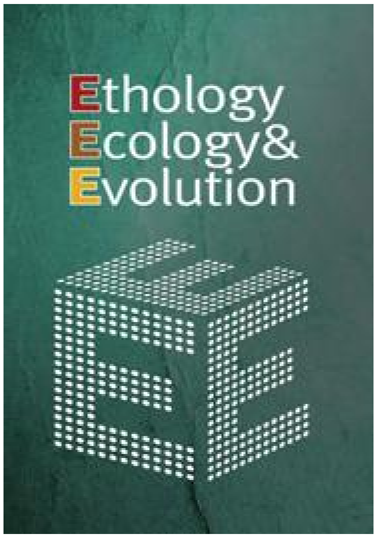

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Journal:	*Ethology Ecology & Evolution*
Manuscript ID	TEEE-2019-0073.R1
Manuscript Type:	Original Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Hisano, Masumi; Lakehead University, Faculty of Natural Resources Management Newman, Christopher; University of Oxford, Wildlife Conservation Research Unit, Department of Zoology
Keywords:	Adaptive foraging, Feeding ecology, Felidae, Hypercarnivory, Iriomote cat

Original Article

Adaptations to prey base in the hypercarnivorous leopard cat *Prionailurus bengalensis*

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ABSTRACT

Investigating biogeographical variations in diet composition can help understand the adaptability and generalism of species. Although the dietary adaptability of omnivorous mesocarnivores is well established, far less work has explored how more specialist hypercarnivores optimise their diets. By reviewing 11 studies of the leopard cat (*Prionailurus bengalensis*), we quantitatively examined how dietary composition varies over the wide range of biomes they occupy in Asia. Specifically, we contrasted the diet of the Iriomote Island sub-species (south-western Japan), where native rodents are absent, with that of the mainland. Leopard cat diet typically comprised mammals, birds, amphibians, reptiles, and invertebrates. In Iriomote Island, however, the low relative frequency of occurrence of small mammals (only introduced rats) was compensated by higher frequencies of reptiles and amphibians compared to the mainland. Consequently, trophic diversity and dietary niche breadth were higher for leopard cats in Iriomote Island than for the mainland. This shows that even hypercarnivorous species can use trophic plasticity to adapt to local prey availability. Given that rodent numbers often fluctuate substantially over time, the availability of alternative prey, such as herptiles, may be vital for the conservation of the leopard cat, and especially the critically endangered Iriomote cat. More generally, the trophic versatility of hypercarnivores must be considered when assessing their vulnerability to environmental change.

Keywords: Adaptive foraging; Feeding ecology; Felidae; Hypercarnivory; Iriomote cat

Introduction

The temporal and spatial distribution of trophic resources can influence life-history (Macdonald and Johnson 2015). Feeding behaviour is, therefore, important for understanding animal ecology (Pineda-Munoz & Alroy 2014). Animals may be primarily herbivorous, omnivorous or carnivorous, but vary in the extent to which they are specialists or generalists within these categories according to their trophic range and the diversity of food types they consume (Virgós et al. 1999; Pineda-Munoz & Alroy 2014). Specialists usually exhibit greater vulnerability to environmental perturbation, while generalists are more versatile and resilient (Clavel et al. 2011).

Dietary adaptability has been well established among members of the Carnivora that have a mesocarnivorous / omnivorous diet (i.e., consuming 50–70% vertebrate prey, with the balance made up of non-vertebrate foods; Van Valkenburgh 2007) (e.g., Virgós et al. 1999; Zhou et al. 2011; Díaz-Ruiz et al. 2013), yet far less work has examined how more specialist hypercarnivores (consuming >70% vertebrate flesh; Van Valkenburgh 2007) may optimise their diets in relation to regional prey availability. Clearly, such adaptability is crucial for obligate carnivores to transcend biomes, resulting in extensive biogeographical distributions. In contrast, predators specialising on a limited, or fixed, variety of key prey species will always be restricted by the distribution of their prey base. In conservation terms, the (in-)flexibility of a carnivore's diet determines their specific vulnerability to prey depletion (Wolf & Ripple 2016), where more versatile carnivores will be more resilient. The implications of a restricted diet for the conservation of many hypercarnivorous Carnivora, must therefore not be overlooked (Kitchener et al. 2017), because many are 'At Risk', notably felids (of 41 felid species from 14 genera,: four species are Endangered (10% of all felid species),: 12 species are Vulnerable (29%), and nine species are Near Threatened: (22%); https://www.iucnredlist.org). Among these, small felids are particularly understudied (Macdonald et al. 2015) due to their lower detectability and approachability (Anile & Devillard 2016).

