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Ecological Flexibility of the Top Predator in an Island Ecosystem – Food Habit of the Iriomote Cat

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1. Introduction

The responses of predators to changes in prey availability, i.e. density and distribution of prey in an environment, are of great interest, especially when they involve both temporal and spatial variations (Lodé, 2000). Variation of prey availability leads to various predator responses (Holling, 1959). For instance, predators specialized in catching particular prey often produce numerical responses to prey availability so that density of the predators mutually fluctuates with the prey density (Krebs & Myers, 1974; Hansson & Henttonen, 1985, 1988). In contrast, non-specialized predators often produce functional responses to prey availability, allowing these predators to switch prey types in relation to availability of alternative resources (Krebs, 1996).

The family Felidae is known as the most successfully evolved and developed predators specialized in feeding on mammalian prey (Kleiman & Eisenberg, 1973; Kruuk, 1982). Hence, they often show numerical response to density of a particular prey (e.g., Andersson & Erlinge, 1977; Krebs & Myers, 1974).

Members of the Felidae, being found at the top of the trophic hierarchy in an ecosystem, usually require extremely large habitat ranges. Thus, most cat species are found only on continents or large islands. The leopard cat *Prionailurus bengalensis*, the most widespread species of East Asian cat, is an exception to this rule, occurring on several small islands as well as larger islands and the Asian continent (Watanabe, 2009). The leopard cat chiefly preys on rodents but occasionally also feeds on other types of animals depending on region. On small islands with a small number of carnivore species, the cat frequently feeds on non-mammalian prey. As an extreme example of this, the Iriomote cat *Prionailurus bengalensis iriomotensis* lives on Iriomote Island, this being the smallest island (284 km²) known to be inhabited by this predator (Watanabe, 2009; Fig. 1).

The felid population on Iriomote Island remained unknown to science until its discovery in 1965 due to the inaccessibility of the dense forest which the cat occupies and to the remoteness of the island (Imaizumi, 1967). The cat had been long considered a separate species due to morphological differences among other small felids of south-east Asia (Imaizumi, 1967; Leyhausen & Pfeleiderer, 1999). This species was listed as endangered in

International Union for Conservation of Nature and Natural Resources [IUCN] (2000) Red List because of its restricted habitat and small population size, estimated at about 100 individuals (Izawa et al., 2000). The population has declined during the last decade due to habitat loss from development and mortality from traffic accidents (Watanabe et al., 2002). Recently, their taxonomical specific distinction has been questioned by molecular methods (Johnson et al., 1999; Masuda et al., 1994).



Fig. 1. An Iriomote cat taken by photo-trap (Mammal Ecology Laboratory, University of the Ryukyus).

The insular fauna of Iriomote Island is unique; there are no autochthonous terrestrial small mammals such as rodents that generally form the principal prey of wild felids. On the other hand, the herpetofauna is relatively abundant. In particular, the density of anurans on the forest floor is extremely high compared with those reported in other tropical forests (Watanabe et al., 2005). In addition, the avifauna is also abundant including many resident and migratory species (see the results). Thus, it is likely that there are unique characteristics of the ecology of the cat as the top predator in the ecosystem of Iriomote Island.

The Iriomote cat preys upon a variety of animals such as birds, reptiles, amphibians, and insects, besides mammals (Sakaguchi & Ono, 1994; Watanabe et al., 2003, Watanabe, 2009). Thus, the Iriomote cat may show functional responses to availability of various alternative prey. Indeed, Sakaguchi & Ono (1994) found a functional response of the Iriomote cat to seasonal variation in prey availability. The cat frequently preys upon *Eumeces* skinks, one of the dominant prey items of the cat, while skinks are abundant during spring and summer; however the cat changes its principal prey during periods of low skink availability.

The purpose of this study is to understand the mechanism that causes temporal variations of diet of the Iriomote cat. I investigate both prey availability and the cat diet in various types

of habitats through all seasons. I then consider how the cat responds to variations of prey availability, in terms of preferences and seasonal patterns of prey eaten. Moreover, I will discuss the role of such ecological flexibility of the cat in order to adapt to the island ecosystem.

2. Materials and methods

2.1 Study area

Field survey was conducted on Iriomote Island (24°20'N, 123°49'E) in the Ryukyu Archipelago, southern Japan (Fig. 2). The island largely consists of highly folded mountains with the highest peak (Mt. Komi) being 469 m above sea level. Its vegetation is mostly natural subtropical evergreen broadleaved forest (83% of the island in area), which is largely composed of *Castanopsis sieboldii* and *Quercus miyagii* in the tree layer of 8-12 m height. The understorey flora is more diverse, consisting of species such as *Daphniphyllum glaucescens*, *Elaeocarpus japonicus*, *Rapanea neriifolia* and *Ardisia quinqueгона* (Miyawaki, 1989; Numata, 1974).

