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Ecological Flexibility of the Top Predator in an Island Ecosystem — The Iriomote Cat Changes Feeding Patterns in Relation to Prey Availability

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1. Introduction

It has long been recognized that islands contain fewer species than comparable pieces of mainland. It is also well-established that the number of species on islands decreases as island area declines. The most successfully established islands species will be those that combine low extinction rates with high immigration rates and where it is generally more difficult for animals without high dispersal ability at higher trophic levels to live on small islands [1]. In particular, carnivorous mammals at the top of terrestrial trophic chain find it most difficult to establish themselves on islands. Extreme examples are considerably large body sized and complete carnivorous species in the family Felidae.

In the region from south-east Asia to the Ryukyu Archipelago in southern Japan, there are thousands of islands of various sizes [2]. In this region, it is well-documented that biodiversity is particularly high among many taxa [3]. The biodiversity of mammalian fauna in this region was summarized in [4]. Among Felidae, seven species are distributed in this region, most of which are distributed only on the continental islands of Java, Sumatra, Borneo and Taiwan [4]. In particular, the leopard cat *Prionailurus bengalensis*, the most widespread species of East Asian wildcats, is an exception to this rule, occurring on several small islands as well as larger islands and the Asian continent [2, 4].

An example of an extreme case is the Iriomote cat *Prionailurus bengalensis iriomotensis* (Figure 1), which lives on the smallest island (284 km², Figure 2) of the Ryukyu Archipelago. The Iriomote cat is unique among the family Felidae, particularly in terms of its food habits [5-8]. Felidae are known as the most successfully evolved and developed predators specialized in feeding on mammalian prey [9, 10]. In contrast, the Iriomote cat preys upon a variety of animals

such as birds, reptiles, amphibians and insects, in addition to mammals [5-8]. The cat shows functional responses according to the availability of various alternative sources of prey [7]. Its principle prey changes seasonally, as the population density of potential prey items change. Moreover, regional differences in the cat's diet have also been reported [5, 11]. The Iriomote cat's diet is more diversified in habitats in which several vegetative environments are included and more similar in habitats where vegetative environments are uniform [11]. For terrestrial vertebrates on the island, distribution of each species is strongly influenced by various topographic and vegetative environmental factors, and distribution patterns vary depending on the type of species [12]. The cat diet changes flexibly in relation to seasonal and regional differences in prey availability [6, 7, 11]. Thus, it is likely that the preferred habitats for this species will also vary depending on seasons and regions.

Figure 1. An Iriomote cat *Prionailurus bengalensis iriomotensis* taken by photo-trap (Mammal Ecology Laboratory, University of the Ryukyus).

Most animals selectively use environments with a good quality of food patches [13, 14]. It is therefore likely that predators specializing in a particular food type that occurs in specific habitats will be habitat specialists, while predators feeding on a range of different food types will be habitat generalists. Variation in prey availability, i.e., the density and distribution of prey animals in an environment, leads to various predator responses [15-18]. For example, predators specialized in catching particular prey types often produce numerical responses to prey availability, so that the density of predators fluctuates alongside prey density [15-17]. In contrast, non-specialized predators often produce functional responses to prey availability, allowing these predators to switch prey types in relation to the availability of alternative resources [18].
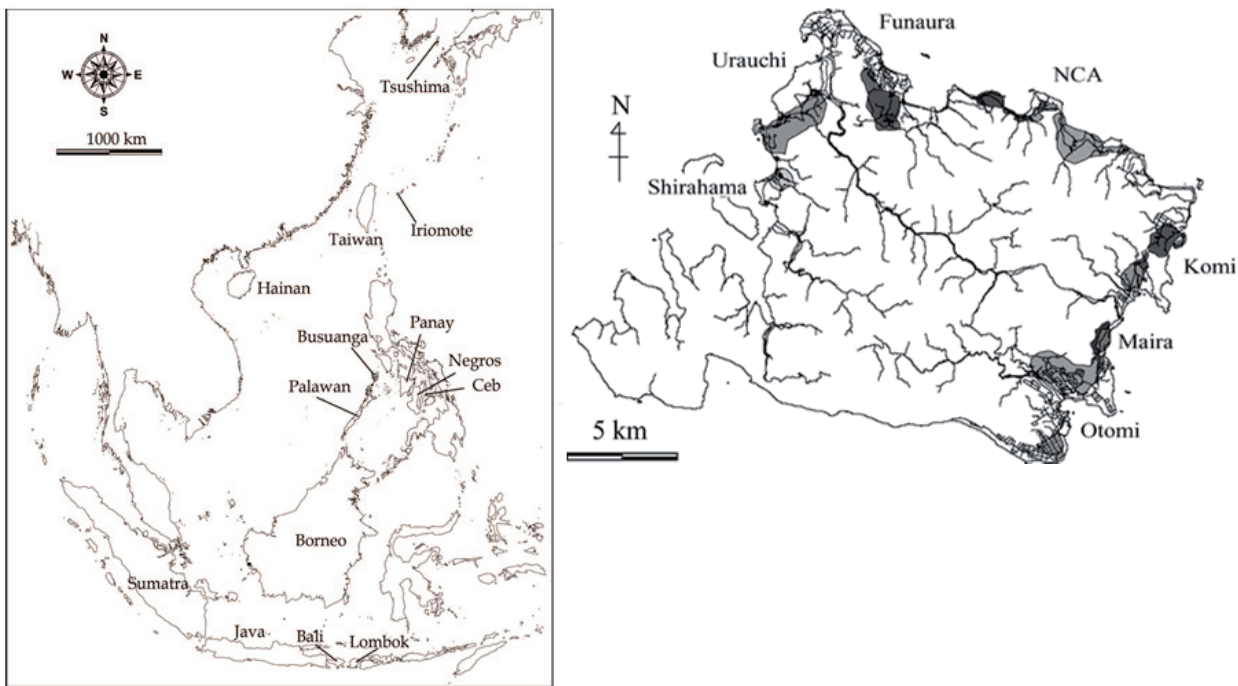
Figure 2. Map of East Asia showing islands with wild felid populations (left) according to [2] and Iriomote Island (Ryukyu Archipelago, Japan, right) showing the locations of seven study sites where radio-tracking were conducted. Each dark area shows the home range of each studied cat, estimated by the 75% harmonic mean method.

In the case of carnivores, food habits are well-documented at interspecific levels [e.g., 19, 20]. Each felid species takes only a few different mammal prey items, while other carnivores eat various food types. The Felidae family is highly specialized in preying on mammals in terms of having developed morphological and behavioural traits [21, 22]. Thus, Felidae are considered typical specialists in terms of food and habitat. Their hunting behaviour is specialized for preying on mammalian prey items [21]. Hence, they often show a numerical response to the density of a particular prey species [e.g., 18, 23].

The Iriomote cat, however, preys on various types of animals. Its diet flexibly changes in relation to seasonal and regional differences of prey availability [5-8; see also the results in the present study]. It is therefore likely that the Iriomote cat makes use of a variety of habitats and movement patterns in response to spatio-temporal variations in prey availability.

A comprehensive and accurate analysis of habitat use and selection, particularly when dealing with large home ranges and high habitat diversity across the geographic range of an animal, must encompass multiple spatial scales [24]. A number of studies have been conducted on the habitat use of the Iriomote cat, but these have only investigated the habitat selection on a univariate scale. Sakaguchi [5] emphasized that the Iriomote prefers to use lowlands (< 50 m above sea level) and avoids highlands, yet other factors potentially affecting their habitat use have not been investigated. In the present study, I will therefore quantify seasonal and regional variations in the habitat use and movement patterns of the Iriomote cat using detailed microhabitat measures at point locations and detailing the movement tracks used by the cat. From the results, I will then discuss their feeding strategies in terms of seasonal and regional

variations in prey availability. Furthermore, I will also present the possible reasons for the presence of this species on Iriomote Island.

Study site	Tracked period		Tracked days	No. of cats		No. of location
				Male	Female	
Otomi	Jul. 12. 1999	Jan. 19. 2001	79	2	1	545
Maira	Jun. 22. 2000	Dec. 25. 2001	33		2	238
Komi	Jun. 04. 1999	Dec. 25. 2001	254	1	2	1211
NCA	Nov. 20. 2001	Mar. 07. 2002	62	3		340
Funaura	Jun. 18. 2000	Feb. 15. 2001	69	1	1	457
Urauchi	Jun. 16. 2000	Aug. 28. 2000	13	1		66
Shirahama	Oct. 12. 1998	Nov. 06. 1999	155	1	1	1229
	Total		665	9	7	4086

Table 1. Summary of the radio-tracking survey in seven study sites on Iriomote Island.

2. Methods

2.1. Field survey

A field survey was conducted on Iriomote Island (24°20′N, 123°49′E) in the Ryukyu Archipelago, southern Japan (Figure 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. Most of the island is protected as a Japanese national park and contains good examples of the natural subtropical forests (see [7] for more information about the island).

