

Ecological Diversification of Insular Terrestrial Reptiles: A Review of the Studies on the Lizard and Snakes of the Izu Islands

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Abstract

Terrestrial vertebrates of the Izu Islands are the subset of species indigenous or endemic to the Japanese main islands, but their species composition is extremely disharmonic both taxonomically and ecologically. Mammals, amphibians and freshwater fishes are impoverished due to isolation, the small area, reduced habitat diversity and lack of permanent freshwater habitats, whereas birds and reptiles are rather rich in endemic species or subspecies with unique ecological characteristics, and those groups of vertebrates maintain higher population densities particularly on the islands without mammalian carnivores. The snake *Elaphe quadrivirgata*, a top predator on most of the islands, shows remarkable diversification in food habits and body size in accordance with inter-island difference in intensity of interspecific competition with other snake species and in availability of prey. The lizard *Eumeces okadae*, a small insectivorous predator in intermediate trophic level, shows variation in life history traits in relation to different predation pressures. The lizard populations exhibiting delayed maturity and lower reproductive rates due to less than annual reproduction exist only on the islands without snakes or mammalian carnivores. Introduction of the weasel for controlling rat pests in agricultural products almost extirpated lizard populations with little adaptation to novel predators, and subsequently caused significant changes in entire island food web structures.

Key words: disharmonic biota, food web, island population, life history, predation by exotic carnivores

1. Introduction

Extinction is much more frequent on islands than continents. Most extinctions in bird, mammal and reptile populations occurring in the past 350 years were recorded from islands (King, 1985; Groombridge, 1992). Extinction is now accelerating, and continental populations are becoming threatened as their natural habitats have been destroyed and fragmented to small areas. The populations in those fragmented habitats are highly vulnerable to extinction, and the extirpation of each small population ultimately lead to species extinction.

Why are insular populations so susceptible to extinction? The proposed reasons are that the species exist only on a single or few islands or that populations consist of few individuals. Environmental variability and demographic stochasticity make small populations much more susceptible to extinction than larger ones. Anthropogenic detrimental impacts such as habitat destruction, fragmentation, deterioration, over-exploitation and hunting, introduction of exotic

species and infectious diseases, together make those smaller island populations much more vulnerable to extinction (Primack, 1995).

Nevertheless, not all species on certain islands would become extinct even if they were exposed to similar environmental changes. Some species would be extirpated, but others would survive the disaster. The same species living on the several similar islands would undergo different population trends even if they suffered identical environmental challenges. Due to stochastic variability, we cannot predict which populations will become extinct or survive, though certain proportions are predicted to become extinct. Differences among species in susceptibility to extinction, in some cases, might be due to some deterministic factors. Differences among species in physiological, behavioral, ecological and life historical attributes are the major deterministic factors responsible for interspecific differences in extinction rates.

Such deterministic factors would explain higher extinction rates of endemic species on remote, oceanic islands, which suffer frequent introduction or inciden-

tal invasion of exotic species. The followings is a scenario explaining why certain species on islands with disharmonic biota are vulnerable to extinction under the threat of carnivore introduction.

1) Biotas of oceanic islands are usually disharmonic in terms of taxonomic composition, because only the taxa that can do over-seas dispersal can become potential colonists.

2) Those disharmonic biotas are characterized by the lack of large predators that require extensive home ranges to sustain their high energetic demands. Consequently, taxa belonging to the next lower trophic level such as insectivorous birds or lizards are able to maintain high population densities, which in turn put significant predation pressure on the organisms in lower trophic levels.

3) The insectivorous birds or lizards on such oceanic islands have to live with permanent deficiency of food and space. As an adaptation to those environmental regimes, certain behavioral and life historical attributes such as relaxation of predator awareness, prolongation of parental care and reduced reproductive output will be developed.

4) Intended or incidental introduction of exotic predators like carnivorous mammals rapidly extirpate those native birds and lizards having little anti-predator adaptation, and food web structures change extensively in comparison with the conditions before introduction.

In this review, I try to show that the above-mentioned scenario is consistent with long-term changes in vertebrate and some invertebrate fauna of the Izu islands, Japan. I will also discuss the evolutionary aspects of community organization in island environments.