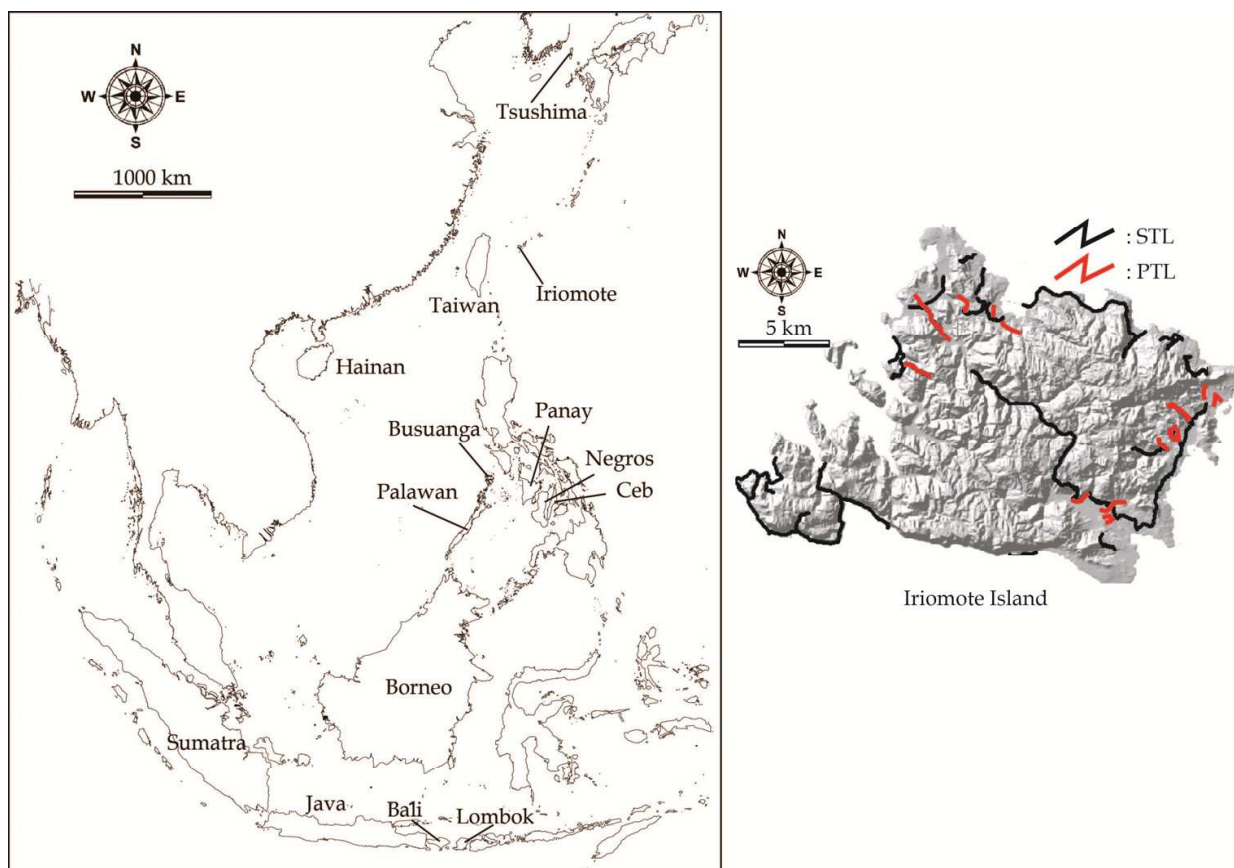


Fig. 2. Maps of East Asia showing islands with wild felid populations as cited in Watanabe (2009), and Iriomote Island (Ryukyu Archipelago, Japan) showing the locations of line transects along which scats of the Iriomote cat were collected (STL) and prey availability was estimated (PTL).

The island, which is located in the humid subtropical zone, includes the long chain of small islands (the Ryukyu Archipelago) which lies to the south of the main island of Japan

between the latitudes 24° and 30°N. However, most of the original, natural vegetation has been lost in this region, as a result of widespread land cultivation, and also due to heavy damage during World War II. Only Iriomote Island, which is now protected as one of the Japanese National Parks, contains good examples of the natural subtropical forests (Numata, 1974).

The climate of Iriomote Island, like that of other Ryukyu Islands, is seasonal with spring (April to June; average monthly temperature is 22.5-27.4°C), summer (July to September; 27.3-28.9°C), autumn (October to December; 19.9-25.1°C), and winter (January to March; 18.3-19.9), and which is largely affected by the south or south-west monsoon during the summer and the north or north-west monsoon during the winter (Ayoade, 1983). The monthly rainfall and relative humidity are 142-274 mm and 73-82%, respectively; the annual rainfall is 2300 mm (Iriomote Meteorological Station).

2.2 Prey census

Prey distribution and abundance, i.e. prey availability, of the cat was estimated by line transect sampling carried out along routes set throughout the island (Fig. 2). The cat is considered as an opportunistic mobile predator which moves around an area seeking out ground-living animals visually (Sakaguchi & Ono, 1994). I thus evaluated potential prey availability for cats by using a line transect method. This method has been effectively used to determine relative abundance of animals in different habitat types (Buckland et al., 2001), which is presumably similar to the feeding pattern of the cat. I estimated relative abundance of various prey in different habitat types, and its distribution and seasonal change were assessed.

Eighteen transects (PTL: prey transect line) varying in length between 190 and 1510 m, with a total transect length of 11.5 km were laid along unpaved trails in several types of forests, along rice fields, crop lands, and pastures (Fig. 2). The trails are 3-4 m in width, and are covered with sparse grass on their ground surface. The PTLs were monitored over 14 periods between August 2001 and April 2003; total transect length in each period varied and resulted in 254 km of transect work. Study periods were divided into four seasons depending on climatic change of the island, particularly depending on the temperature and rainfall (see the study area).

Field surveys were conducted twice a day, daytime (8:00-12:00) and night time (20:00-24:00) depending upon subject animals; diurnal birds, lizards, and skinks were sighted in daytime, nocturnal mammals (flying foxes and bats), nocturnal birds (owls), snakes, frogs, and some insects in night time. Wild boars and crickets were sighted in both time periods. The transect work was carried out under dry weather conditions, by walking at about 2 km h⁻¹ by the author throughout the study. Animals observed or singing in the transect lines and its vicinity (birds within 10 m in radius, lizards, skinks, and frogs within 2 m in radius, and insects were only counted on the transect lines) were located using a handheld Global Positioning System (GPS; model Garmin GPS II plus).

2.3 Scat analysis

Scat analysis was used to estimate the diet of the Iriomote cat, since this method is non-destructive and cost and time effective (Sakaguchi & Ono, 1994; Watanabe et al., 2003; Watanabe & Izawa, 2005). The scats of the Iriomote cat have been collected by trail censuses

as a part of endangered species conservation projects administrated by the Forest Agency and Ministry of the Environment, Japan since 1993. Observers walked along a total length of 91.0 km of transect (STL: scat transect line, Fig. 2) including most parts of the PTLs, along mountain trails, farm roads, paved traffic roads, and coastal lines. Locations of scats found were recorded on the route divided at 250 m intervals (Environment Agency & Forestry Agency, 1998). Although domestic cats (*Felis catus*) also inhabit Iriomote Island, they live mainly in residential areas. In addition, domestic cat scats and those of the Iriomote cat are easily distinguished by specific odours and grooming hairs contained within them (Watanabe et al., 2003).

Collected scats were washed on 1-mm mesh sieve, and dried at a laboratory. Remains such as hair, bone fragments, teeth, feathers, scales, and arthropod chitin of the prey consumed were separated for species identification (Sakaguchi & Ono, 1994; Watanabe et al., 2003). Scats which contained no prey items were excluded from the analysis. I tried to identify prey found in the scats to the level of species using my own reference collection of potential prey species collected on Iriomote Island, e.g. as cited in Watanabe & Izawa (2005) for amphibians. The identification was achieved depending on the type and the quality of the scat sample.

I calculated the frequency of occurrence of each prey item in the scats, i.e. the percentage of the total number of scats that contained a particular prey type for each prey item.

2.4 Prey availability and predation by the cat

2.4.1 Prey preference

To examine food preference in the cat diet, I calculated Jacobs' (1974) modification (D) of Ivlev's Electivity Index for quantification of the diet selection.

$$D = (r - p) / (r + p - 2rp) \quad (1)$$

Where r is the proportion of a given prey item in the total identified items in the scat contents, and p is the proportion of the same prey item in the total number of items found in the prey transects. D varied from -1 to 0 for negative selection and from 0 to +1 for positive selection.