Cats were trapped using box traps during the following six periods, May to July and October in 1999, January, June and November in 2000 and November in 2001. For the captures, box-traps equipped with radio-alarm systems were used. Captured cats were immediately brought to a laboratory and anesthetized by a professional veterinarian with an intramuscular injection of ketamine hydrochloride and xylazine (ketamine hydrochloride 10 mg/kg body weight). The animals were weighed and measured; their age-classes were estimated according to tooth wear, body weight and the delivery history of females [5, 25]. The cats were fitted with 40 g radio collars (Advanced Telemetry Systems Inc., Isanti, Minnesota, USA., or alternatively, collars hand-made in my laboratory).

I captured and radio-tracked a total of 16 adult cats (nine males and seven females) (Table 1) in seven separate study sites (Figure 2). All females were parous when captured, as per

evidence of previous suckling marks on their nipples [5, 25]. Each cat remained in the same study site throughout the study period.

The movements of radio-collared cats were continuously monitored for seven-to 10-day periods, either by car or on foot. Locations used by the cats were taken at intervals of at least one hour using the triangulation software Loas version 2.1 (Ecological Software Solutions) from two-to four-points, marked with a handheld global positioning system (GPS; model Garmin GPS II Plus) on roads or trails. I then determined the universal transverse mercator (UTM; zone 51, WGS84 Datum) coordinates of cats' locations using a geographic information system (GIS) and the IDRISI Kilimanjaro version 14 software (Clark Labs, Clark University, Worcester MA, USA).

2.2. Scat analysis

Seasonal and local variations on diet compositions among the study sites were examined via scat analysis [6-8]. Scats collected in each study site (Figure 2) were used for the analysis. Diet composition and principal prey items were compared among the sites. I calculated the frequency of occurrences for each prey taxon: mammals, birds, reptiles, amphibians, insects, crustaceans and others; this was done for each season and site.

2.3. Data analysis

2.3.1. Environmental measurements

I measured nine environmental variables related to topographic and vegetative characteristics within habitats to determine regional differences in environments among the study sites, as well as the most important factors that influenced the habitat preferences of the Iriomote cat. IDRISI [26], an integrated GIS and remote sensing software, was used for the analysis and display of digital geospatial information. IDRISI is a PC grid-based system that offers tools for researchers and scientists engaged in analysing earth system dynamics for effective and responsible decision making regarding environmental management [26].

Three topographic variables, elevation (El), slope (Sl) and the presence of drainage (Dr), were derived from digital elevation models (Digital Map 50 m Mesh Elevation, published by the Japan Geographical Survey Institute). The topographic data contained elevation values of one meter precision at the centre of grids by latitudinal 1.5 second and longitudinal 2.25 second; the ground length was roughly 50 m. The elevation data were geometrically-corrected in the UTM coordinate as a raster image showing a 50 m x 50 m grid. Sl and Dr were derived from the image using the Surface and Runoff operations of IDRISI. Elevation data generally contain depressions that hinder flow routing; these were removed and then I calculated the accumulation of rainfall units per pixel based on the elevation image. Drainage networks can produce a setting for discovering a threshold on the accumulation of runoff [26]. In the present study, the threshold (50 pixels) was able to detect permanent stable water and as such, streams and rivers in the study area were set. These three variables were subdivided into a 10 m x 10 m grid; images of El and Sl were averaged among neighbouring 5 x 5 pixels using the Filter
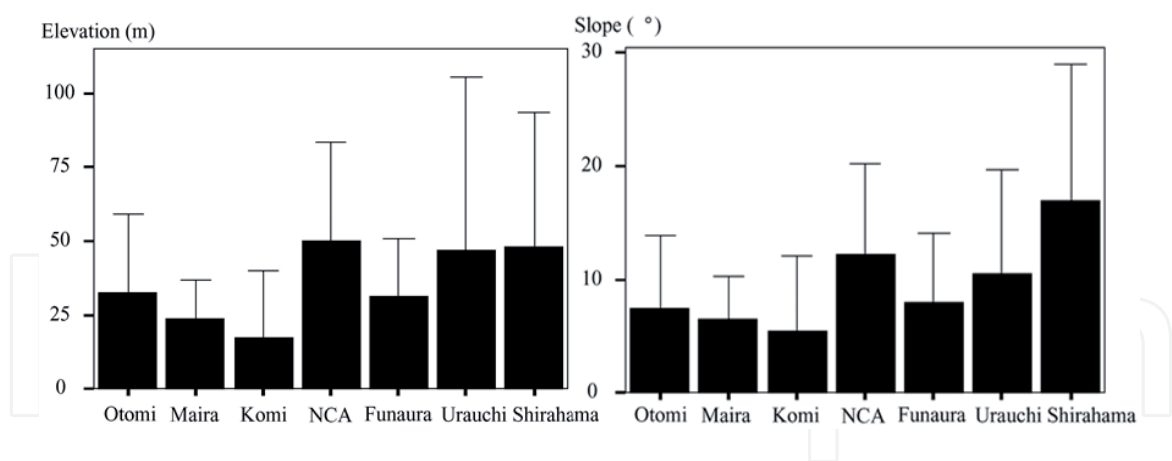
Figure 3. Mean values (+*SD*) of elevation and slope within the home ranges of the Iriomote cat in seven study sites.

operation of IDRISI. Thus, the distance (10 m) and planimetry (100 m²) accuracies in this study were limited by the grid size.

Vegetative variables were derived from a digital vegetation map [27], in which vegetation was classified as 29 categories within the study area. Many categories had a few patches, while some categories were very similar to others. I combined similar habitat types and broadly classified these in the following five categories; natural forest (NF) including subtropical, evergreen and broad-leaved forests; secondary forest (SF), including pine and artificial forests; coastal vegetation (CV), including mangroves and vegetation along shorelines; rice fields and swamps (RS); croplands and postures (CP). The vegetation classified into five categories was also geometrically-correlated in the same UTM coordinate as the raster image showing a 10 m x 10 m grid.

Since the Iriomote cat prefers to use the boundaries of forests and open lands [28, 29], I presumed that the prey availability of some species was high along forest edges, which influenced their food habits. Thus, a variable (FE: presence of forest edges) was derived from the 10 m x 10 m vegetation grid data using the Buffer operation of IDRISI. Forest edge was defined as zones within 50 m toward forests (NF and SF) from other vegetation types.

| Variable | Study site | | | | | | | | | |
	Otomi	Maira	Komi	NCA	Funaura	Urauchi	Shirahama	*G*	*d.f.*	*P*
DR	4.9	6.0	5.9	6.7	5.4	7.0	5.4	190	6	<0.0001
FE	18.9	38.6	12.1	12.5	14.2	9.3	14.6	3957	6	<0.0001

Table 2. Percentages of drainages (Dr) and forest edges (FE) in the home ranges of the Iriomote cat in each study site.

2.3.2. Habitat types in home ranges

I estimated the home range of each radio-collared cat from the coordinates of radio-tracking locations using home range estimation software Biotas version 1.0 (Ecological Software Solutions). The home range (HR) was defined as the area enclosed within the 75% utilization

contour with the harmonic mean [30]. I overlaid HRs of all radio-collared cats in each study site (Figure 2), in which environments concerning the above nine variables were compared among sites. The differences between the continuous variables (El and Sl, see Figure 3) among study sites were subjected to a Kruskal-Wallis test for those that were significantly different, while the seven other categorical variables (Table 2, Figure 4) were subjected to a likelihood-ratio test (*G*-test) for independence to test for differences.
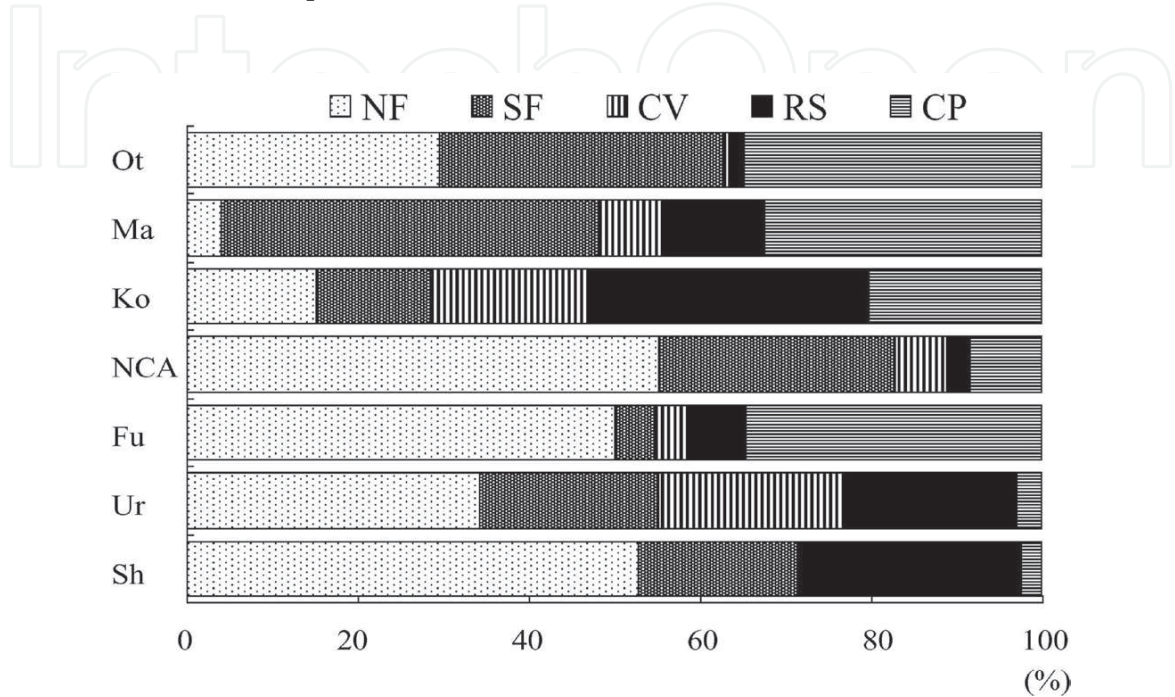
Figure 4. Compositions of vegetation types (NF: natural forest; SF: secondary forest; CV: coastal vegetation; RS: rice fields and swamps; CP: croplands and postures) within the home ranges of the Iriomote cat in seven study sites (Ot: Otomi; Ma: Maira; Ko: Komi; NCA: northern coastal area; Fu: Funaura; Ur: Urauchi; Sh: Shirahama).

