive Alien Species as is the mouse *Mus musculus*. It feeds on animals as well as plants (Yabe 1979), causing a cascade of impact on native fauna and flora or ecosystems in many parts of the world, especially oceanic islands (Fukami et al. 2008). It inhabits nearly all the Bonin Islands, probably as a result of unintentional transportation by humans. Omnivorous black rats cause damage to various native species including plants, land snails, and seabirds, as well as agricultural products. Hashimoto (Chap. 23) reviews the serious impact made by black rats on native species ranging from plant seeds to land snails to adult seabirds.

Many eradication trials have been made against invasive mice or rats in the world, principally utilizing rodenticides, and have proved successful. This suggests the feasibility of eradication of black rats in the Bonins with rodenticides. However, in Japan, virtually no successful eradication has been reported, and the methodology is not established. In addition, when applying rodenticides, we must be careful about their possible effects on non-target species.

Hashimoto (Chap. 23) describes the tactics adopted to eradicate black rats in Nishijima, a small island (49 ha) near Chichijima. Although aerial application of rodenticides is commonly practiced in various parts of the world, Hashimoto used a bait box for application of the rodenticide (diphacinone). The bait box was T-shaped with a horizontal bait platform and a vertical stand, thus pellets of rodenticide were inaccessible to non-target animals. Although diphacinone has very low toxicity to non-rodent mammals or other animals including birds, exposure to non-target animals should be minimized for the first trial of black rat eradication in Japan.

The common buzzard (*Buteo buteo toyoshimai*), a national natural monument of Japan, preferentially preys on rats as a substitute for its original prey (small birds) that have declined in the Bonins. Some people have expressed concern about buzzards accidentally feeding on poisoned rats, which could cause death or weakening of the bird, even though toxicity of the rodenticide is very weak for birds. In order to build a consensus about the application of rodenticide in Nishijima, several briefings were held for inhabitants and/or local government officials of the Bonins.

Application of diphacinone, with about 800 bait stations across the island, was carried out for 2 months in the spring of 2007. No rats or their tracks have been found since then, showing that this is the first successful eradication of black rats in Japan. The initial stage for adaptive management after eradication of an alien species has thus been set on Nishijima. The tactics and methodology developed for Nishijima will contribute to black rat eradication in the other islands.

17.2.4 Bischofia javanica

The *Bischofia javanica* tree is one of the most invasive plants found in the Bonin Islands. It was intentionally introduced from Okinawa as a source of fuel wood about 100 years ago. Although its initial plantations were limited to specific sites, the trees into the natural forests, extensively replacing native tree species (Tanaka 2004; Chap. 15). *Bischofia javanica* has been expanding its range, especially in Hahajima, occupying about 15% of the total island area in 2003. Many native tree species are seriously suppressed in forests dominated by this invasive tree.

Although *B. javanica* has a surprising ability to sprout, and is thus hard to kill by girdling or cutting, Ito (2005) developed a method based on injecting the tree with herbicide. Herbicide injection, together with the removal of seedlings originating from seed banks, makes the eradication of *B. javanica* realistic. In fact, all standing trees were successfully killed within the past few years in Ototojima and Hirashima that had small populations of *B. javanica*. In order to eradicate the tree from Chichijima and Hahajima, where there are a tremendous number of large and old trees, however, we need a long-term strategy.

Tanaka et al. (Chap. 24) show us a road map for accomplishing total eradication of *B. javanica* from these islands within two decades. Their strategy first sets priorities for control of those areas that have a high risk of expansion of the species, cost-effectiveness in terms of control, or a high value from the viewpoint of biodiversity conservation. With the use of herbicide injection, all *B. javanica* trees are killed either simultaneously or gradually, depending on their population density. Forests receive much more sunlight with the removal of *B. javanica*, promoting the growth of seedlings of native species as well as of *B. javanica.* Seedlings of the latter are removed during the following several years. They expect that repeated undertaking of this procedure would accomplish total eradication of *B. javanica* from Chichijima and Hahajima.

In order to select high-priority areas, we need a risk map showing the probabilities of distribution or expansion of *B. javanica* for the entire island. Fukasawa et al. (Chap. 25) developed a mathematical model that incorporates both environmental conditions for species growth and distance from seed source, and give us a map showing area-specific risk of its future invasion in Hahajima. Their model more accurately predicts the invasion process as compared with previous models, and provides us with information indispensable for deciding the priority areas for control of *B. javanica*.

In eradicating alien plant species, we must also be careful about possible effects on the organisms associated with the species to be eradicated (e.g. Zavaleta et al. 2001). Sugiura et al. (Chap. 26) compares beetle assemblages between stands where *B. javanica* trees were left intact and where all *B. javanica* were killed by girdling. These beetles depend on various tree species including *B. javanica*. The results show that the abundance and diversity of beetles did not decrease in the treated stand but instead increased. This is probably because the light intensity of the treated stand increased, attracting various beetles, and because felled trees provided those xylophagous beetles with suitable food. These results suggest that the gradual removal of *B. javanica* trees is not expected to cause negative effects. We need similar information for other taxa before full-scale eradication is implemented.

Papers of this part collectively illustrate the present control status of invasive alien species in the Bonin Islands. Although for some species, eradication is not in sight in the near future, the methodology of eradication has been developed for others. Eradication is not a "stepchild (Simberloff 2002)," but is recognized as a legitimate child for most cases in alien species management. Of course, education and observation are always necessary to properly raise and discipline children to make good adults. Similarly, we definitely need adaptive management and monitoring to ensure that the eradication of invasive species and subsequent recovery of ecosystems is successful.

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Chapter 18

Species Diversity and Conservation of *Mandarina*, an Endemic Land Snail of the Ogasawara Islands

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Abstract

The endemic land snails, genus *Mandarina* of the Ogasawara Islands, have diversified into arboreal, semi-arboreal and ground ecotypes. Shell morphologies of *Mandarina* species have a clear relationship with their respective ecotypes. In addition, marked geographical variations in morphology and genes are found within species. Phylogenetic relationships based on mitochondrial DNA (mtDNA) sequences suggests that *Mandarina* evolved from *Euhadra*, a genus distributed on the mainland of Japan. The inferred phylogeny suggests that similar morphologies and ecotypes appeared independently and rapidly in different lineages and islands at different times. This rapid evolution produced some incongruities among phylogenetic relationships, morphology, species taxonomy, and the level of reproductive isolation. Interspecific hybridization occurs between sympatric species due to environmental change, resulting in an admixture of genetic and morphological characteristics. These findings reveal the importance of *Mandarina* as a model system for evolutionary study. However, a predatory land snail and flatworm have recently been introduced into the Ogasawaras. These predators may rapidly cause the extinction of *Mandarina,* and thus, a conservation program is needed for *Mandarina*. In the conservation program for *Mandarina*, species taxonomy should not be used as a criterion for selection of populations for captive breeding because of incongruence among the phylogeny, morphology, ecology, species taxonomy and reproductive isolation. In addition, the danger of interspecific hybridization should be considered when captive-bred snails are reintroduced into restored or secure habitat.

Key words: adaptive radiation, conservation, hybridization, *Mandarina*, Ogasawara Islands

1. Introduction

Organisms in small isolated locations have great potential in evolutionary studies. Adaptive radiation in endemic organisms inhabiting isolated islands and lakes have been used as general evidence for major evolution. Examples of such adaptive radiations include Darwin's finches in the Galapagos Islands, Hawaiian honey creepers, and African cichlids (*e.g.*, Lack, 1947; Grant, 1986; Freed *et al*., 1987; Schliewen *et al*., 1994). Detailed studies of the processes and causes of adaptive radiation of island organisms have provided excellent data for understanding the process of character divergence.

The endemic *Mandarina* land snails of the Ogasawara Islands offer an exceptional example of character divergence. *Mandarina* has diversified into taxa occupying many habitats, (*e.g.* arboreal, semi-arboreal, terrestrial, dry, and wet habitats) and shows remarkable diversity in shell and genital morphology (Emura, 1943; Habe, 1969; Minato, 1978; Chiba, 1996). Shell diameters range from 15 mm to 80 mm, and 17 species including five extinct species have been described.

The Ogasawara Islands are located in the northwest Pacific, about 1,000 km south of Japan, and they consist of about 30 small volcanic islands. The biggest island among them is only 25 km^2 in area. The Ogasawara Islands have been entirely isolated from other regions, and the biota of these islands (plants, birds, insects and land snails) are characterized by several peculiarities as are the biota in other oceanic islands.

In the last 10 years there have been several studies on the population genetic structure, community structures, the evolutionary history and the process of speciation of *Mandarina*. These studies suggest that large ecological and morphological differences among the species of *Mandarina* have evolved despite a small genetic differentiation among these species. However, these ecological and morphological differences easily disappear when hybridization occurs

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between different species. Reproductive isolation among the species is easily broken in *Mandarina*, resulting in complex geographical variations in morphology and genetics. In this article, I show how morphologically and ecologically divergent species have evolved during a relatively short time, and how morphologically distinct species have hybridized. In addition, I describe how rapid diversification and hybridization is causing a problem with regard to the conservation of island organisms such as *Mandarina*.

2. Divergences in Habitat Preference and Morphology

The Ogasawara Islands are composed of three groups of islands, the Mukojima, Chichijima, and Hahajima groups. Four extant species and five extinct species have been recorded in the Chichijima Group, one extant species has been recorded in the Mukojima Group and six extant species have been recorded in the Hahajima Group. These species are all endemic to each group of islands (Fig. 1). Each species is composed of many local populations with distinctive shell or genital morphologies. In addition, some parapatric species are producing hybrid zones (Chiba, 1997), and thus, geographical variations of *Mandarina* species are markedly complex.

Habitat preference of *Mandarina* was examined for each species in previous studies and the species were divided into arboreal, semi-arboreal and ground ecotypes (Fig. 2) (Minato, 1978; Chiba, 1996). The arboreal ecotypes were found only in trees. These included *M. suenoae* from the Chichijima Islands and *M. hahajimana* from the middle to northern parts of Hahajima. Most of the arboreal species were found at a height of more than 1 m from the ground. Semi-arboreal ecotypes are found both in trees and on the ground, and rest between the trunk and leaf or in the space between thick leaves of pandanus trees or palm trees when they are inactive. These include *M. hirasei* from the Chichijima Islands and *M. exoptata* from Hahajima and *M. hahajimana* from the southern parts of Hahajima, Anejima and Mukoujima. The ground ecotypes are found on the ground and are never found in trees. These include three species from the Chichijima Islands (*M. chichijimana*, *M. mandarina* and *M. anijimana*), four species from the Hahajima Islands (*M. ponderosa*, *M. conus*, *M. aureola* and *M. polita*), *M. hahajimana* from Imotojima and Meijima, and *M. trifasciata* from the Mukojima Islands. There are also differences in preference of microhabitat among the ground ecotypes. The species that have the exposed-ground ecotype prefer to rest or forage in more exposed, thinner, dryer litter than the species that have the hidden-ground ecotype (Chiba, 1999b). For example, *M. anijimana*, which coexists with *M. mandarina* in the central part of Anijima, was found in bushes or in forest litter that was dominated by leaves of pandanus trees and broad-leaved trees, but not in litter dominated by leaves of palm trees. *M. mandarina* was found in all kinds of habitat, but it was relatively rare in bushes or in forest litter that was dominated by leaves of broad-leaved trees when it coexisted with *M. anijimana*.

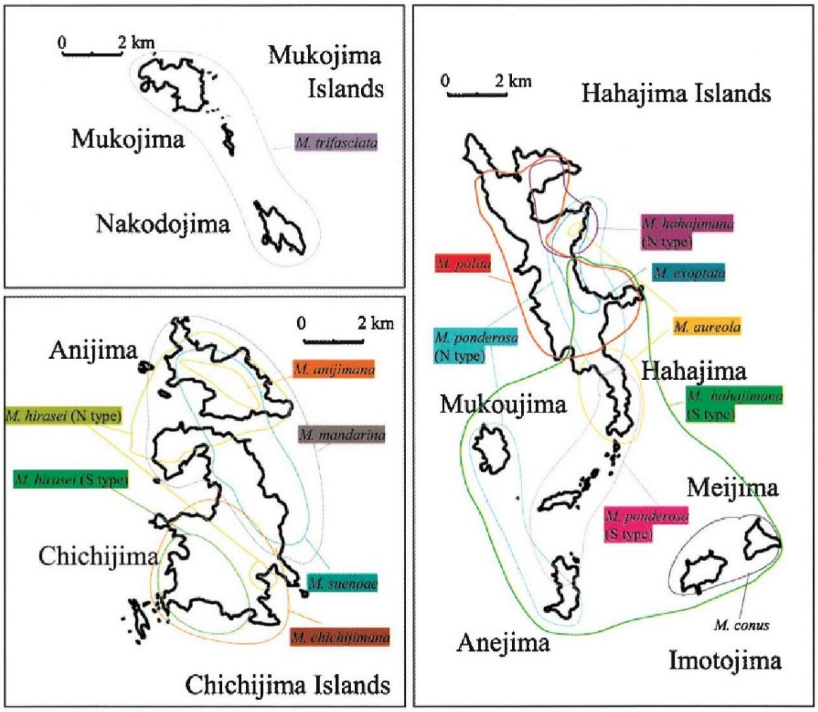

Fig. 1 The Ogasawara Islands, with distributions of species of *Mandarina* indicated.

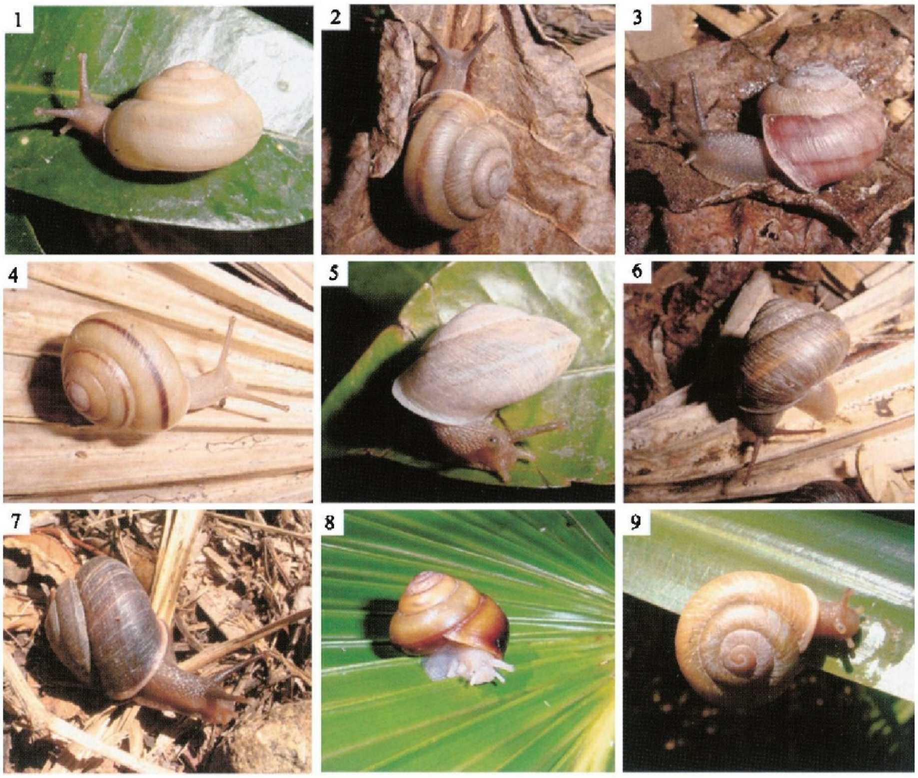

Fig. 2 Diversity of morphology and habitat use in *Mandarina*. 1: *M. hahajimana* N type (Mt. Sakaigatake, Hahajima), 2: *M. aureola* (Minamizaki, Hahajima), 3: *M. polita* (Chibusa-yama, Hahajima), 4: *M. hahajimana* S type (Minamizaki, Hahajima), 5. *M. exoptata* (Chibusa-yama, Hahajima), 6: *M. mandarina* (Yoake-yama, Chichijima), 7: *M. ponderosa* N type (Chibusa-yama, Hahajima), 8: *M. suenoae*, (Anijima), 9: *M. hirasei* S type (Takayama, Chichijima).

There is a clear association between ecotypes and shell morphologies (Fig. 3). The shells of ground-dwelling snails are consistently thicker and heavier, and have a smaller aperture than those of arboreal or semi-arboreal populations. Populations with a similar habitat have similar shell morphology. The remarkable divergence in shell morphology in *Mandarina* is associated with the differences in its habitats (Chiba, 1996). The thinner, larger aperture shells of the arboreal and semi-arboreal populations are possibly adapted for living in trees because they allow the snails to adhere better to trunks and leaves. The species with the exposed-ground ecotype possess flatter and brighter shells than the species with the hidden-ground ecotype. Shells of species with the arboreal and semi-arboreal ecotypes are also brighter than shells of species with the ground ecotype. This relationship between shell color and particular habitats is consistently found in all of the pairs of ground species in *Mandarina*. Bright shells would be expected to have an advantage in sites where snails are largely exposed, because they do not heat up as much as dark shells in the sunlight. Snails with bright shells would be able to avoid overheating in the sun.

3. Parallel Adaptive Radiation of *Mandarina* in the Ogasawara Islands

A comparison between (i) the ecotype and (ii) the phylogenetic relationship of *Mandarina* species estimated by mitochondrial 16SrRNA and 12SrRNA gene sequences suggests that radiation and divergence of arboreal, semi-arboreal, ground ecotypes have occurred repeatedly at different times and in different areas and lineages (Chiba, 1999a). The consistent topology between the 16SrRNA and 12SrRNA trees suggests that radiation and divergence of arboreal and terrestrial species first occurred in the Chichijima Islands. The species migrated to the Hahajima and Mukojima Islands from the Chichijima Islands and diversified on Hahajima, leading to a second radiation. Divergence of different lineages of arboreal, semi-arboreal and terrestrial species occurred repeatedly in the Hahajima Islands.

Although details of the mitochondrial DNA (mtDNA) tree and the population tree may differ because of hybridization between different species, the mtDNA tree suggests that there has been repeated divergence of arboreal and ground ecotypes, because no examples have been found of hybridization between species with the ground ecotypes and those with the arboreal ecotypes. Species with similar shell morphologies appear repeatedly in different lineages (Fig. 3) because shell morphologies are closely related to life habits (Chiba, 1996). Extreme ecological and morphological differences have been found between the arboreal *M. hahajimana* (N type) and the ground-dwelling *M. aureola* (Chiba, 1996). Phylogenetically, however, these populations are very close. Large differences in shell forms and life habits have also been found between (i) phylogenetically close lineages such as *M. exoptata* and *M. ponderosa* and (ii) populations of *M. hahajimana* (S type) from Imotojima and Mukoujima (Fig. 3). Remarkable differences in genitalia occur between genetically and phylogenetically close species. For example, the size of the penis of *M. chichijimana* is no more than 1/5 that of *M. mandarina*, but the genetic distance between these species is only 1.4%. This suggests that shell morphology, genital morphology and the ecotypes of *Mandarina* have all evolved rapidly.

There are some incongruities between phylogenetic patterns of mtDNA and species taxonomy (Fig. 3). The species taxonomy of *Mandarina* is based mainly on differences in genital morphology (Emura, 1943; Minato, 1978). Therefore, some incongruities between species taxonomy and the phylogenetic relationship observed in *Mandarina* can be attributed

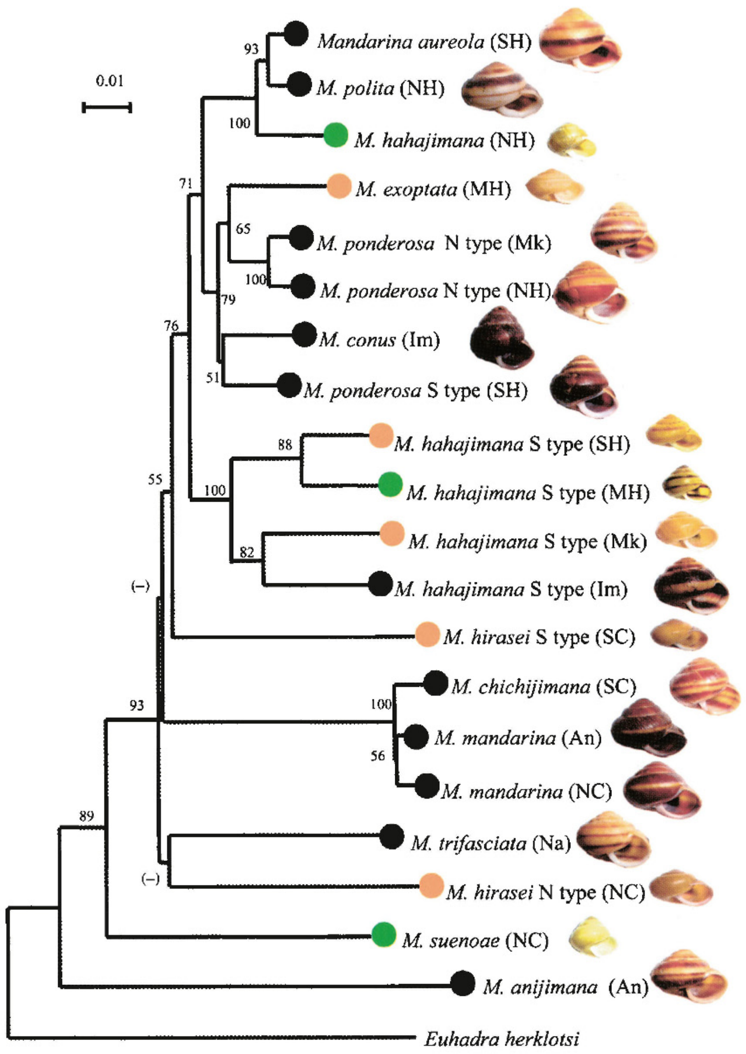

Fig. 3 A neighbor-joining tree for 18 populations of *Mandarina* on combined sequences of 16SrRNA and 12SrRNA genes. Numbers above selected nodes are percentage of times in 500 bootstrap replications that populations occurred in these clades. Bootstrap values lower than 50% were exhibited by (-). Populations with the arboreal ecotype, semi-arboreal ecotype and ground-dwelling ecotype are indicated by green, yellow and black circles respectively. Distribution of each population are also shown in parentheses (NH: north Hahajima, MH: middle Hahajima, SH: south Hahajima, Mk: Mukoujima, Im: Imotojima, Na: Nakodojima (Mukojima Islands), SC: south Chichijima, NC: north Chichijima, An: Anijima. (Modified from Chiba, 1999a). (Note: in black-and-white version, green will be visualized as dark gray and yellow as pale gray.)

to the rapid morphological evolution of this species and to convergent evolution. *M. hahajimana* (N type) from the northern part of Hahajima is phylogenetically closer to *M. aureola* and *M. polita* than other populations of *M. hahajimana*. A similar case is found in the northern and southern populations of *M. hirasei*. The southern populations of *M. hirasei* are phylogenetically closer to the Hahajima species than to other species of Chichijima, and thus, the northern and southern populations of *M. hirasei* should be separated as different species. In addition, the mtDNA tree shows that *M. ponderosa* (N type) from the northern part of Hahajima is phylogenetically closer to *M. exoptata* than to *M. ponderosa* (S type) from the southern part of Hahajima, and these populations of *M. ponderosa* also may be separated as different species. However, these populations of *M. ponderosa* are producing a hybrid zone in the middle range of Hahajima without assortative mating (Chiba, 1993). The incongruence among the morphology, phylogeny, and condition of reproductive isolation makes it difficult to determine the taxonomic positions of these populations.

Mandarina has been generally included in the Camaenidae and is believed to have evolved from Camaenid ancestors distributed in southeast China (Minato, 1978). However, a recent study has suggested that *Mandarina* is not phylogenetically close to Camaenid genera but is closer to Bradybaenid genera (Chiba, 1999a). Phylogenies based on mtDNA showed that *Mandarina* is closest to *Euhadra*, a genus from the mainland of Japan (Chiba, 1999a). The shell and genital morphologies and mating behavior of *Euhadra* distinctly differ from those of *Mandarina*. For example, *Euhadra* possess a dart sac, a mucus gland and complex courtship, all of which are absent in *Mandarina*. *Mandarina* lays a small number of large eggs (one to three eggs larger than 1/5 of adult shell size, see Fig. 4), while *Euhadra* lays a larger number of smaller eggs (more than 20 eggs smaller than 1/10 of adult shell size). *Mandarina* has an extremely solid shell. This suggests that *Mandarina* has changed its reproductive organs, mating behavior, egg size, and morphology to such an extent that it has been placed in a different family. This is also supported by the occurrence of an extinct species, *M. luhuana*, which has a shell morphology similar to that of *Euhadra* from Pleistocene deposits on Chichijima.

Fig. 4 An adult snail of *M. ponderosa* and its huge eggs.

Although the 16SrRNA sequences of the *Mandarina* species diverge considerably among the species of *Mandarina*, this does not imply that the diversifycation of *Mandarina* has a long history, because the divergence rate of the mitochondrial 16SrRNA gene of land snails is extremely fast, approximately 10% per Ma (Hayashi & Chiba, 2000; Thacker & Hadfield, 2000).

Sequence divergences among sympatric species of *Mandarina* from Hahajima (2% - 6%) were mostly smaller than those among local populations within species of *Euhadra* (1% - 14%) (Hayashi & Chiba, 2000; Watanabe & Chiba, 2001). The mean genetic distance of 16SrRNA between *Mandarina* and *Euhadra* (0.188) (Chiba, 1999a) is much smaller than the maximum level of intraspecific genetic distance in *Cepaea nemoralis* (0.25) (Thomaz *et al.*, 1994) and *Ainohelix editha* (0.23) (Teshima *et al.*, 2003). These results imply that the morphological and ecological evolution of *Mandarina* has been accelerated in the Bonin Islands.

Studies of organisms from remote islands such as the Galapagos and Hawaii (Carson & Kaneshiro, 1976; Schluter, 1988, 2000) suggest that morphological and ecological divergence is accelerated in depauperate environments where competitors and predators are fewer. A rapid morphological and ecological evolution of *Mandarina* in the Ogasawara Islands, where competitors and predators are fewer than on the mainland, is consistent with this view. A rapid ecological divergence has also been reported in Hawaiian land snails (Thacker & Hadfield, 2000). These findings suggest that a scarcity of sympatric species soon after the establishment of an island species of land snail will accelerate its ecological divergence.

4. Interspecific Hybridization

Recent studies have shown that the loss or partial loss of reproductive isolation between sympatric species of animals is not as rare an event as was previously thought (Grant & Grant, 1992; Dowling & DeMarais, 1993; Chiba, 1993; Falniowski *et al.*, 1993; Byrne & Anderson, 1994; see a review by Arnold, 1997). Furthermore, such hybridization may have severe effects on genetic variation in island populations (Johnson *et al.*, 1993; Clarke *et al.*, 1998). The influence of sympatric hybridization is especially serious for organisms with geographically limited gene flow.

Genetic and morphologic analyses of populations of *Mandarina* suggest that hybridization between sympatric species has occurred on different islands. In the middle range of Hahajima Island, hybridization between *M. ponderosa* and *M. aureola* has occurred and a complex admixture of genes of these species has been created (Fig. 5) (Chiba, 1993). Although most of these populations are described as *M. aureola* based on their genital morphology, the shells have intermediate characteristics between *M. aureola* and *M. ponderosa*. However, such intermediate shells are not found in the fossil samples (2,000 - 13,000 years ago) collected from Hahajima except for one locality, and thus hybridization between these species has occurred recently (Fig. 6). The past distribution and geographic variation of *M. ponderosa* can be traced from the distribution of *M. ponderosa*-derived genotypes (Chiba, 1993). For example, populations of *M. aureola* in the eastern parts of the middle range of Hahajima possess marker alleles of *M. ponderosa*. *M. ponderosa* is not distributed in this area at present. However, fossils of *M. ponderosa* occur in this area. Thus, the *M. ponderosa* alleles in the populations of *M. aureola* in this area are derived from *M. ponderosa* that has become extinct (Chiba, 1993).

Another example of hybridization is found between the two sympatric species *M. mandarina* and *M. anijimana* on Anijima Island (Chiba, 1998). Intermediate shells and the coexistence of marker alleles between these species are found in populations occupying transitional zones between forest and shrub.

These findings suggest that some ecological factors are causing a partial breakdown of the reproductive isolation between these species. One plausible scenario is "frequency-dependent" hybridization (Chiba, 1998). If one species is rare at a given site and cannot find individuals to mate with, it would mate with individuals of the other sympatric species. This hypothesis seems to be supported by the fact that hybrids have been found in high frequencies in the transitional zone between shrub and forest where *M. anijimana* becomes rare but *M. mandarina* is abundant. Although the exact mechanism of reproductive isolation between sympatric species of *Mandarina* is not clear, it may depend on pre-zygotic isolation by a simple ecological difference as has been shown to be the case with the land snail *Partula* (Johnson *et al.*, 1977; Murray *et al.*, 1982). This kind of isolation would be easily broken and fertile offspring would be produced.

5. Endangerment of *Mandarina* and its Conservation

Human colonization of the islands affects native wildlife both through habitat destruction and through the introduction of domesticated animals and other nonindigenous species. The most prominent cases of the influence of introduced animals are the extinction of *Partula* in Tahiti and the marked decline of endemic land snail faunas of Hawaii and Mauritius due to predation by an introduced carnivorous land snail *Euglandina rosea* (Clarke *et al.*, 1984; Hadfield, 1986; Murray *et al.*, 1988; Griffiths *et al.*, 1993; Wells, 1995). *E. rosea* was introduced (Fig. 7) to control a giant African snail (*Achatina fulica*), a serious agricultural pest. Although *E. rosea* was not the sole cause of the extinction of native snail species, it was a critical factor.

Mandarina has suffered serious destruction of habitat due to cultivation since 100 years ago (Kurozumi, 1988; Tomiyama, 1994). However, the most serious problem is predation by introduced species. For example, a predatory flatworm, *Platydemus monokwari* (Fig. 4) was introduced to the

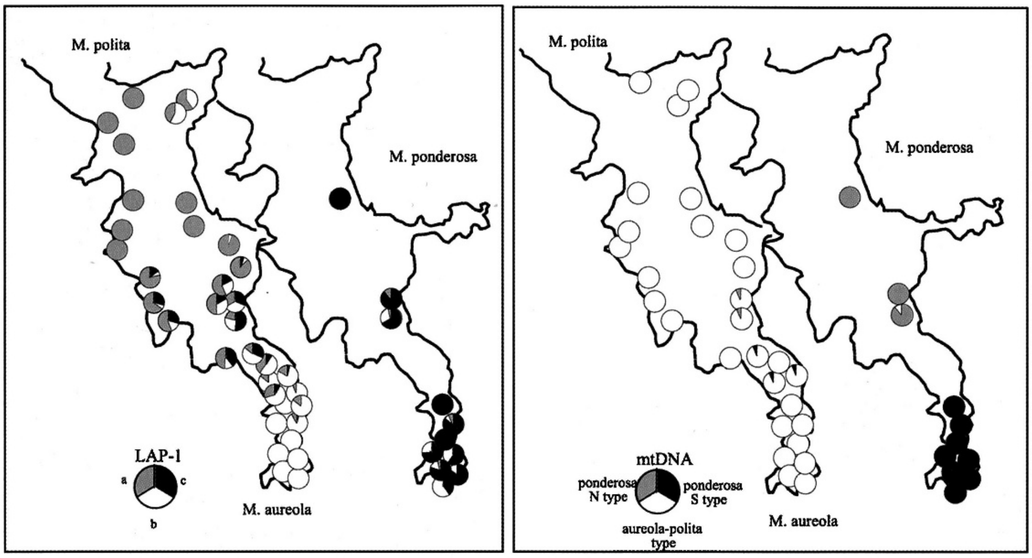

Fig. 5 Geographical variation in an allozyme locus, *Lap-1* and mtDNA (16SrRNA) for *M. aureola*-*M. polita* (left) and M. ponderosa (right).

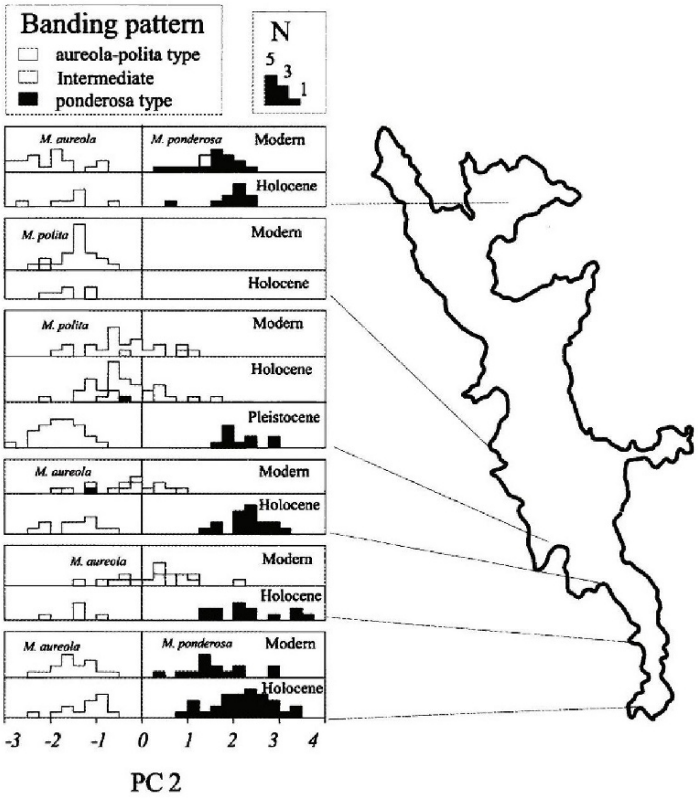

Fig. 6 Historical changes in shell morphologies in living and fossil samples of *M. aureola*, *M. polita* and *M. ponderosa*. The horizontal axis indicates principal component scores on the second principal component. The scores on the principal component were obtained by principal component analysis using 13 shell characters. (Modified from Chiba, 1993).

Fig. 7 Introduced predators: a predatory land snail, *Euglandina rosea* (upper), and a predatory flatworm, *Platydemus monokwari* (lower).

Ogasawaras. This predatory flatworm was introduced to several islands in the Pacific and Indian Oceans as a biological control agent for *Achatina fulica*, and has become a serious threat to the native gastropod fauna of Guam. Some other predatory flatworms were also found in the Ogasawaras, and these flatworms may be one of the causes of the recent decline in land snail species in the Ogasawaras (Kawakatsu *et al.*, 1999; Ohkouchi *et al.*, 1999; Tomiyama, 2002). In addition, the carnivorous land snail *Euglandina rosea*, that led to the extinction of the Tahitian snails, was also introduced to Chichijima. The effect of these introduced predators on native land snail fauna is so serious that they may rapidly cause the extinction of many of the native land snails in the Ogasawaras. The history of disasters caused by these snails to the land snails of Hawaii, Tahiti and other Pacific islands strongly suggest that the same sort of disaster will occur with *Mandarina* in the near future. A conservation program is needed to avoid the extinction of *Mandarina*.

Protection of the native habitat is not enough to avoid the influence of introduced predators such as flatworms and *Euglandina rosea*. The best way to protect *Mandarina* and other endemic land snail species would be to remove all flatworms and *Euglandia rosea* from the Ogasawaras. However, the cases of extinction of land snails in the Pacific islands show that it is very difficult to destroy these alien predators. One approach to avoid the extinction of *Mandarina* would be captive breeding. Reintroduction of captive-bred snails into restored or secure habitats may be one way of preserving *Mandarina*. In the case of *Partula*, more than thousand of these snails are being bred in captivity. The London Zoological Society released the first captive-bred *Partula* into a protected area on the island of Moorea in 1994 (Pearce-Kelly *et al*., 1995).

However, the captive breeding and re-introduction of *Mandarina* species face several problems. First, each species of *Mandarina* is segregated into many genetically and morphologically different local populations. In addition, these local populations produce hybrid zones with complex geographical patterns in morphology and genetics. The best way to recover the present geographical variation is to collect all of the populations living in the islands for captive breeding, and after removing the predators, re-introduce the captive-bred snails to exactly the same sites where the snails were collected. Although this program is not impossible, it is not feasible. Second, the incongruence among morphology, phylogeny, and condition of reproductive isolation make it difficult to identify units for captive breeding and select suitable source populations. For example, taxonomic species should not be used as a unit of conservation, because a species of *Mandarina* includes populations that are genetically and phylogenetically distant from other populations of the same nominal species. In addition, a population reproductively isolated from other populations is not necessarily more distantly related to these populations than a population that is not reproductively isolated from these populations (see section 4). Third, reproductive isolation among sympatric species of *Mandarina* is easily broken by environmental change. Human alterations of environmental conditions and habitats have been shown to have resulted in hybridization in several animals (McDonnell *et al*., 1978; Harrison & Arnold, 1982; Hillis, 1988). Changes in habitat conditions and population density through the re-introduction of captive-bred snails may result in hybridization among species, and thus, the genetic and morphological characteristics of each species may be lost as a result of this program. What is most urgent at this time is research on the breeding of *Mandarina* snails in captivity and at the same time, research on how individuals and populations differ genetically from each other. If we have genetic information for all populations on the islands, we can reconstruct the genetic diversity of *Mandarina* after their extinction in nature, even if we can save only a small part of these populations.