2. Disharmonic Vertebrate Fauna

The Izu archipelago is a group of volcanic islands, which are situated linearly from north (Ohshima:34° 43' N) to south (Aogashima:32°29' N) over a distance of 230 km (Fig. 1). Areas of inhabited major islands range from *ca.* 3 to 90 km². A uniformly mild climate, under the influence of the warm temperate water of the Kuroshio Current, and abundant annual precipitation (2,000-3,000 mm) have made these islands well vegetated with broad-leaved evergreen forests. Terrestrial vertebrates of the Izu Islands are extremely disharmonic both taxonomically and ecologically. Mammals, amphibians and freshwater fishes are impoverished primarily due to isolation, the small area, reduced habitat diversity and lack of permanent freshwater habitats.

Mammalian carnivores have very restricted distribution on the Izu Islands. Common carnivorous mammals found on the main islands of Japan (i.e., the fox *Vulpes vulpes*, the raccoon dog *Nyctereutes procyonoides*, the badger *Meles meles*, and the marten *Martes melampus*) do not occur on the Izu Islands at

all. The native population of the weasel *Mustela itatsi* is restricted to Ohshima, and the other insular populations currently established in this region are of artificial origin. The insectivorous mammals (moles and shrews) and rodents are also poorly represented. The native species are the wood mouse *Apodemus speciosus*, the white-toothed shrew *Crocidula dsinezumi* and two species of bat (Hasegawa & Moriguchi, 1989; Takada *et al.*, 1999; Motokawa *et al.*, 2000). Motokawa *et al.* (2000) suggested a high population density of *C. dsinezumi* on the Izu Islands, though this species is not so common in other areas of Japan.

Twenty-one to 38 species of birds are known to breed in this island group. The scarcity or absence of common terrestrial bird species of the mainland (raptors, pheasants and woodpeckers) characterizes the Izu Islands avifauna (Higuchi, 1973). The grey-headed buzzard eagle (*Butaster indicus*) is the only putative top predator in the insular food web, because other common raptorial species (*Aquila chrysaetos*, *Spizaetus nipalensis*, *Pernis apivorus*, *Accipiter gentilis*, *A.nisus* and *A.gularis*) are absent (Higuchi, 1973; Hasegawa *et al.*, 1996). There are suspected breeding populations of the common buzzard *Buteo buteo* and peregrine falcon *Falco peregrinus* (Higuchi, 1973), but their statuses were not confirmed by a recent survey (Hasegawa *et al.*, 1996).

The reptilian fauna is not so rich in comparison to the mainland. The lizard *Eumeces okadae* is distri-

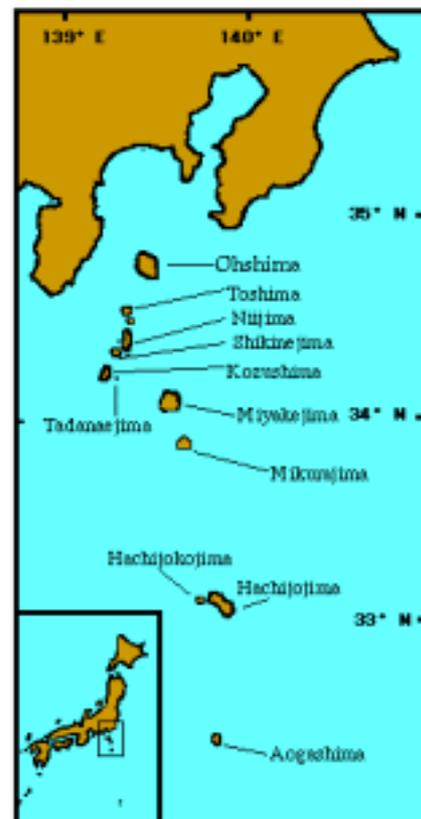


Fig. 1 The Izu Islands, central Japan. Names of major islands are shown in the figure.

buted on all the major islands and several small islets. The number of the snake species varies from zero to five by islands. Among the snakes, *Elaphe quadri-virgata* is a major native predator and has the widest distribution (Hasegawa & Moriguchi, 1989).

All amphibian species currently distributed on the Izu Islands are of recently introduced artificial origins. No systematic survey has been conducted for the freshwater fishes of the Izu Islands. Species now present in several water bodies are of introduced origins.