### 2.3.3. Habitat preferences on cat location

To determine the most important topographic and vegetative characteristics influencing the animals' habitat use, I measured the above nine variables in areas within a 20 m radius of cat location sites fixed by radio-triangulation. To determine seasonal differences in habitat use, the location sites of six cats that were studied during all seasons (spring: April to June; summer: July to September; autumn: November to December; winter: January to March) were compared among seasons with regard to the above environmental characteristics.

To determine the habitat preference of radio-collared cats at each site, environmental characteristics in areas within a 20 m radius at cat location sites were compared with those at random locations. As many random locations as cat locations were chosen from HRs in each study site, using IDRISI. Mean values of El and Sl and the proportions of occurrence of other seven categorical variables were compared between areas within a 30 m radius at cat locations and random locations.

As a first step, these statistical differences were tested using a Mann-Whitney *U*-test for El and Sl, and using a *G*-test for others. Variables remaining after univariate testing were entered into

a logistic regression function following forward stepwise procedures. In the stepwise regression, a forward procedure using the likelihood-ratio statistic was employed, which included a variable in the model at P=0.05 level, which was removed if said variable's significance fell below 0.10. The percentage of sites classified correctly (radio tracking location vs. random location) and coefficients of determination (Nagelkerke R^2) determined by the final logistic models, which were indications of the influence of the logistic regression [31], were calculated in each regression.
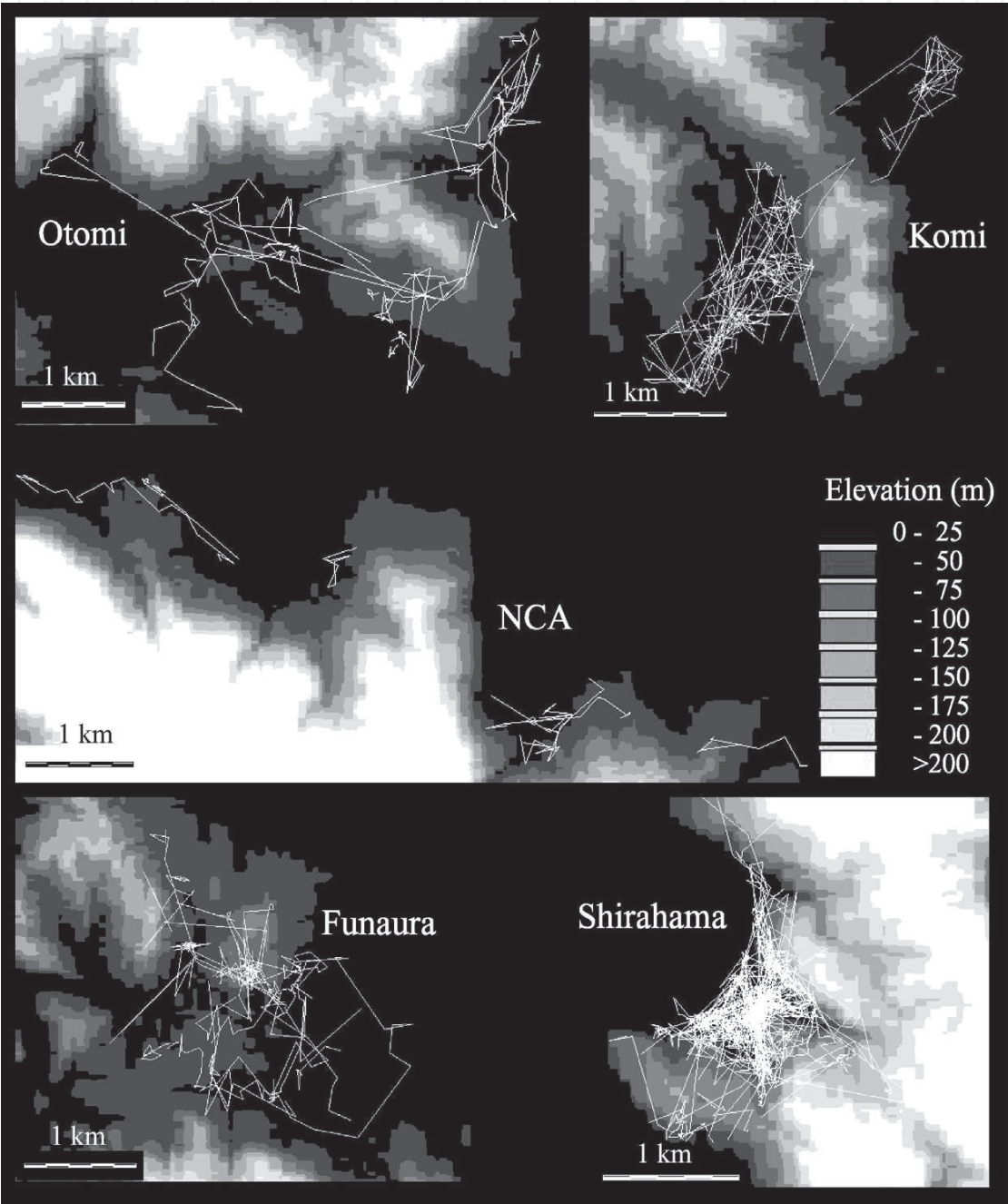
Figure 5. Movement tracks of the Iriomote cat in five study sites shown in digital elevation models. The movement tracks were based on continuous radio-tracking with locations taken every one-to two-hours.
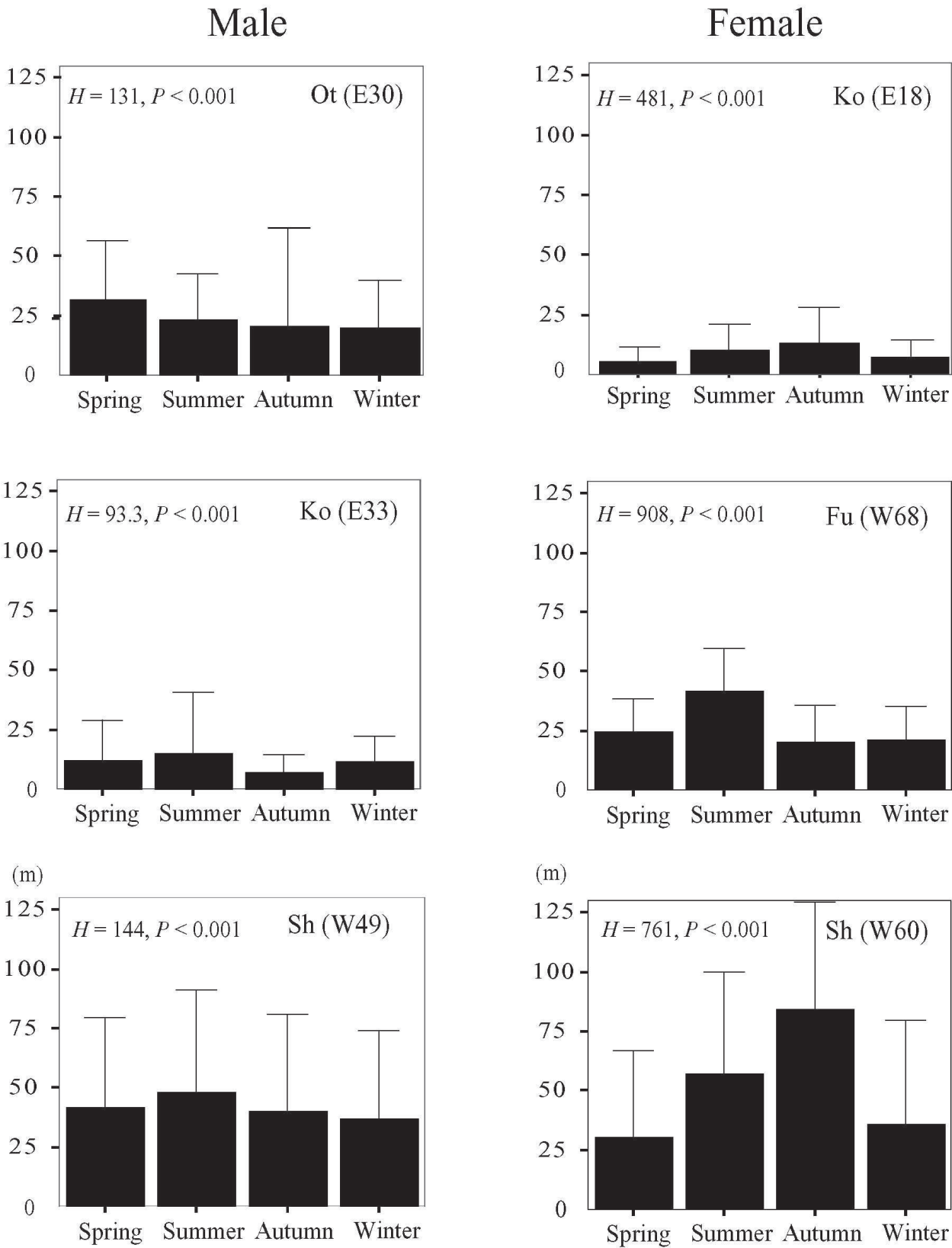
Figure 6. Seasonal elevation changes (mean+*SD*) of the radio-tracking locations of six Iriomote cats in four study sites (Ot: Otomi; Ko: Komi; Fu: Funaura; Sh: Shirahama).