6. Conclusion

Mandarina provides an excellent natural laboratory in which we can test various ecological theories because of its high phenotypic diversity and accelerated evolution. In addition, a high level of geographical variation in *Mandarina* provides an excellent model system for the study of population genetics and speciation processes. The divergence of habitat preference among sympatric species and independent diversification in arboreal, semi-arboreal and ground ecotypes in different lineages at different times on different islands reveal importance of ecological factors in species coexistence and speciation. Hybridization among genetically and phenotypically divergent species suggests that the reproductive isolation of *Mandarina* depends on pre-zygotic isolation by simple ecological differences. These findings should contribute largely to understanding the process of adaptive radiation and evolution. However, at the same time, these findings reveal that it will be difficult to conduct conservation programs for *Mandarina*. Detailed ecological and genetic information as well as captive breeding is needed to keep the loss of genetic diversity of *Mandarin*a to a minimum.

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Chapter 19

Hot water tolerance of soil animals: utility of hot water immersion in preventing invasions of alien soil animals

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Abstract

Introduced soil animals have frequently affected native fauna on oceanic islands that have never been connected to a continental land mass. Alien soil animals can be unintentionally introduced via transfer in potted plants or by commercial trade among islands and continental landmasses. Hot water treatment to destroy pests has recently been used during the quarantine of ornamental plants. To examine the possibility of using hot water treatment for introduced soil animals in potted plants, an experiment was performed to determine whether hot water treatment (immersion in water at 40, 43, 45, 47, and 50°C for 5 min) kills soil animals. I examined four taxa (different phyla) of soil invertebrates that have been introduced to the oceanic Ogasawara (Bonin) Islands, approximately 1,000 km south of the Japanese mainland. The species used were: the invasive alien terrestrial flatworm *Platydemus manokwari* (Platyhelminthes); an unidentified alien species of earthworm (Annelida); the alien snail *Acusta despecta sieboldiana* (Mollusca); and the alien ant *Technomyrmex albipes* (Arthropoda). The water temperature required to kill flatworms (≥43°C) and earthworms (≥43°C) was lower than that to kill snails (≥50°C) and ants (≥47°C). Use of hot water for protection from alien soil animal invasions may mitigate their environmental impacts, particularly on oceanic islands where valuable biota could be threatened.

Key words: Hot water drenching; invasive alien species; Ogasawara Islands; *Platydemus manokwari*; quarantine

INTRODUCTION

Globalization has brought social, cultural, and economic benefits to many people, but it has also caused worldwide biological invasions of alien species (e.g., Reaser et al., 2007). Human activities such as travel, commercial trade, and agroforestry have increased the numbers of introduced organisms at regional and local scales (e.g., Mack et al., 2000). Many introduced species have negatively affected native ecosystems and species (e.g., Elton, 1958; Reaser et al., 2007). This is especially true on oceanic islands that have never been connected to a continental land mass (Elton, 1958; Reaser et al., 2007). For example, the accidental introduction of the brown tree snake, *Boiga irregularis* (Merrem), on Guam Island caused the extinction or dramatic reduction of many native vertebrates, including birds, bats, and reptiles (Fritts and Rodda, 1998); and intentional and accidental introductions of parasitoids to the Hawaiian Islands has caused heavy parasitism of many native moth species (Henneman and Memmott, 2001).

The effects of introduced soil animals have recently been recognized as a serious problem. For example, introduced earthworms have affected native ecosystems by changing nutrient cycling (Bohlen et al., 2004; González et al., 2006); introduced snails such as the giant African snail, *Achatina fulica* Bowdich, have become agricultural pests and have replaced native land snails on islands (Cowie, 2001b); snail-eating flatworms (e.g., *Platydemus manokwari* De Beauchamp) and predatory snails (e.g., *Euglandina rosea* (Férussac)), which were once frequently used for the biological control of introduced giant African snails (Muniappan, 1987, 1990; Eldredge and Smith, 1995; Civeyrel and Simberloff, 1996; Cowie, 2001a,b), have affected native land snail fauna on Pacific islands (Civeyrel and Simberloff, 1996; Cowie,

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2001a, b; Cowie and Robinson, 2003; Ohbayashi et al., 2007); and ants, which are easily introduced via human activities, have affected native vegetation and fauna on many oceanic islands (Holway et al., 2002; O'Dowd et al., 2003). Because soil animals are easily spread in imported potted plants, the transfer of potted plants for any purpose could cause invasions by alien soil animals. Intentional introductions of organisms as biological control agents are now considered more thoroughly. Accidental introduction should be more actively prevented.

Hot water treatment has been used as one quarantine method to destroy plant diseases and pests on cut and potted plants (Hara et al., 1993, 1994, 1996, 1997, 1999; Tsang et al., 1995, 2001; Follett and Neven, 2006); exposure to hot water at 49°C for 12 min kills most pests, including aphids, mealybugs, thrips, soft scale insects, and ants, with minimal effects on vase life and the quality of tropical ornamentals (Hara et al., 1996). Tsang et al. (1995) found that hot water treatment (49°C for 12 min) was not phytotoxic and actually extended the vase life of ornamental flowers and foliage. Therefore, hot water treatment may be useful for killing soil animals introduced with potted plants. To examine the utility of hot water treatment in preventing invasions by alien soil animals in potted plants, hot water treatment (immersion at 40, 43, 45, 47, and 50°C for 5 min) was applied to soil animals from four different taxa, including the invasive alien flatworm *P. manokwari* found on the oceanic Ogasawara (Bonin) Islands.

On the inhabited Ogasawara Island of Chichijima, the invasive alien flatworm *P. manokwari*, among the "100 World's Worst Invader Alien Species" (Lowe et al., 2000), is thought to have been introduced accidentally (probably via soils on plants) and became established in the early 1990s (Kawakatsu et al., 1999). Several studies have confirmed that invasive flatworms have eradicated the endemic land snail fauna on Chichijima (Ohbayashi et al., 2005, 2007; Sugiura et al., 2006b). Although the role of introduced earthworms in the native ecosystem in Ogasawara is unclear, dead earthworms are eaten by the invasive flatworm *P. manokwari*, suggesting that earthworms may support *P. manokwari* populations (Ohbayashi et al., 2005). The native land snail fauna of Ogasawara has been negatively influenced by the introduction of *P. manokwari* and alien land snails such as the giant African snail *A. fulica* (Tomiyama and Kurozumi, 1992). Furthermore, like introduced earthworms, introduced land snail species such as *Acusta despecta sieboldiana* (Pfeiffer) are eaten by *P. manokwari* (Sugiura et al., 2006b). The ant fauna of the Ogasawara Islands includes many alien species that invaded following human immigration (Terayama and Hasegawa, 1991). Some introduced ant species have been reported to influence plant–insect interactions on the Ogasawara Islands (Sugiura et al., 2006a). Flatworms, earthworms, land snails, and ants can readily be transported on or in various materials such as potted plants. Because plants may be transported to islands other than Chichijima for the purpose of vegetation restoration, quarantine methods to prevent their spread are essential.

MATERIALS AND METHODS

Site. The oceanic Ogasawara (Bonin) Islands are located in the northwestern Pacific Ocean, approximately 1,000 km south of the Japanese mainland (Ogasawara Village, Tokyo Metropolitan, Japan; Shimizu, 2003). The mean annual temperature was 23.2°C and the mean annual precipitation was 1,292 mm from 1987 to 1998 on Chichijima (Toyoda, 2003). The climate of the Ogasawara Islands is subtropical. Like other oceanic islands (Carlquist, 1974), the Ogasawara Islands support many endemic species (Shimizu, 2003), including vascular plants (137 species; Toyoda, 2003), insects (338 species; Ohbayashi et al., 2003), and land snails (82 species; Tomiyama and Kurozumi, 1992). However, many organisms are endangered because of human activities (e.g., Tomiyama and Kurozumi, 1992; Chiba, 2003; Toyoda, 2003; Karube, 2004). Furthermore, many alien organisms have invaded the islands, infiltrated the endemic ecosystems, and affected endemic biota (e.g., Yamashita et al., 2000; Ohbayashi et al., 2003; Karube, 2004; Sugiura et al., 2008).

All species samplings and experiments were conducted on the largest island, Chichijima (27°06′N, 142°11′E), in late June 2007.

Species investigated. Four species from different phyla were used: terrestrial flatworms (Platyhelminthes), earthworms (Annelida), land snails (Mollusca), and ants (Arthropoda). Both juveniles and adults of the invasive alien flatworm *Platydemus manokwari* were collected from the Kiyose Experimental Station of the Forestry and Forest Products Research Institute (FFPRI) on Chichijima (27°06′N, 142°11′E). *Platydemus manokwari* can be easily identified on the basis of its morphology and color (Kawakatsu et al., 1999; Sugiura et al., 2006b). Juveniles of an unidentified earthworm species were sampled from Kiyose. Because of the juvenile stage, the species could not be identified; however, all earthworms found in Ogasawara are introduced (Nakamura, 1994). Juveniles and adults of the alien land snail *Acusta despecta sieboldiana* were collected at Okumura on Chichijima (27°05′N, 142°12′E). Workers of the alien ant species *Technomyrmex albipes* (F. Smith) were collected at Asahiyama on Chichijima (27°05′N, 142°12′E). The body length of flatworms, earthworms, and ants, and the shell diameter of land snails were measured to the nearest 1.0 mm using a ruler.

Methods. The following experiments were conducted at the Kiyose Experimental Station or Okumura from 22 June to 12 July 2007. To examine the effective water temperature that kills the target species, individual animals were immersed in water of different temperatures (28, 40, 43, 45, 47, and 50°C) for 5 min. As a control for hot water treatment, water of 28°C was used. The ambient temperature ranged from 27 to 28°C. Soil animals were immersed in 300–500 ml of water in plastic cases (80×110×55 mm). Several treatments were conducted to determine the best water temperature to achieve 100% mortality in each animal group, although not all temperature treatments were applied to all species. I used 15–50 individuals per treatment per animal group. Water temperature was measured using a digital thermometer (Delta SK-1250MC; Sato Keiryoki Mfg. Co., Ltd., Tokyo). To maintain the temperatures (40.0±1.0, 43.0±1.0, 45.0±1.0, 47.0±1.0, and 50.0±1.0°C) during the experimental treatments, a small amount of hot water (ca. 60–70°C) was added, which was boiled in a kettle (3.0 *l*; CV-DT30; Zojirushi, Osaka). In plastic cases (35 mm diameter, 70 mm height), the death of each individual animal after hot water treatment was examined immediately after immersion and again after 1 h. Live and dead individual soil animals were differentiated by a change in body color and/or damage to the body after 1 h.

Data analysis. The body sizes of flatworms (body length, 8–62 mm), earthworms (body length, 20–91 mm), and land snails (shell diameter, 6–21 mm) varied considerably among individuals used in the experiment, but the body size of ants did not differ (body length, 2–3 mm). Therefore, the effects of animal body size, as well as hot water treatment, on survival in flatworms, earthworms, and land snails were analyzed using a generalized linear model (GLM) with binomial error distribution (JMP ver. 6.0; SAS Institute, 2005). Treatments immersed in different water temperatures and body sizes of each individual animal were used as explanatory variables. The response variable was whether an animal was killed (1/0). In ants, only water temperature was used as the explanatory variable, with death (1/0) as the response variable.

RESULTS

Different immersion temperatures significantly affected the mortality of flatworms, earthworms, and land snails, but body size and its interaction with treatment did not (GLM: flatworms: body size, df=1, $\chi^2=0$, $p=1.0$; water temperature, df=3, $\chi^2=80.7$, $p<0.0001$; body size×water temperature, df=3, $\chi^2=0$, $p=1.0$; earthworms: body size, df=1, $\chi^2=0$, $p=1.0$; water temperature, df=2, $\chi^2=93.2$, $p<0.0001$; body size×water temperature, df=2, $\chi^2<0.001$, $p\approx1.0$; land snails: body size, df=1, $\chi^2=0$, $p=1.0$; water temperature, df=4, $\chi^2=72.5$, $p<0.0001$; body size×water temperature, df=4, $\chi^2=0$, $p=1.0$). Exposure to hot water at ≥43, 43, and 50°C for 5 min resulted in 100% mortality of flatworms, earthworms, and land snails, respectively (Table 1). Immersion temperature significantly influenced the mortality of ants (GLM: water temperature, df=5, $\chi^2=207.7$, $p<0.0001$). Exposure to hot water at ≥47°C for 5 min resulted in 100% mortality of ants (Table 1).

DISCUSSION

Exposure to hot water at ≥43, 43, 50, and ≥47°C for 5 min resulted in 100% mortality of flatworms, earthworms, land snails, and ants, respectively (Table 1). In all animal groups, body size did not affect mortality under different treatments. Therefore, the water temperature frequently used in hot water treatment (ca. 50°C) could kill

Table 1. Hot water tolerance of alien soil animals on the Ogasawara Islands

Soil animal (species)	Mortality (%) at each water temperature[a] (*n*)					
	28°C	40°C	43°C	45°C	47°C	50°C
Flatworms (*Platydemus manokwari*)	0.0 (20)	25.0 (20)	100.0 (20)	100.0 (21)	— —	— —
Earthworms (unidentified)	0.0 (28)	3.7 (27)	100.0 (35)	— —	— —	— —
Land snails (*Acusta despecta sieboldiana*)	0.0 (15)	— —	0.0 (15)	0.0 (15)	0.0 (15)	100.0 (15)
Ants (*Technomyrmex albipes*)	0.0 (47)	— —	10.0 (30)	66.0 (50)	100.0 (44)	100.0 (41)

[a] Animals were immersed for 5 min.

—, no treatments at this temperature.

soil animals. Furthermore, the water temperatures that I used may not affect the survival of potted plants because exposure to hot water at 49°C for 12 min is not phytotoxic and has actually been shown to extend the vase life of ornamental flowers and foliage (Tsang et al., 1995). Tsang et al. (2001) designed the hot water drenching system and tested the effect of an increase in temperature using different potting media. The hot water drenching system proposed by Tsang et al. (2001) may be useful for killing soil animals that are frequently introduced with potted plants.

The isolated animals were directly immersed in hot water, but the ability of hot water to kill soil animals in potted soil masses was not examined; soil may protect the animals from direct contact with the hot water. Furthermore, some plant species may not tolerate water temperatures of approximately 50°C because the tolerance is species dependent (F. Kraus, pers. comm.). Therefore, further tests of the practicality of using hot water as a treatment method are needed at a local site (e.g., the Ogasawara Islands). However, hot water treatment is a promising method for preventing biological invasions by alien soil animals because it kills several animal groups such as insects (Hara et al., 1993, 1994, 1996, 1997, 1999; Tsang et al., 1995, 2001; Follett and Neven, 2006), as well as frog eggs (F. Kraus, pers. comm.). Because hot water does not negatively affect the environment, unlike pesticides, hot water treatment could mitigate biological invasions without causing pollution, particularly on oceanic islands that support valuable biota.

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Chapter 20
Endemic Insects in the Ogasawara Islands: Negative Impacts of Alien Species and a Potential Mitigation Strategy

Haruki Karube

Abstract The impact of invasive alien species on endemic insects in the Ogasawara Islands and current efforts to mitigate this impact are described. Endemic insects have probably been impacted most by the green anole (*Anolis carolinensis carolinensis*) as a result of its direct predation pressure, although alien trees such as bishopwood (*Bischofia javanica*) and ironwood (*Casuarina equisetifolia*) have also had substantial indirect impacts.

Factors causing the decline of species that typify individual habitats – endemic odonates, the Ogasawara tiger beetle (*Cicindela bonina* Nakane et Kurosawa, 1959), and the Ogasawara lycaenid butterfly (*Celastrina ogasawaraensis* Pryer, 1883) – have been revealed, and possible conservation efforts have been developed based on these results. Habitat restoration is now underway. Specific examples of these efforts are presented here.

20.1 Introduction

The Ogasawara Islands are a group of oceanic islands lying about 1,000 km south of Tokyo. Starting from the north, the islands consist of four major groups: the Mukojima Group, the Chichijima Group, the Hahajima Group, and the Volcano Islands. Almost all of the islands have been altered by humans as a result of development in the period prior to the start of World War II (Shimizu 2003). Ogasawara is also renowned for yielding numerous endemic insects. New endemic species are still being discovered almost every year, and some 350 endemic insect species have been described so far (Ohbayashi et al. 2003). However, these endemic species began declining rapidly on Chichijima in the 1980s, and a similar dramatic decline occurred on Hahajima in the 1990s. As a result, only a limited number of endemic species have survived on these two islands.

20.2 Factors of the Decline

The Ogasawara Islands have experienced human alterations of the natural environment in various forms, but primarily deforestation, continually since their discovery. However, only one insect extinction, that of the Ogasawara white-spotted longicorn beetle (*Anoplophora ogasawarensis* Makihara, 1976), has documented as a result of this deforestation. Of course, other insect species have likely gone extinct because of the loss of primary forests during early development of the islands (most endemic birds became extinct during this period) as well. When development was at its peak, most parts of the islands were converted to farmland, and those areas currently covered by secondary forest had been used as terraced fields stretching almost to the ridge lines.

Once this intense development subsided, the marked decline in species richness was a major shock, but elucidation of the factors causing this decline took time. One reason for this delay was the absence of domestic entomologists and insect enthusiasts residing on the Ogasawara Islands, which led to a lack of monitoring and a delayed reaction to such unanticipated circumstances.

Unusual changes in Ogasawara's insect fauna became apparent to researchers in the 1990s, and various hypotheses were proffered with regard to the cause of the decline. However, the dramatic decline had almost ended on Chichijima and Hahajima as a whole; after the start of their dramatic decline, most insects were gone in only 10 years.

Potential causes of the decline in insects on Chichijima and Hahajima include (1) the destruction of vegetation by a massive typhoon that hit Ogasawara in the fall of 1983, (2) the dispersal of insecticide to prevent pine wilt, and (3) the various impacts of development. However, studies on neighboring islands revealed that those islands displayed no decline in insects despite being similarly impacted by the typhoon. Also, the dispersal of massive amounts of insecticide was actually not done, and insects were declining dramatically even in out-of-the-way areas of Chichijima and Hahajima that had been unaffected by development. Thus, the aforementioned three reasons do not appear to explain the decline.

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Based on a study of endemic odonates that began in 1997, the author first pointed out in 2001 that these declines might be due to predation pressure from green anoles (*Anolis carolinensis carolinensis*, denoted here simply as anoles; Karube 2001). A study of almost all of the constituent islands found that healthy odonate fauna was present on the islands Anijima and Ototojima, situated beside Chichijima, that endemic odonates survived even on Mukojima where vegetation had been devastated by feral goats, and that the decline was not limited to odonates but affected an extremely large number of taxonomic groups including cicadas, longicorn beetles, jewel beetles, and bees. These affected insects were all diurnal, small, and non-poisonous (lacking a natural repellant; Karube 2004). In other words, the decline in insects may have been caused by a diurnal predator that prefers small insects. In particular, the avoidance of poisonous insects suggested that the cause of the decline was a predator. Anoles emerged as a clear suspect because their range was limited to Chichijima and Hahajima, where insects had declined, and the increase in anoles closely coincided with the decline in insects. Subsequent validation efforts have confirmed this conclusion, and the anole is now considered to be the principal factor in the decline of insects on Chichijima and Hahajima (Makihara et al. 2004; Abe et al. 2008).

Anoles are a type of lizard native to central and southern North America. They feed on insects and have a large mouth and vigorous reproductive ability (Fig. 20.1). The anole population has increased drastically since their arrival on the Bonin Islands, which presumably took place in the late 1960s, because natural enemies are almost non-existent on these oceanic islands. Their range has expanded to all of Chichijima and Hahajima, and their population is now estimated to be several million (Okochi et al. 2006).

Fig. 20.1 A green anole (*Anolis carolinensis carolinensis*) feeding on native cicadas (*Meimuna boninensis* Distant, 1905)

20.3 The Impact of Green Anoles

The dramatic increase in the green anole population has had various impacts, the principal ones of which are noted below.

20.3.1 Extinction of Endemic Species

Many of the endemic insects on the Ogasawara Islands have been impacted enormously by predation pressure from anoles. In particular, species that for some geological or ecological reason are found only on Chichijima or Hahajima face a crisis. At the very least, the tricolored tiger longhorn (*Xylotrechus takakuwai* Kusama, 1977), several species of tumbling flower beetles such as the Ogasawara tumbling flower beetle (*Glipa ogasawarensis* Kono, 1928), and the Ogasawara carabid beetle (*Colpodes boninensis* Kasahara, 1991) are completely missing from recent records and are quite likely already extinct.

20.3.2 Radical Changes in Ecosystems

The ecosystem of Ogasawara has changed dramatically because of the absence of many diurnal insects, a situation difficult to find anywhere else on earth. For example, some plants that had relied on endemic insects for pollination can no longer bear fruit because an alien honey bee (*Apis mellifera* Linnaeus, 1758) does not visit them. Woody plants are long lived, and thus the impacts on them are not immediately apparent; however, the situation may be critical depending on the effects of the insect decline on future generations of these tree species. In addition, the extinction of beetles such as longicorn beetles that eat dead wood means the loss of decomposers from the ecosystem. Also, insects are an important source of food for birds, and thus their sudden disappearance may have a substantial impact on insectivorous birds in the future.

This sudden loss of a group of organisms may render ecosystems on Ogasawara extremely unstable. Future research and monitoring are needed to reveal the long-term impacts, but the case of the green anole on Chichijima and Hahajima shows that just one alien species can lead to disaster.

20.3.3 Various Alien Species and Endemic Insects

While anole predation may be the primary factor in the decline of insects on the Ogasawara Islands, various other alien species have also had impacts.

The black rat (*Rattus rattus*), which feeds directly on insects, inhabits almost all of the Ogasawara islands. Examples of the devastating impacts of the black rat on indigenous insect faunas in places like New Zealand have been reported, but obvious damage to Ogasawara is not yet apparent, and future study is needed. Black rats are known to eat seeds as well and may therefore also impact forest regeneration. Furthermore, this seed predation may also indirectly threaten the survival of insects that depend on vegetation (Dr. Les Molloy personal communication).

The cane toad (*Bufo marinus*) was presumably introduced during the United States' military governance of the Ogasawara Islands. Like the anole, it has increased dramatically on Chichijima and Hahajima and is now distributed over almost the entirety of both islands. Along with the impacts of anoles, cane toads have an enormous influence on ground-dwelling insects. Predation pressure from cane toads is thought to be the reason that the author and colleagues have found almost no Ogasawara vivid metallic ground beetles (*Chlaenius ikedai* Kasahara, 1991) or Ogasawara carabid beetles since their original description. In addition, records exist of American bullfrogs (*Rana catesbeiana*) having been brought to the Ogasawara Islands and found on Chichijima, but they currently survive only on Ototojima. This species lives primarily in ponds, and thus it exerts predation pressure on aquatic organisms like damselflies and dragonflies.

Feral goats have severely damaged the vegetation on islands in the Mukojima and Chichijima Groups. As their feeding damage increases, the topsoil erodes, causing deterioration of vegetation, which likely has an impact on indigenous insects. Only a fraction of the insects that depend on indigenous trees remains on islands like those of the Mukojima Group where the indigenous forest is sparse or has disappeared (Karube et al. unpublished data).

The predatory flatworm *Platydemus manokwari* has had a considerable impact on endemic snails on Chichijima, and the local extinction of snails is proceeding. Thus, ground beetles (undescribed species) that are believed to use endemic snails as food might have the same fate as the extinct endemic land snails.

Alien plants also have a substantial impact on the ecosystems of the islands. The Ogasawara tiger beetle (*Cicindela bonina* Nakane et Kurosawa, 1959; Fig. 20.2) inhabits barren environments, but its local extinction is proceeding as its habitat is invaded by ironwood (*Casuarina equisetifolia*) and luchu pine (*Pinus luchuensis*), whose fallen leaves and needles deeply cover the once-bare ground. Space for reproduction of endemic odonates has also decreased, as bishopwood (*Bischofia javanica*) forms pure closed canopy forests along streams. Moreover, the decline in native trees caused by alien tree invasion is likely to have an impact on their associated phytophagous insects. In this manner, the effects of alien plants are immeasurable.

Fig. 20.2 The Ogasawara tiger beetle (*Cicindela bonina* Nakane et Kurosawa, 1959)

20.4 Mitigating Impacts

The impacts of such alien species on indigenous species became apparent in the 2000s. A research project supported by the Ministry of the Environment's Global Environmental Research Fund, which began in 2004, have led to substantial progress in alien species control.

With regard to insects, efforts were undertaken based on studies by the authors: (1) an Ogasawara version of the Red List (of Threatened Species) was created to prioritize endemic insect conservation in Ogasawara; (2) artificial damselfly and dragonfly ponds were constructed to restore endemic odonates; (3) causes of the decline of the barren-dwelling Ogasawara tiger beetle, remaining only on Anijima, were studied, and captive breeding was attempted; and (4) as for species of wet forests, a conservation project for the Ogasawara lycaenid butterfly (*Celastrina ogasawaraensis* Pryer, 1883), remaining only on Hahajima, was undertaken.

As for effort (1), prioritizing which species to conserve is essential, given the insufficient funding for conservation efforts, a fact not likely to change in the future. The aim of the Red List of Threatened Species is to indicate which insects are currently in critical condition. In the process of creating this list, our surveys re-discovered some species and also discovered new species.

The practices in effort (2) involve a trial to maintain a stable habitat for endemic odonates that remains only on the satellite islands. As mentioned before, endemic odonates have almost completely disappeared from Chichijima and Hahajima, which were formerly their primary habitats [with only an Ogasawara jewel (*Rhinocypha ogasawarensis*) remaining on Hahajima]. Even in these island habitats, the odonates have failed to stably reproduce because of recent droughts; thus, as a supplementary trial damselfly and dragonfly ponds were constructed using large plastic containers (Fig. 20.3). Ponds with more than 4 tons of water have been created on Ototojima and Anijima, and sites for three species, i.e., the Ogasawara damselfly (*Boninagrion ezoin* Asahina, 1952), the Ogasawara green damselfly (*Indolestes boninensis* Asahina, 1952), and the Ogasawara dragonfly (*Hemicordulia ogasawarensis* Oguma, 1913), have successfully been created and maintained. These artificial ponds play a major role as refuge sites when natural bodies of water have disappeared, and these ponds have contributed to an overall increase in the odonate populations. In particular, the Ogasawara dragonfly, whose population was small, has steadily increased on Ototojima and Anijima since the creation of the ponds. In addition, in 2008, the dragonfly was reported twice on Chichijima for the first time in 10 years, since its local extinction on the island. This indicates that individuals from Anijima might have flown across the strait to reach Chichijima. By maintaining the populations of endemic odonates in their current habitats and conserving potential habitats on Chichijima, where they previously existed, populations on Chichijima may recover.

With regard to effort (3), initially, luchu pine and ironwood were not thought to require urgent control, unlike trees such as bishopwood, but these two species have substantially modified barren environments through the accumulation of fallen needles and leaves. Starting in 2008, these alien trees have been cut down in the vicinity of former barren habitats, and monitoring of the restoration of the environment has begun. Captive breeding techniques have been established for the Ogasawara tiger beetle; thus, the conservation of the species should at least be possible regardless of the state of habitat restoration.

Fig. 20.3 Artificial damselfly and dragonfly ponds established for the conservation of native odonates. Successful reproduction of odonates was observed within 2 years of the ponds' construction

Regarding effort (4), adhesive traps developed by Mr. Mitsuhiko Toda (Japan Wildlife Research Center) and his colleagues, have been put to use along with vegetation management. Some 250 traps have been maintained in a small 15 m × 15 m plot, and the area has been monitored for 2 years. This resulted in stable reproduction of the Ogasawara lycaenid butterfly over long periods, from June to December for 2 years running. Such a stable site is unique among the current habitats of the butterfly on Hahajima, indicating the effectiveness of such control anole efforts.

Each individual species we chose typifies its respective environment. By selecting these target species and conserving them, we believe that numerous other organisms inhabiting each environment can be saved as well.

20.5 Development of Techniques to Manage Alien Species

Very few regions like Ogasawara exist in Japan where alien species have become a problem for a wide range of taxonomic groups. This is because the ecosystems of these oceanic islands are more susceptible to invasive species. The importance of responding to the problem of alien species on Ogasawara was noted early on, but most control efforts only started to be developed and implemented in the 2000s.

Starting with the eradication of feral goats, which began in the 1990s, techniques to eliminate alien trees like bishopwood and ironwood using herbicides have been established, and effective techniques have been developed to capture pests (previously done by hand), such as catching bullfrogs in traps like those used for eel and catching anoles in adhesive traps. The development of such techniques for alien species eradication represents a crucial turning point in the eradication or management of alien species.

Previously, even if we knew the area was a habitat for rare insects, the best green anole management strategy was to hand-catch noticeable anoles within an area. Exerting intense predation pressure via traps and other means has increased our chances of defending sites prioritized for conservation. Moreover, a large-scale fence experiment to keep anoles out was started on Hahajima in 2008. If successful, an area free of anole predation should become available on the island – an amazing development considered unachievable 10 years prior. I praise the efforts of the individuals involved.

20.6 Future Developments

Various studies such as those mentioned here have proceeded over the last 5 years, and their findings have been put to use on-site. In the past, the residents of Ogasawara often expressed views such as, “I don’t understand what the researchers are doing” and, “Aren’t they just using the region to make a name for themselves?” However, conservation approaches like those presented here and basic biological research have indicated that we can contribute to the local community in some way, however small, and that a scientific approach is effective at solving various problems.

Although various control methods are now available, many problems still remain. The eradication of some alien species does not mean that it is easy to achieve local clearance of another. Massive amounts of work are still required. In addition, the eradication of one alien species could result in the flourishing of another. For example, feral pigs (*Sus scrofa domesticus*) had caused enormous damage to land snails and vegetation on Ototojima, and removing them was a priority. However, feral pigs fed on bullfrogs, possibly reducing their density; thus, the rapid eradication of feral pigs might have caused an increase in bullfrogs. Therefore, an eradication plan had to be formulated and implemented to first proceed with bullfrog clearance, and only once that had almost been completed could the eradication of feral pigs begin. A similarly complicated situation may exist for anoles feeding on insects, and their eradication may have unforeseen future impacts. However, it is paramount to keep the long-term recovery of native ecosystems in mind and to proceed with control plans, trying to avoid risks as much as possible.

In 2010, 20 years will have passed since the author first visited Ogasawara. At the time of that first visit, the situation on Chichijima was disastrous. Subsequent visits revealed the disappearance of the large populations of the Ogasawara dragonfly and the tiger longhorn from Hahajima. Prospects have finally begun to brighten in the last 5 years, but how much of what was lost will be regained in the next 20 years? I will do what I can, and watch how the islands respond.

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Chapter 21

A decrease in endemic odonates in the Ogasawara Islands, Japan

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Abstract

There are many endemic species in the Japanese Ogasawara Islands. However, many of these endemic species are likely to disappear as a result of reduction of habitat and the introduction of exotic species. Odonates are included within this category of species at risk. If the decrease in endemic odonates is due to a decrease in aquatic habitat, we have only to provide arti" ficial ponds to conserve these species. In this study, we provided artificial ponds as a habitat for odonates in Chichi-jima and Ani-jima, Ogasawara Islands. We then examined the possibility of protection and enhancement of odonate populations. Endemic odonates were found in the natural ponds of Ani-jima and Ototo-jima. In Ani-jima, they could be collected both in the artificial and natural ponds. The artificial pond could provide habitat for endemic odonates. However, in Chichi-jima, few odonates could be collected both in the artificial and natural ponds. Here, invasive species, such as *Gambusia affinis* and *Anolis carolinensis*, are found, which considered to prey upon odonate larvae and adults. Extermination of invasive species may be necessary to conserve the endemic odonates in Chichi-jima.

Key words : *Anolis carolinensis*, endemic species, oceanic islands, odonates, Ogasawara Islands, predator, conservation

Introduction

In Japan, the Ogasawara Islands consist of many small islands, including Chichi-jima, Ani-jima, Ototo-jima, Haha-jima and Iou-jima, and are located about 1,000 km south of the Japanese mainland. These islands are often referred to as "the Galapagos of the Orient". As in many other oceanic islands, many endemic species inhabit the Ogasawara Islands. However, recently many of these endemic species, including odonates, are threatened with extinction (Karube, 2004). Five endemic odonates, *Boninagrion ezoin*, *Hemicordulia ogasawarensis*, *Indolestes boninensis*, *Rhinocypha ogasawarensis* and *Boninthemis insularis* inhabit the Ogasawara Islands. From 1930-1975, adults of endemic odonates could often be found in Chichi-jima (Table 1). Asahina (1976) indicated that many odonates, including endemic species, could be observed on the larger islands, such as Chichi-jima and Haha-jima, which had forest and stream habitat, though on the very smaller islands only more common, non-endemic species could be observed. However, about 1992 it became difficult to find endemic odonates in Chichi-jima, although these species could still be found in Ani-jima and Ototo-jima (Table 1). Most of the endemic odonates are likely to disappear, and this trend is most pronounced in Chichi-jima.

This decline has been blamed on environmental destruction. In Chichi-jima, road construction began in the 1970s. Stream bottoms and banks were lined with concrete blocks, especially at road intersections, and drainage projects along the lengths of the roads were completed. As a result, natural percolation of rainfall through soils decreased, which resulted in reduced natural ponding and pooling of runoff. Construction of complete equipment of water service to the houses also resulted in the diminution of the small water reservoir near the village and then other habitats for odonates have diminished. In addition, introduced plant species that has great fertilization prompts the destruction of endemic plants with decrease in suitable habitat for adult odonates.

If the decrease in endemic odonates is due to a decrease in aquatic habitat, we have only to provide artificial ponds to conserve these species. In this study, we attempted to conserve and increase populations of threatened endemic odonates by providing plastic artificial ponds for habitat in Chichi-jima and Ani-jima, Ogasawara Islands. We also verify the effectiveness of these efforts and discuss the possibility of conservation and enhancement of declining odonates.

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Table 1. Odonates found in the Ogasawara Islands

	Chichi-jima				Ani-jima		Ototo-jima	
	1930s$^{1)}$	1975$^{2)}$	1992$^{3)}$	1997-2000$^{4)}$	1992$^{3)}$	1997-2000$^{4)}$	1992$^{3)}$	1997 ～ 2000$^{4)}$
Boninagrion ezoin	*	*	-	-	*	*	*	*
Hemicordulia ogasawarensis	*	*	-	-	*	*	*	*
Indolestes boninensis	*	*	-	-	-	-	*	*
Rhinocypha ogasawarensis	*	*	-	*	*	*	-	*
Boninthemis insularis	*	*	-	*	*	*	*	*
Ischnura senegalensis	*	*	*		*		*	
Diplacodes bipunctatus	*	*	-		*		*	
Pantala flavescens	*	*	*		*		*	
Tramea transmarina		*	*		-		*	
Tramea virginia	*							
Anax guttatus			-		-		*	
Anax parthenope	*	*						

1): Asahina (1952), 2): Ishida & Kojima (1978), 3): Hirose (1993), 4): Karube (2001), *: Affirmation of living, -: Negation of living, Blank: Not try to be found, Bold letters: endemic species

Materials and methods

The study areas (Chichi-jima, Ani-jima, Ototo-jima) are located on the Ogasawara Islands, about 1,000 km south from Honshu in Japan. In Chichi-jima, one natural pond (CN1) in Yoake-yama (27°05´N, 142°11´E) and one natural pond (CN2) in Mikazuki-yama (27°06´N, 142°10´E) were selected as sampling stations. In Ani-jima, two natural ponds (AN1, AN2) near the shore were selected (27°07´N, 142°11´E) as sampling stations, and in Ototo-jima, two natural ponds (ON1, ON2) were selected (27°11´N, 142°10´E) (Fig. 1). In Chichi-jima, a large (CA1, 3.0 × 1.4 × 0.5 m^3) and a small (CA2, 1.8 × 1.2 × 0.5 m^3) plastic artificial pond were installed at Kiyose (27° 06´N, 142° 11´E) in September, 2000. In Ani-jima, one artificial pond (AA1, 3.0 × 1.4 × 0.5 m^3) was installed near the natural ponds in June, 2001. These installed artificial ponds were left under natural condition.