Systematic investigations of geographical variations in small felid (*Felis* spp.) diet have identified dietary switching. For instance, consumption of rodents by wildcats (*F. sylvestris*) in Europe was significantly reduced in locations where rabbits (*Oryctolagus cuniculus*) were present (Lozano et al. 2006; Apostolico et al. 2015); similarly, the consumption of rabbits by feral cats (*F. catus*) in Australia decreased when consumption of rodents and small dasyurids increased (Doherty et al. 2015). In comparison, assessments of the diets of small felids in Asia are lacking and require further research (Kitchener et al. 2017). Particularly challenging is that small hypercarnivorous felids are especially sensitive to changes in their natural environments, and tend not to be able to exploit the novel niches provided by urbanisation as effectively as many other mesocarnivores (Lewis et al. 2015).

To address this knowledge gap, we focus here on the leopard cat [*Prionailurus bengalensis*; head-body length 500 to 640 mm; weight 2,000 to 3,500 g (based on adults in Thailand; Grassman et al. 2005)], for which sufficient reports exist to support a systematic review (a quantitative assessment) of its dietary flexibility. Leopard cats are common throughout their range and categorised as ‘Least Concern’ in the IUCN Red List of Threatened Species (Ross et al. 2015), although they are locally threatened by poaching and the exotic pet trade (Lau et al. 2010). Leopard cat population status is, however, strongly dependent on habitat quality, and land-use changes threaten leopard cat populations in many areas [e.g., south-western India, Tsuhima Island (western Japan); Ross et al. 2015]. The leopard cat’s diet is comprised mainly by rodents across its range, supplemented by other vertebrates and invertebrates (Watanabe 2009).

The Critically Endangered (IUCN) Iriomote Island subspecies (*P. b. iriomotensis*) in south-western Japan (hereafter Iriomote cat) provides a particularly informative contrast because native rodents are absent from this island (Izawa 2005; Watanabe 2009), although introduced black rats (*Rattus rattus*) are present in low abundance; no house mice (*Mus musculus*) have been introduced (Okinawa Prefecture 2018). Furthermore, there are no intra-guild mammalian predators on Iriomote, except for feral cats, although these are currently restricted to urban areas where they feed predominantly on garbage (Watanabe et al. 2003); given that the presence of sympatric carnivores can influence dietary niche breadth and composition of small cats through competition, modifying their distribution and activity patterns (Drouilly et al. 2018). This unique prey situation in Iriomote provides a particularly stringent test of how leopard cats may adapt their diets according to prey diversity (*cf.* Lozano et al. 2006; Dohety et al. 2015), with implications for their population dynamics (e.g., Pavey et al. 2008).

We base our systematic review on the most contemporary literature, including peer-reviewed articles and regional status reports, which we use to i) quantitatively assess the trophic breadth and adaptability of leopard cats; and ii) how the specific depauperate prey-base in Iriomote might be accommodated by switching to alternative prey types (e.g., Nakanishi & Izawa 2016). We predict that trophic range of Iriomote cats will be broader than mainland populations due to the absence of native rodents on Iriomote. We then use inferences drawn from this systematic review to evaluate how the trophic plasticity and adaptive potential of small hypercanivorous cats may affect their success generally.