2.3.4. Movement pattern

The movement tracks of radio-collared cats were derived from fulfilled radio-tracking locations (Figure 5) following the procedure in [32]. Data were collected at a rate of at least one hour intervals for more than 24 hours. However, if cats moved less than 100 m and rested at a fixed location, the data were accepted. The movement of each cat was characterized by calculating the daily movement distance (DMD: the sum of straight line distances between consecutive locations during 24-hour tracking sessions).

To determine the most important environmental characteristics influencing the animals' movement patterns, I measured the most important predictors derived from the above analyses of the movement tracks of radio-collared cats (MT) and compared them to the same variables for random tracks (RT), which were created by a Monte Carlo simulation using a random walk program in Biotas. A random walk is the most basic process for creating a spatially unpredictable data set. The process was operated with a point pattern using the same number of cat locations and straight line distance of MT during a consecutive tracking session without any specific direction. This process was able to "walk" in any direction within the home range. These statistical differences were tested using a Mann-Whitney *U*-test.

All statistical analyses were carried out using SPSS 11.5 for Windows (SPSS Inc., Illinois, USA). Statistical differences were accepted as significant when $P < 0.05$.

3. Results

3.1. Environmental characteristics among study sites

I measured nine environmental variables within the home ranges of the radio-collared cats and compared them among study sites (Figure 3). Continuous variables (El and Sl) were significantly different among study sites (one-way ANOVA: F=2389 for El and 3468 for Sl, *d.f.*=6, both $P < 0.0001$). Mean values of El were highest in Shirahama, followed by Urauchi and NCA. Those of Otomi, Maira, Funaura and Komi were relatively low. A similar pattern emerged for the case of slopes (Figure 3).

For categorical variables, percentages of drainages (Dr) and forest edges (FE) were also statistically different among sites ($P < 0.001$). Dr was the highest in Urauchi, followed by NCA, Maira and Komi. However, these values varied slightly, ranging from 4.9 to 7.0%, whereas FE varied largely depending on study sites. FE was particularly abundant in Maira, followed by Otomi. These values were lower in other sites.

Composition of vegetation type in each study site is illustrated in Figure 4 and differed significantly among sites (G=66826, *d.f.*=24, $P < 0.0001$). In Otomi, NCA, Funaura and Shirahama, vegetative environments were relatively uniform and mostly occupied by one or two vegetation types; NF and CP in Otomi, NF in NCA, NF and CP in Funaura and NF and SW in Shirahama. On the other hand, vegetative environments were more complex in Maira, Komi and Urauchi, as these were occupied by five vegetation types.
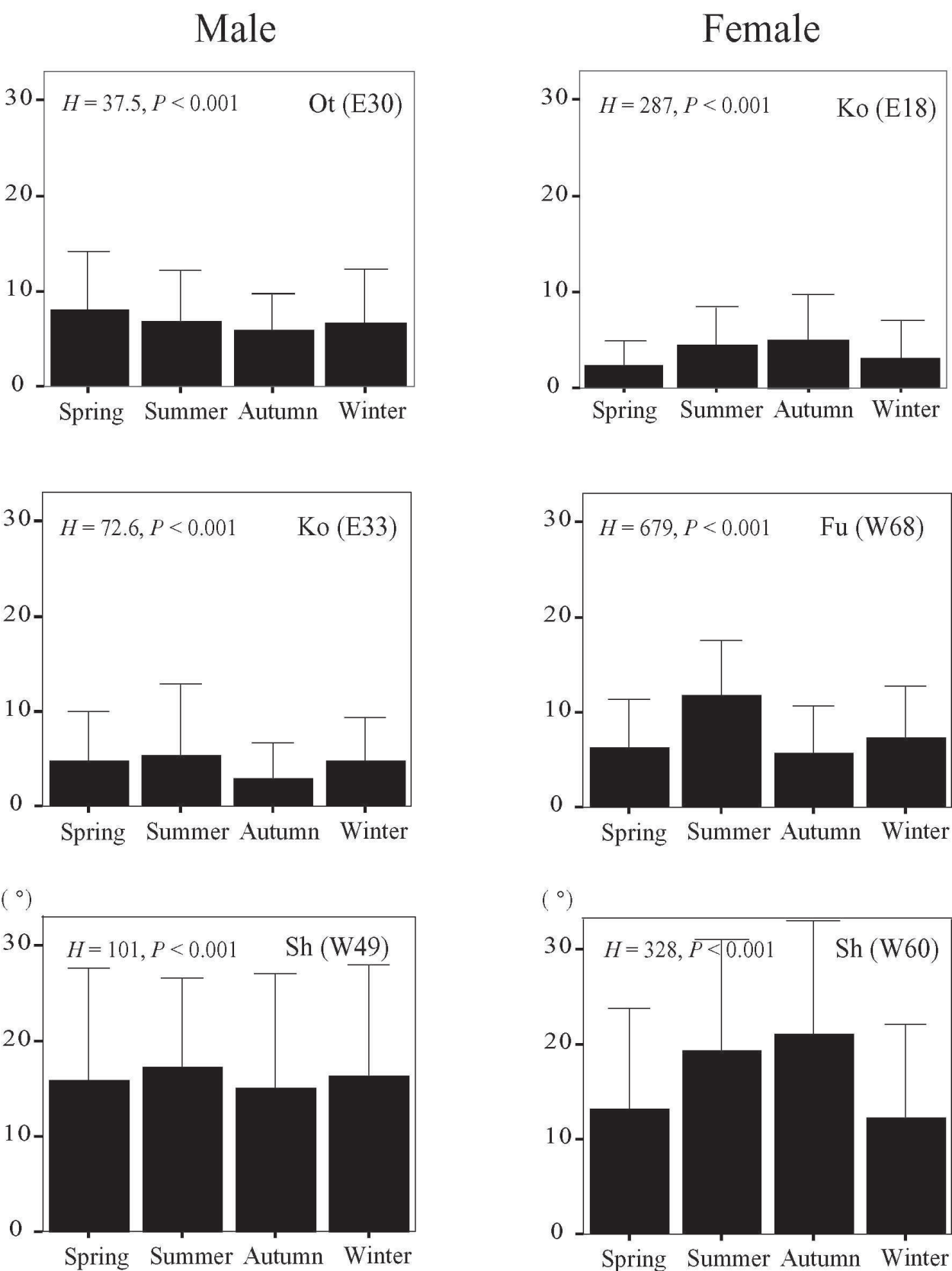
Figure 7. Seasonal slope change (mean+*SD*) of the radio-tracking locations of six Iriomote cats in four study sites (Ot: Otomi; Ko: Komi; Fu: Funaura; Sh: Shirahama).

3.2. Habitat use

3.2.1. Seasonal differences

I measured the seasonal differences for the major environmental characteristics of six radio-collared cats and the results are shown in Figures 6 to 8. For each cat, El and Sl at cat location sites significantly differed among seasons (Kruskal-Wallis test, $P < 0.001$: Figures 6 and 7). Vegetation types at cat locations were also significantly different among seasons for each cat (*G*-test, $P < 0.001$: Figure 8). Seasonal variations for both topographic variables in males were relatively low and varied comparatively more among females. In particular, a female cat in Shirahama used a lowland habitat during winter and spring, and used a higher habitat during summer and autumn (Figures 6 and 7). The vegetative compositions of used habitats varied relatively among females, more so than among males. Although the environments of cat location sites varied seasonally, environmental conditions essentially differed depending on study sites (Figure 8).