I only evaluated prey preference of each bird and amphibian species, respectively, which are two of the major prey groups in the cat diet (see the results). I derived D s for only prey items which were frequently observed within the transect survey, because these indices are vulnerable to sampling errors for prey that are rare in the environment (Jacobs, 1974). From the derived electivity index for each prey item, I considered the feeding pattern of the cat in terms of principal habitats of the major prey species.

2.4.2 Seasonal patterns

To evaluate seasonal patterns of prey availability, frequency of occurrence of each prey species per kilometre on the PTL was calculated in each study period and each season. I used a likelihood ratio test (G -test: Sokal & Rohlf, 1995) to examine the goodness of fit into expected values derived from proportion of transect distance in each season.

Likewise, seasonality of predation of each prey type found in scats was also evaluated. I calculated the frequency of occurrence of prey items in the scats for each season. I used a G -

test to examine the goodness of fit into expected values derived from proportion of analysed scats in each season.

I also performed Principle Component Analysis (PCA: Sokal & Rohlf, 1995) to classify the various prey species in terms of their relative similarity of seasonal variation, availability and predation. This PCA was run after standard VARIMAX rotation of data, the frequency occurrences in PTL and in a scat of each major prey item for each season.

All statistical analyses were carried out using SPSS for Windows version 11.5 (SPSS, Inc.; Chicago, Illinois, USA). Statistical significance was set at the 0.05 level.

3. Results

3.1 Prey availability

From the total of 254 km of transects sampled, I found 8096 individual animal belonging to 72 different prey items including animals which could not be identified to the level of species but were distinguishable from other groups. Most of the prey items are birds (61.6% of the total number of animals found in PTLs), while mammals, reptiles, amphibians, and insects occupied 4.1%, 15.1%, 9.59%, 9.59%, respectively. Insects occupied a low percentage proportion because only three major prey items of insects were recorded. In spite of the species composition, the number of individuals found was dominated by amphibians (62.3% of total number of individuals found in PTLs); particularly, the Indian rice frog *Fejervarya limnocharis* occupied 41.8% of all animals found. In contrast, mammals, birds, reptiles, and insects occupied 1.05%, 24.4%, 7.31%, and 4.92%, respectively.

In the case of mammals, I encountered 85 individuals belonging to three different groups, most of which were the Yaeyama flying fox *Pteropus dasymallus yaeyamae* (65.9% of all encountered mammals). Small-sized chiropterans (24.7%) were the second most frequently encountered animals but not all of them could be identified because I only observed them briefly as they flew across the transect.

In birds, I encountered 1973 individuals belonging to 50 different bird groups in 25 families. The relative abundance of each species was the highest in the Brown-eared bulbul *Hypsipetes amaurotis stejnegeri* (19.6% of all encountered birds), followed by the Oriental turtledove *Streptopelia orientalis* (12.2%), the Jungle crow *Corvus macrorhynchos osai* (9.28%), thrushes in the genus *Turdus* (mostly *T. pallidus* or *T. chrysolaus* although they were difficult to distinguish from each other during the censuses: 7.65%), and *Parus* spp., mostly *P. major* or *P. varius* (7.60%). Thirty-six percent of the identified bird species are arboreal foragers which are sighted mainly on trees or in shrubs, and 52% of the bird species are ground-living terrestrial foragers which are sighted mainly on the ground; the rest of the bird species (12%) are sighted in both habitats, according to our observations during the censuses.

In the case of reptiles, I encountered 572 individuals belonging to seven different groups, most of which were the Sakishima tree lizard *Japalura polygonata ishigakiensis* (41.4% of all encountered reptiles) and *Eumeces* skinks (*Eumeces kishinouyei* or *E. stimpsonii*: 42.1%). I observed four species of snakes, of which the Sakishima habu *Trimeresurus elegans* (10.1%) which is the only venomous snake on the island, was the most frequently observed during censuses.

In amphibians, only anurans were found, of which I encountered 3386 individuals belonging to seven species in three families. The relative abundance of each species was the highest in the Indian rice frog *F. limnocharis* (67.1% of all encountered frogs), followed by the Ryukyu kajika frog *Buergeria japonica* (13.3%), the Ornata narrow-mouthed toad *Microhyla ornata* (10.4%), and the Eiffinger's tree frog *Chirixalus eiffingeri* (4.8%). Most frog species are terrestrial ground-living foragers except for *C. eiffingeri* that inhabits mostly the tree canopy and the Owston's green tree frog *Rhacophorus owstoni* which inhabits mainly tree canopies but comes down to the forest floor during their breeding season (Maeda & Matsui, 1999).

3.2 Predation by the cat

I examined the contents of 947 scats collected in the study area from December 1993 to November 2002. I identified 76 different prey items (four items of mammals, 21 items of birds, seven items of reptiles, five items of amphibians, one item of fish, 26 items of insects, two items of crustaceans, three items of centipedes, six items of arachnids, and one item of gastropod) which include prey items that could not be identified to the level of species but were distinguishable from other prey items. Species identification of mammals and reptiles was accomplished with ease due to the small number of potential species in each taxon and the presence of clearly defined hairs, scales, teeth or mandibles in the scat content. However, birds and insects found in the scat contents were difficult to identify due to a large number of potential prey species, and unclearly characterized body parts in the scat content. Amphibians were also difficult to identify due to only a small number of bone fragments. Thus, these prey taxa include unidentified animal remains at relatively high frequencies. Meanwhile, prey species were diversified in birds (27.6% of total number of identified prey items) and in insects (34.2%).

Only one prey item was found to be contained in 31.5% of total examined scats, while 31.6%, 22.3%, 10.2%, 3.17%, 0.74%, 0.42%, and 0.11% of the scats contained two, three, and four to eight prey items, respectively. Scats containing larger prey items (the estimated liveweight is more than 200 g; Imaizumi et al., 1977) contained significantly fewer prey items (1.92 ± 1.15 , \pm a standard deviation of number of prey items found in the scats) than scats with only smaller prey (< 200 g, 2.37 ± 1.19 ; Mann-Whitney *U*-test, $U = 60202$, $P < 0.001$).

Principle prey species which were frequently found in the scats belonged to a variety of taxonomical groups ranging from mammals to crustaceans. The major prey species are described as follows: the Yaeyama flying fox *Pteropus dasymallus yaeyamae* and the black rat *Rattus rattus* in mammals, egrets *Egretta* spp., the banded crane *Rallina eurizonoides*, the white breasted water hen *Amaurornis phoenicurus*, and thrushes *Turdus* spp. (presumably most of them were the pale thrush *T. pallidus* but difficult to distinguish birds in the genus), in birds, the Sakishima tree lizard *J. p. ishigakiensis*, the Kishinoue's giant skink *E. kishinouyei*, and the Sakishima habu *T. elegans*, in reptiles, the Indian rice frog *F. limnocharis*, the Owston's green tree frog *Rh. owstoni*, and the Ornata narrow-mouthed toad *M. ornata*, in amphibians, the spotted cockroaches *Rhabdoblatta* spp., camel crickets, *Diestrammena* spp., and the spotted cricket *Cardiodactylus novaeguineae*, in insects, and freshwater prawns *Macrobrachium* spp. in crustaceans. Among these prey items, black rats, flying foxes, and rice frogs were the most frequently present species in the cat diet.