3. Four Types of Insular Food Webs

The simple insular vertebrate fauna facilitates the identification of food webs (Fig. 2). From the standpoint of lizards, terrestrial food webs of the Izu islands are classified into four types based on faunal differences in potential native predators: groups of islands with just avian; avian and ophidian; and avian, ophidian and mammalian predators; and the fourth type, that on the small islands with rich sea bird colonies. This sort of classification reflects potential differences in food web structures present in the Izu islands (Hasegawa, 2001).

The first group consists of three islands (Miyakejima, Aogashima and Hachijo-kojima) that were originally free of snake and weasel predators.

The absence of these predators on these islands apparently made possible the high abundance of *E.okadae* (Hasegawa, 1994) and insectivorous bird species, especially the thrush *Turdus celaenops* (Higuchi, 1973). In time-constrained censuses conducted during the mating season in the late 1970s and early 1980s, 100 or more lizards were regularly seen per hour of survey (Hasegawa, 1994). Male *E.okadae* on those islands were heavily paracitised during the mating season by the tick *Ixodes asanumai* specialized to *E.okadae* (Hayashi & Hasegawa, 1984). Lizards on Miyakejima had experienced food shortages under high population density (Hasegawa, 1997) and were presumably forced to eat otherwise unpalatable prey such as worker ants (Hasegawa, 1994; Hasegawa & Taniguchi, 1993). The fauna of ground and soil dwelling invertebrates of this island group were characterized by a greater abundance of amphipods and lesser abundances of isopods and earthworms compared to those on other islands (Hasegawa, 1994). Abundances of ants, centipedes, and spiders seemed to be similar at the time of the samplings.

The second group consists of populations on Toshima, Mikurajima, Kozushima, Niijima, Shikinejima and Hachijojima, which lacked only mammalian predators. These islands supported moderate densities of the lizard (Hasegawa, 1994a),

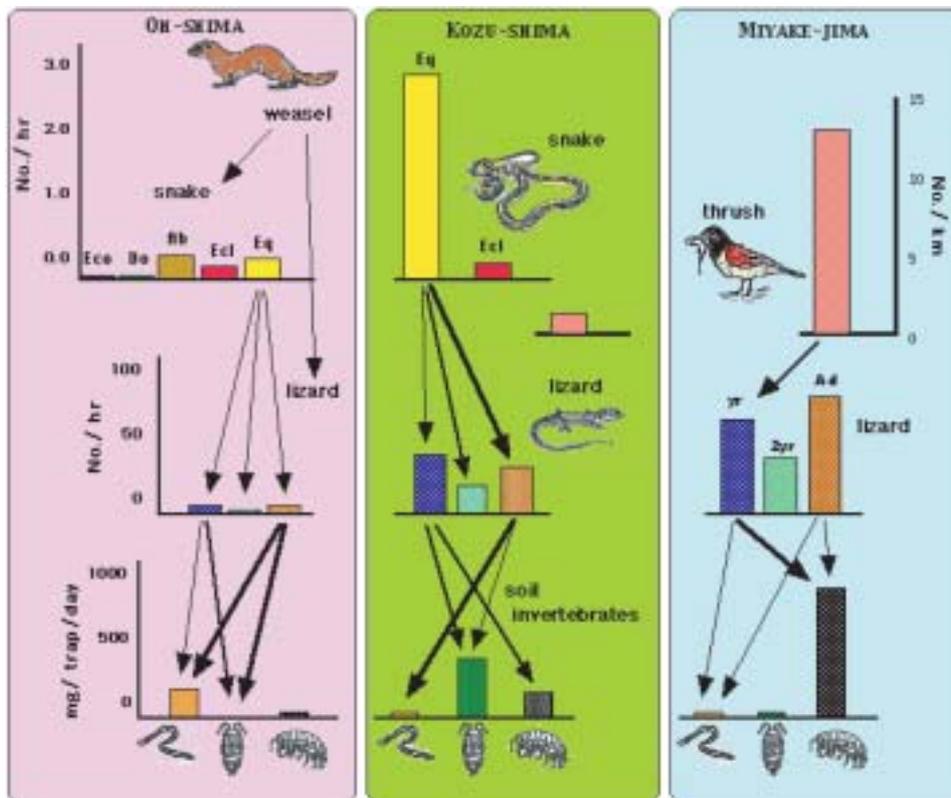


Fig. 2 Abundances of predatory snakes, thrushes and three major prey invertebrates (earthworms, woodlice and landhoppers) of *Eumeces okadae* on three representative islands. Abundances are shown in terms of appropriate indices such as number of individuals encountered in time- or distance- constrained survey, or amount of prey organisms captured per trap-day. Arrows in the figure indicate predation and their thickness indicate relative frequency of predation revealed by stomach content analysis or direct observations.