Study site	Logistic coefficient of covariate							Correct ratio (%)	Nagelkerke (R^2)	χ^2	P
	El	Sl	FE	SF	CV	RS	Intercept				
Otomi	-0.030		0.463		-2.073		1.13	83.3	0.366	21.9	0.0051
Maira	-0.035		0.821				0.65	85.0	0.339	19.2	0.0138
Komi	-0.040			0.745		1.488	0.50	78.9	0.405	42.7	<0.0001
NCA	-0.037						2.25	97.4	0.688	16.1	0.0414
Funaura	-0.023				-2.385	0.932	1.00	76.4	0.220	23.0	0.0033
Urauchi	-0.015						0.71	81.8	0.202	24.7	0.0017
Shirahama	-0.015	0.036		-1.483		1.041	0.75	83.0	0.502	18.1	0.0208

Table 3. Results of final logistic regression models regarding environmental variables (El: elevation; Sl: slope; FE: forest edges; SF: secondary forest; CV: coastal vegetation, rice fields and swamps) predicting radio-tracking locations vs. random locations in each study site.

3.2.2. Regional differences

I measured habitat variables at radio-tracking locations and random locations in each of the study sites; radio-tracking locations were significantly influenced by one to four environmental variables depending on study sites. These environmental variables were employed in forward stepwise procedures. By doing so, I obtained predictive models for cat location sites that were correctly classified at 76.4 to 97.4% (Table 3).

Elevation (El) was the only predictor selected in the models in all study sites, which indicates that the cat preferred lowland and avoided areas at higher altitudes in all study sites. In NCA and Urauchi, El was the only important predictor of cat locations. The cat preferred lowland, regardless of vegetative types. In four of five study sites (other than Funaura), El was the most important predictor of cat locations. Slope (Sl) was only chosen in the model in Shirahama that indicates the cat preferred sloping lands.
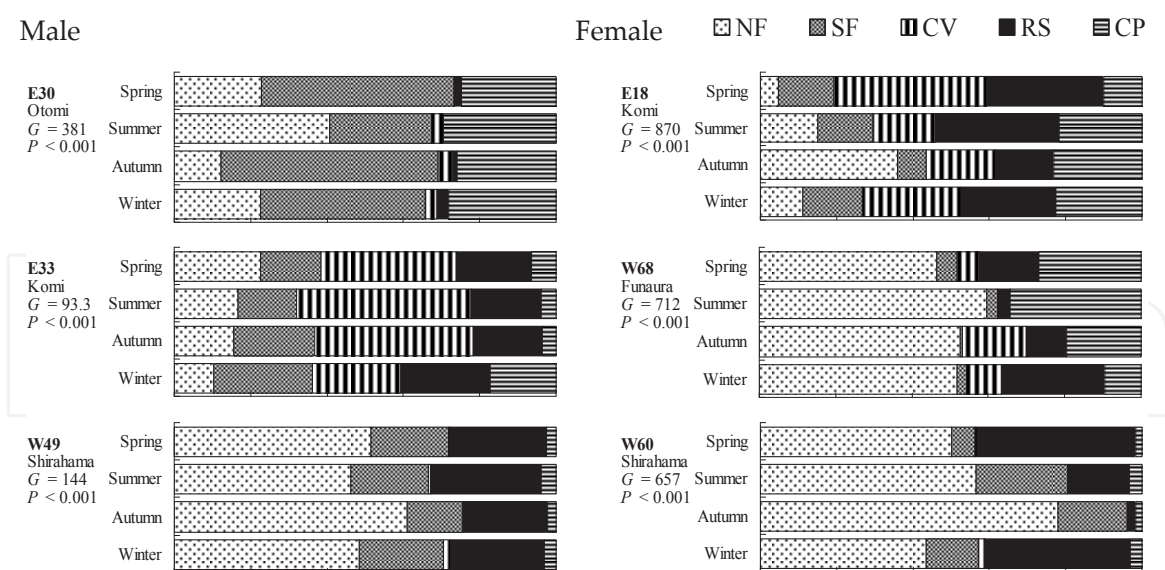
Figure 8. Seasonal vegetative changes for the radio-tracking locations of six Iriomote cats in four study sites (Ot: Oto-mi; Ko: Komi; Fu: Funaura; Sh: Shirahama).

Although vegetative variables also employed in the models of the five study sites, the influence varied depending on the sites. According to each predictive model, besides lowland areas, the cat preferred areas near forest edges in Maira and Otomi; preferred swamps in Komi, Funaura, and Shirahama; preferred secondary forests in Komi but it was avoided in Shirahama; the cat avoided coastal vegetation in Otomi and Funaura.

3.3. Movement pattern

I analysed the movement patterns of 11 cats (five males and six females, see Table 5). The total tracked time and distance were 3012 h and 359.6 km, respectively. DMD of each individual was calculated and is shown in Table 4. The DMD was slightly longer for males (3.36±1.04 km: x ±SD, N=5) than females (3.02±0.80 km, N=6), but lacked the same statistical support (Mann-Whitney U-test, U=14, P=0.93). Despite slight differences between the sexes, the DMD varied largely among study sites and was the longest in Funaura (4.61 km, N=2), followed by Otomi (3.06 km, N=1), Komi (3.04 km, N=2), Maira (3.03 km, N=2), NCA (2.80 km, N=2) and Shirahama (2.26 km, N=2), in this order. The DMD was positively related with home range size but lacked statistical supports (r=0.522, N=5, P=0.182, for males; r=0.575, N=6, P=0.116, for females).

Correlations of HR sizes and DMD against mean values of elevation and slopes in HR are shown in Figure 9. For male cats, DMD and HR were negatively closely related with mean values of slope, though not related with mean values of elevation. Meanwhile, there was not significant correlation between elevation and slope ($P > 0.05$).

The values of elevation and slope on movement tracks of the cats were compared with random tracks created by the random walk simulation (Table 5). Both variables were significantly lower on movement tracks than those on random tracks in all individuals (Mann-Whitney U-test, $P < 0.001$).

Study site	Cat name	Sex	Distance (m)	Track hour (h)	DMD (km)	HR (km^2)	El (m)	Sl (°)
Otomi	E30	M	32880	229	3.45	3.35	47.5	9.60
Maira	E36	F	9674	90	2.58	0.70	32.4	8.51
	E39	F	7750	53	3.48	0.49	15.6	5.66
Komi	E18	F	52196	458	2.73	0.66	28.4	8.07
	E32	F	20419	146	3.36	1.55	37.6	9.79
NCA	W86	M	2898	28	2.46	2.79	67.3	12.2
	W89	M	7936	61	3.14	2.63	66.3	12.3
Funaura	W61	M	10536	50	5.09	2.65	47.7	10.4
	W68	F	46518	270	4.13	1.75	24.9	6.92
Shirahama	W49	M	140572	1257	2.68	0.55	93.3	16.2
	W60	F	28253	369	1.84	0.76	75.9	16.0

Table 4. Movement characteristics of each individual Iriomote cat. DMD (daily movement distance), HR (home range size, estimated by 75% harmonic mean method), mean values of elevation (El) and slope (Sl) in HR.

Study site		N	Elevation (m: mean± SD)		U	P	Slope (°: mean± SD)		U	P
			Random	Movement			Random	Movement		
Otomi	E30	3036	67.9±49.0	25.5±21.8	2004615	<0.00001	12.6±8.72	6.53±5.17	2660791	<0.00001
Maira	E36	882	56.9±51.1	22.1±15.9	229749	<0.00001	12.0±8.50	6.44±4.94	209086	<0.00001
	E39	694	26.9±15.0	10.8±7.08	67732	<0.00001	7.44±6.04	4.82±3.13	166544	<0.00001
Komi	E18	4669	24.8±29.9	10.8±12.8	7670419	<0.00001	7.39±7.39	4.36±4.86	7626407	<0.00001
	E32	1788	37.1±37.4	9.41±13.9	553259	<0.00001	9.17±8.26	3.58±4.51	725216	<0.00001
NCA	W86	268	48.2±37.4	16.0±12.8	15260	<0.00001	10.2±6.17	5.08±3.65	18011	<0.00001
	W89	719	49.3±38.7	21.6±15.8	145632	<0.00001	11.2±6.92	7.80±5.28	183296	<0.00001
Funaura	W61	966	38.4±30.2	28.4±15.6	399199	<0.00001	10.1±7.72	6.54±4.52	311399	<0.00001
	W68	4191	44.2±46.1	28.7±22.1	6874122	<0.00001	9.33±7.11	8.68±6.55	8301671	0.00047
Shirahama	W49	12720	114 ±80.4	38.8±39.0	33984231	<0.00001	17.6±10.2	15.3±11.1	69846145	<0.00001
	W60	2503	107 ±62.1	43.2±42.9	1248043	<0.00001	19.5±10.7	16.4±12.4	2583308	<0.00001

Table 5. Elevation and slope ranges for the movement tracks of the Iriomote cat and for random tracks created by random walk simulations.

The movement tracks that were analysed are shown on the digital elevation model in Figure 5. When the cats went on long-distance walks, they avoided higher lands and selected flat routes to another area. In Otomi, Komi and Funaura, where flat lands largely occur, the movement tracks were distributed relatively uniform, whereas they were concentrated in flat lands in NCA and Shirahama, where these types of area are extremely limited.

3.4. Regional differences of the diet compositions

I analysed the contents of 805 scats collected within HRs of radio-collared cats: 70 scats in Otomi, 182 scats in Maira, 166 scats in Komi, 169 scats in NCA, 81 scats in Funaura, 45 scats in Urauchi and 92 scats in Shirahama. The result of the scat analysis is summarized in Figure 10.