The overall frequency of occurrence in each taxon was calculated as follows: 30.9% in mammals, 47.7% in birds, 33.1% in reptiles, 34.3% in amphibians, 2.96% in fish, 24.3% in insects, 4.22% in crustaceans, and 3.27% in others.

3.3 Prey preference

I calculated Jacobs’ electivity indices for 18 bird groups in which taxonomically similar species with a small number of samples were combined, and for seven amphibian species (Table 1). The result show that the cat preferred preying on some bird items; egrets, rails (*R. eurizonoides* and *A. phoenicurus*), *Halcyon coromanda*, and wagtails in the genus *Motacilla*, all of which were terrestrial foragers. However, *Hirundo tahitica*, *Pericrocotus divaricatus*, *H. amaurotis*, *Cettia diphone*, *Terpsiphone atrocaudata*, *Parus* spp., *Zosterops japonica*, and *Passer montanus*, all of which were arboreal foragers, were not preferred or were avoided by the cat.

Among amphibians, the cat preferred preying on *R. supranarina* and *Rh. owstoni* while *R. psaltes*, *C. eiffingeri*, *B. japonica*, *F. limnocharis*, and *M. ornata* were not preferred or was avoided for predation by the cat (Table 1).

Prey item		Habitat* ¹	Migration* ²	Liveweight (g)* ³	Available N (%)	Consumed N (%)	Electivity Index (D)	Preference
Bird;								
Ardeidae	Egrets	T	R,W	>500	176 (9.2)	22 (12.7)	0.18	+
Anatidae	Ducks	T	R,W	>500	131 (6.8)	15 (8.7)	0.13	+
Rallidae	Rails	T	R	200	49 (2.6)	48 (27.7)	0.87	+
Scolopacidae	Snipes	T	W	200	21 (1.1)	2 (1.2)	0.03	+
Columbidae	Pigeon	A,T	R	200	260 (13.6)	21 (12.1)	-0.07	-
Strigidae	Owls	A	R	120	89 (4.7)	6 (3.5)	-0.15	-
Alcedinidae	<i>Halcyon coromanda</i>	T	S	100	18 (0.9)	6 (3.5)	0.58	+
Hirundinidae	<i>Hirundo tahitica</i>	A	W	20	22 (1.2)			-
Motacillidae	<i>Motacilla</i> spp.	T	W	30	34 (1.8)	7 (4.0)	0.40	+
Campephagidae	<i>Pericrocotus divaricatus</i>	A	R	20	26 (1.4)			-
Pycnonotidae	<i>Hypsipetes amaurotis</i>	A	R	30	386 (20.2)	2 (1.2)	-0.91	-
Turdidae	<i>Turdus</i> spp.	T	W	80	159 (8.3)	27 (15.6)	0.34	+
Sylviidae	<i>Cettia diphone</i>	A	R	20	61 (3.2)			-
Monarchidae	<i>Terpsiphone atrocaudata</i>	A	R	20	23 (1.2)			-
Paridae	<i>Parus</i> spp.	A	R	20	150 (7.8)	2 (1.2)	-0.76	-
Zosteropidae	<i>Zosterops japonica</i>	A	R	20	87 (4.6)	2 (1.2)	-0.61	-
Ploceidae	<i>Passer montanus</i>	A	R	20	36 (1.9)			-
Corvidae	<i>Corvus macrorhynchos</i>	A,T	R	300	183 (9.6)	13 (7.5)	-0.13	-
Frog;								
Ranidae	<i>Rana supranarina</i>	T		60	27 (0.5)	7 (2.8)	0.69	+
	<i>Rana psaltes</i>	T		10	128 (2.5)			-
	<i>Fejervarya limnocharis</i>	T		20	3,386 (67.1)	142 (57.0)	-0.20	-
Rhacophoridae	<i>Rhacophorus owstoni</i>	A,T		20	68 (1.3)	55 (22.3)	0.91	+
	<i>Chirixalus eiffingeri</i>	A		4	242 (4.8)			-
	<i>Buergeria japonica</i>	T		4	669 (13.3)	14 (5.7)	-0.44	-
Microhylidae	<i>Microhyla ornata</i>	T		4	526 (10.4)	29 (11.7)	0.07	+

Table 1. Prey preferences of 25 prey items by the Iriomote cat, indicated by Jacobs (1974) electivity index (D). *¹Principal habitat of each species: arboreal (A), terrestrial (T), and both (A, T), depending on where species were often observed during the censuses. *²Migration of each species; residents (R), summer migrators (S) and winter migrators (W), according to Takano (1982) and Committee for Check-List of Japanese Birds (2000). *³Estimated liveweight from weighing my reference collection or Imaizumi et al. (1977).

3.4 Seasonal variation

3.4.1 Prey availability

The frequency of occurrence of most species changed seasonally. Within an identified 72 species found in the PTLs, 66 species were absent in some periods or present in limited periods of the study years. Although six species, *S. orientalis*, *H. amaurotis*, and *C. macrorhynchos*, of birds, and *B. japonica* and *M. ornata* of amphibians, and *Diestrammena* spp. of insects, were found in all the study periods, these frequencies also largely varied depending on season.

In the bird species, 44 percent of species are residents on the island, while the rest are seasonal migrators: winter birds migrating from north to the island during autumn and winter for overwintering (40%), summer birds migrating from south to the island during spring and summer for breeding (2.0%), and transient migrators stopping off briefly on the island during migration from north to further south of the island (4.0%: Takano, 1982; Committee for Check-List of Japanese Birds, 2000). The relative abundances of principal bird species observed in prey censuses during each season were derived. During all seasons, four species of resident birds, *H. amaurotis*, *S. orientalis*, *C. macrorhynchos*, and *Parus* spp., were relatively abundant. Meanwhile, during autumn and winter, two groups of migrators, *Turdus* spp. and ducks, were also abundant, which occupied respectively high proportions of the avifauna.

Among the amphibians, in spring to autumn, *F. limnocharis* was the most abundant, followed by *M. ornata*, *B. japonica*, and *C. eiffingeri*. Meanwhile, *M. ornata* was the most abundant during winter, followed by *F. limnocharis*, *R. supranarina*, *C. eiffingeri*, and *Rh. owstoni*.