and the parasitic load by *Ixodes asanumai* on male *E.okadae* was low (<1%) on these islands (Hayashi & Hasegawa, unpublished data). The lizards were not so food-limited because their stomach contents consisted of relatively large and palatable prey such as lepidopteran larvae and earthworms (Hasegawa, 1994; Hasegawa & Taniguchi, 1996). The snake *El.quadrivirgata* was moderately abundant and the frequency of sighting ranged from 0.5/hr on Shikinejima to 2.8/hr on Kozushima during spring censuses in 1981-1988 (Hasegawa & Moriguchi, 1989). Densities of insectivorous birds were low on these islands (Higuchi, 1973), probably due to the high densities of snakes, which also preyed on birds (Hasegawa & Moriguchi, 1989; Hasegawa, unpublished data). The raptorial bird *B.indicus*, a potential predator on both *E.okadae* and *El. quadrivirgata* have breeding populations consisting of less than 10 pairs on those islands (Hasegawa *et al.*, 1996). Long-term monitoring of both *E.okadae* and *El. quadrivirgata* suggested that the prey-predator system has been stable on the second group of the islands for over nearly two decades.

The third group consists solely of the population on Ohshima. This island accommodated the highest diversity of predators. Potential native predators included the weasel *Mustela itatsi* and five species of snakes (*El. quadrivirgata*, *El. climacophora*, *El. conspiciata*, *Dinodon orientale* and *Agkistrodon blomhoffii*). The density of *E.okadae* on Ohshima was lowest among the Izu islands, being less than six adult males seen per hour in the spring. Lizards experienced no parasitic load and enjoyed high prey availability (Hasegawa, 1994). The prey-predators system of Ohshima seemed stable, as was suggested by the long-term stability of the *E.okadae* population. Recent establishment of introduced frogs (Hasegawa, 1999), however, might influence dietary compositions of native predators.

The fourth island group consists of the relatively

small unpopulated islands ($1 < \text{km}^2$) that accommodate colonies of several sea bird species (*Phalacrocorax filamentosus*, *Synthliboramphus wumizusume*, *Calonectris leucomelas*, *Oceanodroma tristrami*, and *Larus crassirostris*) (Carter *et al.*, 2002; Moyer, 1959; Hasegawa, 1984). The islands differ in the presence or absence of snake predators. On the islands of Jinaijima, Onbasejima, Onoharajima, and Kojine, the lizard *E.okadae* is only terrestrial vertebrate except breeding land and sea birds, whereas the islands of Udonejima, Hanshima, and Tadanaejima are inhabited by the snake *El. quadrivirgata*. Because of the smaller island size, forest vegetation is rarely developed there, and extensive areas are covered by either short or tall grasslands. In addition, on Tadanaejima, dense populations of the grasshopper *Parapodisma* sp. and a beetle were observed almost every summer, and they were capable of defoliating several bushy trees. Also observed were dense web spider populations that consumed those insects. Terrestrial organisms of these small islands would certainly be under the strong influence by nutritional input from marine food webs via the breeding activities of the sea birds (*e.g.*, Polis & Hurd, 1996).

4. Snake Ecology in Relation to Prey and Competitor Fauna

Snakes are predators high in trophic position, and predator communities in general may be regulated by prey abundance and interspecific competition (Hairstone, 1989). The snakes of the respective Izu Islands are thus expected to vary ecologically in relation to prey and competitor fauna (Fig. 3).

Distributions of the snake species of the Izu Islands are related to their food habits. The principal prey of mainland *El. quadrivirgata* is frogs (Uchida & Imaizumi, 1939; Fukada, 1959), but is the lizards and birds on the islands (Hasegawa & Moriguchi, 1989),



Fig. 3 A Gigantic female *Elaphe quadrivirgata* from Tadanaejima reef (left) in comparison with an average sized female from Kozushima island (right).

whereas prey items of *El. climacophora* are primarily endothermic vertebrates both on the mainland (Uchida & Imaizumi, 1939; Fukada, 1959) and on the islands (Hasegawa & Moriguchi, 1989). Its flexible feeding habits may enable *El. quadrivirgata* to inhabit various islands with variable prey fauna. Conservative food habits would limit the distribution of *El. climacophora*. The other two species with the most specialized diets (*Dinodon orientalis* takes small reptiles, and *Elaphe conspicillata*, small mammals) are confined only to a single island (Hasegawa & Moriguchi, 1989).