Materials and methods

Literature and data compilation

We searched for studies quantifying leopard cat diet composition written in English, Japanese, and Chinese up until March 2018, using *Google Scholar* (https://scholar.google.com) and *ISI Web of Science* (http://apps.webofknowledge.com). We used various combinations of keywords: in English, "leopard cat", "*Prionailurus bengalensis*", "*Felis bengalensis*" (a synonym), "diet", "food"; in Japanese, "Iriomote-yamaneko" (the subspecies in Iriomote), "Tsuhima-yamaneko" (the subspecies in Tsushima Island; *P. b. euptilurus*), and "shokusei" (diet); and in Chinese, "bàomāo" (leopard cat), "shíxìng" (diet), and "shíwù" (food).

We compiled leopard cat diet data from reviewed literature that met the following criteria. Studies must have: (i) examined >20 scats or stomach contents (Doherty et al. 2015) with sufficient detail to re-calculate the number of items belonging to each food category that occurred, and relative frequency of occurrence [RFO (%) = the number of occurrences of each food category / the total number of food categories occurring × 100] of different food categories against the total number of all food items (Zhou et al. 2011; Hisano et al. 2019); (ii) presented all recognisable prey taxa present in faeces / stomachs (i.e., those reports focusing only on the presence of a single taxa, such as frogs, without describing other prey categories, were excluded); and (iii) covered at least one entire year (Zhou et al. 2011; Doherty et al. 2015), to ensure that both dry and rainy (or, fire and non-fire) seasons in tropical/sub-tropical areas, or all four seasons in temperate/sub-alpine areas (Hisano et al. 2019) were included.

To compile dietary data, we divided prey types consumed into seven main categories based on Doherty et al. (2015): 'small mammals' (<500 g: rodents, insectivores, pikas; *Rattus* *norvegicus* was the largest rodent recorded in the studies reviewed), 'other mammals' (i.e., medium and larger mammals >500g including rabbits/hares, flying foxes, and ungulates), 'birds', 'reptiles', 'amphibians', 'fishes', and 'invertebrates'. We then extracted, or re-calculated, RFO according to the food item categories represented in each study used (following Zhou et al. 2011; Hisano et al. 2019). We also calculated Shannon's diversity index ($H' = \sum_{i=1}^{S} P_i ln P_i$) and Levins' niche breadth index ($B = {}^{1}/\sum_{i=1}^{S} P^2{}_i$) based on RFO values to quantify trophic diversity.

Statistical analysis

After standardising for sampling method inconsistencies (see *Supplementary Information*), we conducted Friedman's test to examine whether diet composition (RFO) differed overall between all the study sites. In a second step we then also compared diet between mainland sites only, excluding Iriomote. We applied Mann-Witney *U* tests to examine whether Shannon's and Levins' indices varied between the mainland and the population living on Iriomote. We also performed a permutational multivariate analysis of variance (PERMANOVA; see Hisano et al. 2016, 2019) to assess the extent to which diet composition (RFO) differed between 'Iriomote Island' *versus* 'mainland (i.e., all other study areas)'. If overall dissimilarity in dietary composition was found between the geographical categories, Chi-squared tests were applied to compare RFO of each food category following the methodology of previous studies (Hisano et al. 2019). Finally, we performed a principal component analysis (PCA), based on RFO, to visualise the spatial ordination of the seven food categories (see above) and geographical locations.

We also performed additional tests, described in *Supplementary Information*, to examine whether the source of dietary data (stomach contents vs faeces), or the role of carrion in some study sites had any bearing on our conclusions.