To assess seasonal variation of more general compositions of prey availability, I calculated seasonal variations of frequency occurrences of 18 major prey groups in prey censuses which were also frequently eaten by the cat. The results are summarized in Table 2. Some prey groups including taxonomically similar prey species (ducks in the family Anatidae, the genera of egrets *Egretta* spp., thrushes *Turdus* spp., skinks *Eumeces* spp., cockroaches *Rhabdoblatta* spp., and camel crickets *Diestrammena* spp.) were combined within the taxonomical group and the data were pooled.

Frequency occurrence of 14 prey groups showed significant seasonal variations (G-test, $P < 0.05$). Although other groups, water hens, *S. orientalis*, *T. elegans*, and *R. supranarina*, thrushes, and *J. polygonata*, did not show significant seasonal variations (G-test, $P > 0.05$), these frequency occurrences also differed among seasons in varying degrees.

A more detailed picture of seasonality of prey availability of the cat emerges from applying a PCA model to the data matrix in Table 2. The first and second principal components of PCA explained 61.2% and 25.0% of the total variability, respectively, and the scores of the first and second factors are presented in Table 3. In the score plot of each prey species on factors, the main variables ordering the various species along factor 1 were “winter-summer”, and those ordering the species along factor 2 were “spring-autumn”, which were sufficient to illustrate the main structure of prey availability among seasons (Fig. 3).

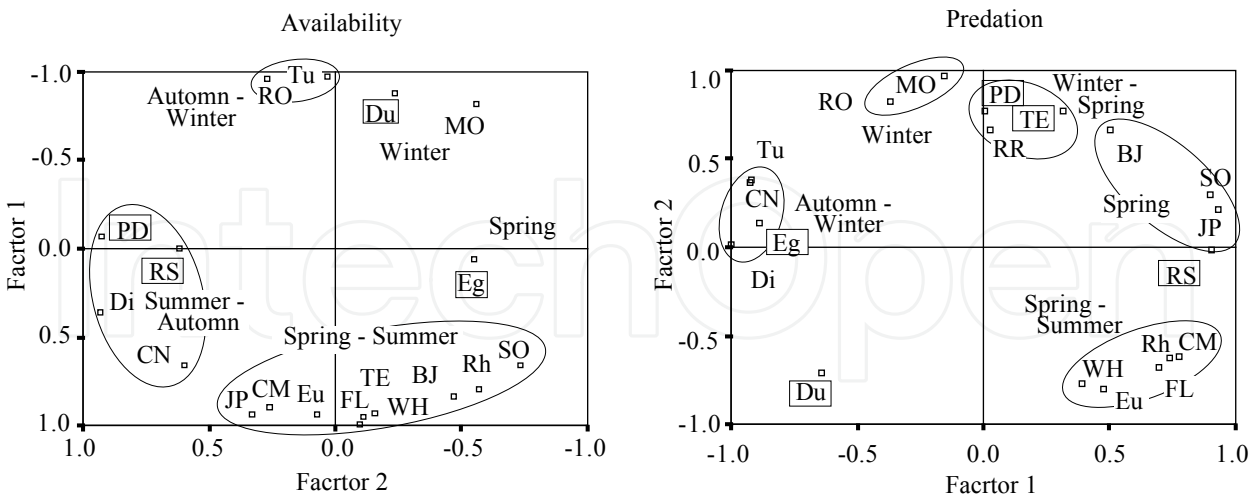


Fig. 3. Seasonal variation of potential prey availability and diet of the Iriomote cat. Two dimensional-plots of scores for each prey items on first two factors using VARIMAX rotation model PCAs showing mainly four season prey groups. PD: *Pteropus dasymallus*, RR: *Rattus rattus*, CM: *Corvus macrorhynchos*, Du: ducks, Eg: egrets, SO: *Streptopelia orientalis*, Tu: *Turdus* spp., WH: water hens, Eu: *Eumeces* spp., JP: *Japalura polygonata*, TE: *Trimeresurus elegans*, BJ: *Buergeria japonica*, MO: *Microhyla ornata*, FL: *Fejervarya limnocharis*, RS: *Rana supranarina*, RO: *Rhacophorus owstonii*, Di: *Diestrammena* spp., Rh: *Rhabdoblatta* spp., CN: *Cardiodactylus novaeguineae*.

Prey items	Frequency of occurrence (%) in scats							Frequency of occurrence (individuals km ⁻¹) in PTLs						
	Spring	Summer	Autumn	Winter	Overall	G	P	Spring	Summer	Autumn	Winter	Overall	G	P
Mammals														
<i>Pteropus dasymallus</i> (Yaeyama flying fox)	12.9	5.3	10.4	11.2	10.5	8.43	0.038 *	0.29	0.46	0.69	0.31	0.42	14.9	0.002 *
<i>Rattus rattus</i> (black rat)	17.7	19.0	13.4	26.2	20.2	11.8	0.008 *							
Birds														
Egrets	1.29	0.53	5.22	3.19	2.32	12.2	0.007 *	2.45	0.31	1.41	0.79	1.26	31.0	<0.001 **
Ducks	0.32	2.65	5.22	0.64	1.58	15.3	0.002 *	0.60	0.31	1.29	4.45	1.08	52.0	<0.001 **
Water hens	3.22	6.35	2.99	2.56	3.59	6.14	0.105	0.47	0.42	0.32	0.22	0.39	0.63	0.890
<i>Streptopelia orientalis</i> (Oriental turtle dove)	1.93	1.06	0.75	0.96	1.27	1.61	0.657	2.17	2.01	1.65	1.87	1.97	1.39	0.708
<i>Turdus</i> spp. (thrushes)	1.29	1.06	4.48	4.47	2.75	5.85	0.119	0.18	0.00	3.02	5.53	1.30	155	<0.001 **
<i>Corvus macrorhynchos</i> (jungle crow)	1.93	2.65	0.75	0.32	1.37	6.59	0.086	1.23	2.39	0.85	0.57	1.50	16.8	<0.001 **
Reptiles														
<i>Japalura polygonata</i> (Sakishima tree lizard)	6.75	4.23	2.99	3.51	4.65	4.76	0.190	1.64	3.22	1.21	0.00	1.95	43.7	<0.001 **
<i>Eumeces</i> spp. (skinks)	30.5	34.4	27.6	3.83	22.1	112	<0.001 **	1.80	3.68	0.24	0.07	1.98	93.1	<0.001 **
<i>Trimeresurus elegans</i> (viper)	2.25	1.59	0.00	3.51	2.22	8.46	0.037 *	0.64	0.59	0.34	0.12	0.44	0.97	0.810
Amphibians														
<i>Rana supranarina</i> (large tip-nosed frog)	3.54	1.59	0.75	0.32	1.69	8.85	0.031 *	0.20	0.15	0.50	0.03	0.20	3.73	0.292
<i>Fejervarya limnocharis</i> (Indian rice frog)	17.4	24.3	11.2	8.63	15.0	25.7	<0.001 **	36.5	45.1	9.95	3.30	25.7	383	<0.001 **
<i>Rhacophorus owstoni</i> (Owston's green tree frog)	1.93	0.00	1.49	15.0	5.81	75.0	<0.001 **	0.06	0.05	1.03	1.14	0.52	60.9	<0.001 **
<i>Buergeria japonica</i> (Ryukyu kajika frog)	2.89	0.00	0.75	1.28	1.48	9.67	0.022 *	10.53	6.42	1.68	0.37	5.07	36.7	<0.001 **
<i>Microhyla ornata</i> (Ornata narrow-mouthed toad)	2.89	0.53	1.49	5.43	3.06	12.4	0.006 *	4.28	1.87	3.60	6.54	3.99	102	<0.001 **
Insects														
<i>Rhabdoblatta</i> spp. (spotted cockroaches)	8.04	13.2	2.24	0.96	5.91	41.1	<0.001 **	0.20	0.18	0.04	0.09	0.14	9.19	0.027 *
<i>Diestrammena</i> spp. (camel crickets)	0.64	3.70	10.4	8.31	5.17	32.1	<0.001 **	1.40	2.48	2.30	1.48	1.92	29.0	<0.001 **
<i>Cardiodactylus novaeguineae</i> (spotted cricket)	1.29	1.06	13.4	13.7	6.97	61.5	<0.001 **	0.00	1.07	0.26	0.00	0.41	93.7	<0.001 **
Summary														
Number of examined scats								Distance (km)						
								Day	38.32	44.78	24.83	13.92	122	
								Night	34.38	39.07	26.14	32.40	132	
								Total	72.70	83.85	50.97	46.32	254	