Principal prey groups were different among sites; reptiles and birds in Otomi, reptiles and amphibians in Maira, birds and amphibians in Komi, birds and reptiles in NCA, birds, reptiles and amphibians in Funaura, mammals and birds in Urauchi, and birds in Shirahama, were most frequently preyed upon, respectively.

The cats' diets were relatively diversified with high frequencies of several prey groups in Otomi, Maira, Komi, NCA and Funaura; however, their diets were narrowed to mainly birds in Urauchi and Shirahama (Figure10).
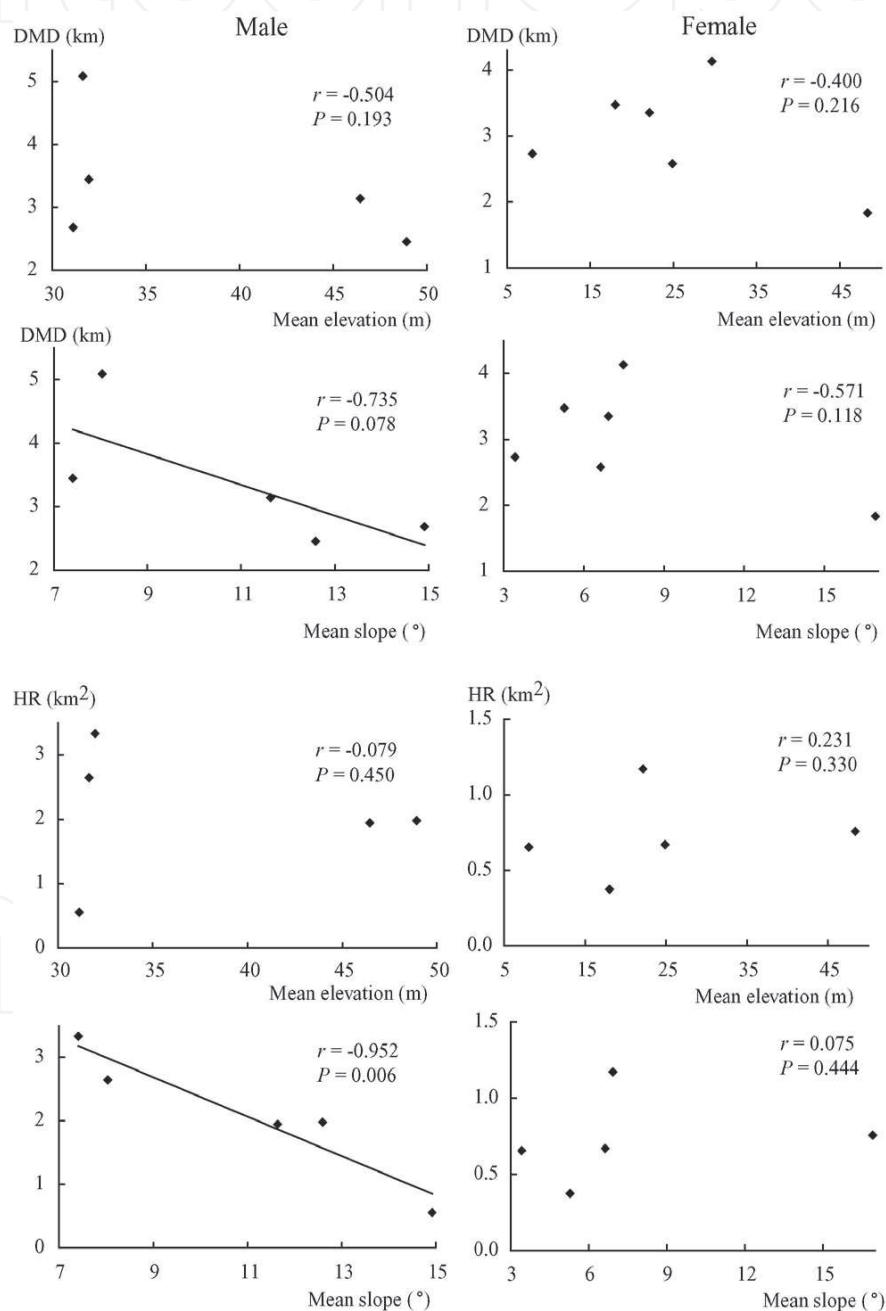
Figure 9. Correlations for daily movement distance (DMD) and home range size (HR) against mean values of elevation and slope in HRs.
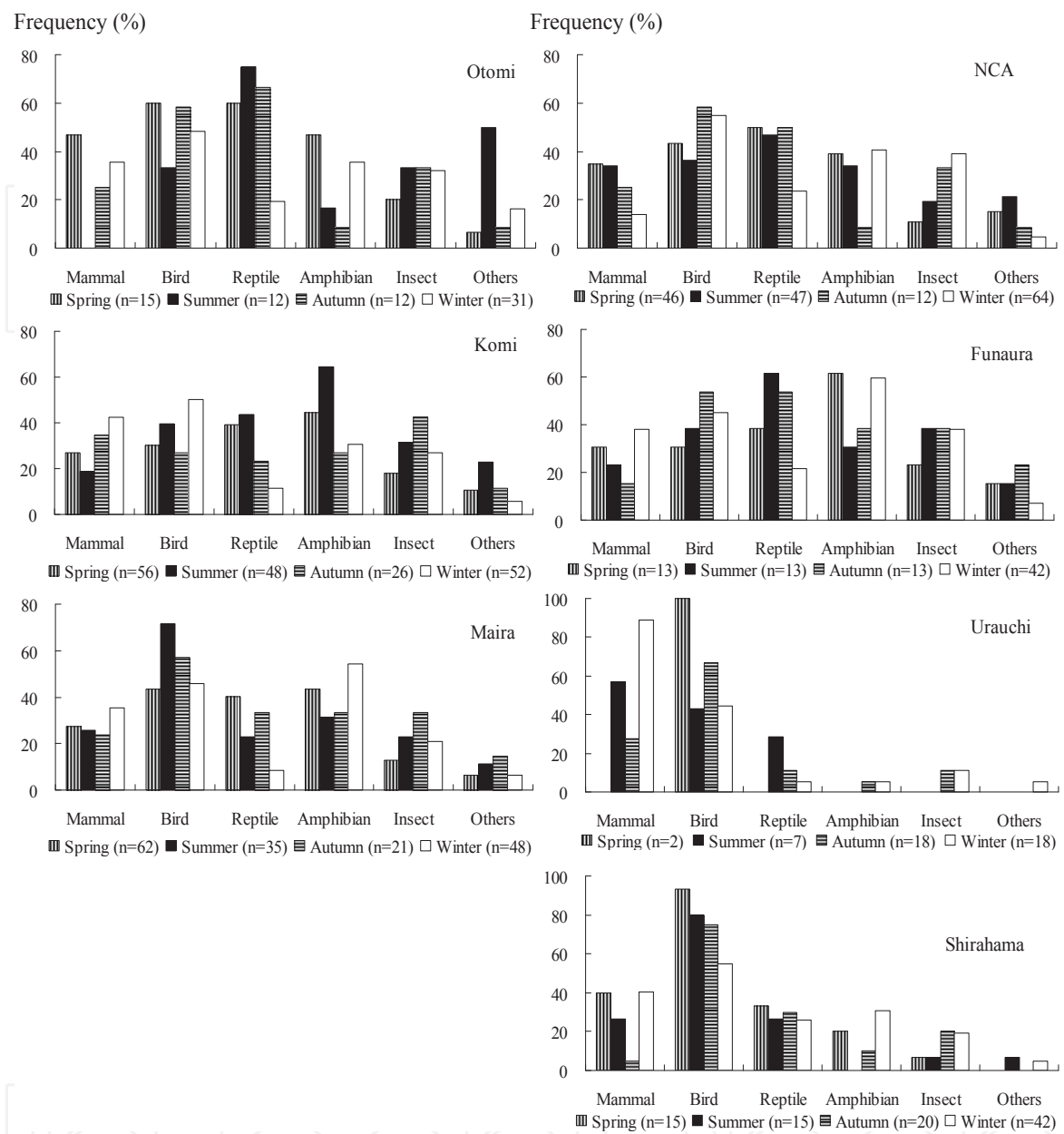
Figure 10. Seasonal and regional patterns of frequency occurrences (%) of prey groups found in 805 scats of the Irio-mote cat.

4. Discussion

4.1. Feeding strategy of the Iriomote cat

The results of the present study showed seasonal variance in the habitat use of the Iriomote cat. Several studies have shown seasonal effects on the movements and habitat use of felids at various scales [33-39]. Deep snow and severe winter weather were shown to restrict home

range size and habitat use [33, 36], as well as the movement patterns [37] of felids. Severe drought during the dry season was similarly shown to restrict movement patterns and the habitat use of some felids [38, 39]. In contrast with the study areas noted above, the climate of the Iriomote is extremely warm and humid throughout the year [40]. Thus, I believe that the seasonal variations in the habitat use of the Iriomote cat in the present study must be related to other factors.