The patterns of inter-island variation in body sizes and feeding ecologies differ among the snake species. In *El. quadrivirgata*, body size has diverged toward both 'giants' (e.g., Tadanaejima) and 'dwarfs' (e.g., Ohshima), whereas the body size of *El. climacophora* has changed little (Ohshima and Niijima) or dwarfed slightly (Kozushima) in comparison with the mainland populations (Fukada, 1972, 1978). The pattern of body size variation in *El. quadrivirgata* is very similar to that reported for the Australian tiger snake *Notechis ater* (Schwaner, 1985). In both species, dwarfism occurs on islands where the snakes mainly exploit lizards (body mass < 20 g), and gigantism occurs on the islands with the colonies of sea birds. Dwarfism is strongly linked to saurophagy (lizard eating), but the underlying factors leading to saurophagy may differ between the two island groups. Dwarfed *N. ater* of Roxby I. takes skinks as its major prey, because skinks are the only potential prey there but abundant, whereas *E. quadrivirgata* of Ohshima takes *E. okadae* as the major prey, although these skinks are not so abundant and seven other prey types are available.

The hypothesis of resource partitioning may explain such a pattern of prey use. *El. quadrivirgata* on Ohshima is a diurnally active specialist to the skink under the presence of other snake species. By contrast, the body size of *El. quadrivirgata* has become larger on the two-species islands where it is sympatric only with *El. climacophora* (i.e., Kozushima) in accordance with a wider diet breadth. The broader feeding niche of *El. quadrivirgata* on two-species islands than a five-species island is related to a corresponding increase in their abundance.

Gigantism both in the Japanese and Australian insular snake populations with sea bird colonies is quite interesting, but the exact mechanism may differ between the two. *El. quadrivirgata* is the only snake species on Mikurajima and Tadanaejima, and it exploits a wide array of available prey exclusively. Its gigantic body size on the two islands may have evolved (or been attained) directly in response to exploiting plentiful sea birds' eggs and chicks.

Therefore, available data suggest that differences in prey fauna are important on offshore islands of southern Australia, whereas interspecific competition plays an important role in the evolution of body size for the insular snake populations of the Izu Islands.

5. Life History and Diet of Lizards in Relation to Predation Regime

The lizard *Eumeces okadae* (Figs. 4 & 5) a small insectivorous predator at an intermediate trophic level, shows considerable intraspecific geographic variation in life history traits in relation to different predation pressures. Some *E. okadae* populations have a suite of traits including small body size, early maturity, production of small and many eggs, low frequency of failure in follicle development, annual reproduction, high relative clutch mass and low post-reproductive mass of females. Whereas others have a suite of the opposite character states. The populations with the richest predator fauna (Ohshima) exhibit suites of life history traits characterized by early maturity and high fecundity, and the populations on the islands with only avian predators (Miyakejima and Aogashima) employ late maturity and low fecundity. The populations on the islands where snakes are a major vertebrate predator (Shikinejima, Kozushima and Mikurajima) are intermediate between these two extremes. The predation regime (age-specificity and intensity) has a direct role in molding the observed divergence of life history traits. Predation impacts directly upon demographic parameters of lizard populations and indirectly upon prey availability via intraspecific competition under different population densities (Reznick & Endler, 1982). The adaptive significance of life history traits under different predation regimes is quite interesting, but its discussion is beyond the scope of this review.

Differences in the intensity and age specificity of predation affect population density (Schoener & Schoener, 1978, 1980, 1982), and explain inter-island differences in the abundances of *E. okadae*. High mortality of hatchlings relative to adult lizards on Miyakejima (Hasegawa, 1990b) suggests that accumulation of long-lived adults results in high density, not high survivorship, of juveniles. The population on Miyakejima attains a density of ca. 4,000/ha exclusive of hatchlings (Hasegawa, 1990b). The reverse pattern, low density with predators capable of consuming adult lizards, may be true on the other islands.