Table 2. Seasonal variations of availability and predation of principal prey items observed in prey censuses and found in scats of the Iriomote cat. * $P < 0.05$; ** $P < 0.001$.

Prey items	Availability		Predation	
	Factor 1	Factor 2	Factor 1	Factor 2
Mammals				
<i>Pteropus dasymallus</i> (Yaeyama flying fox)	-0.072	0.920	0.004	0.773
<i>Rattus rattus</i> (black rat)	—	—	0.027	0.665
Birds				
Egrets	0.059	-0.553	-0.888	0.138
Ducks	-0.882	-0.239	-0.639	-0.709
Water hens	0.929	-0.161	0.393	-0.771
<i>Streptopelia orientalis</i> (Oriental turtle dove)	0.659	-0.737	0.896	0.301
<i>Turdus</i> spp. (thrushes)	-0.978	0.025	-0.920	0.379
<i>Corvus macrorhynchos</i> (jungle crow)	0.899	0.256	0.774	-0.617
Reptiles				
<i>Japalura polygonata</i> (Sakishima tree lizard)	0.940	0.324	0.930	0.211
<i>Eumeces</i> spp. (skinks)	0.938	0.068	0.476	-0.802
<i>Trimeresurus elegans</i> (viper)	0.954	-0.116	0.317	0.771
Amphibians				
<i>Rana supranarina</i> (large tip-nosed frog)	-0.003	0.614	0.902	-0.016
<i>Fejervarya limnocharis</i> (Indian rice frog)	0.991	-0.102	0.695	-0.676
<i>Rhacophorus owstoni</i> (Owston’s green tree frog)	-0.964	0.266	-0.366	0.826
<i>Buergeria japonica</i> (Ryukyu kajika frog)	0.837	-0.476	0.505	0.663
<i>Microhyla ornata</i> (Ornata narrow-mouthed toad)	-0.824	-0.563	-0.156	0.973
Insects				
<i>Rhabdoblatta</i> spp. (spotted cockroaches)	0.797	-0.576	0.736	-0.624
<i>Diestrammena</i> spp. (camel crickets)	0.359	0.927	-1.000	0.012
<i>Cardiodactylus novaeguineae</i> (spotted cricket)	0.657	0.592	-0.927	0.369
Eigenvalue	11.01	4.51	10.07	5.93
% Explained variance	61.17	25.05	53.02	31.20

Table 3. Results of principle component analysis for seasonal variations of availability and predation of principal prey items found in prey censuses and scats of the Iriomote cat.

Ducks and *M. ornata* were the most abundant in winter. Egrets were the most abundant in spring. *Streptopelia orientalis*, *Rhabdoblatta* spp., *B. japonica*, water hens, *T. elegans*, *F. limnocharis*, *Eumeces* spp., *C. macrorhynchos*, and *J. polygonata*, were more abundant in spring and summer. *Cardiodactylus novaeguineae*, *Diestrammena* spp., *R. supranarina*, *P. dasymallus*, were more abundant in summer and autumn. *Rhacophorus owstoni* and *Turdus* spp. were more abundant in autumn and winter.

3.4.2 Predation by the cat

The frequency occurrence of most prey species in scat contents changed monthly or seasonally. Within an identified 76 prey items in the scat content, 72 prey items were absent in some months or present in limited months of the years. Although four species, black rats, flying foxes, rice frogs, and freshwater prawns, were found at all months, these frequencies also greatly varied on a monthly basis.

The frequency occurrences for each season of 19 major prey groups which were frequently found in the scats were calculated, and the seasonal variations were compared among seasons (Table 2). Fifteen groups of the prey items showed significant seasonality (G-test, $P < 0.05$). Four prey species, water hens, *S. orientalis*, thrushes, and *J. polygonata* did not show statistically significant seasonality (G-test, $P > 0.05$), but these frequency occurrences also varied among seasons.

A more detailed picture of seasonality of the diet composition emerges from applying a PCA model to the data matrix in Table 2. The first and second principal components of PCA explained 53.0% and 31.2% of the total variability, respectively, and the scores of the first and second factors are presented in Table 3. In the score plot of each prey species on factors, the main variables ordering the various species along factor 1 were “autumn-spring”, and those ordering the species along factor 2 were “summer-winter”, which were sufficient to illustrate the main structure of diet composition among seasons (Fig. 3).

Rhacophorus owstoni and *M. ornata* were most frequently eaten in winter. *P. dasymallus*, *Rattus ratuus*, and *T. elegans* were more frequently eaten in winter and spring. *Buergeria japonica*, *S. orientalis*, *J. polygonata*, and *R. supranarina* were most frequently eaten in spring. *Corvus macrorhynchos*, *Rhabdoblatta* spp., *F. limnocharis*, water hens, and *Eumeces* spp., were more frequently eaten in spring and summer. Ducks were eaten most frequently in autumn. *Diastrammena* spp., egrets, *C. novaeguineae*, and *Turdus* spp., were eaten more frequently in autumn and winter.