Collection of aquatic invertebrates was done four times in 2001, 2002 and 2003. In 2001, collections were on September 18 and November 25 at the natural ponds, September 16 and November 22 at the artificial ponds in Chichi-jima, September 17 and November 29 in Ani-jima and September 14 and November 24 in Ototo-jima. In 2002, collections were on July 18 in Chichi-jima, July 20 in Ani-jima and July 19 in Ototo-jima. In 2003, collections were on June 11 in Chichi-jima, and June 8 in Ani-jima and Ototo-jima.

At each collection, a "D"-frame net was placed at the base of vegetation growing on the pondbed near the bank and was swung back and forth. Collections in the natural pond were done about 10 m along the bank for five minutes. In the artificial ponds, all the invertebrates in the pond were collected. Aquatic invertebrates were preserved in 80% ethanol and later identified.

Aquatic invertebrate presence-absence data were pooled according to the nine sampling stations through the four collection events, and similarities were assessed with Sorensen's similarity coefficient. The unweighted pair-group method using an arithmetic average (UPGMA) was used to cluster the data.

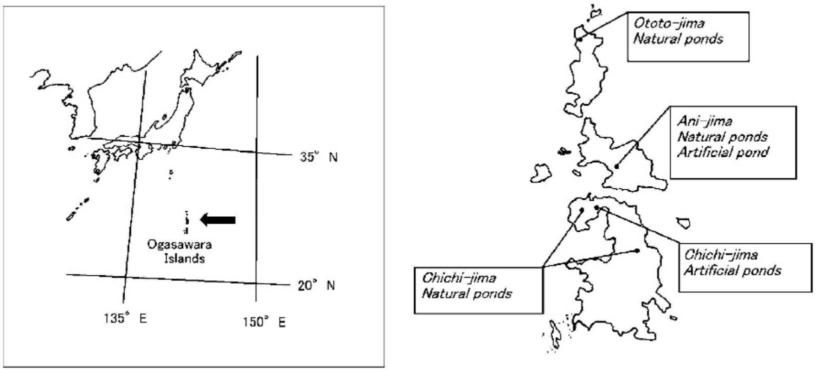

Fig. 1. Map of the Ogasawara Islands and study ponds

Results

We collected seventeen families of aquatic invertebrates and vertebrates over three years in the natural ponds of Ogasawara Island (Table 2). Most of the species were found on every island. However, odonates were not found only in Chichi-jima.

Cluster analysis showed that the aquatic invertebrate assemblage of natural ponds on Ani-jima and Ototo-jima was similar within the islands, but there was little in common between the islands (Fig. 2). The aquatic invertebrate assemblage in artificial ponds was also similar to that of natural ponds in Ani-jima. In Chichi-jima, the aquatic invertebrate assemblage was different depending upon the pond. Many individuals of *Gambusia affinis* and *Bufo marinus* were found in CN2 and its aquatic invertebrate assemblage was greatly different from other ponds.

Odonates could not be found (except for one individual) in Chichi-jima, though they could be found in Ani-jima and Ototo-jima (Fig. 3). Most of the species collected in Ani-jima and Ototo-jima were common, oceanic odonates, and only one endemic, *Boninagrion ezoin*, was collected. This endemic species could be collected both in natural ponds at Ani-jima and Ototo-jima and also in

Table 2. Aquatic invertebrates and vertebrates found in the natural ponds of the Ogasawara Islands

		Chichi-jima		Ani-jima		Ototo-jima	
		CN1	CN2	AN1	AN2	ON1	ON2
Diptera							
Chironomidae	*Chironomus* sp.	**		**		**	**
	Polypedilum sp.	*		*	**		
Culicidae	*Culex tritaeniorhynchus*	***	*	***	**	**	*
	Culex boninensis			**	*	*	
Hemiptera							
Veliidae	*Microvelia* sp.	***		**		**	
	Xiphovelia boninensis		*				
Notonectidae	*Anisops ogasawarensis*	**		**	**	***	***
Mesoveliidae	*Mesovelia* sp.			*			
Corixidae	*Nipponasellus* sp.					*	*
Coleoptera							
Dytiscidae	*Copelatus* sp. 1	*					
	Copelatus sp. 2	*					
	Rhantus sp.	*			*		
	Copelatus ogasawarensis	*				*	
Hydrophilidae	*Borosus signaticollis*	*			*		*
	Coelostoma stultum				*		*
Odonata							
Libellulidae	*Diplacodes bipunctatus*			**	**		**
	Tramea spp.			*	**		*
	Pantala flavescens						**
Coenagrionidae	*Ischnura senegalensis*			*	**	**	***
	Boninagrion ezoin			**	**	**	**
	Ischnura aurora					**	*
Aeschnidae	*Anax guttatus*						*
	Anax parthenope						*
Collembola							
Hypogastruridae	*Hypogastruridae* Gen. sp.		*				
Entomobryidae	*Entomobryidae* Gen. sp.			*			
Podocopa							
Cypridae	*Cypridae* Gen. sp.	***				*	*
Decapoda							
Atyidae	*Caridina typus*		**				
Cyprinodontiformes							
Poeciliidae	*Gambusia affinis*		**				
	Poecilia reticulate	*					
Anura							
Bufonidae	*Bufo marinus*		**				

Number of individuals ***: ≥ 100; **: < 100, ≥ 10; *: <10

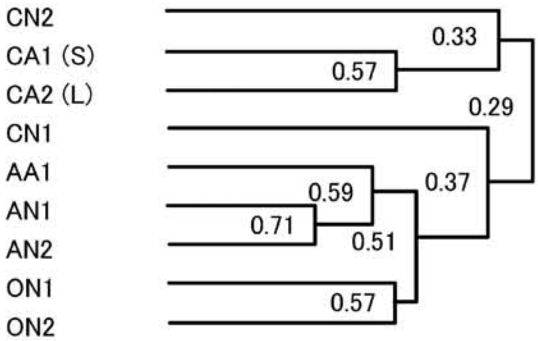

Fig. 2. Cluster analysis of aquatic invertebrates assemblages among nine sampling stations. Similarities assessed with Sorensen's similarity coefficient. The unweighted pair-group method using an arithmetic average (UPGMA) was used to cluster the data.

artificial ponds at Ani-jima. In May 2002, we could find molts of endemic species, *Hemicordulia ogasawarensis* and *Boninthemis insularis*, at the artificial pond in Ani-jima.

Discussion

In this study, we found odonates in both natural and artificial ponds at Ani-jima, including three endemic species. We have shown that artificial ponds could provide habitat for odonates. It is considered that serving water place would be the most expedient way to conserve odonates. However, in Chichi-jima, we found no odonates in either natural or artificial ponds, except for one individual in the artificial pond in November, 2001.

The aquatic invertebrate assemblages of natural and artificial ponds in Chichi-jima were largely different from ponds on other islands. Since people reside only on Chichi-jima, the observed differences in assemblages here may be partly due to human activities beginning in the 1970's. *Gambusia affinis* was introduced to Chichi-jima for mosquito control after reversion of the Ogasawara Islands to Japan. Many *Gambusia affinis* and *Bufo marinus* were found in CN2 of Chichi-jima. While *Gambusia affinis* preys upon mosquitoes, they prey upon many other organisms (Rupp, 1996; Offill & Walton, 1999). They eat treefrog tadpoles (Goodsell & Kats, 1999), and they may eat odonate larvae also. The lack of odonates in Chichi-jima might be partially explained by predation by exotic species.

Only in Chichi-jima, many individuals of introduced predator lizard, *Anolis carolinensis*, could be found (Miyashita, 1991). Numbers of *Anolis carolinensis* have been increasing and their range expanding (Miyashita, 1991) since they were introduced to Chichi-jima in the 1960s (Hasegawa, 1986). Only one native lizard, *Cryptoblepharus boutoni nigropunctatus*, also inhabits Chichi-jima. Both lizards are insectivorous and diurnal. However, as a result of competition between the two species, *Cryptoblepharus boutoni nigropunctatus* tends to be found in habitat where it is difficult for *Anolis carolinensis* to survive (Miyashita, 1991; Suzuki, 1999).

Anolis carolinensis eats various kinds of small insects, including odonates (Makihara et al., 2004; Karube & Suda, 2004). One individual can eat more than two dragonflies per day (Makihara et al., 2004). An endemic cicada (*Meimuna boninensis*) is eaten

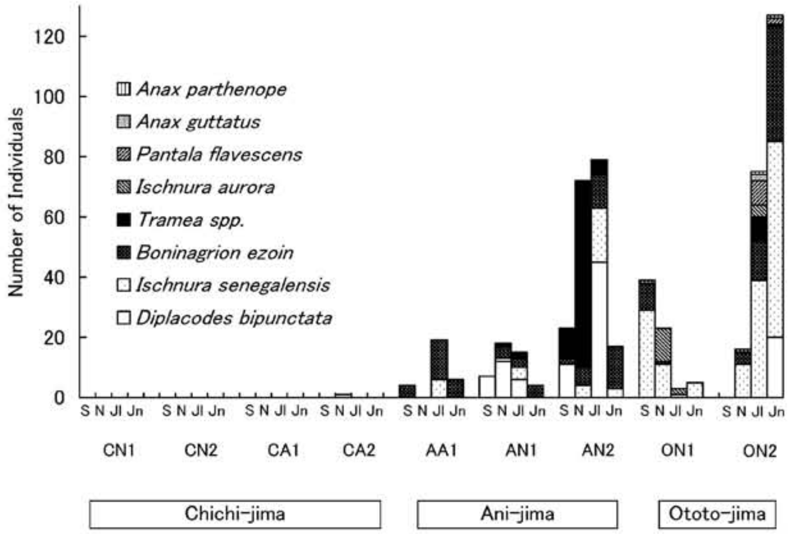

Fig. 3. Number of odonate individuals collected in nine sampling stations of three islands. S: September, N: November, Jl: July, Jn: June.

by *Anolis carolinensis* in the field (Oobayashi, 2001). Under laboratory conditions, another cicada (*Meimuna opalifera*) is usually injured by the mouth of *Anolis carolinensis* although they are not eaten (Makihara et al., 2004). The number of diurnal longicorn beetles has been decreasing while that of nocturnal ones has been almost constant in the field (Makihara et al., 2004). They considered the reason of this decrease as the predation by *Anolis carolinensis*. All the odonates are diurnal species, so odonates might be also eaten by this lizard in Chichi-jima. Therefore, the decrease in the odonate population in Chichi-jima could be largely explained by *Anolis carolinensis* predation.

This lizard was also introduced to Okinawa, Guam and Hawaii (Ota et al., 1995). However, at these sites impacts upon insect populations by predation have not been reported. In the Ogasawara Islands, the lizard fauna is impoverished. Although some birds, such as *Monticola solitarius* and *Buteo buteo*, eat *Anolis carolinensis* (Miyashita, 1991), predation pressure from birds is thought to be low. Therefore, it is possible that the density of *Anolis carolinensis* may be higher in the Ogasawara Islands than in Okinawa, Guam and Hawaii. Sword (2001) reports that a species of grasshopper (*Schistocerca emarginata*) that eats *Ptelea trifoliata* escapes predation by *Anolis carolinensis*, though individuals not feeding upon this plant are caught and eaten by the lizard. Apparently, grasshoppers eating *Ptelea trifoliata* are distasteful and lizards reject them. However, insects in the Ogasawara Islands have not developed this kind of anti-predation strategy against *Anolis carolinensis*.

In Chichi-jima, a priority before providing suitable aquatic habitat for odonates should be to minimize the effects of predation by *Anolis carolinensis*. At present, even if we provide aquatic habitat in Chichi-jima, the ponds would not facilitate conservation and enhancement of odonate populations. In this study, we did not investigate the southern part of Chichi-jima, where human impacts to the environment are fewer. Though Miyashita (1991) reports the range of *Anolis carolinensis* now expanding to southern Chichi-jima, many odonates may still be found there. Accordingly, we see a need to confirm the existence of viable odonate populations in this relatively untouched part of Chichi-jima.

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Chapter 22
Ecology and Control of the Green Anole (*Anolis carolinensis*), an Invasive Alien Species on the Ogasawara Islands

Mitsuhiko Toda, Hiroo Takahashi, Naomi Nakagawa, and Naozumi Sukigara

Abstract The green anole (*Anolis carolinensis*) was introduced from North America to the Ogasawara Islands, where it has become established. The feeding behavior of these animals causes insect population collapse on the islands, and thus the species has been listed as an Invasive Alien Species in Japan since June 2005. Although the green anole population on the islands has not grown rapidly in recent times, its density could nevertheless approach hundreds to thousands of individuals per hectare. Given the biological and ecological characteristics of the species, highest management priority should be given to preventing dispersal to non-invaded islands. Area-specific control is the most practical approach for eradicating established populations. In a series of control projects conducted by Japanese Ministry of the Environment, adhesive traps for animal capture and Teflon sheet fencing to restrict movement were developed. With this technology, continuous green anole capture is now under way around the harbor of Chichijima to prevent dispersal to neighboring uninhabited islands. In addition, an experimental project for regional eradication has been set up on Hahajima in an attempt to resurrect the insect community.

22.1 Introduction

The Ogasawara Islands comprise an oceanic archipelago geographically isolated from any continental land mass, which makes the biological community very distinctive and prevents the immigration of potential predators. Under such conditions, many endemic insect species have evolved, forming a rich fauna on the islands. Recently, the green anole (*Anolis carolinensis*) was introduced artificially, leading to intense predation on native insect populations that have consequently suffered serious declines (Makihara et al. 2004; Karube 2005; Yoshimura and Okochi 2005). Accordingly, in June 2005, the green anole was listed in the Invasive Alien Species by the government of Japan. Many endemic insects on the islands are threatened with extinction (Ministry of the Environment 2006), and conservation of their populations is a matter of great urgency.

To protect these endemic insects, a series of projects are now under way on the Ogasawara Islands. This is probably the first attempt in the world to exterminate an invasive alien lizard species from a habitat in which it is established. The project is being undertaken by Japanese Ministry of the Environment and consists of three parts: prevention of the green anole dispersal to non-invaded islands; establishment of habitat restoration areas for insects native to the Ogasawara Islands, after extirpation of green anole populations; and promotion of the recovery of native insect communities in these habitat restoration areas.

We investigated the status of green anole populations on the islands prior to project implementation, and the results suggested that population control would be laborious. Green anole's population density is high in Chichijima and Hahajima, where the topography is rugged and steep. Since there have been few studies of lizard population control, there are few guidelines. However, while seeking technical solutions to the problem, we conclude that labor-intensive methods are effective for population control, and regional eradication is technically feasible.

Here we summarize results obtained from the field investigation since 2004 and from previous reports on lizard control. We also introduce the Ministry of the Environment approaches that aim at natural environment recovery and prevention and control of the green anole.

22.2 Characteristics of the Green Anole

22.2.1 Genus Anolis

Anolis belongs to the Iguanidae. This is the largest reptile genus, containing about 400 species that are widely distributed from southeastern North America to northern South America.

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These lizards are diurnal, small or medium-sized, and arboreal. They have rows of lamellae, or ruffled structures, on the bottoms of their toes, similar to the Gekkonidae. Like geckos, anoles can move quickly on smooth vertical surfaces (Savage 2002; Lovern et al. 2004). The lamellae of the Gekkonidae stick to vertical surfaces through intermolecular attraction (Autumn et al. 2002), and green anole lamellae are thought to function in the same manner, allowing the animals to climb smooth glass surfaces. Hence, designing fences to exclude green anoles is extremely difficult.

Many species of *Anolis* have green or brown bodies that can blend into their surroundings. However, most have a dewlap on their throat (a fan-shaped structure supported by hyoid bone and used for communication) that is vivid in color (Nicholson et al. 2007). The dewlaps of male anoles are distended when fighting other males or courting females. The body sizes of males are larger than those of females in most species (Savage 2002). Many species of *Anolis* coexist in particular regions of Cuba but use different micro habitats. Each arboreal species prefers different micro habitat among tree crowns, trunks, branches, and twigs. Others occur on flat ground and on cliffs. There are specialized anole "ecomorphs" in each micro habitat (Williams 1969).

22.2.2 The Green Anole as an Alien Species

The anoles introduced to Ogasawara were green anoles (Hasegawa 1986). The species is native to the southeastern United States (ranging from North Carolina to Florida and Texas in the east); other anoles occur mostly in Mexico, Cuba and central and south America. The natural distribution range of the green anole overlaps with those of other species only where there are anthropogenic influences (Behler and King 1979). This is the only anole species whose natural distribution range extends into temperate zones.

Green anoles are medium-sized and have well-developed limbs. They are arboreal and specialized to live in tree crowns. Even though the body is generally green, the lizards can change to greenish brown or blackish brown within about 1 min.

This species has been transported to islands in the Pacific Ocean. It is currently found on the Hawaiian islands of Kauai, Oafu, Molokai, Maui, and Hawaii; and on Guam, Saipan, Tinian, Lota, Yap, Palau, Okinawajima, Chichijima, and Hahajima (Hasegawa 1986; Hasegawa et al. 1988; Ota et al. 1995; McKeown 1996).

Although quantitative data are insufficient, green anoles have not formed large populations on the Micronesian islands (Arthur C. Echternachit, personal communication). Preliminary investigations on Okinawajima (Naha city) were undertaken in February 2006 and November 2007. The presence of the green anole was confirmed, but the population density was thought to be much lower than on the Ogasawara Islands (Mitsuhiko Toda, unpublished data). The underlying factors accounting for limited population development on islands other than Ogasawara have not been identified but may include the organization of the islands' natural biological communities (including natural enemies or competitors).

22.3 Ecology and Population Control of Anoles on Ogasawara

22.3.1 Introduction and Expansion of Population Range

There is no definitive information on how green anoles arrived on Ogasawara. Circumstantial evidence indicates that they came to Ohmura on Chichijima in about 1965 or 1966 and became established between 1968 and 1972 (Hasegawa 1986; Hasegawa et al. 1988; Miyashita 1991; Suzuki 2000). Because Chichijima was under the jurisdiction of American forces at the time of their introduction, anoles may have been brought unintentionally from Guam with supplies or as pets of American military personnel (Levern 2003). They were first found in Ohmura in 1972 and in Komagari in 1979, and later range expansion radiated from these two locations. The anoles then came to occupy the whole island (Miyashita 1991; Suzuki 2000).

Another suggestion is that green anoles were brought into the southernmost village (Motochi) on Hahajima from Chichijima more than once in the early 1980s (Suzuki 2000). Distribution expanded from Motochi to either northern or southern parts of the island (Miyashita 1991). The animals were seen in 1994 around Kitamura, located in the northern section of the island, and they were later found throughout Hahajima (Suzuki 2000).

There are no comprehensive data on the current distribution range. Based on our own knowledge and on anecdotal information from other researchers and locals, green anoles may be distributed over almost all of Chichijima and Hahajima. Except for harbors, where there is no vegetation, the lizards are widely reported from the coasts to the mountains, in natural and secondary forests, in urban districts and farmland. The distribution area of this species in Ogasawara is estimated at 44 km^2.

22.3.2 Population Density

We estimated anole population density in an arboretum operated by the Forestry and Forest Products Research Institute in Kiyose on Chichijima in autumn 2004. The area consists of secondary forest containing rosewood (*Schima mertensiana*), among other species. A mark and recapture program was run for 19 days from mid-September to the beginning of October. A total of 171 anoles were marked. On the assumption that the population was closed, an analysis done with "Capture" software (http://www.mbr-pwrc.usgs.gov/software/capture.html) estimated a population density of 1,450 individuals/ha within the study area. The estimated number of anoles on all of the Ogasawara Islands was 6.38 million (calculated using density estimates within the distribution ranges on Chichijima and Hahajima).

Population density has been continually monitored in the study area. Estimates were made 12 times over two or three 1-week periods per year from autumn 2004 to autumn of 2008 (*1). In each study week, we estimated density (using the Lincoln Index Method) at about 500–800 individual/ha (Fig. 22.1). At this site, anole density decreased over time. Sex ratio varied spatially, with a male majority in the Forestry and Forest Products Research Institute arboretum in Kiyose, a 50:50 ratio in some areas, and a female majority in others. More females were seen in grassland and shrub areas, whereas more males were seen in areas with poorly developed swards of grass.

Okochi et al. (2006) reported the population densities of anoles on Chichijima. They used a mark and recapture method at 11 sites on Chichijima in June 2004, and estimated a population density of 600–2,570 individuals/ha, with an average of 1,270. Our results are in line with this.

In sum, the population density of anoles on Ogasawara is several hundred to several thousand per hectare. On the whole islands, there are several million.

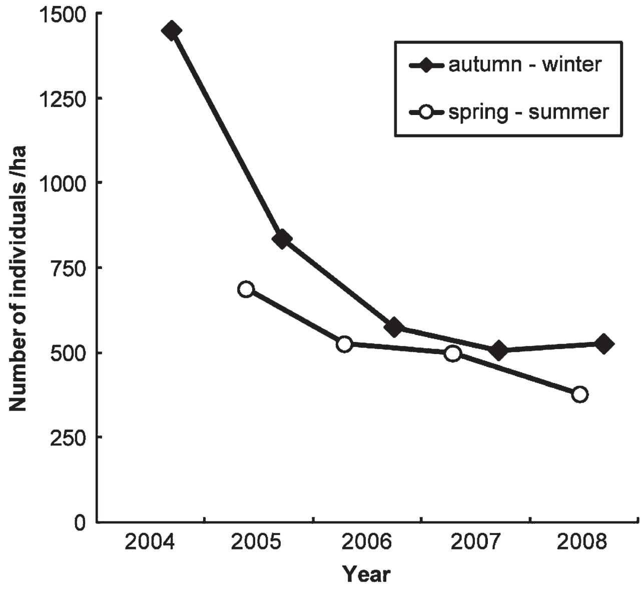

Fig. 22.1 Fluctuation of population density of green anoles in Kiyose, Chichijima

22.3.3 Growth and Maturation

Unlike other lizards, anoles lay only one egg, which is produced in alternating sequence by the left and right ovaries (Savage 2002; Lovern et al. 2004). Ten Female anoles from Chichijima lay 138 eggs from May to October in captivity, and the average number of eggs laid in one season by one female is 13.8 (Noriyuki Komatsu, personal communication, *1).

The incubation period is about 40 days (Hasegawa 1994). The snout-vent length (SVL) in five individuals just after incubation in captivity was 21.7–24.9 mm. A field survey of hatchling anoles demonstrated SVLs of 20–30 mm. Hatchlings started to appear from the beginning of June. They were seen most frequently in September and were not found from December to May of following year. Because immature individuals are absent from May to the beginning of June, the breeding season of this species is estimated to extend from April to October, with a maturation period of about 1 year.

According to Suzuki (2000), the SVL of the smallest male with visibly distinguishable penis or testes is 42 mm and the smallest SVL of a female with an egg is 43 mm, thus it is considered these are the sizes of sexual maturity for the two sexes. From observations of immature marked individuals, we confirmed that SVL reaches 40–60 mm 1 year after hatching. However, it is not clear whether small males of about 42–55 mm can breed in the wild.

Males of this species are much larger than females. The SVL of Ogasawara males reaches a maximum of 74 mm, whereas that of a female attains a maximum of only 60 mm. Tail length is about double SVL; total length of the largest individuals is 210 mm, and maximum weight is about 8 g.

Maximum longevity in the United States exceeds 7 years and 1 month in captivity (Bowler 1977); the oldest individual from the Ogasawara Islands attained more than 6 years and 3 months (Toda 2005). Because all individuals in the Ogasawara Islands study were males and were already mature when captured, the potential longevity of this species is estimated to exceed 7–8 years.

22.3.4 Feeding Behavior and Its Impact on the Ecosystem

Many kinds of lizards are secondary consumers in food webs, preying on small animals including insects and spiders, and being preyed upon by birds, snakes, or mammals. Green anoles are also insectivorous, preying mainly on Coleoptera, Hemiptera, and Araneia on Hahajima, according to Suzuki (2000). Moreover, according to analyses of stomach contents by the Japan Forest Technology Association, anoles prey most frequently on Hemiptera and Coleoptera on Chichijima and Hahajima; they also eat Lepidoptera (mainly larvae) and Hymenoptera (mainly ants; Japan Forest Technology Association 2005). Because of the relationship between the expanding distribution range of anoles and the depleted numbers of entomofauna, local extinctions or decreases in the endemic butterfly *Celastrina ogasawarensis*, endemic Odonata, diurnal Cerambycidae, and endemic cicada *Meimuna boninensis* are considered to be the result of anole predation (Karube 2004; Makihara et al. 2004; Takakuwa and Suda 2004; Karube 2005; Yoshimura and Okochi 2005; Karube and Suda 2004).

The Ogasawara snake-eyed skink *Cryptoblepharus nigropunctatus* is the only terrestrial reptile native to Chichijima and Hahajima. Anoles have a body only slightly larger than that of the skink but have a much more massive head and mouth (head width is 1.6-fold larger, on average; Japan Wildlife Research Center, unpublished data). Anoles have powerful jaws and well-developed teeth. When they prey on large insects, they chew up the prey in a few minutes and then swallow it, breaking the exoskeleton. The cicada *Meimuna boninensis* is one of the largest anole preys; in one instance after catching a cicada, a male anole cut it into small strips and abraded it against a tree after chewing the thorax. The lizard subsequently swallowed only one portion of the cicada (Mitsuhiko Toda, unpublished data). Green anoles are able to prey on much larger insects than native skinks, and the anole toe lamellae allow the animals to hunt on narrow branches and leaves. Anoles also have superior jumping abilities due to their long hind legs. The animals occur in a variety of environments at high densities, and their impact on the insect populations of Chichijima and Hahajima is likely enormous. Within the food chains of these islands, the primary consumers (insects) are in a state of decline, whereas the new secondary consumer (alien green anole) is flourishing. Hence, the structure of the island ecosystem has been massively altered.

Anoles are competitors and predators of the native skink, whose population may have significantly decreased compared with pre-invasion densities (Suzuki 2000). Reptile census data from 1984 (Hasegawa et al. 1988) and preliminary enumerations made by the Japan Wildlife Research Center (unpublished data) show that as the distribution of anoles extends, skink population density decreases.

Nevertheless, skinks may be more frequently observed than anoles in some parts of Hahajima (Mitsuhiko Toda, unpublished data); apparently, coexistence is possible at certain times and places. Unfortunately, there are no data on skink population densities before the green anole invasion, making definitive historical statements on impacts impossible. However, the ecological relationships between the two reptile species can be quantitatively analyzed within the current ecosystem structure, making it possible to construct projections of likely outcomes of the interaction of skinks and anoles.

22.3.5 Population Structure

From the results of anole surveys with continuous mark and recapture methods between 2004 and 2008, the survival rate at each life stage was calculated (Table 22.1, *1), and a life table was constructed as follows: the average number of eggs laid in one season by one female was 13.8 (*1), the hatching rate was 0.9 (from Lovern et al. 2004), the survival rate from hatchling to yearling adult was 11.5%, from 1 to 2 years of age was 35.5% (*1), and from 2 to 3 years of age was 33.3%; females produced eggs in the year after hatching; the sex ratio was estimated to be 50:50. Based on these values, it was estimated that from 1,000 eggs, 103.5, 36.7, 12.2, 4.1, 1.4 individuals would survive after 1, 2, 3, 4, 5 years, respectively (*1).

Age-specific survival and fertility rates were used to construct a matrix projection model of the population (using Ramas EcoLab, http://www.ramas.com/ecolab.htm). The starting population density in the model was the value obtained in autumn 2004 (1,450 individuals/ha). The virtual population increased 14.5-fold after 15 years when there was no trapping of reptiles. This projection does not match empirical observations of changes in population density through age classes; the number of eggs produced or the survival rate was likely overestimated. We also made a projection assuming that 90% of adults were trapped and removed from the population each year. The outcome was complete extirpation in 4 years.

22.3.6 Basic Concepts of Population Control

The life span and reproductive rate of green anoles are very similar to those of mammals and birds. Females produce about 14 eggs per year, comparable to prolific mammals and birds. The green anole has an 8-year life span and a 30–50% survival rate after maturity, both much higher than in the case of small rodents. The body mass of the green anole is several grams, which is less than most mammals and birds but greater than insects. However, green anole population density is estimated to exceed 1,000 individuals/ha, much higher than for mammals and birds but similar to large insects. Hence, the green anole appears to have biological characteristics intermediate between those of large terrestrial animals (e.g. mammals and birds) and small animals (e.g. insects). This should be taken into account

Table 22.1 Life table for Kiyose population of green anole

Stage	x	N_x	S_x	M_x
Egg		1,000.0		
0–1 yr	0	900.0*	0.115	6.165
1–2 yr	1	103.5	0.355	6.165
2–3 yr	2	36.7	0.333	6.165
3–4 yr	3	12.2	0.333	6.165
4–5 yr	4	4.1	0.115	6.165

* hatchling rate was estimated from Lovern and Passek (2002).

when determining the direction of the green anole population control project.

Below we summarize basic concepts that must be considered when attempting to control the green anole population on the Ogasawara Islands.

22.3.6.1 Prevention of Population Dispersal

The green anole is widely distributed on both Chichijima and Hahajima, but we have not measured increases in densities. Although population declines of endemic insects have been reported for both islands, endemic insects are frequently observed on neighboring islands that have not been invaded (Yoshimura and Okochi 2005). Because eradication after invasion is so difficult, highest priority should be given to preventing anole dispersal to these neighboring islands. The green anole has a strong tolerance for starvation; it is very evasive, is well camouflaged, and spreads rapidly. Eradication after establishment is extremely labor intensive. Of particular importance is control of vectors such as building supplies and materials in which anoles can hide. Preventing its range expansion to other islands should take priority over controlling the population on the infested islands of Chichijima and Hahajima.

22.3.6.2 Area-Specific Control

The population of green anoles in Chichijima and Hahajima is estimated to be in the millions; simultaneous eradication of all of these individuals would involve a huge effort. As a first step to total eradication, green anoles should be excluded from those areas that are most important for biodiversity conservation (e.g. the points from which green anoles disperse and where native insects still exist). It is also necessary to block their movement so as to fragment their distribution range.

22.3.6.3 Establishing a Method for Capture

Green anoles are small, they reproduce rapidly, and their population density on the Ogasawara Islands is high. Thus, methods used to capture large mammals and birds will likely be unsuitable. Instead, techniques for pest control, such as setting traps and spraying pesticide, would be more appropriate. A preferred method would exert continuous pressure on the green anole population in key areas, even when capture rate per unit time is inefficient.

22.3.6.4 Regional Characteristics

Green anoles occur in various population densities in forests, grasslands, farmlands, urban areas, and a variety of other habitats. Ease of capture and accessibility of trapping sites also vary by habitat. Thus, it is necessary to develop and apply techniques according to regional characteristics.

22.3.6.5 Adaptive Management to Monitoring Data

Periodic measurements are necessary to evaluate the efficacy of population control in targeted sites, and management plans should be developed based on these evaluations. It is important to monitor the population and community structure of both the eradication target (green anole) and the conservation target (native insects). These monitoring data should be taken into account during the continuous improvement of the management plan.

22.4 Ongoing Projects on the Ogasawara Islands

The Ministry of the Environment has an ongoing project for population control of the green anole based on basic tenets outlined in Sect. 22.3. Two projects, "Control around the harbor in Chichijima to prevent unintentional dispersal to neighboring islands" and "Regional eradication within the habitat of endemic insects in Hahajima," have been running concurrently since 2005, using methods developed during previous studies to capture green anoles. Here we outline these methods and the equipment being used to restrict the movement of the green anole.

22.4.1 Development of Methods for Regional Eradication of Anoles

22.4.1.1 Capturing Methods

Small reptiles are not important as human foodstuff, nor do they cause any serious damage in agriculture and forestry. Hence, there are no traditional reptile-capture techniques to match those available for hunting, fishing, and insect control (Toda and Yoshida 2005). Developing such reptile-capture techniques is important to control the green anole. To proceed, the following should be clear:

- No special technology should be required, and regular work staff must be able to operate any devices.
- It should be possible to capture anoles during periods of inactivity, thus maintaining long-term continuous pressure on their populations.
- Effects on native species (that are being conserved), the natural environment, and human health must be minimized.

Since 2004, angling has been used to capture animals during ecological surveys. Although this method is efficient (a skilled worker can catch 20–30 anoles per hour when angling in high-density habitats on sunny mornings from April to June) it is restricted by season, time of day, and weather, and can only be used when anoles are feeding.

Repellent spray against habu vipers is available to consumers. Its efficacy against anoles was investigated, but the possibility of negative environmental impacts precluded its adoption.

Dr. Tsuyoshi Ono of the Subtropical Agriculture Center of Tokyo Metropolitan Government advised us that anoles are often caught by the adhesive traps that are used outdoors for insect surveys. Thus, adhesive traps for cockroaches were set on tree trunks, and many anoles were caught.

In 2005, we paint-marked 13–41% of anoles and set 700 adhesive traps per hectare on some plots in Chichijima. Within a few days, 10–50% of the marked individuals were caught. Anoles can be trapped on tree trunks without baiting as they frequently pass between the crown and the ground. Although capture is much less efficient than angling, use of adhesive traps is superior because each trap exerts long-term continuous pressure. We made improvements in terms of ease of trap deployment, replacement, and collection. Weather resistance was upgraded, and traps were fabricated for repeated use. Traps were also designed for easy separation into burnable and nonflammable waste after use, and production cost was reduced. Currently, polypropylene traps are being developed during previous studies used on Chichijima and Hahajima (Fig. 22.2).

22.4.1.2 Exclusion Barriers

Field surveys showed that individuals caught by adhesive traps were replaced by immigrants from elsewhere. Consequently, blocks to immigration were required. It is difficult to design fences to guard against anoles because anoles can rapidly climb smooth barriers. Pacara et al. (1983) introduced fences against anoles that had an added roof on the top. The roof was 20 cm wide and made of polypropylene. At the Caribbean study site, vegetation was pruned for 2 m outside the fence to prevent anoles from jumping over the barrier. Three species of *Anolis* (not *A. carolinensis*) released inside the fence were unable to escape over a period of weeks.

Because the landscape of the Ogasawara Islands is complicated and the area is prone to large typhoons, adding a roof to the top of fences was considered impractical. Indoor and field trials showed that Teflon sheeting was the most appropriate material because the intermolecular attraction is small, making it difficult for anoles to climb, and the plastic is highly weather resistant and easy to fabricate. A Teflon sheet 30 cm high was installed on the top of a stainless-steel mesh fence 0.8–1 m high. The whole structure was inclined outward about 15°. Anoles were unable to scale this two-piece fence. It was necessary to remove vegetation from 2-m wide buffer zones on either side of the barrier to prevent lizards from jumping from surrounding trees or shrubs. A 4-m wide clearing could be problematic for native tree vegetation. However, careful selection of a fence route through alien vegetation would serve a second function of reducing stands of plant invaders.

An exclusion fence has been installed on Hahajima (Fig. 22.3) as part of an operation to keep anoles out of 4 ha of naturally regenerated vegetation.

Fig. 22.2 An adhesive trap for capturing green anoles

22.4.2 Capturing Anoles in the Vicinity of the Harbor to Prevent Dispersal to Neighboring Islands

Most sightseeing ships heading to islands of the Chichijima group (e.g. the uninhabited islands Anijima, Ototojima) and Mukojima leave from Futami harbor. Although no anoles have been recorded on these islands, there is always a risk of some being transported there. Tourists are taken aboard from four piers for transport to the uninhabited islands. Our goal was to reduce anole population density around the piers and to make it difficult for anoles to board the ships. Mr. Yuji Takafuji, a Chichijima resident, played a central role in implementing this concept. He worked with seven other laypeople who kindly contributed their time. About 1,000 traps were deployed around the piers from December 2006 through August 2009 (*1). In addition, 34 volunteers trapped lizards in a residential area not far from the piers. More than 5,000 (*1) animals were caught. By comparing densities around the harbor before trap deployment with data from October 2007, we concluded that the procedure reduced density around the harbor by 35%.

Although the number of anoles declined from spring to early summer 2007, there was a rapid increase in trapping from August to October. We believe most of the autumn increase occurred through the immigration of individuals from the mountainsides, across a paved road, and onto the dock. We had expected this double-lane road to act as a barrier to anole movement, but this was not the case. Unfortunately, it is difficult to set barrier fences along roads or in urban areas.

After 3 years (*1) of capturing anoles, we have identified transit points through which the animals frequently pass. These should be future sites of intense trap deployment, preferably with barrier fences to block anole movement.