Results

A total of 24 studies was reviewed (Table S1) for which data quality in 11 was sufficient to support analysis (Table 1; Fig. 1). Overall, leopard cats ate a similar diet composition across mainland regions (Friedman test: $P = 0.863$); however, including Iriomote study data substantially increased diet dissimilarity (Friedman test: $P = 0.124$) (Table 1). Specifically contrasting Iriomote cat to the mainland leopard cat studies clarified this significant dissimilarity (PERMANOVA: $F = 15.70$, $R^2 = 0.64$, $P = 0.011$). This arose from differences in the RFO of specific food categories between Iriomote and the mainland. The RFO of reptiles [e.g., lizards, skinks; $\chi^2 = 9.73$, $P = 0.002$) and amphibians (frogs; $\chi^2 = 10.17$, $P = 0.001$); Fig. 2], was significantly greater in Iriomote (with the result for birds being marginally below significance (Chi-squared test: $\chi^2 = 2.63$, $P = 0.105$), compensating for the significantly lower reliance on small mammals (Chi-squared test: $\chi^2 = 59.6$, $P < 0.001$), due to the absence of native rodents. Our results were robust as alternative approaches (G-test, Mann-Whitney's *U* test) also produced the same results (see *Supplementary Information*). This resulted in the Iriomote cat exhibiting greater trophic diversity (Mann-Whitney *U* test: $P = 0.006$) and niche breadth ($P = 0.006$) indices than the mainland dataset (Table 1).

The first two axes of PCA based on RFO explained 78.57 % (PC1: 53.37 %, PC2: 25.20 %) of the overall variation in leopard cat food composition across studies (Fig. 3; Table S2). The first PCA factor, PC1 represented a greater frequency of amphibians (PC1 = 0.48) and birds (0.44) in the diet, with a lower frequency of small mammals (-0.50). In Iriomote, the positive loading on PC1 corroborated that cats ate a higher RFO of amphibians and birds; in contrast, the negative PC1 loading showed that in the Philippines, India, Korea, and Borneo consumed a higher RFO of small mammals (Fig. 3). PC2 loadings indicated a greater frequency of other mammals (PC2 = 0.60) and fishes (0.38), and a lower frequency of invertebrates (-0.55) and reptiles (-0.39). Leopard cats in India and Iriomote “Ir4” consumed ‘other mammals’ and fishes with higher frequency (positive PC2); while those in Iriomote “Ir1” and Singapore ate reptiles and invertebrates with higher frequency (negative PC2; Fig. 3; Table S2).

We detected no substantial effect of data source (stomachs vs faces) or the role of carrion influencing our findings (see *Supplementary Information*).

Discussion

This is the first study to quantitatively examine the adaptability of leopard cat diet. We found that, despite being an obligate hypercarnivore, the leopard cat still exhibited wide trophic diversity, particularly through its capability to adapt to the different food types available on Iriomote Island. This resulted in a Shannon index of 1.07 (range, 0.69–1.66) and a Levins index of 2.49 (range, 1.49–4.74; Table 1). These indices are very comparable to those for the much more generalist and omnivorous Carnivora genus *Martes* range, respectively 1.38–2.08 and 2.07–3.69, (Zhou et al. 2011). This trophic plasticity, and the leopard cats’ capacity to modify the RFO of key food categories comprising its diet, likely contributes to its occupation of a wide geographic range throughout Asia (Ross et al. 2015) over a diverse range of habitats (Mohamed et al. 2016).