6. Food Web Dynamics after Weasel Introduction

Biological control of rats was the primary purpose for the introduction of the weasel onto most small islands in Japan (Shiraishi, 1982). This was the true for most of the Izu islands. The weasel (*M. itatsi*) was introduced onto the four islands (Toshima, Miyakejima, Hachijojima, and Aogashima; Nishikata, 1986), where effective native predators of rats were absent or present but in low density. Miyakejima and Aogashima are free from snakes and native carnivorous mammals, whereas Toshima has a snake



Fig. 4 Dense basking aggregation of *Eumeces okadae* observed on April 1983. As many as 10 lizards can be recognized within a square meter. Every lizard was individually marked by painting different colour spots on its back. (Photo by H. Higuchi.)



Fig. 5 Newly hatched *Eumeces okadae* from Kozushima with vivid blue tail and creamy white longitudinal stripes on the body.

(*El. quadrivirgata*) but in low density. Hachijojima may appear exceptional, because the pit-viper *A. blomhoffii* was formerly abundant (Goris, 1967). However, it is questionable as to whether the pit-viper was capable of controlling rats to the level at which their agricultural damage was negligible.

Weasel predation on certain island organisms was so dramatic that this phenomenon has been repeatedly highlighted in a number of recent publications (e.g., Hasegawa, 1986, 1994, 1999; Moyer *et al.*, 1985; Hasegawa & Nishikata, 1991; Takagi & Higuchi, 1992). In fact, introduction of the weasel caused a

catastrophic decline in the endemic lizard *Eumeces okadae* (Moyer *et al.*, 1985; Hasegawa, 1986, 1994; Hasegawa & Nishikata, 1991), as well as in endemic avifauna such as the seven island thrush *Turdus celaenops* and Ijima's willow warbler *Phylloscopus ijimae* (Higuchi, 1981; Takagi & Higuchi, 1992). Recent frequent outbreaks of herbivorous lepidopteran larvae on Hachijojima were attributed to the oversimplification of food web structure on this island caused by colonization of the weasel (Kunimi, 1982).

The density of *E. okadae* on Miyakejima was reduced to the level of a thousandth or ten thousandth of

that prior to the introduction of the weasel (Fig. 6). In the summer of 1993, a decade after the illegal introduction of the weasel, the average number of *E.okadae* seen per hour was only 0.1, being 0.0006 of the value obtained before weasel introduction. The decline in the lizard population was first documented in 1984, followed by a more rapid reduction to an extremely low level (*ca.* <1.0 lizards/hr). The period of such a catastrophic decline of the lizard coincided well with that of a remarkable increase of the weasel. Although an insectivorous bird, *T.celaenops*, actually decreased from densities of 23.4-33.4 birds/km in 1973-1980 to 6.7-11.1 birds/km in 1990-1991 (Takagi & Higuchi, 1992), this degree of decrease is much smaller than that of the lizard. It is reasonable to assume that the birds in general are less vulnerable to capture by the weasel due to their ability to escape by flight.

In order to evaluate the weasel's impact on the lizard's potential prey on Miyakejima, pitfall trap samplings were repeated in 1993 at the same sampling sites as 1983. This time, I saw no *E. okadae* at all during the sampling period. Animals trapped in this survey were large numbers of carrion beetles (genus *Eusilpha*) that had never been seen in such a high abundance in the previous trapping bouts. During the 1993 sampling, this beetle was also frequently observed along the roadside. This suggests that considerable changes have occurred in the ground invertebrate community with the possible local extinction of lizards in the late 1980s.

Comparisons of food web elements (abundances of detritivores, omnivores, and carnivores) showed a drastic increase in the carnivorous beetles from 1983 (0.1/trap) to 1993 (61.0/trap). Other changes included a slight increase in earthworms (from 0.2 in 1983 to 1.3 in 1993), and a slight decrease in ants

(from 34.8 in 1983 to 20.4 in 1993). Before resuming the pitfall trap sampling in 1993, I expected that amphipods that had been consumed by *E.okadae* in large numbers would show a remarkable increase. However, there was no substantial difference between the abundance of amphipods in 1983 and 1993. The abundance of isopods and spiders did not change appreciably. In summary, the addition of the weasel to an island food web as a large carnivore has led a medium carnivore (lizard) to near extinction, small carnivores (carnivorous beetles) to drastic increase, and one detritivore (earthworm) to a slight increase. On the other hand, it apparently did not much affect densities of other small carnivores (spiders), omnivores (ants) and detritivores (amphipods and isopods).