4. Discussion

The results of this scat analysis show that the Iriomote cat fed on various types of prey, as observed in earlier studies (Sakaguchi & Ono, 1994; Watanabe et al., 2003). I observed 76 prey items of the cat demonstrating considerable diversity among the dietary studies. In other studies, scats analysed were collected from parts of the island during several years while scats analysed in the present study were collected from the whole island over a long-time period. Thus, a large number of scat contents were analysed, and many differences such as seasonal variation and localities of a variety of prey items could be estimated. Therefore, I believe that the results show general representation of the cat diet in the present study.

The Iriomote cat fed considerably more on avian prey than other animals in the present study although birds are almost always not principal prey among other wild felids (Kruuk, 1982; M. Sunquist & F. Sunquist, 2002). Some other small cats such as *Felis margarita*, *F. silvestris*, *Herpailurus yaguarondi*, *Leptailurus serval*, and *Oncifelis geoffroyi*, occasionally hunt bird prey, but the frequency of these occurrences are much lower than that of the Iriomote cat (M. Sunquist & F. Sunquist, 2002). It is therefore likely that the hunting pattern of the Iriomote cat is the most developed in focusing on bird prey among the cat family.

Of eighteen avian groups which were frequently observed in the prey censuses, thirteen groups were eaten by the cat; others are all arboreal foragers. Sakaguchi & Ono (1994) suggested that the cat may hunt mainly on the ground because all nine bird species found in their analysis were mainly foraging on the ground. I found that the cat occasionally preyed

on arboreal species such as *H. amaurotis* and *Parus* spp., suggesting the Iriomote cats arboreal activities. However, prey preferences of the cat for arboreal birds were much lower than those for terrestrial foraging bird species. Thus, I support the prediction of Sakaguchi & Ono (1994) that the cat is a species foraging mainly on the ground, as opposed to in trees.

Species compositions of avifauna as potential prey resources of the cat drastically changed in relation to migrations of birds. This island with such abundant small vertebrates is known as a way station or breeding place for many migrant birds; 191 species belonging to 15 orders, 43 families, and 106 genera are recorded on this island, 83% of which are seasonal migrators while resident bird species occupy at least 17% of the total avifauna on the island (Okinawa Prefectural Education, 1985). In the cat diet, these avian prey items were present at high frequency. Thus, I presumed that such drastic seasonal changes of potential food resources of the cat in relation to migrations of large numbers of birds would strongly influence the feeding habits of the Iriomote cat.

Consequently, bird migrations largely affected the cat diet, particularly during winter by some migrators such as *Turdus* spp., ducks, *Motacilla* spp., and egrets. Most species of resident birds on the island breed during spring and summer (Takano, 1985); many juvenile birds were observed from June to August during the prey censuses. Particularly, *A. phoenicurus* and *C. macrorhynchos* were frequently preyed upon during spring and summer. It is likely that more vulnerable juveniles were frequently eaten during these periods. Although reptiles are principal prey items during spring and summer, the availability of this prey decrease during winter due to their low physiological activity under low temperature (Sakaguchi & Ono, 1994). It is, therefore, likely that the migrations of winter birds largely contribute to supply a deficiency of food resource during winter.

In dietary studies of other *P. bengalensis* populations, the cat diet is monopolized by mammalian prey in a continental habitat (Thailand), bird prey were present at less than 2% of their scats (Rabinowitz, 1990). On an island site, Tsushima Islands, Japan, although mammalian prey are also the most important food in the diet, the cat also preys heavily on birds (41.7% for the frequency of occurrence in the scats: Inoue, 1972). Unfortunately, there is little available information for diets of other wild felids on island sites. However, I could find those of feral domestic cat, *Felis catus*, populations which are widespread all over the world, and they had been introduced to many islands (Fitzgerald & Tuner, 2000). Dietary studies of domestic cats on continents show that mammals are usually the main prey eaten by cats, while birds are much less important than mammals. However, birds are much more important in the diet of domestic cats on islands than on continents. Particularly, on islands where seabirds are recorded in the diet, birds are present on average at 60% of frequency of occurrence in their scats (Fitzgerald & Tuner, 2000). Although small mammals such as rodents or lagomorphs are available on many islands, feral cat populations can persist on islands that lack mammalian prey but are abundant in birds (Kirkpatrick & Rauzon, 1986). Therefore, I suggest that the Iriomote cat can endure on its small island despite a poor mammalian fauna by means of shifting principal prey items to seasonal migrators, particularly during winter. It is during this winter period, that the mating season of the cat takes place (Okamura et al., 2000); home range size and activity of male cats increase (Nakanishi et al., 2005; Schmidt et al., 2003, 2009). Thus, the food requirement of the cat should increase in that time. Therefore, it is likely that winter migrators supply an increment of food requirement for reproduction of the cat.

In addition, the number of migrant birds on this island largely fluctuated year by year, particularly *Turdus* spp.; the species were rarely encountered in some years while they have been abundant in most years during this decade (Iriomote Wildlife Conservation Center pers. comm.). The incidence of winter migrators may influence survival rate and breeding success of the Iriomote cat.

In the case of the other main prey items of the Iriomote cat, amphibians were the second most frequent prey eaten in the cat diet. The Iriomote cat is also unique among the cat family in feeding on amphibians. For other carnivores, however, numerous mustelids are found to prey upon anurans. Although otters *Lutra lutra*, American mink *Mustela vison*, and badger *Meles meles* sometimes consume a significant quantity of frogs and toads, the occurrences of amphibians in the diet of carnivores remain generally low (Chanin & Linn, 1980; Erlinge, 1969; Webb, 1975; Wise et al., 1981). Exceptionally, polecats *Mustela putorius* feed heavily on anurans. Anurans occupy about 46% of the total number of prey which is almost the same as that of mammalian prey. However, the predation of anurans is limited only during spring while the availability of anurans is particularly high in relation to their breeding season (Lodé, 1996). In the present study, the Iriomote cat frequently feeds on anurans throughout the year. The abundance of amphibian fauna on the island is the highest so far reported in Old and New world tropics; that is relatively high throughout the year due to different breeding periods of several species (Watanabe et al., 2005). The availability of the frog species most frequently eaten, *F. limnocharis*, is high during spring and summer due to their breeding season (Watanabe et al., 2005). The frogs were mainly eaten during these periods. From autumn to winter, the availability of the frogs drastically decreased and they were not frequently eaten by the cat. During winter, the availability of two other species, *Rh. owstoni* and *M. ornata*, were high and they were mainly eaten during this period. Therefore anurans on the island are available food for the Iriomote cat throughout the year.