As a particular case in point, we found that in the special instance of Iriomote Island, in the absence of native rodents, leopard (Iriomote) cats compensated by making greater use of herptiles (Nakanishi & Izawa 2016) and marginally birds, especially flightless rails (Rallidae). In addition, they also scavenged wild boar (*Sus scrofa*), and utilised novel food sources, such as Ryukyu flying foxes (*Pteropus dasymallus*; a species of Chiropteran endemic to the Ryukyu Islands, south-western Japan). These medium-/large- carrion species were reported by both the "Ir4" (Nakanishi & Izawa 2016) and "Ir1-3" (Sakaguchi and Ono 1994; Watanabe et al. 2003; Watanabe 2012) studies. Consequently, these studies produced Shannon's and Levin's indices of 1.66 and 4.74, much broader than the 0.99 and 2.17 typifying mainland sites. This shows that although leopard cats tend not to predate on herptiles or birds substantially under normal circumstances of prey availability (RFO <10%; Fig. 2), they exhibit dietary switching (as seen in omnivorous carnivores — Zhou et al. 2011; Coogan et al. 2018; Hisano et al. 2019) to utilise unusual prey to a greater extent in the absence of their favoured food categories. On Iriomote, they exploited amphibians, reptiles, and birds at respectively 21.2%, 21.9%, and 23.0% (RFO) of their total diet, versus just 2.4%, 4.5%, and 12.3% elsewhere. Indeed, even within Iriomote, the marked spread of the four studies on Axis PC2 of the ordination (Fig. 3), suggests that, even on a small island, there may still be substantial flexibility in diet. We were able to discount that this 'within-Iriomote' variation could have arisen simply from sampling methodology inconsistency across our study sample set (i.e., Nakanishi & Izawa (2016) analysed stomach contents vs the other 10 studies that examined faeces, where faecal analysis may underestimate certain prey items due to differences in the proportion of indigestible parts (Klare et al. 2011)) by excluding Nakanishi's & Izawa's (2016) study, which still gave similar results (see *Supplementary Information*).

Across study sites, leopard cats also adapted their diets to best utilise suitable local prey availability within community compositions. For example, in India the leopard cat consumes a variety of ungulate carrion (16.7% RFO vs 0-5% elsewhere), including gorals (*Naemorhedus goral*), cattle (*Boss* spp.), and dzos (*B. grunniens* × *B. primigenius*) (Bashir et al. 2014). This demonstrates that they can meet their dietary needs, even with much less reliance on actively hunting. Moreover, in India their diet included the novel consumption of locally abundant pikas (*Ochotona* spp.; RFO >20%) in addition to other rodents (Bashir et al. 2014). Consuming these atypical food sources enables leopard cats to adapt to habitats above 3000 m (asl) in the Himalayas (Table 1). The substantial consumption of carrion in India versus hunting living prey did not influence our conclusion, however, as evidenced by excluding scavenged items (ungulates) from the PERMANOVA, which yielded consistently similar results (see *Supplementary Information*).

Intra-guild prey competition can also constrain the prey types consumed by carnivores (Tatara & Doi 1994; May et al. 2008). Across most of its range, the leopard cat competes within diverse carnivore communities (e.g., Cheyne & Macdonald 2011), where we confirmed from the literature that all mainland study areas included at least two other wild sympatric carnivore species (potential competitors). On Iriomote Island the feral cat was the only other mammalian predator present (Motokawa 2000; Watanabe et al. 2003); however these feral cats typically inhabit human residential areas and rely heavily on refuse [>85% absolute frequency of occurrence (FO: the number of each food item occurred / the total number of faeces examined × 100)] with animal prey FO <10%. This lack of natural competitors in their natural habitat potentially enables Iriomote cats to solely occupy the top mammalian predator trophic niche on the island. However, feral cat populations are expanding in Iriomote, risking dietary niche overlap and competition for resources with Iriomote cats. Future studies should examine in more detail how interactions with sympatric carnivores can affect leopard cat diet.

Given the trophic adaptability of leopard cats, we infer that they will not be especially vulnerable to changes in prey base arising from changing seasonality (Pucek et al. 1993), or climate change (Kausrud et al. 2008). They may, however, be vulnerable to intensified land-use (Blaum et al. 2007) if this substantially reduces gross prey abundance across multiple categories per population (e.g., Mohamed et al. 2016). In such human-altered environments, the conservation of herptiles (e.g., Renken et al. 2004) may benefit leopard cats, while the protection of forested habitat is important for conserving their denning sites (Mohamed et al. 2016).

Our broad conclusion is that non-specialised hypercarnivores, especially felids, may utilise prey switching to succeed across various prey communities in different regions, mirroring the trophic adaptability of omnivorous generalists (Zhou et al. 2011; Hisano et al. 2019).