7. Conservation Implications

It is obvious that the weasel has had a serious impact on the insular vertebrate and invertebrate fauna. Whether the introduction of an exotic predator has significant effects on prey animals might depend not only on the type of the predator but also on the life history traits and anti-predation mechanisms of prey populations. Differences in diet preference and predation intensity among predators certainly result in different predation impacts on their prey populations (Winemiller & Polis, 1996).

Evolutionary differences in life history traits among prey species may be a factor responsible for differential vulnerability to exotic predators. The life history traits of *E.okadae* on the weasel-free islands is characterized by low reproductive rate (biennial reproduction, small clutches of large eggs, and delayed maturity with a large mature size) and low natural mortality rate (Hasegawa, 1994). This type of life history and demographic traits seem to be particularly

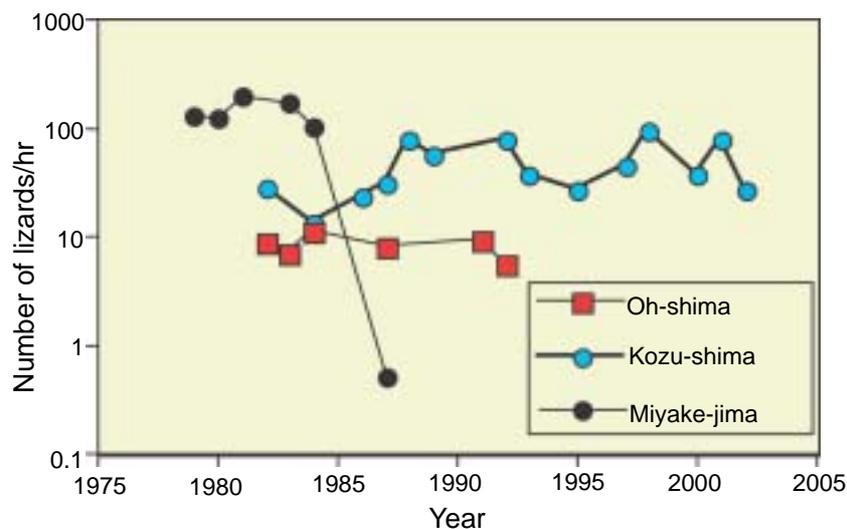


Fig. 6 Long-term changes in the abundance of *Eumeces okadae* on three representative islands (Ohshima, Kozushima and Miyakejima). Abundance is the mean number of lizards excluding hatchlings seen per man-hr of census during July, August and September. Abundance on Miyakejima decreased sharply after an appreciable increase of the sighting records of *Mustela itatsi* since 1983.

vulnerable to exotic predators, because the balance between natality and mortality can be upset due to the introduction of exotic predators. An evolutionary response towards such high predation intensity is a combination of life history traits leading to high natality. A suite of traits including annual reproduction, large clutches of small eggs, and earlier maturity with a small mature size was found in the population of *E.okadae* on Ohshima where the weasel is native (Hasegawa, 1994). However, *E.okadae* can not adjust its life history traits to cope with a weasel population rapidly established within an ecological time scale (<10 yr), despite *E.okadae*'s capability of reproducing annually when its population density is experimentally reduced (Hasegawa, 1997).

Behavioral traits also vary among populations under different predation regimes. Anti-predator responses by newly hatched *E.okadae* was compared between the islands with and without snake predators (Mori & Hasegawa, 1999). The results were consistent with the hypothesis that lizards from snake islands have evolved the ability to recognize chemical cues from snake predators. The lizards from snake-free islands were less efficient at recognition or lacked recognition of snake chemicals. Such a loss of predator recognition or reduced wariness against predators would explain the greater vulnerability of insular lizards to exotic predators.

The different islands of the Izu Islands support biological communities of differing structures and organizations. This is not only due to different species compositions, but more importantly due to different life history traits, resource utilization tactics and predator avoidance mechanisms exhibited by the component species. The impact of introduced species on the recipient community varies enormously from case to case (Case & Bolger, 1991), and Diamond and Case (1986) explained much of this variation is related to the extent of its prior experience with functionally similar species. Most species in the disharmonic insular communities have been evolved under fewer biological relationships than continental counterparts. This evolutionary view of insular biological communities is indispensable in considering conservation of island biota.

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