There are eight species of the amphibian fauna of Iriomote Island, of which five species were found in the scat contents of the cat. Of the other three species, *R. utsunomiyaorum*, lives chiefly near streams in montane forests (Maeda & Matsui, 1999); this species is rarely found and was not found during these censuses. Although *C. eiffingeri* was frequently observed during the censuses, I found this frog by mainly identifying their calls when made by individuals located on trees, whilst these frogs were rarely found on the ground. This species was not observed on the ground during the prey census in this study. Thus, the result also supports the prediction that the cat mainly hunts animals on the ground. *Rana psaltes* was a ground-dwelling species but the species was not found in the scat samples. It is not clear why the species was absent in the cat diet but it is possible that the density of this species is particularly low compared with those of other anurans in the habitats of the cat, or the identification of this species was not successfully achieved in the scat analysis.

The frogs eaten by the cat, *R. supranarina* and *Rh. Owstoni*, were only selectively preyed upon. For estimation of prey value for each species, a species with large mass is probably higher than a species with a small mass. It is because, from the results estimating body mass of *F. limnocharis* in scat contents of the Iriomote cat, the cat selectively preys on large sized frogs and avoids immature small frogs (Watanabe & Izawa, 2005). *Rana supranarina* is the largest frog species of the amphibian fauna. The size of adult *Rh. owstoni* is almost same as *F. limnocharis* but only breeding adults *Rh. owstoni* were observed during winter. *Buergeria*

japonica and *M. ornata* are both small species, thus the values for the cat diet are presumably lower than those of larger frogs. Therefore the selectivity of frog species by the cat resulted from the differences of prey values, environments inhabited, and breeding cycles of each species.

From spring to summer, the availability of many reptiles, frogs, and resident birds are high; thus, the cat feeds on various prey types during the period. Meanwhile, availability of these prey species decreases during winter. Thus, the cat changes principal prey during winter. Additionally, the cat frequently preys on small-sized prey items such as frogs and insects, *M. ornata*, *B. japonica*, and *Diestrammena* spp., during winter.

Even if prey resources seasonally decreased or occasionally disappeared in habitats of open environment such as on continents, predators would move to search for other habitats encompassing plenty of food. Indeed, home ranges of leopard cats on the continent largely shift depending on wet and dry seasons and its sizes are much larger (Rabinowitz, 1990; Grassman, 2000, 2005) than those of Iriomote cats (Nakanishi et al., 2005; Schmidt et al., 2003). In restricted habitats such as small islands, however, predators have to remain in the same habitats during periods of prey resource scarcity.

The feeding pattern of leopard cats is presumed to be one of randomly foraging within a wide area with a relatively high abundance of their prey, and these cats prey on encountered animals; that is indicating an opportunistic feeding pattern (Fitzgerald & Tuner, 2000). The results in this study support that Iriomote cats are also opportunistic predators due to their non-selective varied diet representing prey availability with seasonal variations. The Iriomote cat is more likely to opportunistically forage in areas of abundant prey resources, feeding on various prey. However, it is unlikely that cats travel within their habitat and chase encountered volant birds. It is more effective that cats ambush and then attack a bird coming within close reach of the cat; that is using an ambushing feeding pattern. Therefore, the cats may shift their feeding tactics when switching their principal prey items. The movement pattern of the Iriomote cat varies in relation to seasons and local differences of habitats (Nakanishi et al., 2005; Sakaguchi, 1991; Schmidt et al., 2003, 2009). It may also vary in relation to shifting feeding patterns of the cat depending on seasonal difference of principal prey items. These patterns will be more clarified by comparison of movement patterns and prey availability of the cat in the further study.

From the above results, I considered that the broad range of the food niche of the Iriomote cat probably resulted from making the best possible use of fauna on the small subtropical island. Furthermore, the cat adapts to the islandwide environment to change principal prey items and feeding patterns in relation to temporal variations of food availability. I suggest that such flexibility of food habits of the Iriomote cat plays an important role for its existence on the small isolated habitat. Most small felids may potentially have such flexible properties in their ecology. However, I believe that it is revealed only in the peculiar fauna of the insular environment of Iriomote Island.

5. Conclusion

The leopard cat, *Prionailurus bengalensis*, is one of most widespread felids and is distributed throughout Asia. The Iriomote cat *Prionailurus bengalensis iriomotensis*, a subspecies of the

leopard cat, lives only on Iriomote Island of the Ryukyu Archipelago in southern Japan. Although there are thousands of islands of various sizes within the range of distribution of the species, the Iriomote cat is the only population on such a small island (284 km²). Moreover, on the island, there are no autochthonous terrestrial small mammals such as rodents that are generally the principal prey of wild felids. Thus, it is likely that there are unique characteristics of the ecology of the cat as the top predator in the ecosystem. In the present study, I aim to clarify characteristics of the cat population inhabiting the most limited environment for wild felids.

The cat diet was examined regarding prey preference and seasonal pattern of each prey item by analysing their 947 scat contents collected from various environments throughout the island. I also investigated potential prey availability for the cat using a total length of 242 km of transects conducted over two years.

In the cat diet, 76 prey items were found, this being the most diversified diet in the cat family. Seasonal patterns of 19 principal prey items were examined, which was compared with those of prey availability. Both prey availability and predation varied between seasons. The cat seasonally shifted principal prey items in relation to prey availability. The seasonal patterns of prey availability were chiefly influenced by seasonal migration of birds, by temperature variation for reptiles, by reproductive cycles for insects and by temperature variation and reproductive cycles for amphibians, respectively.

From the above results, I considered that the broad range of the food niche of the Iriomote cat probably resulted from making the best possible use of fauna on the small subtropical island. Furthermore, the cat adapts to the islandwide environment to change principal prey items and feeding patterns in relation to temporal variations of prey availability.

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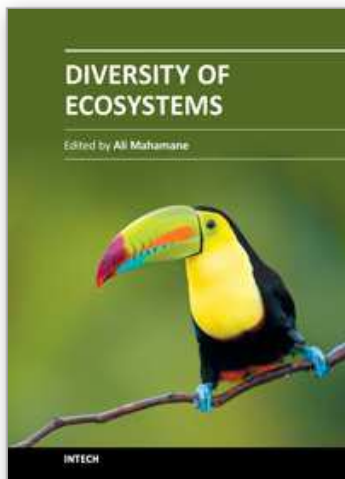
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The ecosystems present a great diversity worldwide and use various functionalities according to ecologic regions. In this new context of variability and climatic changes, these ecosystems undergo notable modifications amplified by domestic uses of which it was subjected to. Indeed the ecosystems render diverse services to humanity from their composition and structure but the tolerable levels are unknown. The preservation of these ecosystemic services needs a clear understanding of their complexity. The role of research is not only to characterise the ecosystems but also to clearly define the tolerable usage levels. Their characterisation proves to be important not only for the local populations that use it but also for the conservation of biodiversity. Hence, the measurement, management and protection of ecosystems need innovative and diverse methods. For all these reasons, the aim of this book is to bring out a general view on the function of ecosystems, modelling, sampling strategies, invading species, the response of organisms to modifications, the carbon dynamics, the mathematical models and theories that can be applied in diverse conditions.

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