Fig. 22.3 A fence to block green anoles invading the nature revitalization area in Shin-Yuhigaoka, Hahajima

22.4.3 Preventing Local Extinction of Insect Species Endemic to the Ogasawara Islands

On Hahajima, the history of anole invasion is quite short. There are more surviving native insects on Hahajima than on Chichijima, where there have been no sightings in the past decade of the endemic butterfly *Celastrina ogasawarensis* or the endemic dragonfly *Rhinocypha ogasawarensis* (a few of each survive on Hahajima; Karube 2004; Takakuwa and Suda 2004). The sighting frequency of native skink is also higher on Hahajima than on Chichijima. In the Hahajima island group, there is no alternative environment to forest vegetation for insects that occur specifically within this habitat. Hahajima should be given priority over Chichijima in attempts to regenerate natural vegetation through the control of anoles. Procedures should be aimed at maintaining the native insect community and other flora and fauna.

The Ministry of the Environment first installed a fence in 2006 to control anole invasion in an attempt to regenerate natural vegetation. Shin-Yuhigaoka was selected as the first site on Hahajima. The second site chosen was at the southern tip of Minamizaki. Shin-Yuhigaoka supported many native insects characteristic of the Ogasawara Islands. A local organization for native butterfly conservation ("Ogasawarashijimi no Kai") and "Japan Butterfly Conservation Society," a nationwide nonprofit organization, have conducted continuous censuses of insect species, patrolled for poachers, and controlled anoles. The two sites chosen for this work are important in the local community. Furthermore, as roads are very winding, deforestation is minimized around the fences.

At Shin-Yuhigaoka, forests consisting of rosewood *Schima mertensiana* have been regenerated and maintained. Exotic trees such as *Bischofia javanica* and *Morus australis* have been trimmed, and experience has shown that the anole exclusion fences can help regenerate insect populations. A fence of more than 944 m (*1) was completed in spring 2008 (Fig. 22.3). In summer 2008, more than 5,300 adhesive traps were deployed in a naturally regenerating area (ca. 2 ha) surrounded by fence. Anole and insect monitoring continue, and a project for the regional eradication of anoles has progressed.

A fence blocking cats and anoles has been completed at the southern tip of Minamizaki on Hahajima. Within the 2-ha area enclosed, there has been an attempt to recover a breeding colony of the brown booby *Sula leucogaster*. This seabird no longer breeds on the inhabited Ogasawara Islands. In addition to the seabird colony, the management is attempting to restore grassland vegetation and native insect fauna.

22.5 Epilogue

Genus *Anolis,* a world largest lizard genus, are very diverse in morphology, ecology, and behavior, ranging from about 10 to 50 cm in length. Caribbean *Anolis* has been the subject of evolutionary biology studies for more than 40 years. Green anoles have been paid particular attention, and, among reptiles, sequencing of their genome is the most advanced.

However, anoles have achieved notoriety as alien invaders of Pacific islands. Their destructive effects on native ecosystems should be terminated. This is particularly important on Okinawajima, which was invaded only 14 years ago (*1), and where the alien lizard population seems to be in a type of incubation period that precedes an outbreak (as was the case on Chichijima). The Okinawajima anole population should be extirpated before it does irreparable damage.

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Chapter 23
Eradication and Ecosystem Impacts of Rats in the Ogasawara Islands

Takuma Hashimoto

Abstract Alien rat species have severe negative impacts on ecosystems in many regions, including the Ogasawara Islands. In some cases urgent countermeasures are required, for example, when predation by rats endangers populations of seabirds breeding on uninhabited islands. Some countries, notably New Zealand, have had success eradicating rats from islands using rodenticides. In 2007, we attempted to eradicate the black rat *Rattus rattus* from Nishijima, in the Ogasawara Islands. We achieved almost complete eradication using bait stations and using diphacinone as a rodenticide; we were also able to minimize risks to non-target animals and secondary poisoning events. Rodenticide has been broadcast aerially in Mukojima and Higashijima, and we are still monitoring the progress of this program. We will attempt to eradicate more alien rats in the Ogasawara Islands by considering geographical factors, operating conditions, and impacts on non-target animals.

23.1 Introduction

Invasive species control has become one of the most important issues in biodiversity conservation. Predatory invasive animals have tremendous effects on ecosystems, especially on islands, where many open niches without predators often exist, allowing for easy invasion.

The oceanic Ogasawara Islands have never been connected to a continent. Their fauna consists of species belonging to an extremely limited number of species groups, especially limited in mammals, which do not have the dispersal ability of birds and insects. For example, Bonin flying foxes *Pteropus pselaphon* and Sturdee's pipistrelles *Pipistrellus sturdeei* (extinct) are the only two bat species native to the Ogasawara Islands (the latter is possibly misrecorded; Abe et al. 2005). Mammals that cannot fly are not able to migrate from the mainland over distances of more than 1,000 km; thus, the only terrestrial mammal in the native ecosystem of the Ogasawara Islands is the bat.

However, since the nineteenth century, various alien species have invaded the Ogasawara Islands as a result of human settlement. Goats (*Capra hircus*) were intentionally introduced as an emergency food source for whale hunters, dogs (*Canis familiaris*) and cats (*Felis catus*) as companion animals, and pigs (*Sus scrofa domesticus*) as livestock. Rats were incidentally introduced into the Ogasawara Islands via ships.

Three species of rodents are confirmed inhabitants of the Ogasawara Islands: Norway rat (*Rattus norvegicus*), black rat (*R. rattus*), and house mouse (*Mus musculus*) (Kawakami 2002). These species, so-called cosmopolitan species, have expanded their distribution worldwide from various origins (*R. norvegicus* from central Asia, *R. rattus* from southeast Asia, and *M. musculus* from southwest Asia). These pioneers of invasive mammals have invaded and persisted in new habitats all over the world for centuries or millennia (Yabe 2008). The two *Rattus* species have large bodies, generally weighing more than 100 g and sometimes >300 g, but *M. musculus* is small, weighing less than 20 g. These alien rodents have successfully invaded almost all areas of Japan and have detrimental effects on humans. *R. norvegicus* and *R. rattus* damage human food, cause sanitation problems and disease, and cut cables (Yabe 1998). *M. musculus* feeds on crops in fields or in storage.

23.2 Effects of Alien Rats on Ecosystems

Until recently, little attention has been paid in Japan to the effects of *R. norvegicus*, *R. rattus*, and *M. musculus*. One possible reason for this is that with the exception of limited warm areas such as in big cities, the temperature of the Japanese mainland is too low for the successful establishment of the two *Rattus* species. Yet on tropical and subtropical islands outside of Japan, the severe impacts of *Rattus* on island ecosystems have been of great concern since the early twentieth century. *R. rattus* and *M. musculus* are both included on the list of "100

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of the World's Worst Invasive Alien Species" selected by the IUCN (Lowe et al. 2000). However, none of the three species is included on the list of "100 of Japan's Worst Invasive Alien Species" (Murakami and Washitani 2002).

Only recently have the impacts of alien rats on ecosystems of subtropical islands such as the Nansei and Ogasawara Islands started to be reported. In 1997, an outbreak of *R. rattus* in the Amami Islands caused damage to the bark of fruit trees such as *Citrus tankan* (Yabe 1997). Subsequently, damage to the bark of field plants such as *Leucaena leucocephala* was reported on many of the Ogasawara Islands (Kitahara and Sato 2000; Nobushima 2003; Watanabe et al. 2003). Surveys of vegetation damage caused by rats on uninhabited islands of the Ogasawara Islands such as Mukojima revealed that more than 30 plant species have been damaged in some way, including seed damage to *Pandanus boninensis* and *Terminalia catappa* and small branch damage to *Orchrosia nakaiana* and *Hibiscus glaber* (Watanabe et al. 2003; Fig. 23.1). In Mukojima, damage by rats may be why attempts to restore native vegetation have not been successful despite success in eradicating feral goats in 2004 (Ogasawara Islands Branch Office of the Tokyo Metropolitan Government and JWRC 2007).

In the Ogasawara Islands, native animals as well as plants have been impacted by rats. In Anijima, the change in population density of land snails over 17 years, together with evidence of rat attacks on snail shells, indicates that predation by rats could be a cause of the observed decrease in the population of native land snails (Chiba 2007). Moreover, in 2006 researchers found that rats preyed on seabirds such as *Bulweria bulwerii* and *Oceanodroma tristrami* (listed as VU on the IUCN Red List) breeding in Higashijima (Horikoshi et al. 2007). We found *B. bulwerii* feathers in the stomach contents of some *R. rattus* captured in Higashijima (Hashimoto et al. unpublished data).

Fig. 23.1 Fruits of *Pandanus boninensis* damaged by alien rats. The epicarp has been removed and seeds had been all consumed

A list of studies on the ecological impacts of alien rats on the Ogasawara Islands is shown in Table 23.1. Predation damage to plants has been reported in many islands. Some researchers have suggested that rat predation on seeds affects the regeneration of native trees (Yamashita et al. 2003; Abe 2007). To date, the impacts of rats on animals in the islands have not been well reported, and information is available for only a few islands, such as Anijima (land snail decrease) and Higashijima (seabird predation). Survey efforts on other islands have not been sufficient to provide a clear understanding of the potential impacts of alien rat species on native animals.

As mentioned previously, in some countries, the ecological impacts of alien rats have been studied since the early twentieth century and are well known. The earliest study concerned rat predation on seabirds at seabird breeding sites. In 1912, it was suggested that predation by rats could be a cause of the observed decrease in the population of white-tailed tropicbirds (*Phaethon lepturus*) breeding in the Bermuda Islands (Gross 1912). The avian community on Lord Howe Island in Australia, now a World Heritage site, suffered from devastating damage caused by rat predation (Hindwood 1940). Birds are not the only victims. Eggs and juveniles of green sea turtles (*Chelonia mydas*) are heavily preyed upon by rats on Sangalaki Island in Indonesia (Meier 2003), and the number of palm crabs (*Birgus*

Table 23.1 Damage to plants and animals by invasive rodents on the Ogasawara Islands

Island	Damage	Reference
Mukojima group		
Mukojima	Seeds of *Rhaphiolepis indica*	Kato (2002)
Mukojima	Seeds and twigs of endemics	Watanabe et al. (2003)
Torishima	Eggs and chicks of *Oceanodroma tristrami*	Hasegawa (1992)
Chichijima group		
Chichijima	Bark of *Leucaena leucocephala*	Kitahara and Sato (2000)
Chichijima	Seeds if *Elaeocarpus photiniaefolius* and *Neolitsea gilva*	Kanto Regional Forest Office (1999)
Anijima	Land snails	Chiba (2007)
Nishijima	Seeds of endemic plants such as *Neolitsea aurata*, *Livistona chinensis* var. *boninensis* and *Pandanus boninensis*	Abe (2007)
Higashijima	Eggs, chicks and adults of seabirds such as *Bulweria bulwerii*	Horikoshi et al. (2007)
Minamijima	Birds and hatching turtles	Jayasekara (2005)
Hahajima group		
Hahajima	Seeds of *Elaeocarpus photiniaefolius*	Yamashita et al. (2003)
Hahajima	Twigs of trees such as *Hibiscus glaber*	Nobushima (2003)

latro) in the Chagos Archipelago has been decreasing because of competition with rats for resources (Page and Meier 2006). An extreme example of rat predation can be found in the extinction of the great short-tailed bat (*Mystacina robusta*) in New Zealand. This ground hunting bat underwent a unique evolution in New Zealand, where few predatory mammals exist, and disappeared only 5 years after the rats invaded (Atkinson and Taylor 1991). There is an enormous number of studies examining rat predation on plants.

These case studies show that alien rat species have wider ecological impacts and can drive native species to extinction more quickly than researchers once thought. Researchers might understand only a small portion of the total impact of rats on native species of the Ogasawara Islands. There is even the possibility that the current ecosystem of the Ogasawara Islands has already partly destroyed by alien rats.

23.3 Distribution of Alien Rats in the Ogasawara Islands

Three alien rodent species, *R. norvegicus*, *R. rattus*, and *M. musculus*, inhabit the Ogasawara Islands (Table 23.2). *R. norvegicus* has been found on only three islands, Chichijima, Hahajima, and Hirashima (Kawakami 2002). However, there have been no recent observations of the species on Chichijima, suggesting that it could have been extirpated. We do not have sufficient information to determine whether *R. norvegicus* still survives on Hirashima. *M. musculus* has invaded only two inhabited islands, Chichijima and Hahajima, where agricultural land serves as its main habitat.

The most common rodents in the Ogasawara Islands is *R. rattus*; it survives on those islands inhabited by humans and on almost all uninhabited islands that have been explored. The only island on which *R. rattus* has not been found despite sufficient survey efforts is Minamiiwoto, one of the Volcano Islands (Ishii 1982; Kato et al. 2008). *R. rattus* has even settled on the small uninhabited islands of Torishima in the Mukojima group (11 ha) and Higashijima (28 ha) and Minamijima (34 ha) in the Chichijima group. *R. rattus* can settle on a tiny island with an area of less than 1 ha (Towns and Broome 2002), indicating that *R. rattus* might have already invaded some small islands that have not yet been explored.

23.4 Is Rat Eradication Possible? Examples from Around The World

There have been campaigns to eradicate rats from many countries. The earliest was in New Zealand, the leader in the management of alien species. In New Zealand, small-scale eradication campaigns started with rodenticides in the 1950s in an attempt to conserve the breeding habitats of seabirds. At the time it was thought to be impossible to eradicate rats completely. Thus, these attempts only achieved temporary decreases in rat populations and only around breeding habitats.

However, some of these attempts succeeded in accidental eradication. The first example in New Zealand was from Maria Island, whose area is less than 1 ha (Towns and Broome 2002). There, a rodenticide (warfarin) was used for the conservation of shearwaters in 1961, and the eradication of *R. norvegicus* was confirmed after a few years (Moors 1985). In the 1960s and 1970s, more examples of eradication were reported. The eradication of rats from Titi Island, located in the Cook Strait between the South and North Islands of New Zealand, showed that eradication was possible on a relatively large island (32 ha). This bolstered the impetus of rat control programs in the 1980s to aim for the complete eradication of rats (Towns and Broome 2002). At around the same time, eradication techniques improved, resulting in more effective rodenticides (second-generation anticoagulants) and aerial application methods. After the 1980s, campaigns were planned with eradication as their ultimate goal, and many more campaigns began to succeed. In the 1990s, the number of successful eradications came to 23 islands (100%) for *Rattus exulans*, 8 islands (100%) for *R. rattus*, 22 islands (86%) for *R. norvegicus*, and 19 islands (68%) for *M. musculus* (Towns and Broome 2002). After 2000, *R. norvegicus* was successfully eradicated from Campbell Island (113,000 ha), the largest island to date on which rodent eradication has been successful. On some islands, single projects have eradicated multiple target species (e.g. *R. rattus* and *R. norvegicus*; Towns and Broome 2002).

As eradication methods have improved, there have been at least 113 examples of eradication in New Zealand. Howald et al. (2007) stated that “the eradication of invasive rodents from islands…is no longer a rare event.”

There are also monitoring data on ecosystem restoration following rodent eradication. For example, in Rarotonga, one of the Cook Islands, the breeding success of Rarotonga monarchs (*Pomarea dimidiata*) in rodent-poisoned territories was three times higher than in unpoisoned territories (Robertson et al. 1994). In Fajou Island off Guadeloupe, French West Indies, rat predation on the eggs of hawksbill sea turtles *Eretmochelys imbricata* was stopped, clapper rails *Rallus longirostris* expanded its distribution, and the land crab population recovered after the eradication of small Asian mongoose *Herpestes javanicus* and *R. rattus* (Lorvelec and Pascal 2005). These studies show that ecosystem recovery can often occur soon after rat eradication.

Table 23.2 Current information of rodent distribution in the Ogasawara Islands (>10 ha)

Island	Rodent invasion	Area (ha)	Maximum altitude (m)
	Mukojima group		
Kitanoshima	Unknown	19	52
Mukojima	RR	257	88
Torishima	RR	11	33
Nakodojima	RR	158	155
Yomejima	RR	85	105
Maejima	Unknown	11	128
	Chichijima group		
Magojima	Unknown	16	134
Ototojima	RR	530	235
Anijima	RR	785	254
Nishijima	RR	49	100
Chichijima	RN[a], RR, MM	2,395	318
Higashijima	RR	28	92
Minamijima	RR	34	60
	Hahajima group		
Hahajima	RN, RR, MM	2,021	463
Hirashima	RN, RR	60	62
Mukoujima	RR	138	137
Anejima	RR	143	117
Imotojima	RR	122	216
Meijima	RR	133	113
	Others		
Nishinoshima	Unknown	29	25
Minamitorishima	RR?	151	9
Kitaiwoto	RR	557	792
Iwoto	RR	2,316	161
Kangokuiwa	Unknown	15	14
Minamiiwoto	None	357	916

RN *Rattus norvegicus*, RR *R. rattus*, MM *Mus musculus*

[a] Not found recently

23.5 Rat Eradication Methods

Rat eradication methods used on islands can be broadly classified into two categories: trapping and poisoning. Most eradications have been achieved using rodenticide. There are a few examples of rats having been successfully eradicated using only traps, though these are restricted to very small islands (<14 ha; Howald et al. 2007). The use of rodenticide is more suitable than traps for eradication, because poisoned bait, when made with well chosen drug formulation, is preferred by all rats and will not arouse suspicion. The most important issues to consider when planning rat eradication with rodenticide are (1) choice of rodenticide, (2) application methods, and (3) effects on non-target animals.

Acute toxin and chronic toxin are the two major types of rodenticides (Table 23.3). Acute toxin kills with a single small dose, whereas chronic toxin is lethal only after multiple doses. In general, acute toxins have strong toxicity and thus are highly efficient at killing animals, including non-target animals. Some acute toxins are toxic enough to kill even humans. However, use of chronic toxin rodenticides enables one to manage the risk to non-target animals by controlling their chances of coming into contact with the rodenticide. Baits loaded with chronic toxin rodenticides do not kill until the animal's toxin intake has reached a certain level. Moreover, some chronic toxin rodenticides have weaker toxicity for animals other than rats. Because of this, cumulotoxin rodenticides are used in most rat eradication campaigns. Anticoagulant rodenticide is the most commonly used chronic toxin rodenticide. This rodenticide inhibits blood clotting and leads to death by internal bleeding. Anticoagulant rodenticide consists of first-generation formulae, which contain relatively weak toxins; and second-generation types, which are slightly stronger. To date, brodifacoum, a second-generation anticoagulant, has been used most often in eradication campaigns, but use of diphacinone, a first-generation rodenticide, has become more common because the toxin is less harmful to non-target animals.

Table 23.3 Main rodenticide products and its characteristics

Rodenticide	Characteristics	Major products
Acutes	Lethal with a single small dose	Sodium fluoroacetate (1,080), Zinc phosphide
Chronics	Lethal after multiple doses	
Anticoagulant	Inhibit blood clotting and cause internal bleeding	
1st Generation	Less potent toxin	Warfarin, Diphacinone
2nd Generation	Relatively powerful toxin	Brodifacoum
ATP inhibitor	Disrupt ATP formation	Bromethalin
Vitamin D analogue	Cause high blood calcium levels and acute renal failure	Cholecalciferol

Rodenticide application methods are roughly divided into three types: bait station, hand broadcast, and aerial broadcast (Table 23.4). The method should be chosen based on the terrain and the area of the target island, budget, and effects on non-target animals. The bait station method emphasizes minimizing damage to non-target animals. Baits are not placed directly on the ground but into bait stations designed to make them harder for animals other than rats to approach. Hand and aerial broadcast involves placing baits directly onto the ground; in these cases, the risk to non-target animals cannot be fully controlled. Aerial broadcast is sometimes the most effective (and can be the only) method when the island is large or the terrain does not allow for ground-based work.

The range and intensity of risks to non-target animals will depend on the kind of rodenticide and application method

Table 23.4 Application methods of rodenticides in the field

Method	Description
Hand broadcast	Spraying rodenticides directly onto the ground by hand without specialized equipment
Aerial broadcast	Spraying rodenticides onto the ground from helicopters
Bait station	Locating rodenticides in special containers in order to minimize damage to non-target animals

used. It is important to formulate an eradication plan that minimizes these risks, especially on islands containing protected animals or those inhabited by predators that can be affected by secondary poisoning events.

23.6 Rat Eradication in the Ogasawara Islands: Nishijima

Efforts to control alien rat species on the islands of Japan have lagged behind those of other countries. The 1987–1988 *R. norvegicus* campaign on Koyajima (1.8 ha) in Fukuoka prefecture was the pioneering work and was aimed at conserving a Japanese Murrelet *Synthliboramphus wumizusume* breeding site. Trapping efforts continued until 1991, but no individuals were captured, indicating that the eradication campaign had been successful (Fukuoka Forest Research and Extension Center 2000). There are a few similar examples of alien rat eradication from small islands, but no eradication effort had been made on any of the larger islands before the case outlined here.

After 2000, as the impacts of rats on vegetation, seabirds, and land snails have been revealed, control of alien rat species was required in the Ogasawara Islands. Under the project "Studies on eradication of introduced species and the recovery of ecosystems in the Ogasawara Islands" (Global Environment Research Fund), conducted by the Forestry and Forest Products Research Institute, a campaign was begun in 2005 to eradicate alien rat species and to monitor ecosystems before and after eradication on Nishijima, in the Chichijima group. This was the first attempt at alien rat eradication in the Ogasawara Islands and represented a massive manipulated field experiment to reveal the ecosystem effects of rat eradication.

Nishijima is an uninhabited island 49 ha in area belonging to the Chichijima group. The island is located 1.8 km northwest of Chichijima, and its maximum elevation is 100 m. The coastal area of the island has a steep drop-off, but its central area is gently sloped. Most of the island is covered by pure forest of invasive *Casuarina equisetufolium*, and only a small area of native forest (e.g. *Livistona chinensis*, *Hibiscus glaber*, and *Terminalia catappa*) remains.

From 2005 to 2007, we deployed snap traps and cage traps to capture rats in a preliminary survey and conducted stomach content analysis and age determination by measuring eyeball weight. The results showed that *R. rattus* was the only rat species inhabiting Nishijima. In April 2006, we set four quadrats on the island and placed 30 cage traps in each quadrat. We captured rats for five successive days; captured individuals were marked and released. The population estimates from this mark–recapture study indicated that the rat population density could be as high as 90 individuals per ha (5–90 individuals/ha). It was also revealed that in Nishijima, *R. rattus* fed mainly on the seeds of gramineous plants, reproduced throughout the year, and were least active in winter (January–March). These results suggest that the most effective time for eradication would be around March, when the rat population density would be at its lowest and food resources scarce. The non-target animals that could have possibly fed on the baits were assumed to be *Coenobita* and land birds such as blue rock-thrushes *Monticola solitarius*. We thought that common buzzards *Buteo buteo toyoshimai* might be affected by secondary poisoning events, as this species preys heavily on *R. rattus*. We took all of these preliminary results into consideration when planning our eradication campaign, and we organized a meeting before the start of the campaign to explain our plans to related organizations (e.g. the government, companies, NPO) and local residents.

The *R. rattus* eradication campaign in Nishijima started in March 2007. We used bait stations and chose diphacinone, a first-generation anticoagulant, as the rodenticide. This choice was made to reduce the risk to non-target animals (diphacinone poses almost no lethal risk to birds), to lower the risk of secondary poisoning events, and to appeal to the preferences of *R. rattus*. To prevent the poisoning of non-target animals, we designed the bait stations to be higher than 10 cm so that *Coenobita* could not climb into them, and we placed the baits more than 5 cm away from the entrance of the traps to make it difficult for land birds to reach them. After field trials, we decided to use both T-shaped (Fig. 23.2) and cage (Fig. 23.3) stations. We placed 773 of these stations at 25-m intervals all over the island and visited them almost every day to check the amount of bait that had been removed and to replenish them. The stations were visited continuously until the end of April 2007, during which 69 kg bait was removed and 49 dead *R. rattus* were found. The number of dead *R. rattus* was far less than the estimated population, but this could have been because many *R. rattus* that had fed on the toxic baits died underground in their nests.

From April 2007 to September 2008, five monitoring surveys were conducted to examine whether any rats remained on the island. We did not capture any rats despite placing 4,328 cage traps in total. Moreover, no evidence of the existence of rats was found either on automatic video or from field surveys. All of these facts led us to determine that *R. rattus* had been eradicated from Nishijima.

Fig. 23.2 T-shaped bait station used for black rat eradication in Nishijima

Fig. 23.3 Cage bait station used for black rat eradication in Nishijima

We observed no damage to non-target animals during visits to the bait stations, and migration of *B. buteo toyoshimai* to Nishijima was not observed during our program.

23.7 Future Control of Rats in the Ogasawara Islands

After the success in Nishijima, in 2008 the Ministry of the Environment conducted rat eradication campaigns on Mukojima (including the satellite island Torishima) of the Mukojima group and on Higashijima of the Chichijima group. *R. rattus* predation on vegetation and on seabirds was catastrophic on these islands, and the highest priority was to restore the natural ecosystems. Mukojima is large (268 ha including Torishima), making eradication using only non-aerial application difficult. Higashijima is relatively small (28 ha) but hard to approach because of the surrounding ocean current, and thus equally unsuitable for non-aerial application. Therefore, diphacinone was broadcast aerially by helicopter on these two islands. The campaigns were conducted after careful preliminary surveying, consensus-building with local residents through meetings, and action planning for possible effects on non-target animals. Rodenticides were applied in August 2008. About 11 kg/ha rodenticide was applied on each island, for a total of 2,800 kg on Mukojima and 300 kg on Higashijima. In September 2008, traps were set to examine rat occurrence, but no evidence of rats was found. Thus far, no evidence of effects on non-target animals has been found.

To restore natural ecosystems, rat eradication is still needed on many islands. On Anijima of the Chichijima group, rat predation is damaging native land snails, and on Minamijima, its effect on seabirds is of great concern. It is very important to operate eradication campaigns in a way that will cause the least amount of damage to the environment, including non-target animals. Continued monitoring of rat occurrence in Nishijima, Mukojima, and Higashijima, where rat eradication has been achieved, is also vital. Although rats have had large negative impacts on vegetation, they are also an important food resource for an endemic protected species, *B. buteo toyoshimai*. Therefore, it is necessary for eradication programs to consider the effects of eradication in important habitats of the *B. buteo toyoshimai*. We must also monitor islands to check for reinvasion after eradication. Studies in New Zealand have shown that reinvasions occurred from habitats 500 m (*R. rattus*) and 2,250 m (*R. norvegicus*) away (Clout and Russell 2006). Anijima, a candidate island for the next eradication campaign, is only 500 m from Chichijima and will be always exposed to the risk of reinvasion. Reinvasion countermeasures, such as the development of survey methods to promptly detect reinvasions and regular monitoring using traps, are necessary.

The control of alien rat species in the Ogasawara Islands and in Japan is still in its infancy. Our successful eradication of rats on Nishijima has motivated eradication attempts on other islands, such as Mukojima and Higashijima, and also on Moyururi in Hokkaido for the conservation of the tufted puffin *Fratercula cirrhata* breeding habitat (Kushiro Nature Conservation Office, Ministry of the Environment 2008). As eradication methods are now well established worldwide, more attempts will be made in more regions in the future. The ecological characteristics of rats vary according to the environmental conditions unique to a given region, and rats can have unusual feeding habits and breeding seasons, especially on small and isolated islands. Therefore, it is important to plan eradication campaigns that are optimal to a region by collecting fundamental biological information on the target animals and by anticipating the effects of eradication efforts on non-target animals. The occurrence of alien rat species has still not been explored on some Ogasawara Islands. Such basic information should be obtained quickly. When using rodenticides, it is necessary to explain the campaign to local residents at meetings and to achieve their buy-in, even if the risk of damage to the environment is thought to be small.

The eradication of alien rat species is one way to restore an island's unique native ecosystem. If our attempts at rat eradication prove to be effective, and if long-term ecosystem monitoring indicates the recovery of native ecosystems through increased numbers of breeding seabirds and the restoration of native plants, this will give extreme satisfaction to we who are involved in these campaigns.

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Chapter 24
Eradication of the Invasive Tree Species *Bischofia javanica* and Restoration of Native Forests on the Ogasawara Islands

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Abstract *Bischofia javanica* is the most invasive alien tree species on the Ogasawara Islands; it is seen as a significant problem for biodiversity conservation. *B. javanica* has colonized four Ogasawara islands, namely, Ototojima, Chichijima, Hahajima and Hirashima. On Ototojima, *B. javanica* was never abundant and has been almost eliminated through actions of an eradication project operating since 2005. However, larger numbers of the alien trees are distributed over wider areas on Chichijima and Hahajima, and eradication will be problematic. Aerial images captured in 2003 showed that the invaded areas on Chichijima and Hahajima covered 50.9 ha (2.1%) and 296.5 ha (14.7%) of the islands, respectively. The potentially invasible habitat area on Hahajima was estimated to be 59.2% of terrain (judged from the vegetation type distribution on the island). A model predicting the alien tree's distribution on Hahajima was developed by mapping environmental factors (elevation, slope, drainage basin, curvature, and topographic openness) and distance from seed source. We developed an occurrence probability map (potential habitat map) estimated solely from measured environmental factors. The expected risk of invasion was estimated by comparing present distributions with potential habitat areas. A survey of forest development after clear-cutting *B. javanica* stands demonstrated natural regeneration potential in a diversity of native tree species. Based on available ecological knowledge and the results of eradication projects, we propose a management system aiming to eradicate *B. javanica* from whole island systems.

24.1 Introduction

Island ecosystems are vulnerable to alien species invasion, and their introductions to islands have caused enormous problems worldwide. Examples include *Myrica faya* on Hawaii and *Cinchona pubescens* on the Galapagos (Itow 1994). Among alien tree species that have colonized the Ogasawara Islands, bishopwood (*Bischofia javanica*, Japanese name: akagi) is the most problematic. It has negative impacts on individual native tree species and on insular ecosystems. *B. javanica* is listed as one of the 100 worst invasive alien species in Japan (Murakami and Washitani 2002). Although many cases of expanding alien herbaceous species distribution exist on mainland Japan, few examples of natural forest invasion by introduced tree species have been reported. It is a dioecious tropical member of the Euphorbiaceae that forms evergreen forest canopy. Its natural distribution extends through Taiwan, southern China, Southeast Asia, India, and South Pacific islands such as Polynesia and Papua New Guinea. It is widespread in the tropics but is just one of a diverse array of canopy species. *B. javanica* does not dominate forest stands within its natural range (Tanaka and Sakurai 1996). However, it is dominant on the Ogasawara Islands, where it outcompetes native species. *B. javanica* is one of the largest tree species on the Ogasawara archipelago, and native species are unable to coexist when it is dominant. Apart from effects on island plants, there is concern that the tree has negative impacts on indigenous birds and invertebrates that are dependent on native flora.

To conserve native ecosystems on the islands, it is necessary to control and eradicate alien species like *B. javanica*. Complete eradication is the most effective strategy against invasive species on the Ogasawara Islands, as little risk of re-colonization exists following extirpation, and, of course, management costs for control would be avoided. Although many examples of invasive plant control have been reported, cases of complete eradication are limited (Myers and Bazely 2003). Four islands in the Ogasawaras, Ototojima, Chichijima, Hahajima, and Hirashima (the Hahajima group) have been invaded by *B. javanica*. On Ototojima, the invasion

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was limited to a small number of individuals, and *B. javanica* has been almost eliminated by actions of an eradication project in operation since 2005. Eradication was almost complete on Hirashima by 2008. However, on the other two islands, larger numbers of invading trees cover a greater area of terrain, and eradication will be difficult.

B. javanica was recognised as a threat to forest ecosystems on the Ogasawara Islands by about 1975 (Toyoda 1975, 1981), and ecological research on the species started in the 1980s (Shimizu 1988; Toyoda and Tanimoto 1991; Tanimoto and Toyoda 1996). The Forestry Agency conducted a survey of *B. javanica* spread in 1993 and developed strategies for control (Forestry Agency of Japan 1994). In 1994, the Tokyo Regional Forestry Office (subsequently the Kanto Regional Forest Office) started experimental girdling of *B. javanica* trees and underplanting of native species in a National Forest surrounding Kuwanokiyama (Hahajima) in order to develop methods for controlling the expansion of *B. javanica* stands (Tokyo Branch of Kanto Regional Forest Office 2000; Uchida 2002). In 2005, the Japanese Ministry of the Environment initiated a *B. javanica* elimination project on Ototojima and Hirashima and in a National Park on Hahajima as a pilot study. The Forestry and Forest Products Research Institute (FFPRI) conducted a project to develop technologies for alien species eradication and restoration of native ecosystems on the Ogasawara Islands from 1995 to 2009 (Agriculture, Forestry and Fisheries Research Council 2001). Here, we document the distribution and ecology of *B. javanica*, review experiments and projects for its eradication, and propose a management system for eradication of the invader and restoration of native forests.

24.2 Assessing the Expansion of *B. javanica* Distribution on the Ogasawara Islands

24.2.1 Introduction of B. javanica

The Forestry Agency has reported the history of *B. javanica* introduction and range expansion on the Ogasawara Islands (Forestry Agency of Japan 1994). Cultivation of sugar cane was successful on the islands from 1889 onwards, but was accompanied by a shortage of firewood and charcoal for sugar production. *B. javanica* was one of the plantation tree species introduced before 1905 for fuel wood production. Plantation experiments in Renjudani (Chichijima) started in 1928; however, the plantation area was mere 0.51 ha by 1934. *B. javanica* was first introduced to Hahajima in the former Hyogidaira nursery during the early Showa period, and saplings were planted in Sekimon, Nagahama, the highland part of Uchuzawa, and along the old Kuwanokiyama path. A survey in 1977 showed that the range of *B. javanica* was restricted to areas around former plantations (Forestry Agency of Japan 1994). Typhoon No. 17 in 1983 caused considerable windfall of trees across Hahajima, and a large number of canopy gaps formed. The distribution of *B. javanica* has increased rapidly since then (Shimizu 1988). It is believed that range expansion followed windfalls caused by major typhoons on the islands in October 1989, June, October and November 1997.

24.2.2 Vegetation Types Colonized by B. javanica

Figure 24.1 shows the 1997 distribution of Chichijima and Hahajima forests in which *B. javanica* had become a canopy species (Tanaka 2005). Canopies of *B. javanica* and other species on Chichijima were visually identified on site and recorded on a map. The Forestry Agency made identifications at ground level on Hahajima and marked them on a map (Forestry Agency of Japan 1994). Areas colonized by *B. javanica* covered 2.7% of Chichijima and 11.1% of Hahajima in 1997.

In Chichijima, *B. javanica* is distributed in a patchy fashion in the western central and northern parts; in eastern to southern regions, distribution was limited. On Hahajima, concentrated canopies were present in the central part, as well as another patch along the road on the north side of the island. Invasions of the northern and southern capes were very limited. *B. javanica* mixed forests were also found in Sekimon, a Special Protection Area of a National Park. According to vegetation maps (Shimizu 1989), characteristic vegetation is (C) *Distylium–Schima* dry forest and (E) *Distylium–Pouteria* dry scrub on Chichijima, with (A) *Elaeocarpus–Ardisia* mesic forest and (F) *Dendrocacalia–Fatsia* mesic scrub at high altitudes on Hahajima (Fig. 24.2). Analysis of spatial relationships between *B. javanica* colonization and mapped vegetation types demonstrated a high proportion of invaded areas in (A) *Elaeocarpus–Ardisia* mesic forest, (B) *Schima* mesic forest (secondary vegetation of forest type A), and (F) *Dendrocacalia–Fatsia* mesic scrub. Invaded areas were limited in dry vegetation types such as (C) *Distylium–Schima* dry forest, (D) *Rhaphiolepis–Livistona* dry forest and (E) *Distylium–Pouteria* dry scrub (Fig. 24.3). Humid environments appeared to provide suitable habitat for *B. javanica* on the islands, as it was most frequent in three types of mesic vegetation.