In the present study, there were different levels of seasonal variations between sexes. Male cats had small seasonal variations; meanwhile, female cats used lowland habitats during winter and spring. The different seasonal patterns of habitat use between sexes may be connected to the gender differences in breeding cost. Female Iriomote cats breed and raise their young, while males are not involved in the raising of offspring [25, 41]. The breeding cycle of the cat is not seasonally restricted but a mating peak is recognized between February and April, and females deliver litters between April and June [41]. Accordingly, females need suitable habitats for breeding dens and for nursing their young [25, 41]. Three females were parous when they were captured. Thus, the females preferred and used lowland habitats during breeding; meanwhile, the habitat use of males were not as related to the breeding cycle.

Some studies of carnivores have suggested that suitable structures and sites for breeding dens are essential and limited within the animals' habitats. The distribution of breeding sites affects the habitat use of breeding females [42-45]. The breeding habitat use of Iberian lynxes *Lynx pardinus* is more strongly influenced by distribution of natal hollow trees than by prey availability and breeding females use old growth forests during breeding season [45]. It has also been reported that a female Iriomote cat used a hollow tree for breeding [46]. On Iriomote Island, hollow trees that are large enough in size for the breeding purposes of Iriomote cats were identified among several tree species, mostly *Quercus miyagii*, *Castanopsis sieboldii* and *Machilus thunbergii* (Watanabe, unpub. data); these only occurred in the NF vegetative category in the present study. Contrarily, females used lowland habitats with a low proportion of NF during the breeding season, suggesting that the availability of den sites was not the only important factor for the habitat use of breeding Iriomote cats. They may also use other structures or sites for breeding and as such, it is likely that an increase in food requirements for nursing influences the habitat use of female cats during breeding.

During nursing periods, females with young concentrated their movements near the den [47]. In the present study, the proportions of rice fields and swamps in home ranges of three females were higher than those of other vegetation types during the period. There were an abundance of birds and frogs in the habitat type during this period [7, 12, 40, 48]. Thus, the females intensively used the habitat to prey on abundant food sources for nursing their young.

In addition to seasonal differences, I observed significant alterations of habitat use among the Iriomote cats in different study sites. The habitat use of several widespread felids such as bobcats, lynxes, leopards and tigers have been studied in broad geographic ranges across several climatic zones [39]; the habitat use of each species varies somewhat according to region. This is likely the result of different climates, vegetation structures, or the principal prey species present in completely different environments. For leopard cats *Prionailurus bengalensis*, home range sizes differ among broad regions in Thailand [49-51], in Borneo [52], on Tsushima Island

[53] and on Iriomote [5, 47, 54]. On Iriomote, the vegetative and topographic conditions significantly differed among the study sites, which were only several kilometres away from one another. The narrow-regional differences among environments strongly affected the habitat use, movement pattern and diet of the Iriomote cats.

Bekoff et al. [19] assumed that prey distribution strongly affects the habitat use of predators. Generally, vegetation types have a larger effect on the prey distribution of carnivores [e.g., 55-60]. The distribution of principal prey items of the Iriomote cat is also chiefly determined by vegetative environment [7]. The habitat use of the Iriomote cat varied in relation to the regional differences of vegetative environments. Preferred vegetation types differed among regions. In addition, diet composition of the Iriomote cat differed between regions. Therefore, it is my conclusion that the cats changed their use of habitat in order to adapt to differences in prey distribution.

Although most environmental variables affected the habitat use of the Iriomote cat, only elevation showed strong and similar effects within all study sites. All radio-collared cats preferred using lowland habitats, mainly with elevation of less than 50 m, while they hardly used highlands with elevation more than 200 m. In particular, the effect of elevation was more highly correlated with the habitat use of the cats in rough terrains (NCA, Urauchi and Shirahama). Sometimes, elevation contributed as a factor for determining vegetation type and affected the mammalian fauna [e.g., 61-63]. However, this effect was the result of climatic changes that required a vertical interval of several thousand metres. In this study, a vertical interval of only 50 m limited the habitat use and movement of the Iriomote cat. Thus, the small difference of elevation did not cause climatic changes.

Sakaguchi [5] also reported that the Iriomote cat avoided highlands and suggested this to be due to scarce prey resources in the highlands. However, some principal prey items of the Iriomote cat such as reptiles and insects are more abundant in montane forests than in lowland habitats [7]. Thus, I believe that highlands encompass abundant prey items at a similar level of that found in lowland habitats and that prey availability is not a principal factor affecting the avoidance of highlands.

The habitat uses of predators are likely determined by how efficiently they seek and acquire food. This is because predators perform optimum feeding to maximize the efficiency of their energy acquirements [13]. In this regard, prey availability will be an important factor for habitat use. However, at the same time, if there is a high cost for acquiring food, the results will be inefficient. Schoener [64] assumed that energy acquirement efficiency fluctuated according to the relationship between food availability and the cost demanded for acquiring the food.

According to the feeding patterns of the Iriomote cat, the animal is considered to be an opportunistic mobile predator [5]; as such, the feeding cost can be represented as the movement cost expended when seeking prey. Several studies have suggested that movement cost is highly correlated with topographic condition, particularly slope [e.g. 65-67]. Walking speed decreases as the slope on walking routes increase [65] and the energy requirements of humans [66] and goats [67] during walking are much higher on a slope than on a flat surface. In the analysis results of movement tracks of the Iriomote cat, it was shown in all study sites that the animal

preferred to move on areas with a lower slope and lower elevation. Thus, I hypothesize that the avoidance of highland areas by the Iriomote cat is a consequence of increasing movement cost based on the optimal feeding strategy: the cat performs habitat use to maximize the energy acquirement efficiency, depending on the cost and benefit of feeding.

Several studies of felids have suggested that the availability of suitable foraging spots in an area is limited [9, 68] and that felids flexibly shift their home range uses in response to prey availability. In studies of bobcats *Lynx rufus*, it has been suggested that prey availability affects home range sizes and large home ranges were reported in habitats with limited prey resources [33]. A cat in an area with scarce prey resources needs to expand its home range to acquire essential hunting spots and prey. However, in the present study, home range sizes tended to contract as the slope in home range increased. If a cat enlarged the home range in hilly habitats where the movement cost was particularly high, the cat acquired more food, but spent much more energy seeking out said prey than it acquired energy.

Corbett [69] reported that feral cats with larger ranges were more likely to use mobile than stationary or ambush hunting strategies, while cats with smaller ranges used stationary or ambush strategies more often. In this study, the movements of cats in hilly areas (NCA and Shirahama) were concentrated in limited lowlands, whereas cats with wide lowland habitats (Otomi, Komi and Funaura) utilized their home ranges uniformly. Thus, it is likely that cats in areas with wide lowland habitats used mobile opportunistic hunting strategies, whereas cats in areas with hilly lands were more inclined to using stationary or ambush hunting strategies in order to raise their feeding efficiency. Consequently, the cats kept small home ranges in hilly areas with high movement cost.

4.2. Evolution of flexible habits of the Iriomote cat

Consumers can be roughly classified as either specialists with a narrow diet range and generalists with a broad diet range. Discussions on the general or specialist characteristics of predators are common in ecological literature [70]. The distribution of diet widths, i.e., the range of food types eaten by an animal, differs among the various types of consumers [71]. In the case of carnivores, the topic is well-documented at interspecific levels [e.g., 19, 20]. Each felid species takes only a few different prey items of mammals, while other carnivores eat various food types. The family Felidae is highly specialized for preying on mammals in terms of developing their morphological and behavioural traits [21, 22]. Thus, Felidae is considered a typical food specialist. These patterns appear to be in diets of *P. bengalensis* in that they feed mostly on mice and rats [39, 51, 72]. However, the Iriomote cat is also considered as being a generalist, because they prey on various types of animals besides mammals [6-8]. What then generalizes their diet?

From an ecological perspective, the diet width of an animal is chiefly determined by the functional limitations of their feeding ability, that is, how many food types in its habitat the animal can consume [71]. For instance, all felids cannot digest vegetable matter due to physiological limitations, though other carnivorous families such as some mustelids and all ursids can. In addition, solitary felids generally do not hunt animals bigger than themselves, due to their morphological and behavioural limitations; however, felid species do hunt in

groups, as lions and canids often do [22, 73]. In the diet of the Iriomote cat, *Sus scorfa* (wild pig), the largest animals on Iriomote Island, are hardly eaten. In addition, the Iriomote cat mostly preys on ground-living animals, while arboreal species are infrequently preyed upon [7]. This is likely due to limitations of their feeding ability. However, the Iriomote cat preys on nearly a hundred prey items belonging to wide range of taxonomical groups [7]. Thus, it is possible that they have developed a high feeding technique ability to prey on most types of ground-living animals.

The ancestral species of the Iriomote cat is common to other species of the genus *Prionailurus* [74], which presumably fed on small mammals living in continental environments, in which small mammals coexisted. As such, it is assumed that the Iriomote cat acquired a more diverse diet through further development of feeding functions to include a larger variety of animals.