Acknowledgements

We are grateful to Xingwen Loy for his courtesy to provide the graphic art of the leopard cat. We also thank Dr. Shota Deguchi for his insights into the manuscript.

Funding: This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Conflict of Interest: The authors declare that there is no conflict of interest.

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Figure legends

Fig. 1. Geographical locations of leopard cat dietary studies used in the meta-analysis. **Ir** (Iriomote Island, Japan), **Si** (Singapore), **Ba** (Bangladesh), **Ph** (Philippines), **Bo** (Borneo, Malaysia), **In** (India), **Ko** (Korea), **Ts** (Tsushima Island, Japan). Leopard cat distribution range is shaded on the map (based on Ross et al. 2015). The leopard cat illustration was provided courtesy of Xingwen Loy.

Fig. 2. Comparing food composition of the leopard cat between the 'mainland' ($N = 7$) and 'Iriomote Island' ($N = 4$), shown as the relative frequency of occurrence (RFO). Boxplots show median (horizontal bars) with 25 and 75% quartiles and vertical bars give maximum and minimum values. $^{*}P < 0.05$ (significance detected only by Mann-Whitney *U* test). $^{**}P < 0.05$ (significance detected by Chi-squared test, *G*-test, and Mann-Whitney *U* test; see *Supplementary Information*).

Fig. 3. Geographical variations in leopard cat food composition depicted by principal component analysis. Abbreviations: **SMamm** = Small mammals, **OthMamm** = Other mammals, **Rept** = Reptiles, **Amp** = Amphibians, **Inv** = Invertebrates; **Ir1-4** = Iriomote Island, **Si** = Singapore, **Ba** = Bangladesh, **Ph** = Philippines, **Bo** = Borneo, **In** = India, **Ko** = Korea, **Ts** = Tsushima Island (see references in Table 1).

Table 1. Summary of study areas from the reviewed papers of the leopard cat across Asia. ‘Iriomote’ = Iriomote Island, Japan; ‘Mainland’ = the rest of other study areas (see Fig. 1).

	‘Iriomote’	**‘Mainland’**							**Total**
	Ir1-Ir4	**Si**	**Ba**	**Ph**	**Bo**	**In**	**Ko**	**Ts**	
Compiled publication (N)	4	1	1	1	1	1	1	1	11
Analysed sample (n)[a]	1311	65	21	51	72	37	280	350	2187
Trophic diversity									
Shannon's diversity index (H')[b]	1.66 ± 0.06	1.16	1.18	0.93	0.94	0.7	0.69	1.32	1.07 ± 0.11
Levins' niche breadth index (B)[b]	4.74 ± 0.34	2.63	2.94	1.72	1.81	1.64	1.49	2.93	2.49 ± 0.36
Geo-climatic variable									
Latitude (°)[c]	24.2	1.2	21.9	10.4	5.1	27.3	37.9	34.2	20.3 ± 4.4
Elevation (m)[d]	300	10	10	506	72	3562	1068	200	716 ± 398
Annual mean temperature (°C)[e]	23.1	35.8	22.9	28.9	32.8	5.8	5.8	14.8	21.2 ± 3.8
Annual mean precipitation (mm)[e]	2073.4	1269.9	614.3	1064.2	1194.1	437.8	1088.7	2060.9	1225.4 ± 196.0
Inhabitation by native rodents[f]	Absent	Present	Present	Present	Present	Present	Present	Present	-

Ir1 (Sakaguchi & Ono 1994; analysed sample $n = 177$), **Ir2** (Watanabe et al. 2003; $n = 156$), **Ir3** (Watanabe 2012; $n = 947$), **Ir4** (Nakanishi & Izawa 2016; $n = 31$), **Si** (Singapore: Chua et al. 2016), **Ba** (Bangladesh: Khan 2004), **Ph** (Philippines: Lorica & Heaney, 2013), **Bo** (Borneo, Malaysia: Rajaratnam et al. 2007), **In** (India: Bashir et al. 2014), **Ko** (Korea: Lee et al. 2014), **Ts** (Tsushima

Island, Japan: Tatara & Doi 1994).