24.2.3 Distribution Map of B. javanica Based on Aerial Photographs

A distribution map of *B. javanica* is necessary for planning control and monitoring its range. Direct visual measurement from the ground has the advantage of providing detailed

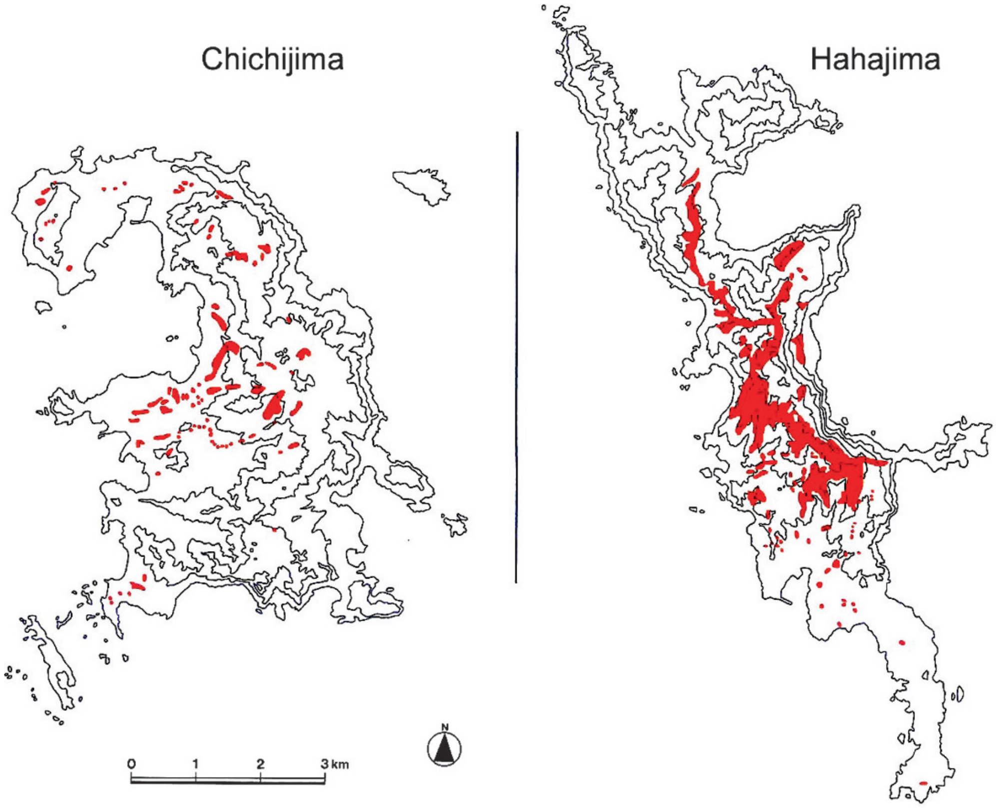

Fig. 24.1 Distribution of forests invaded by *B. javanica* (as a canopy species) by 1997. The forests were visually identified on site (Tanaka 2005)

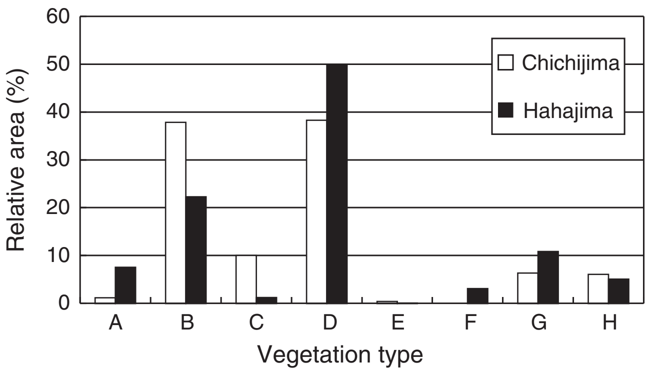

Fig. 24.2 Relative area of each vegetation type on Chichijima and Hahajima. A: *Elaeocarpus–Ardisia* mesic forest, B: *Schima* mesic forest, C: *Distylium–Schima* dry forest, D: *Rhaphiolepis–Livistona* dry forest, E: *Distylium–Pouteria* dry scrub, F: *Dendrocacalia–Fatsia* mesic scrub, G: *Leucaena* forest, H: Others

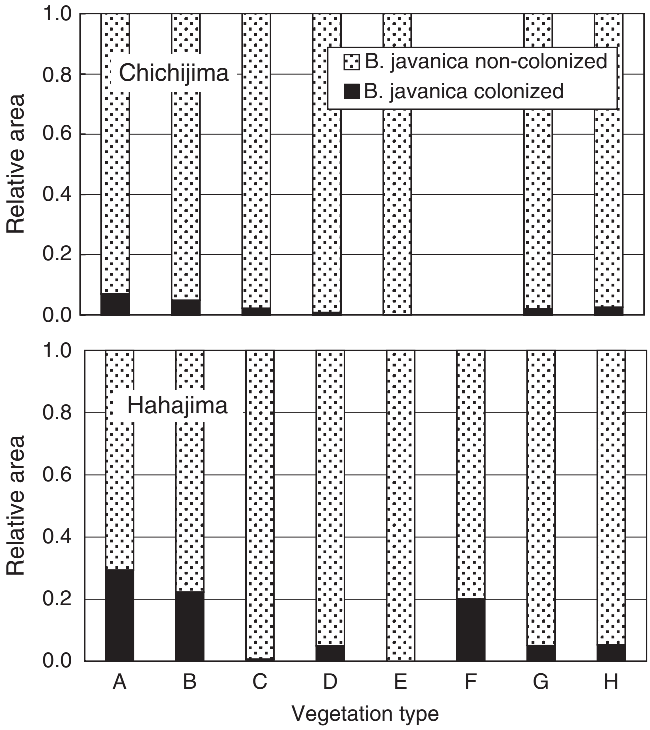

Fig. 24.3 Relative area of *B. javanica*-colonized areas and non-colonized areas for each vegetation type. A: *Elaeocarpus–Ardisia* mesic forest, B: *Schima* mesic forest, C: *Distylium–Schima* dry forest, D: *Rhaphiolepis–Livistona* dry forest, E: *Distylium–Pouteria* dry scrub, F: *Dendrocacalia–Fatsia* mesic scrub, G: *Leucaena* forest, H: Others

records for accessible areas; however, it is of limited use on difficult terrain with restricted access by foot. In such regions, a more precise mapping is provided by aerial photography whenever possible to identify canopies of a focal tree species. *B. javanica* canopies can be most easily distinguished from those of other tree species in spring when its new leaves change the canopy colour to bright green. Distribution maps of *B. javanica* canopy density on Chichijima and Hahajima were produced from aerial images captured in March 2003 (Fig. 24.4; Japan Forest Technology Association 2004; Kanto Regional Forest Office and Japan Forestry Foundation 2004; Ministry of the Environment 2007). The proportion of *B. javanica* canopy in a uniform forest area was categorised into five classes, with minimum forest area set to 0.1 ha. Ground-truthing was done to improve the accuracy of these interpretations. The *B. javanica* colonized forest areas were 50.9 ha on Chichijima (2.1% of the island) and 296.5 ha (14.7%) on Hahajima (Table 24.1). The original plantation areas on the two islands were small and similar, and the greater range expansion on Hahajima may indicate that environmental conditions on this island are more suitable than are those on Chichijima.

Overlays of spatial distributions of *B. javanica* canopy density on the vegetation map of Hahajima (Okutomi et al. 1985) identified (by vegetation type) potential habitats with high risk of invasion (Fig. 24.5). These were primary vegetation of the *Pisonia umbellifera*–*Elaeocarpus photiniifolius* community, the *Dendrocacalia crepidifolia* community, the *Ardisia sieboldii*–*Machilus boninensis* community, the *Schima mertensiana*–*Ardisia sieboldii* community, and secondary vegetation of communities with *Celtis boninensis*, *Trema orientalis*, *Acacia confusa*, and *Calophyllum inophyllum*. The

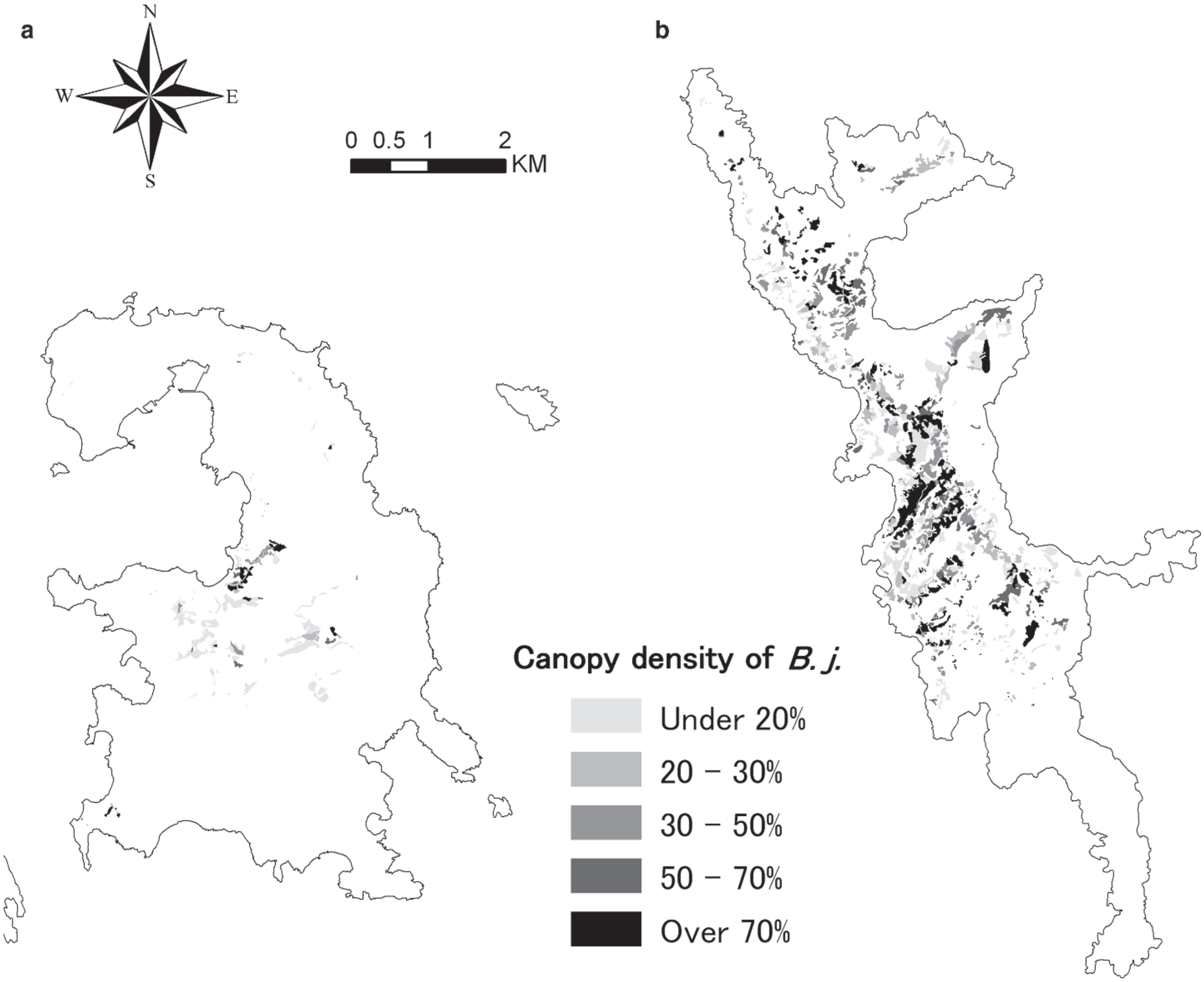

Fig. 24.4 Distribution of *B. javanica* canopy densities based on aerial images captured in March 2003 on (**a**) Chichijima and (**b**) Hahajima (Ministry of the Environment 2007). Minimum identified area is 0.1 ha

Table 24.1 Areas of *B. javanica* canopy density classes on Chichijima and Hahajima based on aerial images captured in March 2003

	Chichijima	Hahajima
Canopy density	ha (%)	ha (%)
Under 20%	35.4 (1.5)	86.4 (4.3)
20–30%	3.0 (0.1)	36.9 (1.8)
30–50%	3.9 (0.2)	47.7 (2.4)
50–70%	2.1 (0.1)	39.6 (2.0)
Over 70%	6.5 (0.3)	85.8 (4.3)
Total	50.9 (2.1)	296.5 (14.7)
Total area of island	2,380.0 (100.0)	2,021.0 (100.0)

potential habitat area estimated in this way was up to 1194.4 ha (59.2% of the island), covering most of Hahajima, except for narrow capes in the north and the south.

24.2.4 B. javanica Occurrence Probability and Evaluation of Colonization Risk

B. javanica on the Ogasawara Islands has expanded its range by replacing native tree species in canopy gaps. Identification of potential habitats for *B. javanica* to enable identification of areas with high risk of invasion is important in planning an eradication program on the islands. Initial surveys used vegetation types to project future range increases. This method employs biological indicator communities and has proven reliable. However, it does not identify environmental factors that affect the distribution of the invader. A predictive distribution model (Higgins et al. 1999) that uses environmental factors as explanatory variables has been increasingly used. In the case of an invasive species undergoing range expansion, however, areas exist that are physiologically suitable but not yet colonized. Hence, this model underestimates both potential habitats for the invasive species and the risk of colonization (Kriticos et al. 2003).

In order to solve this constraint, we developed a process-based statistical model to predict distributions of *B. javanica* using environmental factors and distance from a seed source (Kanto Regional Forest Office 2008). We estimated potential habitats and colonization risk for the whole island of Hahajima. The model uses the present (as of 2003) distribution of *B. javanica* as a response variable and environmental factors and distance from the 1977 range boundary (Forestry Agency of Japan 1994) as explanatory variables. A *B. javanica* distribution map (Fig. 24.4b) based on aerial images was used to extract presence/absence data for the species. Environmental factors were elevation, slope, drainage basin, curvature, and topographic openness calculated from 10-m DEM data. The model identified major controlling environmental factors and showed a high probability of occurrence on gentle slopes at high altitude.

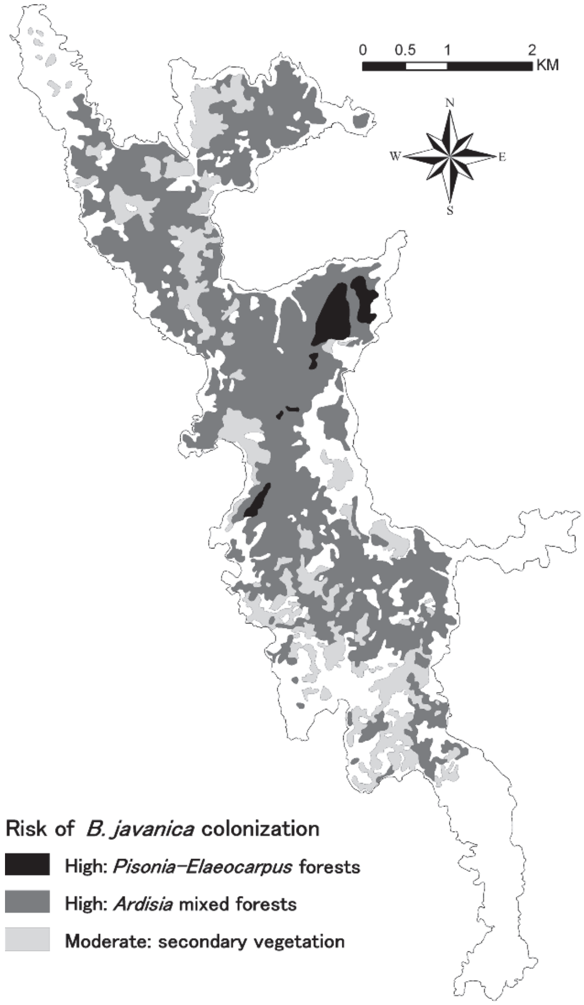

Fig. 24.5 Potential habitats for *B. javanica* estimated from the vegetation map (Japan Forest Technology Association 2004)

Figure 24.6a maps the present occurrence probability of *B. javanica* estimated by the model. Areas of high probability matched present distribution (Fig. 24.4b). In Fig. 24.6b, the effect of seed supply has been eliminated, so that the probability map is based only on environmental factors, i.e., it is a potential habitat map. This can be regarded as a future occurrence probability map after *B. javanica* has spread to all eco-physiologically suitable habitats. We predict that *B. javanica* seeds would distribute across the island and that the species would invade every suitable habitat if we were not to implement an eradication program. A comparison of the present map (Fig. 24.6a) and the projected future distribution (Fig. 24.6b) shows possible invasion to the south of Chibusayama and to Higashidai and Nishidai. Lack of seed supply has restricted *B. javanica* expansion into these areas, but the future invasion risk is considered high. Such high risk

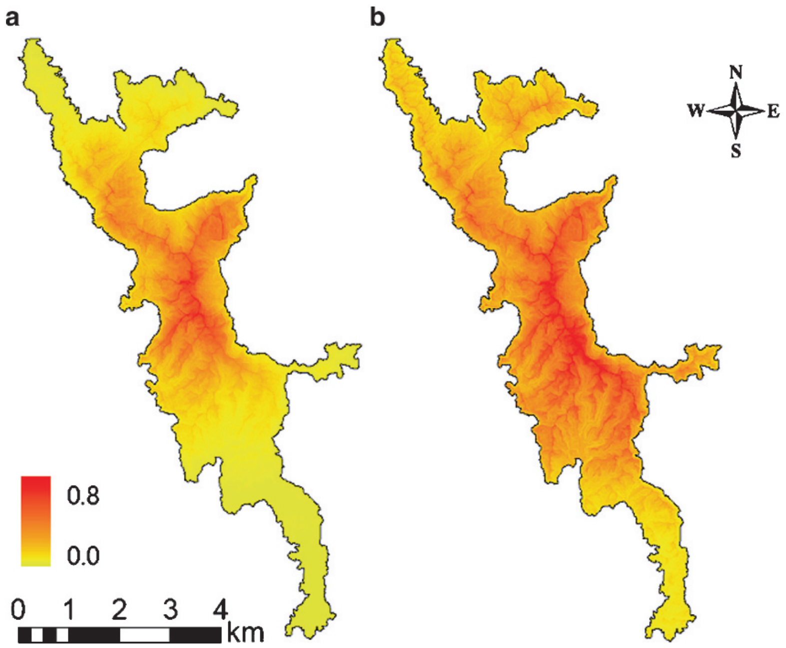

Fig. 24.6 Occurrence probability of *B. javanica* estimated by a model. (**a**) Probabilities based on both environmental factors and distance from seed source; (**b**) probabilities based on environmental factors only, showing potential habitats

areas that are little invaded are given priority status for eradication. The extirpation process is economical because invasion area is limited, and long term benefits are derived from taking early action to save the much larger regions that are not yet densely colonized, but that are suitable habitat for *B. javanica.*

24.3 Ecology of *B. javanica* and Impact of Its Reproduction

24.3.1 Reasons for Enhanced B. javanica Population Growth

B. javanica in its native range is just one component in forests with diverse tree species (Tanaka and Sakurai 1996). Many factors are thought to suppress reproduction in the native range, e.g., the abiotic environment including severe dry seasons, presence of many competitive species (fast growing, shade-tolerant, tall or long-lived species), and physical disturbance from fungi and animals. The following causes are considered as drivers of enhanced *B. javanica* reproduction on the Ogasawara Islands.

Female trees of this dioecious species produce large numbers of seeds, which drop to the forest floor below. Seed density reaches 3,082/m^2 in a *B. javanica*-native mixed forest in Kuwanokiyama (Yamashita et al. 2003). In addition, some seeds are dispersed over long distances by birds such as the brown-eared bulbul *Hypsipetes amaurotis*. The proportion of viable seeds is high (88–96%), and few seeds are lost to foraging by alien black rats (*Rattus rattus*) or invertebrates (Yamashita et al. 2003). Many seeds and seedlings survive in the vicinity of a mother tree. Seedling 2-year survival rate after germination in deep forest shade is reported to be 17% (Yamashita et al. 2003). Continuous germination supplies large numbers of seedlings, which occur densely on the forest floor.

Short-lived breaks in the forest canopy following typhoon damage produce elevated illumination on the forest floor, and seedlings grow rapidly into 30 cm tall saplings. Saplings under canopy gaps grow faster than those of most native species (Hata et al. 2006). Large saplings of *B. javanica* tolerate the shade that develops following canopy re-growth. The responses of *B. javanica* to high and low light levels endow the species with a high adaptability not found in native tree species (Yamashita et al. 2000). Native pioneer tree species such as *Trema orientalis* and *Zanthoxylum ailanthoides* occasionally grow faster than *B. javanica*; however, these natives do not grow as tall as *B. javanica* and are short-lived. The maximum height of *B. javanica* exceeds those of native tree species. On drainage basins with a deep soil layer and low wind velocity, *B. javanica* can exceed 25 m in height and reach a DBH > 80 cm. *B. javanica* also shows vigorous growth of sprouts. Even if the tree is blown down by strong wind, it does not die and able to produce sprouts. Furthermore, *B. javanica* can grow with sprouts from stumps after cutting or girdling. Branches damaged in typhoons recover in less than 1 year.

The population growth of native tree species is inferior to that of *B. javanica* (Yamashita 2002; Yamashita et al. 2003). For example, the majority of *Elaeocarpus photiniifolius* seeds are eaten by rats, and the seedling density and survival rate in this species are substantially lower than those of *B. javanica*. *Morus boninensis* has few mother trees, amounting to a total of approximately 200 individuals across the islands of Ototojima, Chichijima, and Hahajima combined, and it produces hybrids with the alien species *M. australis* (Kawahara and Yoshimaru 2002; Tani 2003). Hence very few genetically pure seedlings exist. *Ardisia sieboldii* is shade tolerant and occurs at high density, but its maximum size is much less than that of *B. javanica*.

24.3.2 Impact of *B. javanica* Expansion

B. javanica exploits habitats of native tree species and forest floor plants. When *B. javanica* invades *Elaeocarpus–Ardisia* or *Schima* mesic forests, it becomes gradually dominant as densities of native trees decline, resulting in the formation of pure *B. javanica* stands with little understory vegetation. Rare tree species such as *Claoxylon centenarium* and *Ficus iidaiana* were virtually eliminated in Kuwanokiyama following formation of *B. javanica*-dominated forest (Shimizu 2002).

Surveys of forests with different *B. javanica* densities demonstrated that the negative impact is limited when this species has a canopy cover <34%. Densities of native tree species declined, but species number did not in forests with *B. javanica* canopy covers between 43 and 64%; when alien cover exceeded 70%, both native tree density and species richness decreased markedly (Toyoda and Kawaoka 2005). Among diverse tree species in mesic forests, *Pisonia umbellata* disappears first as *B. javanica* density increases; subsequently *Melia azedarach* and *Planchonella obovata* are eliminated, resulting in forests with limited densities of *Zanthoxylum ailanthoides*, *Trema orientalis*, and *Ardisia sieboldii*.

Replacement of native forests by stands of *B. javanica* destroys habitat for native fauna. For example, the endangered bird species *Columba janthina nitens* feeds mainly on seeds of native canopy tree species, including *Elaeocarpus photiniifolius*, *Neolitsea boninensis*, *Zanthoxylum ailanthoides*, *Melia azedarach*, *Ardisia sieboldii*, and *Planchonella obovata*, whose numbers are greatly diminished following invasion, with obviously negative impacts on the native tree-dependent pigeon.

24.4 Recovery of Native Tree Species After Clear-Cutting in a *B. javanica* Forest

The objective of *B. javanica* eradication is restoration of native forests. The regeneration of native tree species is highly likely in forests with low abundances of *B. javanica* because of the high densities of native tree seeds and saplings. However, prospects for regeneration are of concern when *B. javanica* is dominant. Here, we present an example of regeneration in a clear-cut *B. javanica* forest located on private land at Nagahama in Hahajima.

Herbicide was experimentally applied to trees in 2005 within a 1.3 ha *B. javanica* forest in the Nagahama valley (Japan Forest Technology Association 2006). Seventy-two *B. javanica* trees spanning 5–60 cm DBH were cut down, resulting in the creation of a large canopy gap. To investigate tree regeneration capability, three plots of 10 × 10 m^2 were established in the gap 26 months after felling. All individuals over 2 m in height were recorded by species, DBH, and height.

A total of 261 young trees >2 m tall were identified across plots (300 m^2). *B. javanica* accounted for 26%, and *Elaeocarpus photiniifolius*, *Ardisia sieboldii*, and *Zanthoxylum ailanthoides* each accounted for >15% (Table 24.2). Eleven native species regenerated in the plots. Among them, two were pioneer subcanopy tree species (*Z. ailanthoides*, *Trema orientalis*), six were sub-canopy tree and shrub species (*A. sieboldii*, *Rhaphiolepis indica* var. *umbellata*, *Planchonella obovata*, *Tarenna subsessilis*, *Psychotria homalosperma*, *Syzygium cleyerifolium* var. *microphyllum*), and three were canopy species (*E. photiniifolius*, *P. obovata*, *Schima mertensiana*). The average tree height was 2.7 m, and the average DBH was 2.3 cm. Little differences were observed in height and DBH between *B. javanica* and native species. Previous studies suggested poor recovery of late successional species such as *E. Photiniifolius* (Tanaka 2003). In this study site where *B. javanica* previously dominated, young trees of *E. photiniifolius*, *P. obovata* and other native species regenerated densely. Hence, we expect that a native forest would develop in this site if saplings and young trees of *B. javanica* were eliminated for a few years. A *B. javanica* forest survey in Kuwanokiyama demonstrated saplings and a seed bank comprising diverse native tree species (Tokyo Branch of Kanto Regional Forest Office 2000), indicating the potential for natural forest recovery.

Even in *B. javanica*-dominated forests, a potential for natural regeneration of various native tree species exists when *B. javanica* trees are killed. Changed environmental conditions after the elimination of *B. javanica* canopy would likely lead to native species regeneration, including the re-growth of suppressed saplings and germination from the soil seed bank. Germination of seeds dispersed by birds and wind is also expected.

Table 24.2 Numbers and sizes of regenerated trees in *B. javanica* clear-cut plots in Nagahama, Hahajima

Species	Stem no. (no./300 m^2)	Hight (m)	SD (m)	DBH (cm)	SD (cm)
Bischofia javanica	94	3.0	0.9	2.8	1.3
Elaeocarpus photiniifolius	42	2.8	0.9	2.2	0.9
Ardisia sieboldii	41	3.1	1.1	3.0	1.3
Zanthoxylum ailanthoides	39	2.1	0.3	2.0	0.5
Rhaphiolepis indica var. *umbellata*	16	2.7	1.0	1.7	0.8
Trema orientalis	15	3.1	1.1	2.7	1.0
Planchonella obovata	7	3.1	1.7	2.1	2.3
Ligustrum micranthum	3	2.3	0.2	1.7	1.0
Tarenna subsessilis	1	2.0	–	1.3	–
Psychotria homalosperma	1	2.7	–	2.4	–
Syzygium cleyerifolium var. *microphyllum*	1	3.0	–	2.0	–
Schima mertensiana	1	3.0	–	3.2	–
Total	261				

24.5 Eradication of *B. javanica* on Hahajima by Girdling and Cutting

The Kanto Regional Forest Office started a *B. javanica* eradication project in National Forest areas on Hahajima in 2002 (Tanaka 2003, 2004). To transform *B. javanica*-dominated or mixed forests into native forests, the project targeted areas with high invader densities, namely, Kuwanokiyama, Nagahama, and Uchuzawa. Recovery of native tree species by natural regeneration and planting was expected after girdling and felling of *B. javanica* canopy trees. The procedure was performed in 30 target forest units with a total of 21.5 ha in the period 2002–2003. After 2003, the project moved to the stage of *B. javanica* regeneration control and the promotion of native tree species recovery. A brief description of the methodologies employed follows.

The target area was divided into forest units of about 1 ha each. Each procedure was implemented in these units. All *B. javanica* trees <20 cm DBH were cut. Trees >20 cm DBH (canopy-forming individuals) were girdled. When the proportion of *B. javanica* trees >20 cm DBH made up <30% of the total, all trees were girdled; when this proportion exceeded 30%, female trees were preferentially girdled until they made up 30% of the total. After the following year, young trees >30 cm tall were uprooted, and sprouts were removed annually. In some areas, native tree species saplings were planted. Following the girdling and cutting treatments, individual trees in monitoring plots are surveyed after a few years, and methods and schedules are to be revised according to the forest regeneration condition.

After the girdling and cutting treatments, forest floors received more light and the regeneration of pioneer tree species, e.g. *Zanthoxylum ailanthoides*, *Trema orientalis*, *Ardisia sieboldii*, and *B. javanica*, began within ten months. However, we needed to monitor regeneration of late-successional tree species such as *Elaeocarpus photiniifolius* and *Pisonia umbellifera*. Some female *B. javanica* trees were left uncut because of difficulties in sex identification. Nevertheless, seed supply was estimated to have fallen through the reduction in the numbers of mother trees. Because sprouts grew rapidly on girdled and cut trees, substantial investments of labour and cost were necessary for sprout removal even through 2009, 6 years after treatment. It is difficult to kill *B. javanica* stumps by removing sprouts once or twice a year. The strategy for sprout control is an important issue for *B. javanica* eradication. This eradication project aimed to develop technologies to restore native forests previously invaded by *B. javanica*. Concerns about the achievability of this aim persist. The girdling treatment was chosen to prevent abrupt changes in the forest environment by removing canopy. However, as shown in a Nagahama forest (Chapter 24.4), regeneration of native tree species is possible with large forest canopy gaps. Furthermore, stumps do not die after girdling treatment, and they rapidly sprout in spite of intensive removal. Thus, this treatment holds little merit.

24.6 Herbicidal Eradication of *B. javanica* on Ototojima

The selection of an extermination method must be appropriate to local circumstances. Since Chichijima and Hahajima have large, dense stands of *B. javanica*, an efficient method killing *B. javanica* trees is necessary. A herbicidal eradication procedure was selected on Ototojima by the Ministry of the Environment. Treatment began in 2005. Glyphosate, which is used worldwide, was selected. This is a non-selective amino acid-based herbicide sold and used on the Ogasawara Islands. Once absorbed into a plant, the chemicals spread via sap flow. It prevents amino acids synthesis at growing points and kills the plant. It decomposes into nitrogen and phosphorus in the soil and does not produce any harmful substance

(Yoneyama 2002). It is listed by the Poisonous and Deleterious Substances Control Law as the least hazardous ubiquitous substance. A method was developed for killing standing *B. javanica* trees with this herbicide (Ito 2004, 2005; Ito and Otsu 2007; Ito et al. 2009).

A total of 550 individual *B. javanica* trees >0.5 m tall were counted on Ototojima (Fig. 24.7; Otsu and Ito 2007). Many seedlings and saplings occurred around mother trees, and browsing damage from goats was observable. Herbicide was injected into the stems from October 2005 to January 2006. The treated trees started to lose leaves within two weeks and became completely leafless. Of the trees treated, 90% were killed in 4 months. Similar experiments done in Koromodate (on Hahajima) produced a 100% death rate among 54 treated trees over 1 year (Japan Forest Technology Association 2006). All *B. javanica* trees were killed by this method on Ototojima, and labour costs were low. The seed supply from mother trees has ceased, and it is estimated that complete eradication will be accomplished within 3 years through additional seedling removal.

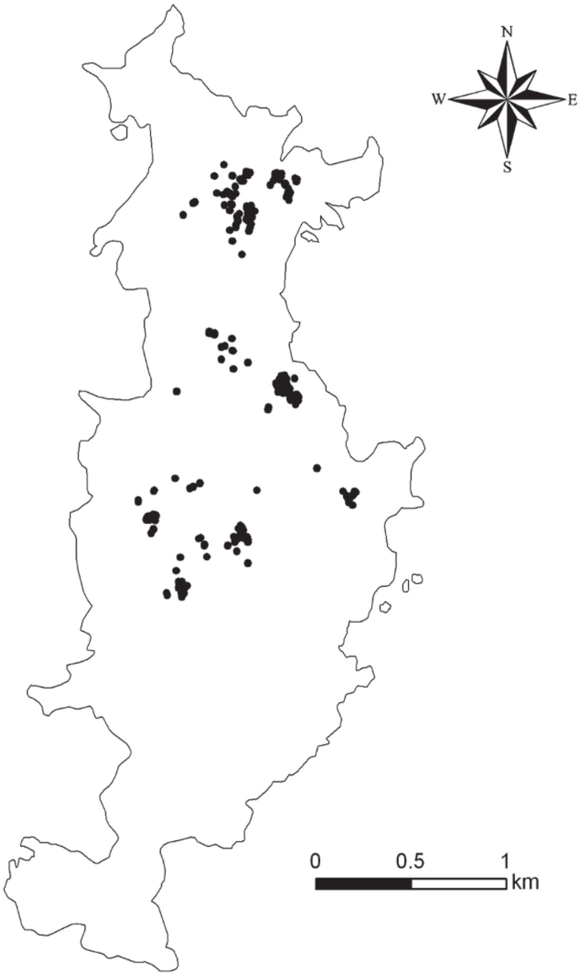

Fig. 24.7 Distribution of *B. javanica* individuals on Ototojima (Ministry of the Environment 2007)

24.7 Management System for Whole-Island Eradication of *B. javanica*

A forest management recommendation was proposed for the Ogasawara Islands (Tokyo Branch of Kanto Regional Forest Office 2000; Tanaka 2002). It stated that an adaptive whole-island management system (including private forests) was needed to integrate conservation projects and monitoring; the recommendation stressed the importance of achieving a consensus in management. However, no management recommendation is available for complete eradication of *B. javanica* from all islands. The master plan for conservation and restoration of the Ogasawara natural environment was produced in 2007 (Ministry of the Environment 2007), and it put forward the strategy, methodologies and future challenges for eradication of *B. javanica* based on agreement among organisations and stakeholders.

It may seem impossible to exterminate the aggressive *B. javanica* invaders from the extensive area of occupancy on Hahajima and Chichijima. However, combined treatments of herbicide to effectively kill trees and manual removal of saplings were effective on Ototojima. Low invader densities on this island made it easy to achieve eradication. When the invader occurs at low densities, many native tree species remain, and their natural regeneration after the treatment is easy. We propose a management system to eradicate *B. javanica* and to restore natural forests on Hahajima (Fig. 24.8). As a first step, a master plan laying out the priority order of eradication areas should be prepared. To build such a plan, a variety of maps should be used, e.g., maps of *B. javanica* invasion (Fig. 24.4), important native species, vegetation types, potential habitats and *B. javanica* colonization risk (Figs. 24.5 and 24.6), conservation areas, and land ownership. Based on these maps, an island should be zoned for management and the priority order of regions for efficient *B. javanica* eradication should be determined. The target region should then be divided into unit forest areas for identical treatments. In each forest unit, a tree census should be conducted, and plots should be set up to monitor forest dynamics. It is particularly important to select target *B. javanica* trees for killing to effectively implement eradication. Target trees for killing are selected from tree censuses. In a forest with low *B. javanica* density, all individuals should be killed. When densities are high, the treatment is limited to a proportion of invader trees in such a way as to prevent adverse effects on the forest, such as soil erosion. It is important to kill all mother trees to terminate the seed supply, and remaining male trees are killed after the regeneration of native trees. *B. javanica* trees <21 cm DBH are predominantly non-flowering; in trees

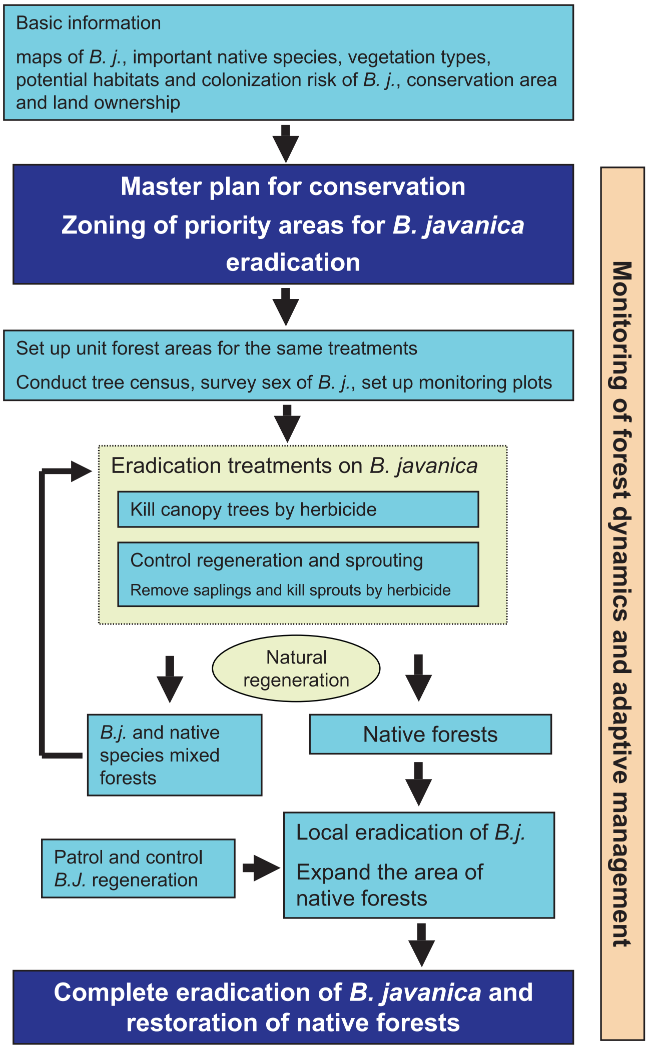

Fig. 24.8 Management system aiming for complete eradication of *B. javanica* on an island

>34 cm DBH, most trees are flowering, and the gender ratio is close to one; an intermediate pattern is observed among trees between 22 and 33 cm DBH (Yamashita and Abe 2002). Small trees <21 cm DBH will grow rapidly to reproductive maturity if left uncut, and females will produce seeds. Therefore, it is important to kill all small trees to reduce reproduction.