To improve feeding ability, species are likely to develop morphological or behavioural functions for hunting [22, 73]. However, there is no notable morphological distinction between the Iriomote cat and other closely related species [74]. In addition, it has been reported that the hunting methods of the Iriomote cat have not been well-developed in relation to each of its prey types and is much more primitive than those of other small felids [75]. Furthermore, if a species develop its feeding patterns in relation to feeding on particular food types, they are likely to specialize in a narrow range of food types [76]. According to the dietary studies of *P. bengalensis* in other regions, in addition to mammals, they also eat birds, reptiles, amphibians and insects, though at low frequencies [2, 39, 51]. This suggests that the cats are also capable of feeding on these types of prey but that these prey types may be in the minority in environments, or are avoided by the cats. Therefore, it is likely that the Iriomote cat's well-developed hunting techniques are related to each of its various prey items.

It is more likely that regional differences of potential food resources influence diet widths of *P. bengalensis*. The insular fauna on Iriomote Island is characterized by a geological history that caused the absence of native non-volant small mammals [2], by the humid-subtropical climate that leads to the high abundance of floor-dwelling amphibians [40] and by the island's geographically suitable location for migrant birds that has led to the drastic seasonal changes in the abundance of and species composition of the avifauna [7]. Thus, small vertebrates are remarkably abundant on the island in spite of the scarcity of small mammalian fauna, which may be responsible for large differences in terms of the potential food resources of cats. However, these small vertebrates eaten by the Iriomote cat are commonly also eaten in other regions by other carnivores such as mustelids, viverrids and herpestids [21].

Absolute limits of diet widths are primarily defined by the cats' feeding abilities, but very few animals actually eat all of the different food types they are capable of consuming, thereby exhibiting their fundamental niche. This fundamental niche of a species in the absence of competitors from other species may be restricted to a realized niche in the presence of competitors [71]. In other regions where wild felid populations are present, several species of other carnivores coexist. Interspecific differences of morphological traits and diets among sympatric carnivore species have been reported as evidence for interspecific competition [e.g., 77-79]. Thus, it is likely that sympatric carnivore species compete with felids in the habitats, causing the diet widths of cats to be narrowed. There is no strong competitor for the cat on

Iriomote. Thus, its broad diet width range is possibly as evolutionary consequences of ecological release [e.g.70], due to the absence of competitors.

However, even when a competitor species is absent in a habitat, the species present will select food types with good quality in order to maximize reward intake [13, 80]. As such, its diet width will be narrower than its fundamental niche. At the one extreme, if the qualities of all food types are uniform and scarce, the predator may employ a generalist strategy that will tend to exhibit a broad diet, i.e., it will hunt and eat many of the food items that it comes into contact with. At the other extreme, if a food type with remarkably high quality is abundant in a habitat, the predator may employ a specialist strategy, have a narrow diet and ignore many of the prey items it comes across, preferring to search for a few specific types of food. In general, animals exhibit strategies ranging across a continuum between these two extremes in relation to food condition in their habitats [13, 80]. In addition, strategies will be more generalized when the food condition in a habitat is scarcer [14].

Food quality is generally determined by its energy content and its feeding efficiency, i.e., the ease of predation [13]. For small felids, food types with good quality are the most common prey item, for example, small terrestrial mammals such as rodents. However, these food types are scarce on Iriomote Island [2, 7]. If preferred food types with good qualities decreased in a habitat, the predator has two choices. First, it might maintain the selectivity of its diet and migrate to another suitable habitat; alternatively, it risks starving by staying in the same habitat. Second, the predator changes the selectivity of its diet and adapts to environmental changes by preying on other food types in the same habitat. In general, such flexible adaptations to environmental changes in the second choice are more difficult for specialized species [14]. Thus, it is likely that most felid species will opt for the first choice during food scarcity.

In general, island habitats are restricted in terms of food resources compared to those on continents. For animals living in continental habitats, if food conditions worsen, they may escape from starvation by migrating to other habitats with more resources. Indeed, it has been reported that the home ranges of *P. bengalensis* on the continent shifts seasonally, seeing them move to other habitats or enlarging their habitat in relation to prey distribution [51]. However, where animals in insular habitats are confined to the same habitats all the time, food conditions can vary. Thus, animals in insular habitats likely need some ecological flexibility in order to adapt to environmental variations. Consequently, it is likely that animals that have adapted to island habitats often have peculiar habits when compared to those found in continental sites [81]. For example, some insectivorous lizards adapted to insular environments have expanded their diets to include nectar, pollen and fruit [82]. To respond to flexibly as it concerns different food types, it may be better for feeding patterns to be unspecialized when it comes to particular food types. This is why the feeding behaviour of the Iriomote cat is more primitive and undeveloped when it comes to particular prey. It is also likely that the opportunistic feeding pattern of the Iriomote cat is suited for flexibly responding to variations in food availability.

Prionailurus bengalensis is considered a habitat generalist when compared to other small felids. While other species in the genus inhabit narrow habitat types [39], the habitat of *P. bengalensis* varies [2]. Such flexible habitat use may also play a role allowing the felid population to be present in such a small island. However, the results of the present study showed that the

Iriomote cat does not randomly forage for food in its habitat. They might instead have learned about food availability in relation to density and the distribution of prey from short-term experience, and as a result, adopt the most efficient feeding tactics. These flexible feeding patterns, as well as their diversified diets, are uncommon among Felidae. It is likely that the Iriomote cat optimizes most of habitat types on the island.

Therefore, the wide range of food habits of the Iriomote cat results significantly from the peculiar prey fauna of Iriomote Island [7, 40], the lack of competitors on the island [2] and the limited environment due to small island effects [7]. Moreover, I believe that the potential environmental adaptability, i.e., the fundamental niche of *P. bengalensis* appears only on Iriomote Island, which is therefore an essential area of study for the behavioural evolution of Felidae.

5. Conclusion

The leopard cat, *Prionailurus bengalensis*, is one of most widespread felids distributed through-out Asia. Although there are thousands of islands of various sizes within the range of distri-bution of the species, the species lives on several small islands as well as larger islands and the Asian continent. Iriomote Island (284 km^2) of the Ryukyu Archipelago in southern Japan, is the smallest habitat of this species, on which the Iriomote cat *Prionailurus bengalensis iriomo-tensis*, a subspecies of leopard cats, lives.

On Iriomote Island, there are no autochthonous terrestrial small mammals such as rodents, which are generally principal prey of wild felids. Thus, it is likely that there are unique characteristics in the biodiversity of the island and in the ecology of this particular cat as the top predator in the ecosystem. In the present study, I investigated the characteristics of the ecology of the Iriomote cat concerning food habits, habitat use and movement patterns.

I conducted radio-tracking surveys in seven study sites. I examined a location fixed by the radio-tracking in each study site in terms of the cats' habitat preferences related to nine topographic and vegetative variables by using a geographic information system (GIS). Then, the seasonal and regional patterns of the cats' habitat use were examined in terms of feeding patterns.

The results showed that all studied cats selectively used their habitats. Cat locations were significantly influenced by six to eight environmental variables, depending on the study sites. To determine the most important topographic and vegetative factors influencing their habitat use, I attempted a logistic regression function following a forward stepwise approach and with environmental determinants in each study site. Suitable habitats evaluated from logistic regression models more or less differed among study sites. For the comparison of habitat use among study sites, elevation was the only variable to significantly relate to the cats' habitat use in all study sites, while the effects of other variables varied depending on the particular study site. In the results of assessing the prey availability of the cat, distribution and the abundance of their principal prey species were chiefly influenced by vegetative environments.

The compositions of vegetative types differed among study sites. Thus, prey distribution and abundance also varied according to site, which potentially influenced the regional differences of suitable habitats.

The diet of the Iriomote cat was examined in terms of the seasonal and regional differences of each prey type by analysing 805 Iriomote cat scat contents collected from various environments in the seven study sites. The results showed that the cat seasonally shifted principal prey items as it concerned food availability. They preyed on items that were abundant in environments. In addition to seasonal differences, the diet compositions also differed among study sites. Thus, it is likely that the cat feeds on abundant prey types depending on the regional differences of environments, as well as seasonal differences.

To determine the most important topographic characteristics influencing Iriomote cats' movement patterns, I measured the elevation and slope of the movement tracks of radio-collared cats and compared them to the same variables on random tracks created by Monte Carlo simulations. The results showed that values of elevation and slope were significantly lower in all individuals on movement tracks than those on random tracks. This suggests that the cat moves from one area to another to avoiding steep paths.

Predators maximize the energy acquirement efficiencies that fluctuate within the relationship between prey abundance and the demanded cost for acquiring prey. For mobile predators such as the Iriomote cat, demanded costs for feeding are significantly determined by costs required for foraging. Thus, highly folded habitats will increase feeding costs. In addition, the cat may avoid areas at high elevation, irrespective of prey abundance.

From the above results, I have concluded that the broad range of food niches of the Iriomote cat likely resulted from making the best possible use of fauna on the small subtropical island. Furthermore, the cat has adapted to the island-wide environment in order to change its principal prey items and feeding patterns in relation to the spatial and temporal variations of food availability. Most small felids may potentially have such flexibility in their ecology. However, this might only be the case in the uniquely biodiverse environment of Iriomote Island.

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