In the second step, *B. javanica* individuals are killed. Standing trees die within a month of herbicide application. It is best to cut the dead trees early before dangerous branch falls occur in areas frequented by people. Growths of seedlings and sprouts of native tree species and of *B. javanica* are promoted on a brighter forest floor after the treatment. Regeneration of *B. javanica* can be controlled by herbicide application on stumps producing sprouts and by removal of saplings. *B. javanica* occasionally changes sex (Yamashita and Abe 2002). Once detected, any female trees produced by this process should be promptly killed. In this way, areas of eradication will expand and *B. javanica* distribution will contract.

We stress that the restoration of native forests should be by natural regeneration of native tree species. After trees of *B. javanica* have been killed, we suggest that further actions should be limited to controlling its regeneration and overseeing natural regeneration by monitoring and patrolling. Artificial planting carries a risk of disturbing genetic structure of species population, and it is also expensive. Natural regeneration is best. Of course, adaptive management is essential; the approach must be adjusted according to results of monitoring over a few yearly cycles.

The time necessary to achieve eradication from all the islands depends upon the efficiency of eradication in high-density areas. In these areas, a second treatment should be implemented after native tree species regeneration following first treatment. It is difficult to accurately estimate the time required for native tree species regeneration. Considering that it took 23 years (the period between the end of WWII and the return of the islands to the Japanese Government) for pre-war cropland to convert to secondary forest, we propose that the time required for eradication be set at 20 years.

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Chapter 25

SPECIAL FEATURE **Ecological risk management**

**Keita Fukasawa · Fumito Koike · Nobuyuki Tanaka
Kayo Otsu**

Predicting future invasion of an invasive alien tree in a Japanese oceanic island by process-based statistical models using recent distribution maps

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Abstract Modelling and predicting the potential habitat and future range expansion of invasive species can help managers to mitigate the impact of such species. Because habitat suitability and the colonization process are key determinants of range expansion, inferences drawn from invasion patterns should be based on both attributes. To predict the potential habitat and expansion rate of the invasive tree *Bischofia javanica* on Hahajima Island, we used simultaneous models of habitat and dispersal to estimate the effect of environment and dispersal from the source population on the current distribution. We compared the fit and the estimated magnitudes of the environment and dispersal effects in the simultaneous models with those in habitat suitability and colonization kernel models. The values of Akaike's information criterion for the simultaneous models were better than those of the habitat suitability and colonization kernel models, indicating that the current distribution of *Bischofia* was determined by both environment and dispersal. The simultaneous models predicted that the potential habitat of *Bischofia* would be larger than that predicted by the habitat suitability model. The potential habitat distribution and future invasion predicted by the simultaneous models will contribute to the development of specific landscape-scale management plans to control this invasive species.

Keywords Dispersal kernel · Ecological niche model · Exotic species · Potential range · Ogasawara Islands

Introduction

Invasive species can cause irreversible changes in biodiversity (e.g., Mack et al. 2000) and ecosystem functions (Vitousek and Walker 1989; Le Maitre et al. 1996). Control and eradication then become necessary, but mitigating the impacts of the invasion is often difficult (Myers and Bazely 2003; Clout and Russell 2006; Hulme 2006). Modelling and predicting potential habitats of invasive species and their future range expansion offer great advantages in control and eradication projects. Geographical mapping of the invasion risk is useful for establishing a spatially explicit control strategy for invasive species (Higgins et al. 1999; Koike 2006).

In many studies, the potential habitat and rate of range expansion have been estimated independently. The potential habitat of invasive species is often predicted by using a "habitat suitability model" (also referred to as an "ecological niche model") that explains the occurrence of species as a function of environmental factors such as topography and climate (Higgins et al. 1999; Hartley et al. 2006; Usio et al. 2006; Nielsen et al. 2008). Such approaches are based on the observed correlation between environmental factors and the distribution of invasive species, but in many cases the distribution of invasive species is limited not only by environmental factors but also by propagule dispersal from one or more source populations (Higgins et al. 1996; Havel et al. 2002; Rouget and Richardson 2003; Leung and Mandrak 2007). Because suitable sites may not be invaded owing to limitations on propagule

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dispersal, the absence of an invasive species does not always mean that a site is not suitable for colonization by the species, especially in edge regions around the current range. Therefore, distribution data for invasive species are "zero-inflated" (Martin et al. 2005) when they are used as training data of habitat suitability models; that is, they do not account for the zero observations because of the limitations on propagule dispersal. This zero-inflation may lead to biased predictions of potential habitat.

On the other hand, the rate of range expansion has been estimated by using a "colonization kernel" model, which assumes that the occurrence of an invasive species at a given point in time is determined by its dispersal from one or more previous source populations (Facon and David 2006; Koike 2006). Though such models express the decrease in the probability of occurrence as a function of the distance from a source population, environmental heterogeneity has not been incorporated in these models. However, in many cases, there will be sites where the propagules of an invasive species were dispersed but failed to survive due to an unsuitable environment. Therefore, distribution data for invasive species are also zero-inflated when they are used to train colonization kernel models.

To deal with the problem of zero-inflation, and to estimate appropriate potential habitats and colonization kernels, we must establish a statistical model that integrates habitat suitability with a colonization kernel. Because the distribution of an invasive species is determined by the combination of environmental factors with the dispersal process of a species (D'Antonio et al. 2001; Rouget and Richardson 2003), a model based on the pattern of invasion should incorporate both attributes. A simple option would be to develop a logistic regression model for the joint effects of environmental factors and propagule dispersal (Havel et al. 2002; Komuro and Koike 2005). Such models can then incorporate both factors as linear predictors. Alternatively, a simultaneous model with an explicit dispersal kernel can be used, given that invasion of a site occurs when both propagule dispersal and establishment succeed (Leung and Mandrak 2007). If a species is expanding its range, a site will be occupied by the species only if two conditions are satisfied: First, the site must be suitable for the species; second, a propagule of the species must arrive at the site. Thus, the probability that a species will occur at a given site should be the product of two probabilities: the probability that the species can grow in the site's specific environment, and the probability that propagules will arrive at the site during the range-expansion process. These models can account for both habitat and dispersal. However, differences in the predictive accuracy of these models have not yet been determined, and we must also consider how to make decisions based on the model's predictions.

In this study, we predicted the potential habitat and future range expansion of the invasive tree *Bischofia javanica* on Hahajima Island, a subtropical oceanic island of the Bonin (Ogasawara) archipelago in the northwestern Pacific Ocean. *Bischofia* is a major threat to the biodiversity of Hahajima Island because it will become the dominant tree in the climax forest at mesic sites (Koike 2001). Prediction of the potential habitat and future range expansion is thus needed to support the development of a spatially explicit control strategy against *Bischofia*. We tested the effect of environment and dispersal on the range expansion of *Bischofia* at a landscape scale by using several models, and we examined the ability of these models to predict the future range expansion of *Bischofia*. In our comparison of the models, we compared two range-expansion scenarios (expansion from the initial introduction to the present, and more recent range expansion) to evaluate whether long-term or short-term expansion could best explain the current range. Because range expansion is a stochastic process, the prediction might become difficult in a longer time scale. We hypothesized that the short-term expansion scenario can explain the current pattern of *Bischofia*. From the predicted habitat and the dispersal, we proposed an index of spatial priority of control that incorporated the stochastic causality of invasion.

Materials and methods

Study site

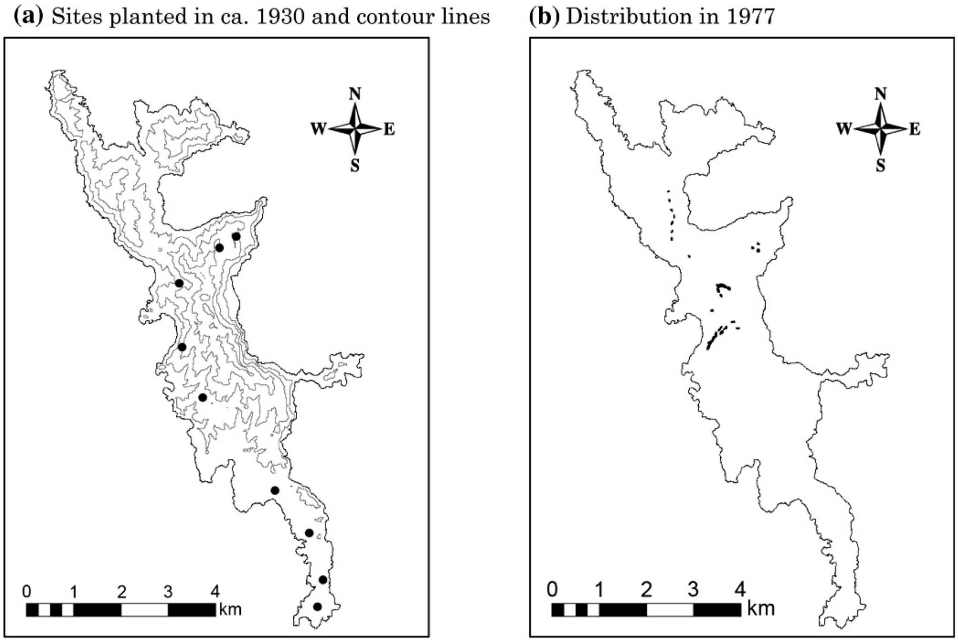
Hahajima Island, in the Bonin Island group, is an oceanic island with an area of 20.21 km^2 located about 1,000 km south of mainland Japan in the northwestern Pacific Ocean (26°39′N, 142°9′E). Although the Bonin group originated as a volcanic archipelago during the Tertiary period, volcanic activity has ceased. The climate is subtropical, with a mean annual temperature of 23.0°C and a mean annual precipitation of 1,268 mm (1971 to 2000; data recorded at Chichijima Island, 50 km north of Hahajima Island). Once every few decades, a large typhoon strikes the island and creates a large disturbance that accelerates regeneration of the island's forests (Shimizu 1994). The Bonin Island group is a biodiversity hotspot because of its endemic and disharmonic biota. About 40% of the plant species, and 70% of the trees, are endemic to the Bonin Islands (Toyoda 1981).

The vegetation types on Hahajima Island are arranged along the altitude and moisture gradients (Shimizu 2003). The island's topography is dominated by peaks at an elevation of around 400 m that are frequently capped by clouds. Humid, windswept scrub vegetation exists on ridges at altitudes above 350 m. The climax vegetation at lower altitudes is the mesic evergreen broadleaved forest. There is also a slightly dry, mixed palm scrub under the influence of a continuous salt breeze on the southern part of the island (Okutomi et al. 1985).

Though many villagers had cultivated agricultural fields throughout the island before World War II, all the people were displaced from the island by a forced evacuation during the war. Until 1968, when the villagers started to return to the island, there were no inhabitants. Most areas of the abandoned agricultural fields had changed into secondary forest.

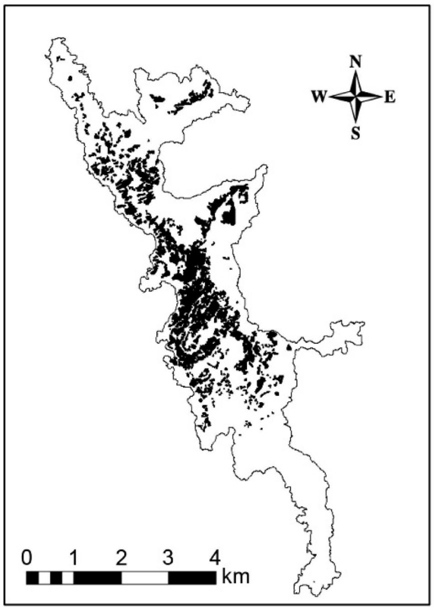
Bischofia javanica (Akagi), belonging to the Euphorbiaceae, is a tree species native to South and Southeast Asia but alien to the study area. It was introduced into Hahajima Island as a part of an afforestation effort in about 1930 (Fig. 1a). Subsequently, the species extended its range gradually from the successful afforestation sites (Fig. 1b), and after a large typhoon disturbance in 1983 it spread rapidly across a wide range of sites on Hahajima Island. As of 2003, *Bischofia* dominated about 14% of the island's area (Fig. 1c). *Bischofia* is a sex-reversing dioecious plant species (Yamashita and Abe 2002), and has pulpy fruits that are eaten and dispersed by birds. The rapid invasion success of this species after a large disturbance may be due to its high fecundity, high shade tolerance (Yamashita et al. 2003), and rapid photosynthetic acclimation (Yamashita et al. 2000, 2002). In light of its ecophysiological characteristics, such as shade tolerance and maximum tree height, *Bischofia* is expected to become the dominant species of the island's climax forest (Koike 2001).

Fig. 1 **a** Sites planted with *Bischofia javanica* in ca. 1930 and the topography of Hahajima Island. The distributions of *Bischofia javanica* in **b** 1977 and **c** 2003. The *contour lines* in **a** represent 100-m intervals. **a** Sites planted in ca. 1930 and contour lines. **b** Distribution in 1977. **c** Distribution in 2003


(a) Sites planted in ca. 1930 and contour lines

(b) Distribution in 1977

(c) Distribution in 2003



Distribution maps

We surveyed the distributions of *Bischofia* on Hahajima Island at three points in time: at the time of the initial plantings in ca. 1930 (Fig. 1a; Forestry Agency of Japan 1994), in 1977 (Fig. 1b; T. Toyoda, a former researcher of the Forestry and Forest Products Research Institute of Japan, unpublished data), and in 2003 (Fig. 1c; Forestry Agency of Japan and Japan Forestry Foundation 2004; Ministry of the Environment of Japan 2004). The locations of the initial plantings were confirmed by means of interviews with old villagers. The distribution of *Bischofia* in 1977 was determined by means of a field survey that targeted the canopy or subcanopy trees. The distribution of *Bischofia* in 2003 was determined from aerial photographs and validated by field surveys. Maps of the *Bischofia* forest in 2003 were polygon-based, and the minimum unit size in this survey was 0.1 ha. To permit spatial alignment among data layers for each of the 3 years, all distribution maps were converted into 10-m-mesh raster presence/absence data using ArcGIS 9.1.

Site environments and distance from seed sources

In our modelling, we parameterized two range-expansion scenarios: the range expansion from 1977 to 2003 (scenario #1, which focuses on recent expansion of the distribution) and the expansion from the initial plantings in the 1930s to 2003 (scenario #2, which focuses on expansion of the distribution since initial establishment of the species). As the predictor for dispersal, we used ArcGIS to calculate the nearest distance from previously occupied locations to each new location on the island.

All variables were derived from the 10-m-mesh DEM (altitude in meters). The environmental factors considered in our analysis were elevation, summit plane elevation (SPE), flow accumulation (FA), slope, curvature, and skyline. SPE is an indicator of cloud occurrence and is defined as the highest elevation within the 2-km buffer surrounding each cell of the mesh. FA is the area of the drainage basin from which a stream flows into each point (i.e., larger values at the bottom of valleys), and was log-transformed to normalize a skewed frequency distribution. Curvature is an index of topographic concavity: a positive value means a convex-upward site, and a negative value means a concave-upward site. The skyline parameter represents the number of directions in which the elevation is higher than that of the focal cell when there is a total of eight directions (starting at 0° and continuing at 45° intervals); it was calculated with the free GIS software "Minna de GIS" (Koike 2004). FA, slope, and curvature were calculated with ArcGIS. We did not consider variation in geological formations (e.g., volcanic vs. limestone), because a previous study had revealed that this parameter did not affect the distribution of *B. javanica* on this island (Mikami and Koike 2005).

Anthropogenic areas such as residential districts, roads, and agricultural fields, which is 3% of total area of the island, were removed from our analysis. To reduce the effect of spatial autocorrelation and to reduce the absolute quantity of data that had to be analyzed, we randomly sampled 5% of the cells (a total of 9,776 cells). All environmental variables and distances from the old ranges were standardized so that the relative importance of each variable could be determined. The correlations among the independent variables were shown in the Electronic Supplementary Material (ESM).

Models

We developed four models: a habitat suitability model, a colonization kernel, and two simultaneous models that included both habitat and dispersal (one based on simple logistic regression and the other with an explicit dispersal kernel). We have summarized the relationship among the objectives, the models, the data, and the predictions in Fig. 2. The habitat suitability model and the colonization kernel model explain the invasion pattern on the basis of environmental factors and the distance from the nearest source population, respectively. Both simultaneous models explain the invasion pattern by combining the environment and the distance from the source population, but the formulations of these models are different, as described below. Thus, the predictions of invasion by these models may differ.

Habitat suitability model

The habitat suitability model, which is based on the relationship between the occurrence of a species and the characteristics of the physical environment, is represented by the following logistic regression model (Higgins et al. 1999; Hosmer and Lemeshow 2001):

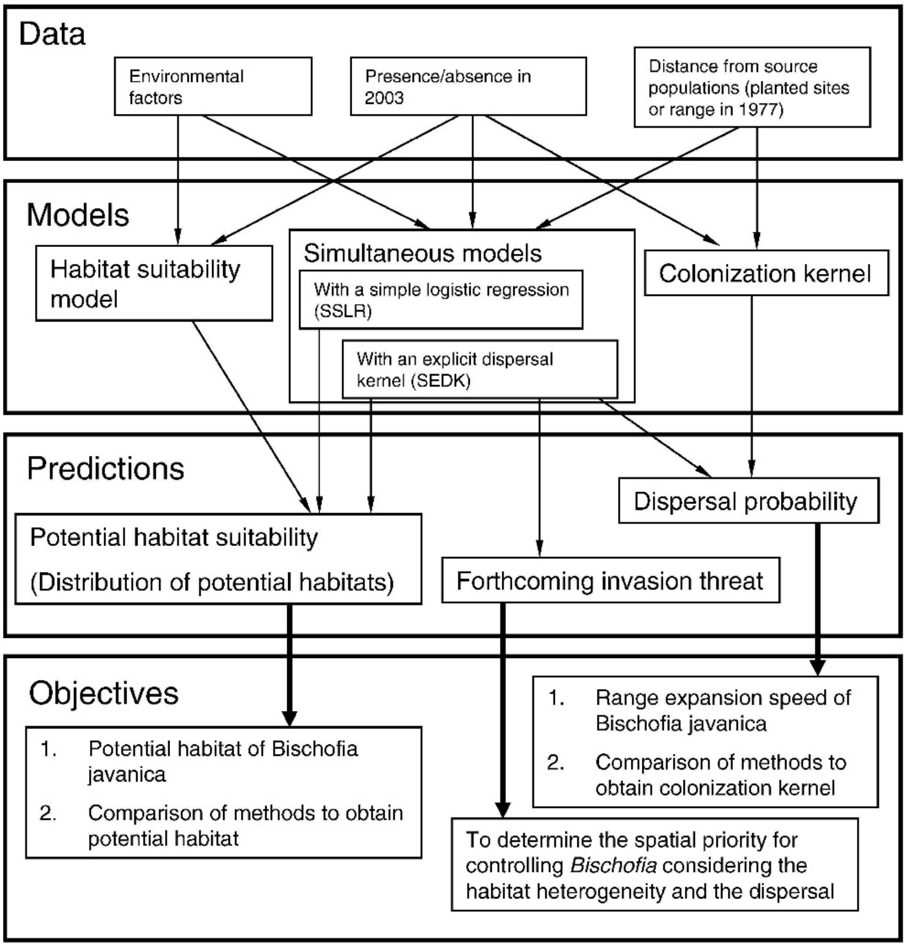
$$\log\left(\frac{Z_i}{1-Z_i}\right) = \alpha + \sum_j \beta_j X_{ij} \tag{1}$$

where Z_i is the probability that the species occurs at site i, α, and β_j are the regression coefficients, and X_{ij} represents the jth environmental variable. The map of predicted Z_i is interpreted as the potential habitat distribution. However, this model assumes that the occurrence of a species is primarily determined by given environmental conditions (Guisan and Zimmermann 2000), and its application to the distribution of invasive species will lead to underestimation of habitat suitability because there are sites where the invasive species can potentially survive, but that it has not yet reached through dispersal (Kriticos et al. 2003).

Colonization kernel

A colonization kernel model is frequently used to estimate distance-dependent dispersal from a source population

Fig. 2 Overview of the relationships among the objectives, the data, the models, and the predictions. *Arrows* from the box "data" to the box "models" indicate the data used to develop each model. *Arrows* from the box "models" to the box "predictions" indicate the parameters each model can predict. *Arrows* from the box "predictions" to the box "objectives" indicate the connections between them



on the basis of the observed temporal change in distribution (Komuro and Koike 2005; Koike 2006). We modelled the colonization kernel as the product of the survival rate and the dispersal probability (a negative exponential kernel) as follows:

$$Z_i = \phi \exp(\gamma D_i) \quad \text{for } \gamma \leq 0 \text{ and } 0 \leq \phi \leq 1 \tag{2}$$

where Z_i is the probability that the species occurs at site i, D_i is the distance from a previously occupied site, and γ is a regression parameter that determines the decay of the probability of dispersal as a function of distance. The survival rate, ϕ, is also a regression parameter. Because this model assumes habitat homogeneity, the distribution of suitable habitat must be specified before the parameterization (which might be quite difficult to specify in a continuously changing environment).

Simultaneous model with simple logistic regression (SSLR)

The potential range and the residence time are vital components that determine the current range of an invasive species (Wilson et al. 2007), and simultaneous modelling of habitat suitability and dispersal is reasonable in this context. The SSLR model can be expressed as a multiple-logistic-regression model of the environmental factors and of distance from the source populations (Komuro and Koike 2005):

$$\log\left(\frac{Z_i}{1 - Z_i}\right) = \alpha + \beta_1 D_i + \sum_j \beta_{2j} X_{ij} \tag{3}$$

where Z_i is the probability that the species occurs at site i, D_i is the distance of site i from an occupied site, β_1, and β_{2j} are regression coefficients, and X_{ij} represents the jth environmental variable.

Simultaneous model with an explicit dispersal kernel (SEDK)

The SEDK is a process-based statistical model. If a species is expanding its range, a site will be occupied by the species only if two conditions are satisfied. First, the site must be suitable for the species; second, a propagule of the species must arrive at the site. Thus, the probability that a species will occur at a given site should be the product of two probabilities: the probability that the species can grow in the site's specific environment (the probability of habitat suitability, p_i) and the probability that propagules will arrive at the site during the range-expansion process (the probability of dispersal, q_i). We used these probabilities to define an SEDK model that accounts for habitat and dispersal:

$$Z_i = p_i q_i. \tag{4}$$

Although this multiplicative formulation for habitat and dispersal is frequently found in process models of invasion (e.g., Bossenbroek et al. 2001; Marco et al. 2002; Gilbert et al. 2005), few studies have attempted to estimate the optimal parameters for a model with this formulation (but see Leung and Mandrak 2007).

The potential habitat suitability probability (p_i) is determined by environmental factors. We assumed a logistic function to describe these factors:

$$\log\left(\frac{p_i}{1-p_i}\right) = \alpha + \sum_j \beta_j X_{ij} \tag{5}$$

where α and β are the regression coefficients, and vector X_{ij} represents the jth environmental variable at site i. This part of our model is the same as the logistic regression model presented by Higgins et al. (1999), and p_i represents the probability that the species will occur at site i after range expansion is complete.

We assumed that the dispersal probability (q_i) is determined by the distance from the nearest site occupied by the mother plants of the species (i.e., the nearest seed source). The nearer a site is to the seed source, the greater the dispersal probability. To express the distance-dependent dispersal, we introduced a negative exponential function:

$$q_i = \exp(\gamma D_i) \quad \text{for } \gamma \leq 0 \tag{6}$$

where D_i is the distance from an occupied site to site i, and γ is a regression parameter that determines the shape of the negative exponential kernel. We assumed that q_i at an occupied site equals one. This assumption means that the probability of the population occurring during the next time step of the simulation may depend on the environment, and this should be evaluated by using p_i in Eq. (5). Equation (6) represents the colonization kernel under a suitable and uniform environment for the invasive species. Theoretically, the colonization kernels of a population (i.e., the probability that at least one propagule will arrive at the site) have a sigmoidal shape if the dispersal kernel of a single propagule follows a negative exponential relationship (Komuro and Koike 2005). Although the logistic function can be used for the colonization kernel (q_i), the parameter estimation procedure did not converge in our preliminary work, so we did not use the logistic kernel in this research. Although long- and short-distance dispersal mechanisms are important determinants of invasion (Buckley et al. 2005), we used a simple exponential kernel to estimate the pattern of dispersal at a landscape scale.

Model estimation and comparison

Curve fitting was performed with version 2.5.0 of the R software (R Development Core Team 2007). The SEDK and colonization kernel models were fitted by means of maximum-likelihood estimation with the Newton-type nonlinear minimization function (nlm), and the SSLR and habitat suitability models were fitted by using the generalized linear model function (glm). All estimates converged successfully for the candidate models.

We compared the goodness of fit of four models by using Akaike's information criterion (AIC, Akaike 1974), a parsimonious approach in which low values of AIC represent better fits. If the AIC is smallest for the SSLR or SEDK models, this means that the distribution of *Bischofia* is determined by both habitat heterogeneity and the dispersal process, not by only one of the two factors. We can evaluate the importance of habitat heterogeneity by comparing these models with the colonization kernel model, and the importance of propagule limitation by comparing these models with the habitat suitability model. We examined two range-expansion scenarios (scenario #1, from 1977 to 2003; scenario #2, from the 1930s to 2003). We selected the best combination of environmental factors for each of environmentally explicit models (i.e., habitat suitability model, SSLR and SEDK) to minimize AIC in advance and considered only the most favored combination.

Map of the potential habitat distribution and forthcoming invasion threat

We predicted the potential habitat of *Bischofia* using the SEDK model in Eqs. (4–6), the SSLR model in Eq. (3), and the habitat suitability model in Eq. (1). In the SEDK model, the map of predicted p defines the potential habitat. The potential habitat suitability in the SSLR model can be determined as the probability predicted on the basis of the environment at each site, excluding the effect of the distance from the nearest seed source:

$$\hat{Z}_{pi} = \frac{1}{1 + \exp\left(-\left(\hat{\alpha} + \sum_j \hat{\beta}_{2j} X_{ij}\right)\right)} \tag{7}$$

where $\hat{Z}_{pi}$ is the predicted potential habitat suitability at site i, $\hat{\alpha}$ and the $\hat{\beta}_{2j}$ are estimated parameters of α and β_{2j} in the SSLR model (Eq. 3), respectively, and vector X_i represents the environmental variables. In the habitat suitability model, the potential habitat is predicted on the basis of the probability of current occurrence, Z_i, in Eq. (1) (Higgins et al. 1999).

In the context of the SEDK model, the value of $p(1 - q)$ is an index of the forthcoming invasion threat. This value represents the probability that the environment of a site is suitable for the invading species (p)

when the species has not yet invaded the site ($1 - q$). A site with a high forthcoming invasion threat represents a high priority for managers to prevent invasion, because it is highly possible that the site will be invaded if no countermeasures against *Bischofia* are taken. The value of $p(1 - q)$ was mapped on the basis of parameters estimated by the SEDK model from range-expansion data from 1977 to 2003.

Results

SEDK scenario #1 (1977 to 2003) provided the best AIC value of all the models, and SSLR scenario #1 provided the second-best AIC value (Table 1). Simultaneous analysis of these factors provided a better fit than the separate analyzes in the habitat suitability model and the colonization kernel model. Fittings over the shorter time range (scenario #1, 1977 to 2003) were better than those over the longer time range (scenario #2, 1930s to 2003) for all models.

Figure 3 indicates the predicted dispersal probability for SEDK scenarios #1 and #2 and for colonization kernel scenario #1 and #2. The colonization kernel model predicted a lower dispersal probability than the SEDK model for both range-expansion scenarios. The SSLR model could not be illustrated in Fig. 3 because the probability of habitat suitability and the dispersal probability could not be separated.

The potential habitats for *Bischofia* predicted by the SEDK and SSLR models were similar, but the potential range predicted by the habitat suitability model was smaller than those of the two simultaneous models (Fig. 4a, b, c).

The favored combinations of environmental variables and their coefficients varied among the models, but the same variables were selected for the SEDK and SSLR models under the same range expansion scenario (Table 2). The site's elevation and SPE were the most important environmental variables in all the environmentally explicit models. In contrast, curvature was not selected in any model.

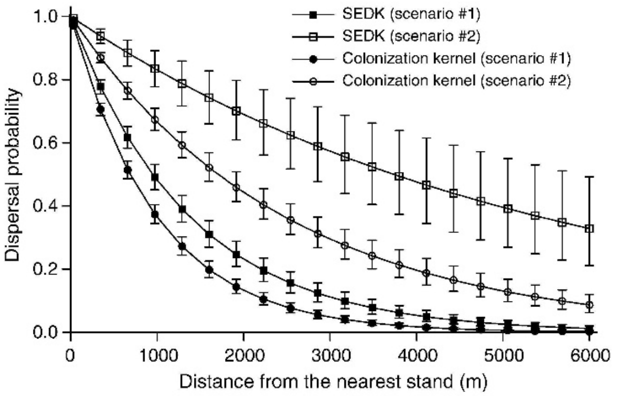


Fig. 3 Dispersal probability of *Bischofia javanica*, predicted by the simultaneous model with an explicit dispersal kernel (SEDK) in scenarios #1 and #2, and by the colonization kernel model in scenarios #1 and #2. *Error bars* indicate 95% bootstrap confidence intervals

Table 1 Values of Akaike's information criterion (AIC) for the simultaneous model with an explicit dispersal kernel (SEDK), the simultaneous model with a simple logistic regression (SSLR), the habitat suitability model, and the colonization kernel model for *Bischofia javanica*

Model	AIC value	Number of parameters
SEDK (scenario #1)	6,806	6
SSLR (scenario #1)	6,816	6
Colonization kernel model (scenario #1)	7,139	2
SEDK (scenario #2)	7,179	7
SSLR (scenario #2)	7,190	7
Habitat suitability model	7,199	5
Colonization kernel model (scenario #2)	8,025	2

Scenario #1 represents the range expansion from 1977 to 2003; scenario #2 represents the expansion from the 1930s to 2003. The table was arranged in ascending order of the models' AIC values

The forthcoming invasion threat, $p(1 - q)$, predicted by the SEDK model is the probability that the environment of a given site is suitable for *Bischofia* and that a propagule has not yet reached that site. Therefore, the value for already-invaded areas is low. The threat of new invasions was highest in the central high-altitude area, located slightly towards the southern part of the island (Fig. 4d).

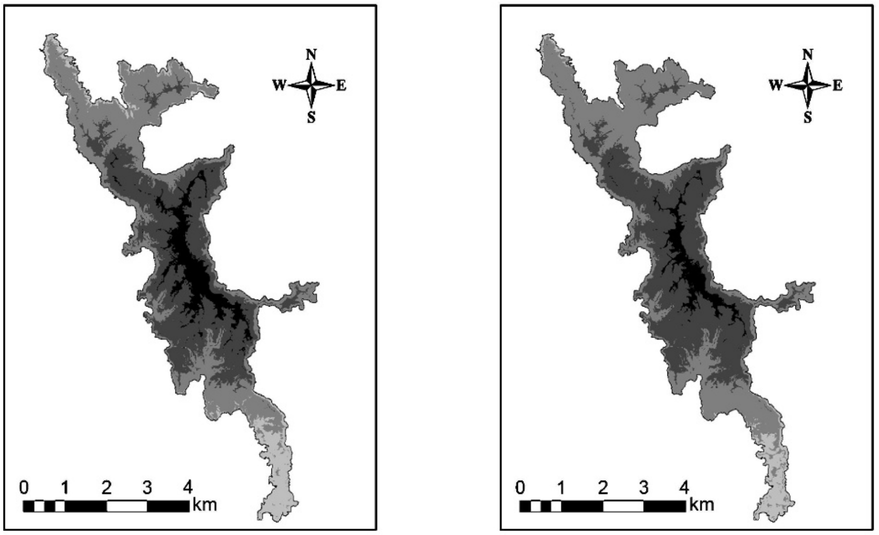
Discussion

When the effect of zero-inflation is negligible, the conventional habitat suitability model (e.g., Higgins et al. 1999) and the colonization kernel approach (Koike 2006) are useful for predicting the range expansion of an invasive species. However, we should develop models that integrate both attributes of the invasion process to estimate an appropriate habitat suitability and colonization kernel under non-equilibrium and environmentally heterogeneous conditions. In the case of *Bischofia*, our simultaneous models explained the range of the species in 2003 better than separate estimation by the habitat suitability model and the colonization kernel model (Table 1), regardless of the scenarios (i.e., based on planted sites in the 1930s or the distribution in 1977). Although the model fit was better for the SEDK model than for the SSLR model, the difference was not big. This suggests that the distribution of *Bischofia* in 2003 was determined not only by environmental parameters but also by dispersal limitations, and that its range will expand as the propagules are disseminated into suitable sites that have not yet been invaded.

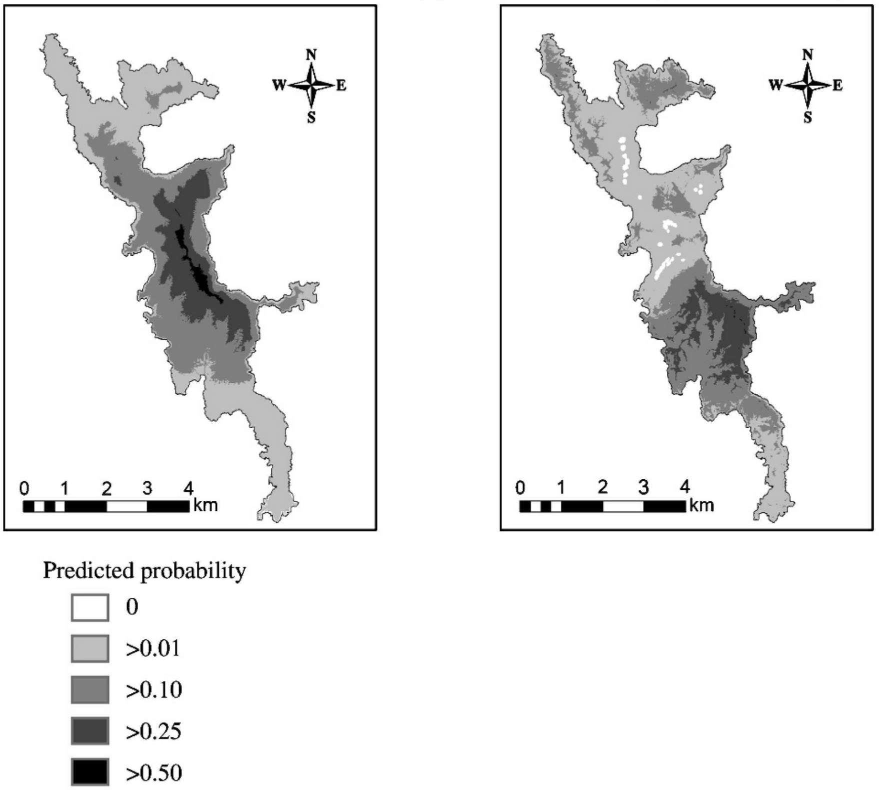
The shorter-term range-expansion data (1977 to 2003, 26 years analytical step) provided a better fit than the longer-term data (1930s to 2003, 73 years analytical step) for the colonization kernel model and the two

Fig. 4 **a** Maps of the potential habitat suitability for *Bischofia javanica*, produced using the simultaneous model with an explicit dispersal kernel (SEDK). **b** The simultaneous model with a simple logistic regression (SSLR). **c** The habitat suitability model. The range expansion from 1977 to 2003 (scenario #1) was used for the estimation in the SEDK and SSLR models. The distribution in 2003 was used in the habitat suitability model. The higher the probability, the greater the habitat suitability for *B. javanica*. **d** Predicted forthcoming invasion threat values, $p(1 - q)$, in the simultaneous model with an explicit dispersal kernel (SEDK) under scenario #1; these values represent the threat of future invasion by *Bischofia javanica*. These values indicate the probability that a site will be suitable for *Bischofia* but has not yet been invaded

(a) SEDK **(b)** SSLR



(c) Habitat suitability model **(d)** Predicted forthcoming invasion threat by the SEDK



simultaneous models (SSLR and SEDK in Table 1). Because range expansion is a stochastic process, the prediction might become difficult in a longer time scale. In addition, dispersal distance in a single analytical step should be longer in multi-generational long-term scenario than in short-term one (Fig. 3), and unrealistic long distance dispersal (e.g., those beyond sea cove) might occur. On the other hand, if the analytical time step was too short (e.g., 1-year analytical step), we could not detect range expansion. Our short-term data might be of suitable period.

The simultaneous models of habitat and dispersal predicted higher habitat suitability for *Bischofia* on Hahajima Island than in the conventional habitat suitability model (Fig. 4a, b, c). This difference suggests that zero-inflation caused by dispersal limitations leads to underestimation of the predicted habitat suitability when the habitat suitability model is used, and that simultaneous

Table 2 Parameter estimates and 95% confidence interval (CI, in brackets) for the simultaneous model with an explicit dispersal kernel (SEDK), the simultaneous model with a simple logistic regression (SSLR), and the habitat suitability model

	SEDK (scenario #1)	SEDK (scenario #2)	SSLR (scenario #1)	SSLR (scenario #2)	Habitat suitability model
Environmental variables					
Elevation	0.460 (0.382 to 0.540)	0.625 (0.557 to 0.693)	0.388 (0.324 to 0.451)	0.587 (0.526 to 0.650)	0.606 (0.549 to 0.667)
Summit plane elevation	0.492 (0.365 to 0.621)	0.552 (0.476 to 0.635)	0.398 (0.280 to 0.522)	0.558 (0.482 to 0.639)	0.661 (0.567 to 0.762)
Flow accumulation	–	0.072 (0.008 to 0.134)	–	0.069 (0.006 to 0.129)	0.058 (−0.001 to 0.114)
Slope	−0.183 (−0.263 to −0.107)	−0.049 (−0.111 to 0.013)	−0.140 (−0.203 to −0.080)	−0.049 (−0.108 to 0.009)	−0.058 (−0.115 to 0.000)
Curvature	–	–	–	–	–
Skyline	−0.154 (−0.236 to −0.076)	−0.056 (−0.123 to 0.010)	−0.120 (−0.181 to −0.056)	−0.048 (−0.112 to 0.018)	–
Dispersal variables					
Nearest distance from the range of *Bischofia* in 1977	-7.31×10^{-4} (-8.18×10^{-4} to -6.49×10^{-4})	–	-8.66×10^{-4} (-9.64×10^{-4} to -7.73×10^{-4})	–	–
Nearest distance from the sites planted in ca. 1930	–	-1.85×10^{-4} (-2.59×10^{-4} to -1.18×10^{-4})	–	-1.51×10^{-4} (-2.28×10^{-4} to -7.80×10^{-5})	–

Scenario #1 represents the range expansion from 1977 to 2003; scenario #2 represents the expansion from the 1930s to 2003. Environmental variables marked with a dash (–) were not selected in the best combination of environmental factors on the basis of Akaike's information criterion (AIC). Environmental variables were standardized so that the relative importance of the variables could be shown. The 95% confidence interval is based on a 5,000-iteration nonparametric bootstrap resampling (Efron and Tibshirani 1986)

models can cope better with this problem. The differences in the habitat distribution predicted by the SSLR and SEDK models were not big. Whereas predictive habitat distribution models such as the habitat suitability model in our study require the assumption of an equilibrium state between the environment and the species' distribution (Guisan and Zimmermann 2000), simultaneous analysis does not require this assumption because the effect of propagule dispersal is intrinsic to the model. Since many suitable sites have not yet been occupied by the spreading invasive species, a habitat suitability model will always underestimate the potential habitat, as shown in Fig. 4c.

The most important environmental predictors for *Bischofia* were elevation and SPE in all the environmentally explicit models; this confirms the results of previous research on the island (Mikami and Koike 2005). The positive effects of elevation and SPE can probably be attributed to the high moisture levels and the avoidance of the salt breeze in upland areas of the island, both of which would facilitate the establishment of *Bischofia*. Some environmental factors used in this study were proxies for direct limiting factors such as moisture conditions (i.e., elevation and SPE) and wind pressure (i.e., skyline). Though the simultaneous models adequately predicted future invasion by *Bischofia* on Hahajima Island, their generalizability to other regions (native range or other invaded range) may be limited. To increase their generality, it would have been helpful to analyze the distribution in other regions, but this requires equivalent information on other regions that is not currently available. It would also be appropriate to investigate whether replacing general site characteristics such as elevation and slope (proxies for proximal factors) with proximal factors such as soil characteristics (e.g., particle size distribution, nutrient content) and environmental characteristics (e.g., temperature, wind direction and speed) would improve the generalizability of the model. Such an analysis would also improve the separability of the effects of the explanatory variables by decreasing the correlations among them.

The effect of dispersal on the current distribution pattern of *Bischofia* was relevant in all the dispersal-explicit models. The colonization kernel model showed a smaller goodness of fit than the SEDK model, probably because of environmental noise. Moreover, the predicted dispersal rate was underestimated by a colonization kernel that ignores habitat heterogeneity (Fig. 3), probably because of false zeros (Martin et al. 2005) in the dispersal process caused by the presence of unsuitable habitats. It is difficult to obtain a fixed dispersal probability in the SSLR model, because the shape of the kernel changes depending on the specific environments as a result of the formulation of the model (Eq. 3).

On this island, there are still areas suitable for invasion by *Bischofia* that have not yet been invaded and that still retain a rich endemic flora. Prediction of future invasions of these sites using the forthcoming invasion threat, $p(1 - q)$, will provide key information to support decision-making designed to protect the endemic flora (Fig. 4d). Young *Bischofia* plants near sites with a higher threat of invasion should be the highest priority for removal to conserve current plant communities of native species, because these *Bischofia* populations will be satellite populations or "nascent foci" (Moody and Mack 1988) that promote invasion, and invasion of environmentally suitable sites from these foci will be facilitated. Our results show that such a future risk map can be easily obtained by means of simultaneous estimation of habitat suitability and the colonization kernel. Integration of the predictions of habitat suitability and dispersal can thus guide the development of specific landscape-scale management plans to control invasive species.

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Chapter 26

Beetle responses to artificial gaps in an oceanic island forest: implications for invasive tree management to conserve endemic species diversity

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Abstract Natural forests are often replaced by invasive alien trees on isolated oceanic islands. Adequate eradication of invasive trees should be conducted with the goal of biodiversity conservation, because islands support many endemic organisms that depend on native forests. An invasive alien tree, *Bischofia javanica* Blume (Euphorbiaceae), has invaded and replaced natural forests on the oceanic Ogasawara (Bonin) Islands, Japan, in the northwestern Pacific Ocean. To determine how the removal of *B. javanica* trees affects insect diversity, we examined flying beetles captured using Malaise traps in *B. javanica* forests on Hahajima. The abundance, species density, and species composition of wood-boring beetles (Coleoptera: Cerambycidae, Elateridae, Mordellidae, and Scolytidae) were compared between closed-canopy sites and gaps created by girdling *B. javanica* trees in alien forests during two seasons (June–July and October–November 2005). Of the collected beetles, 75.8, 87.5, 90.0, and 0.0% of cerambycid, elaterid, mordellid, and scolytid beetle species, respectively, were endemic to the Ogasawara Islands. More cerambycid, elaterid, and mordellid individuals were captured in June–July than in October–November; the number of scolytid individuals did not differ between seasons. More cerambycid, elaterid, and scolytid individuals were captured in artificial gaps than on the closed-canopy forest floor. Although fewer mordellid individuals were captured in gaps, more endemic mordellids were captured in gaps. More cerambycid and scolytid species were captured in artificial gaps than in closed-canopy areas. The positive responses of beetles to artificial gaps suggest that the removal of *B. javanica* increases beetle diversity and the abundance of endemic beetles.

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Keywords Biodiversity · *Bischofia javanica* · Introduced trees · Ogasawara (Bonin) Islands · Subtropical islands

Introduction

Natural forests are often replaced by invasive alien trees (Richardson 1998; Gordon 1998). This is especially true for isolated oceanic islands that have never been connected to a continental landmass (Shimizu and Tabata 1985; Yamashita et al. 2000; Denslow 2003; Daehler et al. 2004). Endemic tree species originally formed unique forests on isolated oceanic islands such as the Hawaiian and Galápagos Islands (Carlquist 1974) because the islands lack major tree groups such as oaks (*Quercus*) that dominate continental forests (Carlquist 1974; Denslow 2003). However, human immigration has resulted in the introduction of various tree species, some of which have invaded and replaced natural forests (Shimizu and Tabata 1985; Yamashita et al. 2000; Denslow 2003; Daehler et al. 2004). Replacement by invasive alien trees affects native forest-dwelling insects, because most native insects depend on native plants for food and habitat (Samways 2005). Endemic organisms are highly concentrated to oceanic islands because of evolution and the speciation of immigrant organisms (Carlquist 1974; Howarth and Mull 1992; Paulay 1994; Whittaker 1998; Gillespie and Roderick 2002). Therefore, eradication of alien trees is needed to conserve endemic insect communities on oceanic islands. Because some of endemic species still inhabit alien forests, adequate removals of invasive trees should be conducted to conserve endemic insects.

Emulation of natural disturbances such as wildfires and natural gaps is one forest management tool for biodiversity conservation (e.g., Niemelä 1999; Perera et al. 2004; Buddle et al. 2006), although natural disturbances might increase the risk of pest outbreaks (Bouget and Duelli 2004). This forest management strategy can be used to eradicate invasive alien trees. However, the impacts of invasive alien tree removal on biodiversity have rarely been studied on islands. Here we examined the responses of wood-boring beetles to gaps created by killing trees in forests that have been replaced by the invasive alien tree *Bischofia javanica* Blume (Euphorbiaceae) on one of the oceanic Ogasawara (Bonin) Islands in the northwestern Pacific Ocean (Fig. 1a). This allowed us to determine whether emulation of natural disturbances such as gaps is an appropriate management strategy for invasive alien trees to conserve endemic species and diversity on the Ogasawara Islands.

The alien tree *B. javanica*, which was introduced and planted on the Ogasawara Islands before 1905 as a forestry tree (Toyoda 2003; Shimizu 2003), has invaded native forests via bird-dispersed seeds (Yamashita et al. 2000; Shimizu 2003; Toyoda 2003). This broad-leaved evergreen tree species grows up to 20 m tall (Toyoda 2003). Because *B. javanica* grows faster and has higher shade tolerance than native tree species, it often replaces native forests (Yamashita et al. 2000). On Hahajima, the second largest of the Ogasawara Islands, *B. javanica* has invaded ca. 14% of the tree crown (Fig. 1b; West 2005). Because *B. javanica* invasion affects native plants, the eradication of *B. javanica* is important for conserving native forests (Shimizu 2003). The Japan Forest Agency recently planned to kill this alien species and recover native forests by transplanting young native trees under the canopy of dead *B. javanica* trees (Shimizu 2003). As a first step toward this management goal, *B. javanica* trees have been killed by girdling (ring barking; Fig. 2a) in gap-sized patches since 2002 (Shimizu 2003). Gaps, which are open-canopy patches, are

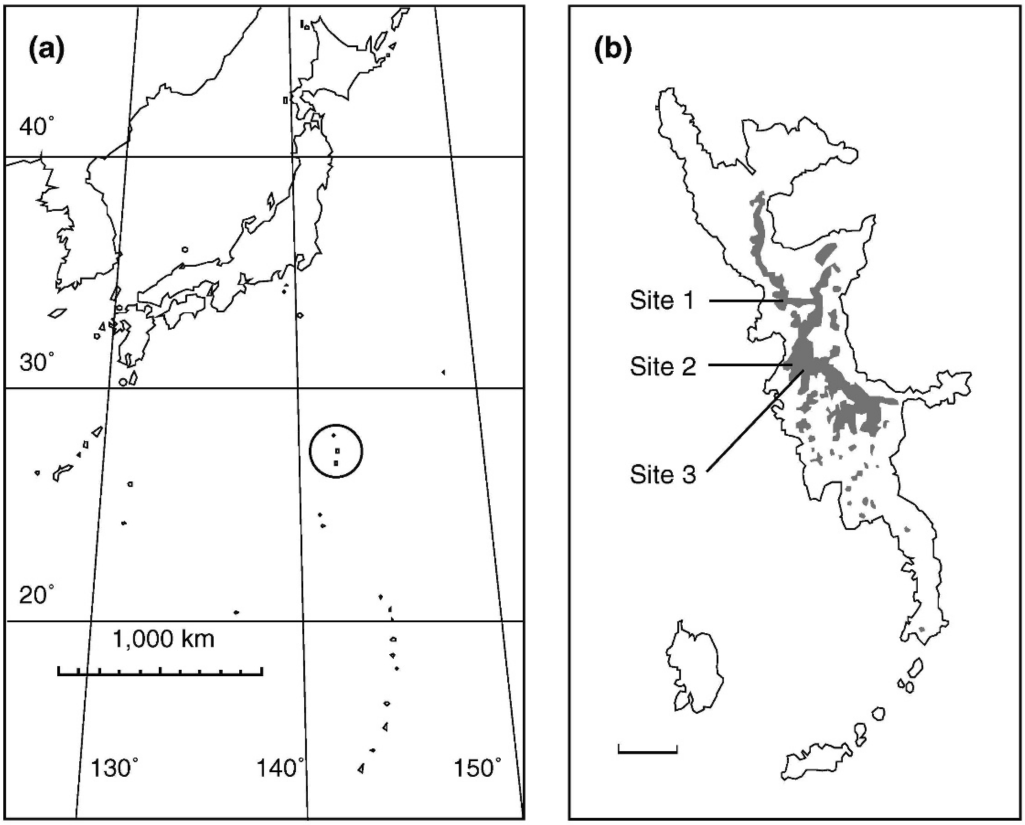


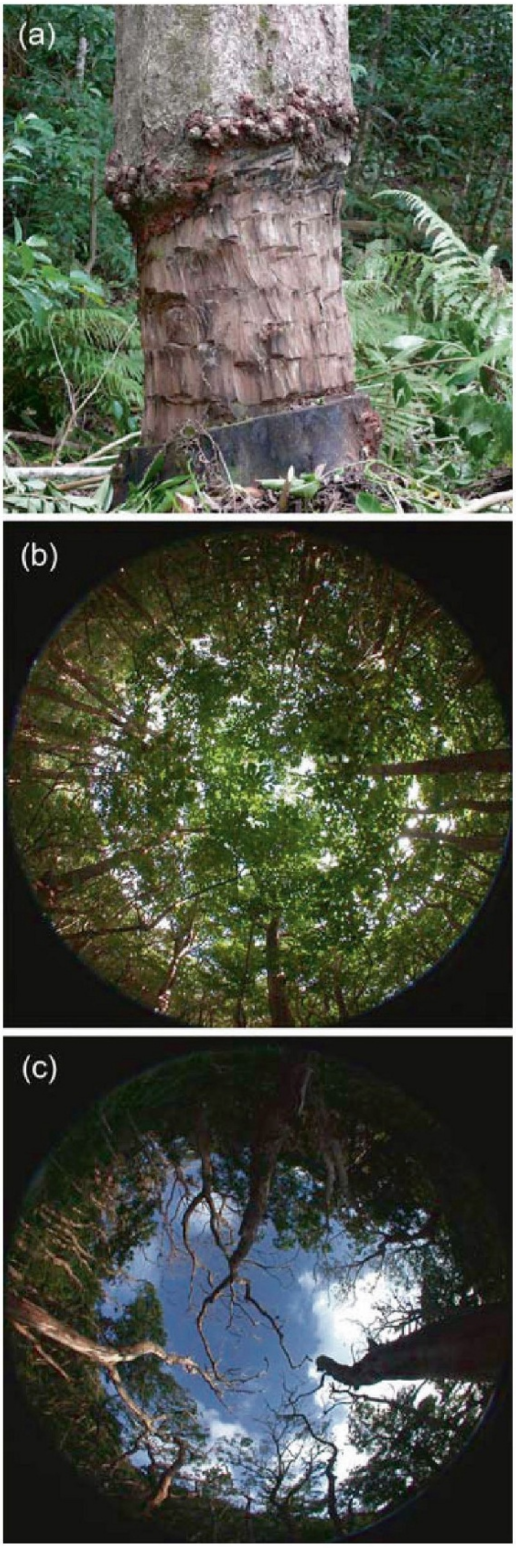
Fig. 1 **a** Location of the Ogasawara Islands (*circled*); scale bar, 1,000 km. **b** Locations of study sites on Hahajima; scale bar, 1 km. The shaded area indicates forests in which the tree crown has been invaded by *B. javanica* (based on data and figures from the Japan Forest Technology Association 2005)

often created in forests of the Ogasawara Islands because several typhoons hit the islands every year and damage the forests (Shimizu 2003). Because emulation of natural disturbances such as gaps is a forest management tool for biodiversity conservation (e.g., Niemelä 1999; Perera et al. 2004), it may be useful for *B. javanica* eradication. However, impacts of this removal method on native organisms other than plants have not been examined. Therefore, we used the artificial gaps created by killing *B. javanica* trees to examine the impact of this management plan on insect diversity.

The insect fauna of the Ogasawara Islands is characterized by forest-dwelling species such as wood-feeding beetles (Kato et al. 1998). The diversity and high endemism of beetles is particularly striking on the Ogasawara Islands (Ohbayashi et al. 2003; Sugiura et al. 2008a, b, 2009). The responses of wood-boring beetles to forest disturbances such as gaps are important for forest management for biodiversity conservation in the Ogasawara Islands, as in other areas (reviewed by Bouget and Duelli 2004).

We compared the abundance, species density (numbers of species per sample unit; Gotelli and Colwell 2001), and species composition of four families of wood-boring beetles between closed-canopy sites (Fig. 2b) and gaps created by killing *B. javanica* trees (Fig. 2c) on Hahajima in two seasons (June–July and October–November). Considering the conservation and protection of island forests, we focused on two types of beetles, endemic and non-endemic (i.e., widely-distributed or introduced) species. Endemic species are

Fig. 2 Tree trunk of *B. javanica* and the forest canopies. **a** Girdling; the complete removal of a strip of bark around a tree's outer circumference. Hemispherical photographs taken above traps using a digital camera **b** at a closed-canopy site in a *B. javanica* forest and **c** at a gap created by killing *B. javanica*



conservation targets on islands, while introduced species might become pests that attack native trees. We examined the responses of beetles to artificial gaps and discuss invasive tree management for biodiversity conservation and pest management.

Materials and methods

Study site

The Ogasawara Islands are extinct volcanic islands in the northwestern Pacific Ocean, approximately 1,000 km south of the Japanese mainland (Shimizu 2003; Fig. 1a). The mean annual temperature is 23.2°C and the mean annual precipitation was 1,292 mm from 1987 to 1998 on Chichijima (Toyoda 2003). Therefore, the climate of the Ogasawara Islands is subtropical. Like other oceanic islands, the Ogasawara Islands support many endemic organisms (Shimizu 2003), including vascular plants (137 species; Toyoda 2003) and insects (338 species; Ohbayashi et al. 2003). However, many organisms are endangered because of human activities (e.g., Shimizu 2003; Toyoda 2003; Karube 2004). Furthermore, many introduced organisms have invaded the islands and have affected native communities (e.g., Yamashita et al. 2000; Shimizu 2003; Ohbayashi et al. 2003; Karube 2004; Sugiura et al. 2008a, b).

Forestry for timber production is no longer conducted in the Ogasawara Islands; forests are conserved as important habitats for endemic organisms (Shimizu 2003). Our study was conducted in *B. javanica* forests on the inhabited island of Hahajima (Fig. 1b; 26°38′ N, 142°9′ E; 20.8 km^2; 0–462.6 m above sea level). We selected three sites in *B. javanica* forests where *B. javanica* trees have been killed by girdling (Fig. 1; site 1, 26°40′ N, 142°89′ E; site 2, 26°39′ N, 142°09′ E; site 3, 26°39′ N, 142°09′ E). The canopy at the study sites was almost completely occupied by *B. javanica* trees (Fig. 2b) although only a few native tree species grew in the forests. Saplings of native trees have been planted after the removal of *B. javanica* trees, because no native tree species grew in the patches where *B. javanica* trees were killed.

Insects

We examined the abundance, species density, and species composition of four families of wood-boring beetles (Coleoptera: Cerambycidae, Elateridae, Mordellidae, and Scolytidae). The diversity and high endemism of Cerambycidae, Elateridae, and Mordellidae are particularly striking on the Ogasawara Islands (Ohbayashi et al. 2003; Sugiura et al. 2008a, 2009). Cerambycid beetles, whose larvae feed on wood and adults, feed on pollen, nectar, or leaves, have frequently been used in investigations of forest biodiversity (e.g., Shibata et al. 1996; Ohsawa 2004a; Makino et al. 2007). Furthermore, approximately 70% of cerambycid species recorded from the Ogasawara Islands are endemic, and some are endangered (Ohbayashi et al. 2003; Karube 2004; Makihara et al. 2004; Sugiura et al. 2008a, b, 2009). Several alien cerambycid species have been unintentionally introduced to these islands by human activities (Makihara et al. 2004); e.g., wood-boring insects can be transported in untreated wood packaging material, and a few species have become established (Makihara et al. 2004; Sugiura et al. 2008a, b). Elaterid beetles, whose larvae are generalist predators of other wood-boring insects or rood feeders, have rarely been examined in detail (except by Ohsawa 2004b). The family Elateridae is also important for endemism conservation in Ogasawara because ca. 70% of elaterid species are endemic, as in the Cerambycidae (Ohbayashi et al. 2003; Makihara and Ôhira 2005; Sugiura et al. 2008a). Mordellid beetles, whose larvae feed on living stems or dead wood and adults feed on pollen and spores (Jackman and Lu 2002), have also rarely been examined in detail, despite the importance of this family for insect conservation in the Ogasawara Islands because of the high rate of endemism (90%; Ohbayashi et al. 2003; Sugiura et al. 2008a,

2009) and their dominance in the Ogasawara Islands. Mordellids account for ca. 37% of beetle individuals captured using Malaise traps in the Ogasawara Islands (Kato et al. 1998). Beetles of these families are good indicators of biodiversity in the Ogasawara Islands because the diversity and endemism of these species depend on natural vegetation (Sugiura et al. 2008a, 2009). Despite the high endemism of other wood-boring beetles, there are no endemic species of Scolytidae in the Ogasawara Islands; the recorded species are widely distributed or introduced (Nobuchi and Ôno 1973; Ohbayashi et al. 2003). Thus, this family is rarely found in the Ogasawara Islands. Scolytid (bark and ambrosia) beetles, whose larvae feed on wood (and/or fungi), are frequently used in studies of biodiversity and forest health because their diversity is high in forests and some are forest pests (Martikainen et al. 1999; Bouget and Duelli 2004; Bouget 2005).

Methods

We used Malaise traps (Townes-style Malaise traps with coarse mesh; 1.8 × 1.2 × 2.0 m length × width × height; Golden Owl Publishers) to capture flying beetles. The collection bottle (500 ml) contained equal amounts of 99% ethanol and 99% polypropylene to preserve collected insects. Malaise traps are frequently used to investigate flying beetles (e.g., Maeto and Makihara 1999; Nakashizuka and Stork 2002; Ohsawa 2004a, b; Makino et al. 2007; Sugiura et al. 2008a, 2009), although other traps such as window traps are also used (e.g., Bouget 2005; Martikainen et al. 1999). We set traps at three forest sites in two seasons, from 18 June to 1 July 2005 and from 19 October to 1 November 2005. Traps were set at two sampling points per site, one in the closed-canopy forest floor and the other in a forest gap created by killing *B. javanica* trees. The traps were set >20 m apart at each site. Furthermore, traps were set at the same sites in both study seasons.

Bischofia javanica trees have been killed by girdling in the Ogasawara Islands (Fig. 2a; Shimizu 2003). Girdling is the complete removal of a strip of bark around a tree's outer circumference, which causes death (Fig. 2a; Fujimori 2001). To examine differences among beetle communities between closed-canopy forest floors and artificial gaps, we used small-sized patches (<100 m^2) as artificial gaps where *B. javanica* trees were killed by girdling in summer 2004. Because the killed trees were not removed, dead trees and twigs were more abundant in artificial gaps than on the closed-canopy forest floor. We used openness (i.e., the proportion of sky not covered by canopy) of the tree crown as a measure of the light environment (Fig. 2b, c). Openness was measured by taking hemispherical photographs above traps using a digital camera (Nikon COOLPIX 995) with a fisheye lens (Nikon FC-E8). The camera was positioned horizontally above the trap (2.0 m above the ground). Photographs were taken on 18 June and 19 October 2005. Openness was calculated using the program CanopOn 2 (http://takenaka-akio.cool.ne.jp/etc/canopon2/). Gaps created by killing *B. javanica* were more open (12.5–32.8%) than closed-canopy sites (5.7–8.5%; Fig. 2b, c; generalized linear mixed models, cf., data analyses; treatment, $\chi^2 = 10.0$, $P < 0.01$; season, $\chi^2 = 0.6$, $P = 0.43$; treatment × season, $\chi^2 = 1.4$, $P = 0.23$). Therefore, the light environment and abundance of dead trees differed between the closed-canopy sites and artificial gaps, but not between seasons. We did not focus on the effects of gap size and isolation on beetle diversity (*sensu* Bouget 2005), although the number of girdled trees and gap size varied among study sites. Because most endemic insect species are endangered (Karube 2004), we could use only a few traps.

Sampled beetles were sorted, pinned, and identified using pictorial encyclopedias or published reports (Nomura 1975; Hatayama and Takakuwa 1985; Makihara et al. 2004; Makihara and Ôhira 2005; Ohbayashi and Nisato 2007). Information on the distribution and ecological properties of beetles was obtained from previous studies (Nobuchi and Ôno 1973; Hatayama and Takakuwa 1985; Takakuwa 1992; Nobuchi 1994; Ohbayashi et al. 2003; Karube 2004; Makihara et al. 2004; Makihara and Ôhira 2005; Sugiura et al. 2008a, b, 2009).

Data analyses

To examine the effects of treatment (i.e., closed-canopy site vs. artificial gap) and season (i.e., June–July vs. October–November) on the abundance (numbers of individuals per trap) and species density (numbers of species per trap; Gotelli and Colwell 2001), of beetles, we used generalized linear mixed models (GLMMs) with a Poisson error distribution. Because we sampled beetles at the same sampling sites in two seasons, sampling sites were not independent between seasons. To consider site effects, we treated sampling site as a random effect (Faraway 2006). We set treatment and season as fixed effects. We also examined the interaction between treatment and season as a fixed effect. In the GLMMs, we used model comparisons to test fixed effects (Faraway 2006, p. 165). We examined models with only random effects ($\text{model}_{\text{null}}$), with random effects and treatment ($\text{model}_{\text{treatment}}$), and with random effects and season ($\text{model}_{\text{season}}$). We compared $\text{model}_{\text{null}}$ to $\text{model}_{\text{treatment}}$ to test for differences between treatments, and compared $\text{model}_{\text{null}}$ to $\text{model}_{\text{season}}$ to test for differences between seasons. We also used model comparisons to test for the effect of the treatment-season interaction. We used models with random effects, treatment, and season ($\text{model}_{\text{treatment+season}}$), and with random effects, treatment, season, and treatment × season interaction ($\text{model}_{\text{interaction}}$). We compared $\text{model}_{\text{treatment+season}}$ to $\text{model}_{\text{interaction}}$ to test for effects of the interaction. GLMMs were conducted on both total species and endemic species (i.e., excluding non-endemic species) in each beetle family. Furthermore, individuals of abundant non-endemic species were separately analyzed. Similarly, we examined the effects of treatment, season, and their interaction on openness using a normal error distribution (cf., methods). We used R Ver. 2.6.1 (R Development Core Team 2006) and lme4 Ver. 0.99875-9 (Bates and Sarkar 2007) for the GLMMs.

To examine the effects of treatment on insect species composition, we conducted a redundancy analysis (RDA) using CANOCO Ver. 4.5 (ter Braak and Smilauer 2002). We pooled the number of individuals of each species collected from the two seasons at each sampling site. The resultant summed value was used as the response variable for each species. Because the response variables of most species had skewed distributions, the response variables were transformed logarithmically. The treatment was coded as a dummy variable in which closed-canopy site was used as a reference category. We conducted the RDA for each insect group. Species were centered and standardized using the option in CANOCO. We used all other CANOCO defaults. The dummy explanatory variable was tested in 999 permutation tests. All statistical tests were conducted at the 0.05 significance level.

Results

Beetle endemism

Twelve, eight, ten, and eight species of cerambycid, elaterid, mordellid, and scolytid, beetle, respectively, were captured in the Malaise traps (Table 1). Of these, 75.8, 87.5, 90.0, and 0.0% of species and 85.2, 99.4, 19.9, and 0.0% of individuals, respectively, were endemic to the Ogasawara Islands (Table 1). In the Cerambycidae, endemic species represented 98.8% of individuals captured in June–July, although the non-endemic (introduced) species *Curtomerus flavus* (Fabricius) represented 42.6% of individuals captured in October–November (Table 1). In the Mordellidae, the non-endemic native species *Ermischiella castanea* (Boheman) accounted for 73.4 and 94.4% of individuals captured in June–July and October–November, respectively (Table 1). Therefore, only 19.9% of mordellid individuals were endemic, even with the high species endemism rate (90.0%). In the Scolytidae, no species were endemic; all captured species are also distributed on mainland Japan and/or in other areas (Table 1; Nobuchi and Ôno 1973).

Beetle responses to artificial gaps

More cerambycid individuals were captured in June–July than in October–November, although species density did not differ between seasons (Fig. 3a, b; Table 2). Cerambycids were more diverse and more abundant in artificial gaps than closed-canopy sites, although the difference in species density was only marginally significant (Fig. 3a, b; Table 2). The interaction between season and treatment was significant for cerambycid abundance (Table 2), suggesting that the positive effects of gaps on cerambycid abundance might be larger in June–July than in October–November (Fig. 3b). Among endemic species, the pattern was similar to that of all species (including non-endemic species), although the difference in endemic species density between closed-canopy and gap sites was not significant (Fig. 4a, b; Table 2). Furthermore, only in *C. flavus,* a non-endemic species, more individuals were captured in artificial gaps than in closed-canopy sites in October–November (Fig. 4g; Table 2).

Elaterids were more abundant and diverse in June–July than in October–November (Fig. 3c, d; Table 2). More elaterid individuals were captured in artificial gaps than in closed-canopy sites, although elaterid species density did not differ among sites (Fig. 3c, d; Table 2). The interaction between season and treatment was marginally significant for elaterid abundance (Table 2). This interaction suggests that the positive effects of gaps on elaterid abundance were detected only in June–July because few elaterids were captured in October–November (Fig. 3c, d). Among endemic species, the pattern was similar to that of all total species (including non-endemic species; Fig. 4c, d; Table 2).

Mordellids were more abundant and diverse in June–July than in October–November (Fig. 3e, f; Table 2). Fewer mordellid individuals were captured in artificial gaps than in closed-canopy sites, although mordellid species density did not differ between sites (Fig. 3e, f; Table 2). The interaction between season and treatment was significant for mordellid abundance (Table 2). This interaction suggests that the negative effects of gaps on mordellid abundance were detected only in October–November (Fig. 3e, f). However, excluding non-endemic species (i.e., *E. castanea*; M8 in Table 1), the pattern differed from that for all species (Fig. 4e, f; Table 2). More individuals of endemic species were captured in artificial gaps than in closed-canopy sites (Fig. 4f; Table 2). In *E. castanea*, fewer individuals were captured in artificial gaps than in closed-canopy sites (Fig. 4h; Table 2). Therefore, the pattern of *E. castanea* influenced that of all species.

The species density and abundance of Scolytidae did not differ between seasons (Fig. 3g, h; Table 2). Scolytids were more diverse and abundant in artificial gaps than in closed-canopy sites, although the difference in species density was only marginally significant (Fig. 3g, h; Table 2). No interaction between season and treatment was detected (Table 2).

Table 1 Abundance of cerambycid, elaterid, mordellid, and scolytid species captured by Malaise traps in *Bischofia javanica* forests in 2005

No.	Family/species	Status[c]	Season[a] Site[b]	J 1 C	J 1 G	J 2 C	J 2 G	J 3 C	J 3 G	O 1 C	O 1 G	O 2 C	O 2 G	O 3 C	O 3 G	Total
	Cerambycidae															
C1	*Psephactus scabripennis* Kusama	Endemic		0	0	0	0	1	0	0	0	0	1	0	0	2
C2	*Nortia kusuii* Kusama et Nara	Endemic		1	1	1	2	1	0	1	0	0	1	0	0	8
C3	*Ceresium unicolor unicolor* (Fabricius)	Wide		0	0	0	0	0	0	1	3	0	0	0	0	4
C4	*Ceresium signaticolle* Matsumura et Matsushita	Endemic		22	16	22	59	12	57	0	0	0	0	0	0	188
C5	*Ceresium simile simile* Gahan	Endemic		0	0	0	0	0	3	0	0	0	0	0	0	3
C6	*Curtomerus flavus* (Fabricius)	Wide		0	0	0	0	0	1	11	32	0	1	1	1	47
C7	*Comusia testacea* (Gressitt)	Wide		0	0	0	2	0	0	0	0	0	0	0	0	2
C8	*Xylotrechus ogasawarensis* Matsushita	Endemic		0	2	0	1	0	0	0	1	0	2	0	1	7
C9	*Mesosa rufa* (Breuning)	Endemic		0	0	0	0	0	0	0	4	0	1	1	0	6
C10	*Acalolepta boninensis* Hayashi	Endemic		0	1	0	0	1	3	0	2	0	0	0	0	7
C11	*Phloeopsis lanata* (N. Ohbayashi)	Endemic		0	0	0	0	0	0	0	3	0	0	0	0	3
C12	*Phloeopsis bioculata* (Matsumura et Matsushita)	Endemic		5	11	3	6	2	13	1	18	3	2	0	16	80
	Elateridae															
E1	*Cryptalaus larvatus pini* (Lewis)	Wide		0	0	1	1	0	0	1	0	1	0	0	0	4
E2	*Lacon* (*Alaotypus*) *boninensis* (Ôhira)	Endemic		1	0	0	0	0	1	0	0	0	0	0	0	2
E3	*Ischiodontus longfordi* (van Zwaluwenburg)	Endemic		7	7	54	132	17	28	1	1	0	1	1	0	249
E4	*Megapenthes kusuii* (Ôhira)	Endemic		0	0	9	7	2	4	0	0	0	0	0	0	22
E5	*Megapenthes makiharai* Ôhira	Endemic		1	1	14	17	12	18	0	0	0	0	0	0	63
E6	*Haterumelater bifoveolatus* (Miwa)	Endemic		3	1	16	17	6	14	0	0	0	0	0	0	57
E7	*Priopus boninensis* (van Zwaluwenburg)	Endemic		30	10	81	97	8	9	0	0	2	0	0	0	237
E8	*Propsephus* sp.	Endemic		0	1	0	0	0	0	0	0	0	0	0	0	1
	Mordellidae															
M1	*Variimorda inomatai* Takakuwa	Endemic		3	1	0	0	0	0	0	0	0	0	0	0	4

Table 1 continued

No.	Family/species	Status[c]	Season[a] Site[b]	J 1 C	J 1 G	J 2 C	J 2 G	J 3 C	J 3 G	O 1 C	O 1 G	O 2 C	O 2 G	O 3 C	O 3 G	Total
M2	*Variimorda ihaii boninensis* Nomura	Endemic		1	3	5	2	2	0	0	1	0	9	0	1	24
M3	*Variimorda* sp.	Endemic		0	0	0	0	0	0	2	0	0	0	0	0	2
M4	*Falsomordellistena formosana boninensis* Nomura	Endemic		1	0	4	1	1	2	0	0	0	0	0	0	9
M5	*Falsomordellistena pseudalpigena* Nomura[e]	Endemic		2	4	0	2	0	1	0	0	0	0	0	0	9
M6	*Falsomordellistena watanabei* Nomura	Endemic		7	14	21	12	2	4	2	1	0	1	1	3	68
M7	*Glipostenoda pseudexcisa* Nomura	Endemic		19	20	19	35	10	48	1	0	0	1	0	0	153
M8	*Ermischiella castanea* (Boheman)	Wide		237	209	104	140	37	9	119	21	186	66	41	18	1,187
M9	*Ermischiella nigriceps* Nomura	Endemic		1	0	4	4	4	0	0	0	0	0	0	0	13
M10	*Ermischiella hahajimana* Nomura	Endemic		1	1	2	1	3	0	1	1	0	0	2	0	12
	Scolytidae															
S1	*Ambrosiodmus lewisi* (Blandford)[d]	Wide		0	0	0	0	0	0	0	0	0	2	0	0	2
S2	*Ambrosiodmus rubricollis* (Eichhoff)[d]	Wide		0	1	0	0	0	0	0	0	0	0	0	0	1
S3	*Xylosandrus brevis* (Eichhoff)[d]	Wide		0	0	0	0	0	0	0	1	0	1	0	0	2
S4	*Xylosandrus compactus* (Eichhoff)[d]	Wide		0	0	0	0	0	0	0	0	0	0	1	0	1
S5	*Xylosandrus crassiusculus* (Motschulsky)[d]	Wide		0	0	0	0	0	1	1	0	0	0	0	0	2
S6	*Xyleborinus saxeseni* (Ratzeburg)[d]	Wide		0	0	1	0	0	0	0	0	1	0	0	1	3
S7	*Hypothenemus birmanus* (Eichhoff)	Wide		0	9	0	0	0	1	0	0	0	2	0	0	12
S8	*Hypothenemus eruditus* Westwood	Wide		0	4	1	1	0	3	0	0	1	4	0	2	16

[a] Sampling period: J, 18 June–1 July 2005; O, 19 October–1 November 2005

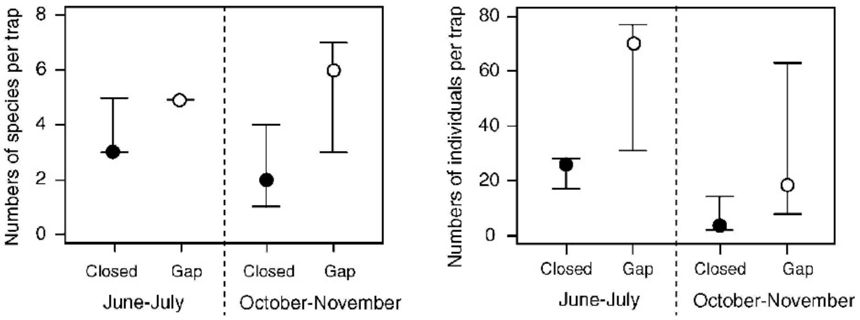
[b] Sampling site: 1–3, site number (see Fig. 1b); C, closed-canopy site; G, gap created by killing trees

[c] Status as endemic or widespread (non-endemic)

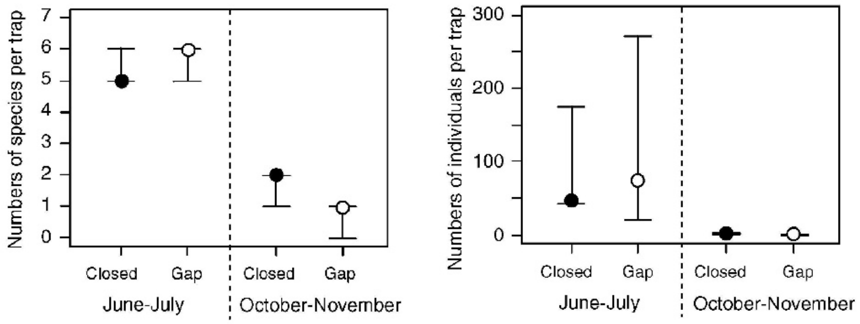
[d] These species are ambrosia beetles, whose larvae feed on fungi carried by adults to the host tree (Nobuchi 1994). Other scolytid species are bark beetles, whose larvae feed on the undersurface of bark (Nobuchi 1994)

[e] Females of the two endemic species *Falsomordellistena pseudalpigena* and *F. rosseoloides* cannot be identified, and the two species can only be distinguished based on male morphology. However, because we found no male *F. rosseoloides*, we considered the females to be *F. pseudalpigena*

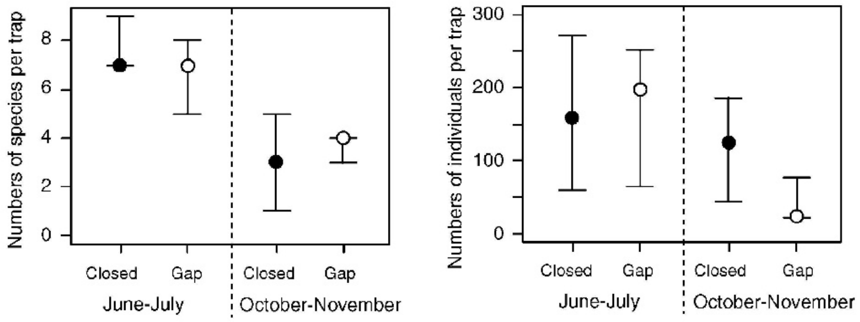
(a) Cerambycidae, species density **(b)** Cerambycidae, abundance



(c) Elateridae, species density **(d)** Elateridae, abundance



(e) Mordellidae, species density **(f)** Mordellidae, abundance



(g) Scolytidae, species density **(h)** Scolytidae, abundance

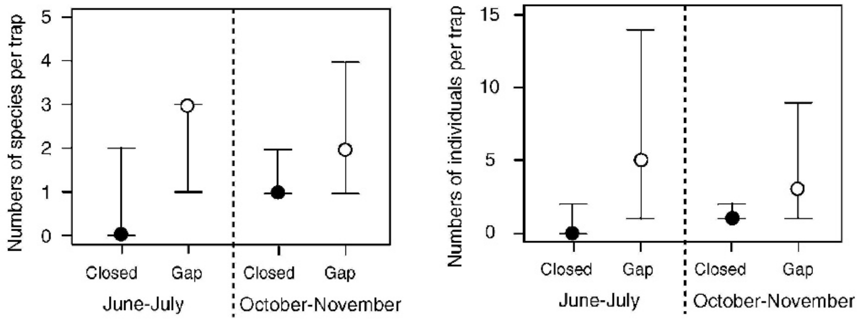


Fig. 3 Differences in species density and abundance between closed-canopy sites (*Closed*) and gaps created by killing *B. javanica* trees (*Gap*): **a** cerambycid species density, **b** cerambycid abundance, **c** elaterid species density, **d** elaterid abundance, **e** mordellid species density, **f** mordellid abundance, **g** scolytid species density, and **h** scolytid abundance. *Circles* indicate the median value. *Bars* indicate the range of values

Table 2 Generalized linear mixed models comparing beetle species richness and abundance between treatments and seasons

Family	Response variables	Treatment[a] ($df = 1$)		Season[b] ($df = 1$)		Treatment × season ($df = 1$)	
		χ^2	P	χ^2	P	χ^2	P
Cerambycidae							
Total species (12 spp.)	Species density	3.5	0.06	0.2	0.67	0.7	0.39
	Abundance	91.8	0.00	57.2	0.00	5.0	0.03
Endemic species (9 spp.)	Species density	2.5	0.11	1.6	0.20	1.8	0.18
	Abundance	77.3	0.00	125.1	0.00	9.9	0.00
Curtomerus flavus (C6[c])	Abundance	11.8	0.00	55.5	0.00	0.6	0.44
Elateridae							
Total species (8 spp.)	Species density	0.1	0.75	18.4	0.00	1.3	0.26
	Abundance	15.5	0.00	794.4	0.00	3.6	0.06
Endemic species (7 spp.)	Species density	0.0	1.00	20.9	0.00	0.2	0.63
	Abundance	16.2	0.00	806.9	0.00	1.5	0.22
Mordellidae							
Total species (10 spp.)	Species density	0.0	0.90	8.6	0.00	0.4	0.53
	Abundance	29.6	0.00	190.2	0.00	88.4	0.00
Endemic species (9 spp.)	Species density	0.0	0.89	10.8	0.00	0.5	0.48
	Abundance	9.2	0.00	227.2	0.00	0.8	0.38
Ermischiella castanea (M8[c])	Abundance	57.9	0.00	69.1	0.00	78.4	0.00
Scolytidae							
Total species (8 spp.)	Species density	3.3	0.07	0.2	0.65	0.5	0.49
	Abundance	20.6	0.00	0.6	0.42	1.5	0.22

[a] Closed-canopy sites vs. gaps created by killing *B. javanica* trees

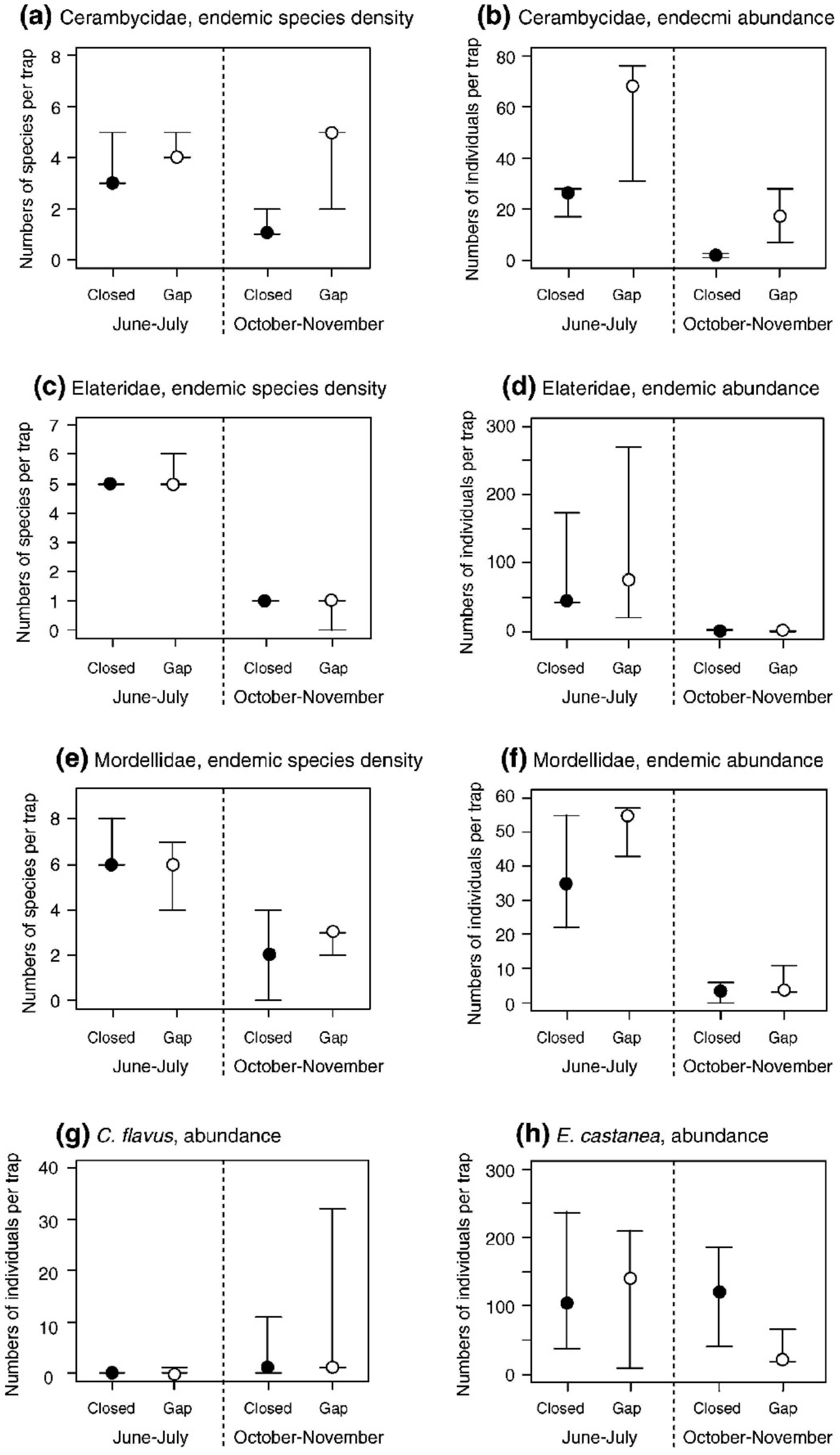
[b] June–July vs. October–November

[c] Code numbers are given in Table 1

Beetle species composition

The results of the RDA indicate the responses of beetle species to artificial gaps (Table 3). In all four families, the dummy explanatory variable was not significant (Table 3). However, the treatment effect differed among beetle families. Of cerambycid, mordellid, and scolytid species composition, 26, 24, and 32%, respectively, were explained by the treatment variable, compared to only 6% of elaterid species composition. Triplots showed that most cerambycid and scolytid species were positively associated with the treatment (i.e., artificial gaps; Fig. 5a, d) and that some mordellid species (e.g., *E. castanea*, M8)

Fig. 4 Differences in endemic and non-endemic species density and abundance between closed-canopy sites (*Closed*) and gaps created by killing *B. javanica* trees (*Gap*): **a** endemic cerambycid species density, **b** endemic cerambycid abundance, **c** endemic elaterid species density, **d** endemic elaterid abundance, **e** endemic mordellid species density, **f** endemic mordellid abundance, **g** non-endemic cerambycid *Curtomerus flavus* (C6 in Table 1) abundance, and **h** non-endemic mordellid *Ermischiella castanea* (M8 in Table 1) abundance. *Circles* indicate the median value. *Bars* indicate the range of values ▶



(a) Cerambycidae, endemic species density

(b) Cerambycidae, endecmi abundance

(c) Elateridae, endemic species density

(d) Elateridae, endemic abundance

(e) Mordellidae, endemic species density

(f) Mordellidae, endemic abundance

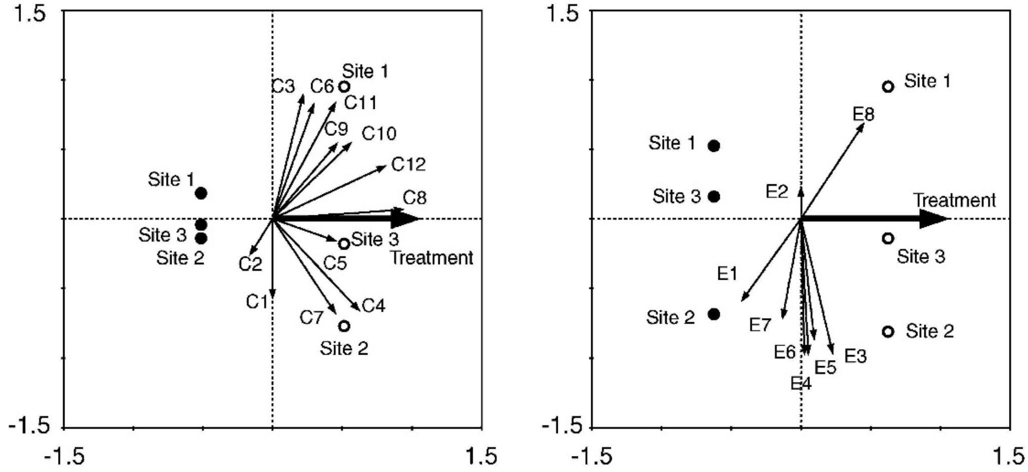
(g) *C. flavus*, abundance

(h) *E. castanea*, abundance

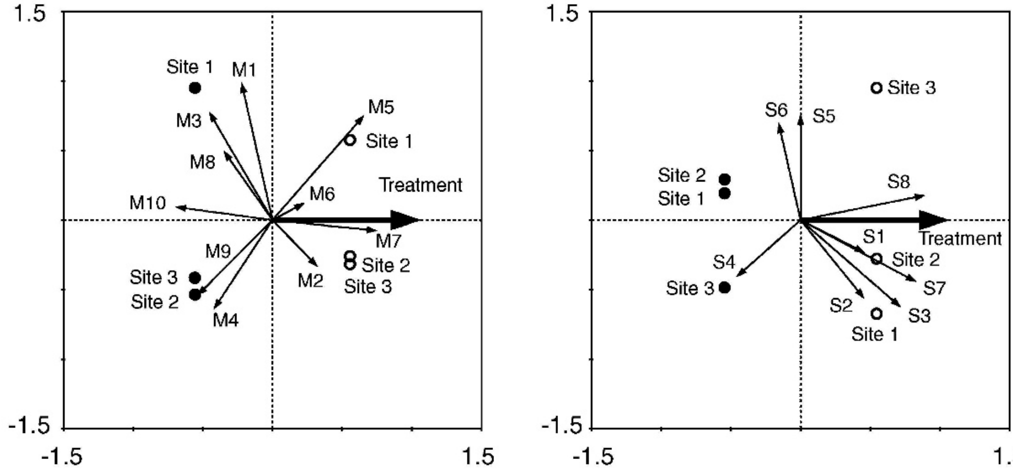
Table 3 Redundancy analysis (RDA) comparing species composition in each beetle family between closed-canopy sites and artificial gaps

Beetle family	*P*	R^2
Cerambycidae	0.10	0.26
Elateridae	0.90	0.06
Mordellidae	0.38	0.24
Scolytidae	0.10	0.32

The dummy explanatory variable was tested by 999 permutations



(a) Cerambycidae **(b)** Elateridae



(c) Mordellidae **(d)** Scolytidae

Fig. 5 Triplots from the RDA summarizing differences in the species composition of **a** cerambycids, **b** elaterids, **c** mordellids, and **d** scolytids between closed-canopy sites and gaps created by killing *B. javanica* trees. Large arrows represent the treatment effect (i.e., response to artificial gaps). Small arrows represent the associations of species with treatment. See Tables 1 and 3 for species codes and results of the RDA, respectively. *Closed* and *open circles* represent closed-canopy sites and artificial gap sites, respectively. Small arrows directed toward a large arrow suggest that the corresponding species more frequently occurred in artificial gaps. Small arrows directed away from a large arrow suggest that the corresponding species less frequently occurred in artificial gaps. For example, triplot **a** suggests that C8 occurred more frequently in artificial gaps than in closed-canopy sites were negatively associated with the treatment (Fig. 5c). However, most elaterid species were not associated with the treatment (Fig. 5b), suggesting that other factors were important for determining elaterid species composition.

Discussion

Seasonal differences in beetle abundance and diversity

In most species, abundance was higher in June–July than in October–November (Fig. 3; Table 1). This result suggests that beetle abundance and diversity have seasonal dynamics, even in the subtropical Ogasawara Islands, although the October–November temperatures were high enough for insects to be active: the mean temperature from October to November ranges from 23.3 to 26.1°C (Toyoda 2003). Sugiura et al. (2008a) also found seasonal changes in bee, wasp, cerambycid, elaterid, and mordellid diversity and abundance on a small island of the Ogasawara Islands. The seasonal pattern of insect abundance and diversity might be related to the flowering or leafing phenology of plants, given that most insects are closely associated with plants. In fact, Shimizu (1983) found seasonal patterns of leafing and flowering in plant communities on the Ogasawara Islands.

Beetle responses to artificial gaps

Most cerambycid and scolytid species were more frequently captured in artificial gaps than in closed-canopy sites (Figs. 3a, g and 5a, d). This finding suggests that most cerambycid and scolytid species fly more frequently in gaps created by killing *B. javanica* than in closed-canopy sites. Because all cerambycid species (except for species C8 in Table 1) fly mainly at night (Makihara et al. 2004), the light environment of gaps might not influence the flight activity of most cerambycids. Rather, most cerambycid species might gather in the dead wood of *B. javanica* for oviposition or mating. Because dead wood of *B. javanica* is a larval food for at least four species of cerambycid (including species C1, C8, and C12 in Table 1; Sugiura et al. 2008b), some captured cerambycids might have emerged from dead *B. javanica* in the artificial gaps. Most of the captured scolytids, whose larvae feed on fungi carried by adults to the host tree (Table 1), use the wood or twigs of various tree species for larval food, and for mating and oviposition sites (Nobuchi 1994). Therefore, scolytid beetles as well as cerambycids might also have gathered on or emerged from dead *B. javanica* in the artificial gaps, although it is difficult to determine whether they have gathered from surrounding forests or emerged from dead trees within the gaps, just based on our trap data.

In contrast to other beetle families, fewer mordellid individuals were captured in artificial gaps than in closed-canopy sites, especially in October–November (Fig. 3f). However, this pattern could be explained by the preferences of the abundant, non-endemic *E. castanea* (M8 in Table 1), which did not prefer gaps to closed-canopy sites (Figs. 4h and 5c). *Ermischiella castanea* represented 80.1% of mordellid individuals captured (Table 1). Excluding *E. castanea* (i.e., examining only endemic species), more mordellid individuals were captured in artificial gaps than in closed-canopy sites (Fig. 4f; Table 2). Sugiura et al. (2008a) showed that *E. castanea* was less frequently captured in open areas (grasslands at forest edges) than in forests on the small island of the Ogasawara Islands. Therefore, *E. castanea* might not prefer open areas such as gaps and forest edges. However, *E. castanea* abundance did not differ between artificial gaps and closed-canopy sites in June–July (Fig. 4f). As found for endemic mordellids (Fig. 4f; Table 2), mordellids generally gather in gaps where dead leaves, twigs, and wood are abundant (Takakuwa 1992).

Most elaterid species, whose larvae attack wood-boring insects, are likely to gather in dead wood. More elaterid individuals were captured in artificial gaps than in closed-canopy sites in June–July (Fig. 3d). However, the effect of treatment on elaterid species composition was weak, and most elaterid species did not prefer gaps (Fig. 5b). Therefore, other factors are more likely to influence elaterid species composition.

Implications for invasive tree management for endemic insect conservation

Because replacement by invasive alien trees reduces the abundance of native forest-dwelling insects on the Ogasawara Islands (Sugiura et al. 2008a), eradication of alien trees is needed to conserve endemic insect communities. However, removal of the invasive tree *B. javanica* should be conducted with a goal of endemic insect conservation, because endemic beetles inhabit *B. javanica* forests (Table 1). In this study, artificial gaps created by killing *B. javanica* trees supported more cerambycid species than closed-canopy sites (Fig. 3a; Table 2). Furthermore, endemic cerambycid, elaterid, and mordellid species more frequently gathered in artificial gaps than in closed-canopy areas (Fig. 4b, d, f; Table 2). These results suggest that removal of *B. javanica* trees increases cerambycid species density and the abundance of endemic beetle species. However, because the gap size was very small in this study (<100 m^2), the situation would be quite different in large-scale cutting for practical removal of *B. javanica*. Because natural gaps frequently act as regional biodiversity hotspots (Bouget and Duelli 2004), emulation of such a natural disturbance is a management tool for biodiversity conservation (Niemelä 1999; Perera et al. 2004). However, natural disturbances might increase the risk of pest outbreaks (Bouget and Duelli 2004). In this study, scolytid species, all of which are non-endemic (Nobuchi 1973), also more frequently gathered in artificial gaps (Fig. 3g, h). Although scolytid beetles did not occur at the outbreak level in this study (Table 1; Fig. 3g, h), some scolytid species are tree pests and could impact native trees (e.g., Masuya 2007). Furthermore, *C. flavus* (species C6 in Table 1), an introduced cerambycid (Makihara et al. 2004; Sugiura et al. 2008b), more frequently gathered in artificial gaps in October–November (Fig. 4g; Table 2). This species attacks live native woody trees (Makihara et al. 2004; Sugiura et al. 2008b). Therefore, inadequate removal of *B. javanica* trees could potentially increase pest outbreaks, which could impact native tree species.

Our study might reflect some short-term effects of alien tree removal on endemic beetles due to the short sampling duration and small number of study sites. However, the impacts of invasive tree management on endemic insect diversity on islands have rarely been explored. Therefore, our findings provide insight into forest management for the conservation of endemic insects in isolated oceanic islands. Further studies examining long-term and gap-size effects are needed to address the management and eradication of invasive alien trees.

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Part IV
Implications for Island Ecosystem Management

Chapter 27
Reconstruction of the Ecosystem in the Bonin Islands

Kazuto Kawakami

Abstract The eradication of invasive species is one way to maintain biodiversity on oceanic islands. In the Bonin Islands, eradication programs for goats, pigs, rats, *Bischofia javanica*, and so on, are either ongoing or complete on several islands. However, the islands are still suffering from the impacts of increasing numbers of invasive species, such as green anoles (*Anolis carolinensis*) and flatworms (*Platydemus manokwari*), which are hard to eradicate completely because of their high density and small body size. Control measures to prevent range expansion have been developed for these species. Techniques to conserve threatened populations, such as through artificial habitats and captive breeding, have also been implemented. Because the number of species introduced to the islands is increasing, an adequate daily monitoring system is required to detect them. Although controlling introduced species is expected to restore the native ecosystem, countermeasures do not always produce the desired outcomes. For example, the eradication of feral goats caused subsequent increases in invasive plants that had been released from heavy grazing pressure. Pre- and post-eradication monitoring is required to ensure the success of eradication programs. A better understanding of interspecific relationships is the only solution to such a problem. When some species in a native ecosystem have gone extinct, their ecosystem function may be filled by long-established introduced species, whose subsequent removal could cause ecosystem collapse. The construction of a sustainable, stable ecosystem including both native and introduced species is the realistic goal of conservation in the Bonin Islands.

27.1 Eradication Efforts

To maintain biodiversity, invasive species on the Bonin Islands must be controlled. Without adequate countermeasures, these species will expand their ranges, exclude native species, and degrade biodiversity. Predators and species that alter habitat structures can severely affect native species (Part 2). When an introduced species is determined to be invasive, elimination is a control method that has been attempted all over the globe (Simberloff 2001; Campbell and Donlan 2005; Howald et al. 2007).

In the Bonin Islands, feral goat eradications have been completed on at least 17 islands and are being conducted on two more islands (Anijima and Ototojima). Eradication programs for pigs (*Sus scrofa domesticus*) and American bullfrogs (*Rana catesbeiana*) are almost complete, and those for black rats (*Rattus rattus*) are ongoing on several islands (Table 1.1; see also Chaps. 8 and 23). We believe that the Bonin Islands will be released from some traditional invasive vertebrate species in the near future. In general, the eradication of introduced plants is more difficult than that of vertebrates, but it is not impossible (Simberloff 2001). Although the eradication of introduced *Bischofia javanica* might be difficult and time consuming, it should be achievable with proper procedures; in fact, its eradication is almost complete on two islands (Chap. 24). Although such achievements are not rare, large-scale eradications are still uncommon in Japan.

27.2 Cat Control

Cat predation has a serious impact on native bird populations worldwide (Nogales et al. 2004). Various countermeasures to control introduced cats are ongoing in the Bonin Islands. For example, the registration of domestic cats with microchips and the sterilization of such cats have been promoted. In the southernmost region of Hahajima, where a seabird colony was destroyed (Chap. 11), a cat fence was erected to separate the colony from the mainland, and all cats were removed from the exclosure. Cat exclosures are also being established around the breeding area of an endangered subspecies of the Japanese wood pigeon *Columba janthina nitens* on Chichijima.

Remarkably, captured cats have never been killed but instead have been transferred to mainland Japan, where they

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train to be domestic pets and are fostered by volunteers (Horikoshi et al. 2008). These efforts have been conducted in partnership with local residents; local NPOs and NGOs; national, metropolitan, and village governments; the Tokyo Veterinary Medical Association; and a shipping company. It is difficult to reach consensus concerning the extermination of captured cats, and thus such collaborations are fundamental when balancing conservation with social opinion. Domestic cats will, however, never disappear completely where humans exist. A social campaign to keep domestic cats indoors or in outdoor enclosures, such as that launched by the American Bird Conservancy in the United States (Cats Indoors! Campaign; http://www.abcbirds.org/cats/), is required to minimize the impacts of cats on natural systems.

27.3 Development of Control Techniques

The ecosystems of the Bonin Islands have been increasingly affected by invasive species such as *Anolis carolinensis*, *Platydemus manokwari*, and *Bischofia javanica*, as well as more traditional invasives. Previously, there were no established proper methods to control these species. Knowledge of the biology of each introduced species was required to formulate a suitable eradication program. Essential ecological data such as seed bank character, habitat preferences, and life tables are very helpful for planning control programs (e.g. Chaps. 15 and 22). New techniques and equipment have been developed for these unfamiliar species. Without basic information, efforts will be wasted. An adequate mix of basic and applied research can produce effective countermeasures.

27.4 Prevention of Range Expansion

Although elimination is one control method, some species are impossible to eradicate from their current ranges because of wide distributions and/or high population densities. Smaller species hidden in shrubs and soils are particularly hard to detect and remove completely. This is the case for both green anoles and flatworms (Chaps. 4, 12, 20 and 22). Once such species have established wild populations, a possible countermeasure is to prevent their range expansion. The distributions of major invasive species are largely limited to two inhabited islands: Chichijima and Hahajima. Various native species that have decreased in population size or vanished from these two islands have survived on their satellite islands (Kato et al. 1999; Chaps. 13 and 21). Thus, introduced species must be confined to their current ranges.

Satellite islands are used by tourists, fishermen, and researchers, all of whom should take particular care to avoid being carriers of introduced species. To prevent their migration, green anoles are currently being removed using sticky traps from the harbor area in Chichijima, from where many boats depart to satellite islands for sightseeing (Chap. 22). A scraper mat with salt water is located at the entrance of Hahajima to remove invasive flatworms that attach to the soles of shoes. Everyone going to satellite islands from Chichijima is also required to scrub the soles of their shoes. Many goods are currently imported to uninvaded areas for use in ecosystem restoration programs (e.g. fencing, monitoring, elimination, patrols). These activities should be conducted with special care, because the target areas are often exceptionally important places.

27.5 Prioritization

Prioritization is also necessary for eradication programs, because in many cases budgets and staff are limited. Although it is best to eradicate whole populations simultaneously, this may be hard to do for species with expanded ranges. In such cases, small populations and range peripheries should be controlled to stop range expansion. In the case of *Bischofia javanica*, eradication measures were first applied to small populations on satellite islands (Ototojima and Hiarashima; Chap. 24) and should subsequently be conducted on the peripheries of the large population on Hahajima (Chap. 25). When introduced species expand their ranges to new islands, they should be eliminated during the initial stages of colonization, before explosive growth. Eradication costs are lower, and the probability of success is greater during these initial stages of invasion.

However, partial eradication is not effective for certain species. If an invasive species has a high rate of reproduction and/or high migration ability, whole populations should be eliminated in the short term. Introduced *Lantana camara*, one of 100 of the World's Worst Invasive Alien Species (Lowe et al. 2000), is a representative example in the islands; its range has spread throughout both inhabited and uninhabited islands. Because its seeds are dispersed by various species of birds (Kawakami 2009; Kawakami et al. 2009), spread of *L. camara* cannot be prevented without either simultaneous total eradication or the eradication of birds. Local eradication is not an effective way to control such a species, although it can lead to delays in range expansion.

27.6 Development of Conservation Methods

Critical populations can recover without special measures after the eradication of deleterious invasive species in some situations. For example, after a rat eradication program, the population of Bulwer's petrels (*Bulweria bulwerii*) on Higashijima would surely recover from severe depletion (Chap. 8). However, alongside eradication programs, measures directed at maintaining and increasing threatened populations are essential for various indigenous species. Insular species often maintain reduced reproductive output per individual in response to increased density and decreased mortality in their original ecosystems (Whittaker 1998). In addition, environmental problems are not limited to invasive species. Other factors, such as habitat loss and anthropogenic disaster, also affect the maintenance of ecosystems.

The development of artificial habitats and captive breeding techniques can be adequate for population maintenance (Chaps. 17, 20 and 21). In addition to the topics mentioned in this book, captive breeding is conducted by Ueno Zoo for endemic subspecies of the Japanese wood pigeon, which is ranked as CR in the Japanese red list. Although successful eradication is praiseworthy, management of both native and introduced species is essential to the restoration of an ecosystem.

27.7 Monitoring Systems

Unfortunately, the cases detailed in this book represent only the tip of the iceberg. For example, the introduced freshwater snail *Melanoides tuberculata*, which was initially found in brackish water areas of Chichijima in 2005 (Satake et al. 2006), replaced the native confamilial (Thiaridae) species *Stenomelania boninensis* via intermediary human disturbance (Sasaki et al. 2009). Also, the number of newly detected introduced insects in the Bonin Islands has rapidly increased over the past two decades (Ohbayashi 2002).

When introduced species are detected in the initial stages of colonization, they are relatively easy to control, and the cost of control is minimal. Thus, daily monitoring is required to detect changes in the current biota. For this purpose, the participation of local guides and naturalists in the monitoring system is essential. Although funding is much easier to obtain if an invasion is already very serious (Cronk and Fuller 2001), it is irresponsible to remain inactive when an invasion has been detected. Governments and researchers should promptly determine whether newly detected species are invasive.

Although the control of introduced species can be expected to restore ecosystems, countermeasures do not always produce the desired outcomes (Zavaleta et al. 2001, Courchamp et al. 2003). Since the eradication of feral goats (*Capra aegagrus*) on Nakodojima in 1999, some areas of bare ground have shifted to grassland because of release from goat herbivory. However, despite the disappearance of the goats, forests have not yet recovered, probably because of the lack of seed rain (Chap. 14). In addition, the invasive alien woody species *Leucaena leucocephala* has expanded its distribution in some areas (Hata and Kachi 2009). In this case, additional measures are needed to restore the vegetation.

The reestablishment of populations of eliminated species must be prevented with monitoring. Introduced species sometimes reinvade their previous ranges (Myers et al. 2000). Although the probability of reintroduction is relatively low for large vertebrates, flying insects and anemochores can be reintroduced relatively easily. On Nishijima, black rats were rediscovered during a monitoring survey conducted in summer 2009, although we believed that they had been completely removed in 2007 (Chap. 23). We do not know whether these individuals remained undetected on the island or reinvaded from other islands. Regardless of their origin, we must eradicate them again. Because each countermeasure is only a step in the right direction, ante- and post-program monitoring is required. Monitoring surveys are currently conducted for almost all countermeasures in the Bonin Islands.

27.8 Interspecific Relationships Between Natives and Aliens

The introduction of new species can sometimes have unexpected ecosystemic effects. For example, the establishment of the green anole likely led to the unpredicted arrival of the bull-headed shrike *Lanius bucephalus* in the Bonin Islands, which frequently foraged on the lizard (Suzuki 1991). In the 1980s, *L. bucephalus* began to breed on Chichijima (Chiba 1990), whereas previously it had been a rare migrant to the islands. The range of the shrike expanded on Chichijima, appearing to follow the expansion route of the green anole. It thus may have become established in the islands because of the sudden appearance of an available prey species. The unpredictable nature of the effects of introduced species is a particularly problematic aspect of their ecology. Incidentally, the shrike population was reduced after their range expanded to Hahajima in the 1990s, and we now have not seen them for some years.

The impacts of introduced species include various indirect effects that can reach multiple trophic levels (e.g. Mulder et al. 2009; Chap. 13). Indirect effects have often been neglected in the control of introduced species, but evaluation of these important effects now has become integral to the assessment of the impacts of introduced species and countermeasures for their control (Caut et al. 2009). Ecological operations may unintentionally harm native species (Bergstrom et al. 2009). This is generally more likely to occur when ecosystems contain more than one invasive species, which is common in oceanic islands (Zavaleta et al. 2001; Caut et al. 2009). Alien herbivore eradication often enhances the reproductive success of invasive plants and causes subsequent problems

(Zavaleta et al. 2001; Courchamp et al. 2003). Goat eradication and the subsequent increase of *Leucaena leucocephala* in the Bonin Islands illustrates this point. The removal of top predators sometimes causes mesopredator release (Courchamp et al. 1999; Rayner et al. 2007). Thus, a better understanding of interspecific relationships is the only solution to such problems. Before feral pigs were eradicated from Ototojima, introduced American bullfrogs, which preyed on threatened dragonflies, were eradicated (Chap. 20). If the pigs had been eradicated first, the frog population could have increased and decimated the dragonfly population.

However, such relationships are sometimes extremely complicated and can take a long time to clarify. Under the present circumstances, countermeasures can afford no further delay, because various indigenous species are in danger of extinction due to the impacts of invasive species. Control programs should include monitoring of ongoing ecosystem shifts, and the flexibility to modify policy in the face of a changing context is required when beginning control efforts. Adaptive management has become a watchword for ecosystem restoration programs in the islands.

Problematically, some introduced species have become essential components of the current ecosystem after long-term naturalization and can sometimes support vulnerable species. For example, the introduced white-eyes *Zosterops japonicus* has likely replaced the lost function of the native Bonin Islands white-eyes *Apalopteron familiare* as an agent of seed dispersal on Chichijima, where the native white-eyes are extinct (Kawakami 2006; Kawakami et al. 2009). Because their function is absolutely necessary to maintaining the ecosystem, they cannot be eradicated. In another case, introduced rats compose half the diet of the endangered subspecies of the common buzzard *Buteo buteo toyoshimai* (Kato and Suzuki 2005), and there is concern as to whether rat eradication could cause food shortages for the birds. However, rats have also caused the decline of small seabird colonies (Chap. 8) whose recovery would provide alternative primary food for the raptors.

27.9 Conclusion

Relying solely on the protection or elimination of particular species is not a convincing solution to the problems caused by invasive organisms. The ultimate goal of countermeasures is the conservation of the overall ecosystemic balance, and each management act is only one step toward achieving that goal. Some components of the original ecosystems have regrettably been lost forever, and current ecosystems may not function without introduced species. In addition, many invasive species are extremely difficult to eradicate. As long as humans live in the Bonin Islands, invasive species will never disappear. We must properly estimate the risk posed by each species and control it accordingly. Preventive frameworks such as quarantine systems and risk assessment systems must be established (e.g. Kato et al. 2006).

A realistic goal of conservation is not the reconstruction of the primary environment but the construction of a sustainable and stable ecosystem including both native and introduced species. Although the shortest path to this destination is not obvious, we know the general direction in which we must proceed. The important thing is not to stop working with the cooperation of local communities, NPOs, NGOs, related organizations (including private corporations), national and local governments, and scientists.

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