[a] Summed across studies for Iriomote Island and total (the sample size for each study in Iriomote Island is noted in the footnote above).

[b] Values are the mean and standard error for Iriomote Island and total.

[c] Extracted from each publication and averaged across provided range in each study.

[d] Extracted from each publication. When the information was not provided, we used the elevation function in *R* package *rgbif* to extract data from *Google Maps*.

[e] Obtained by *BioSIM 11* software based on latitude, longitude, and elevation information (between 1982 and 2010).

[f] Absent: native rodents were absent in the study area. Present: native rodents were present in the study area.

Fig. 1

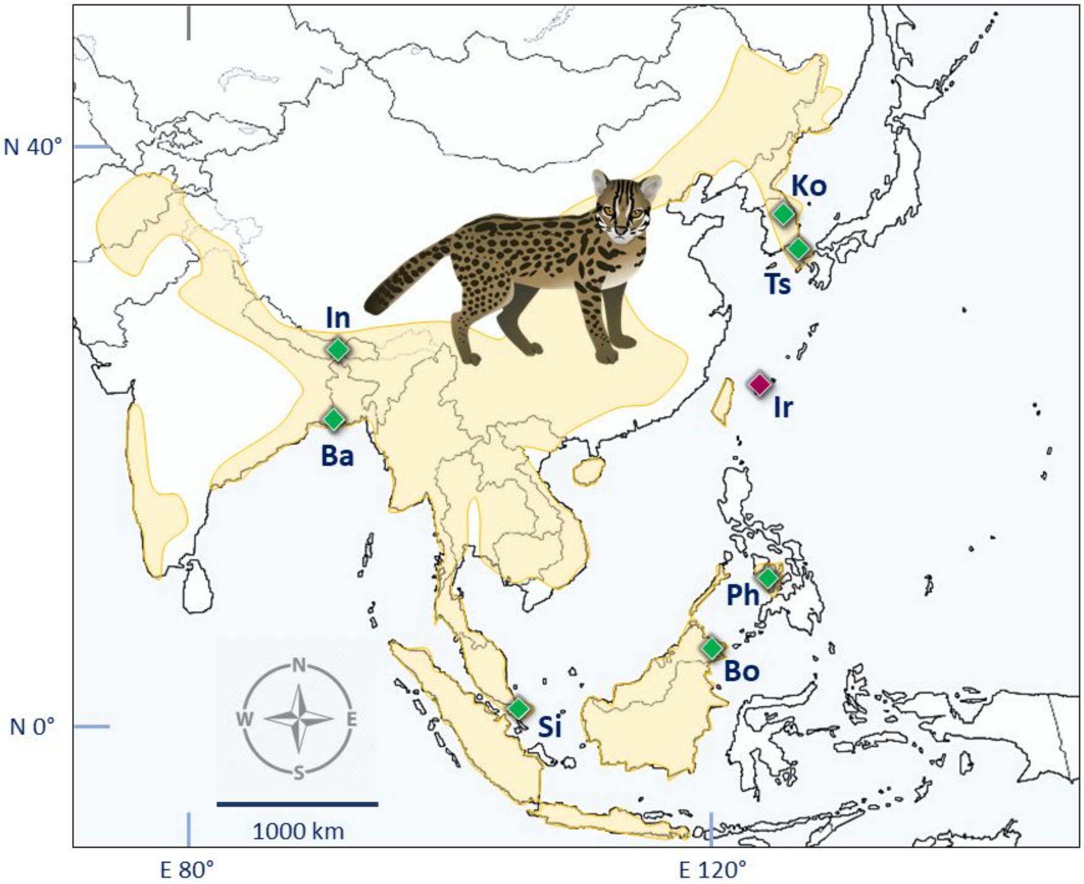
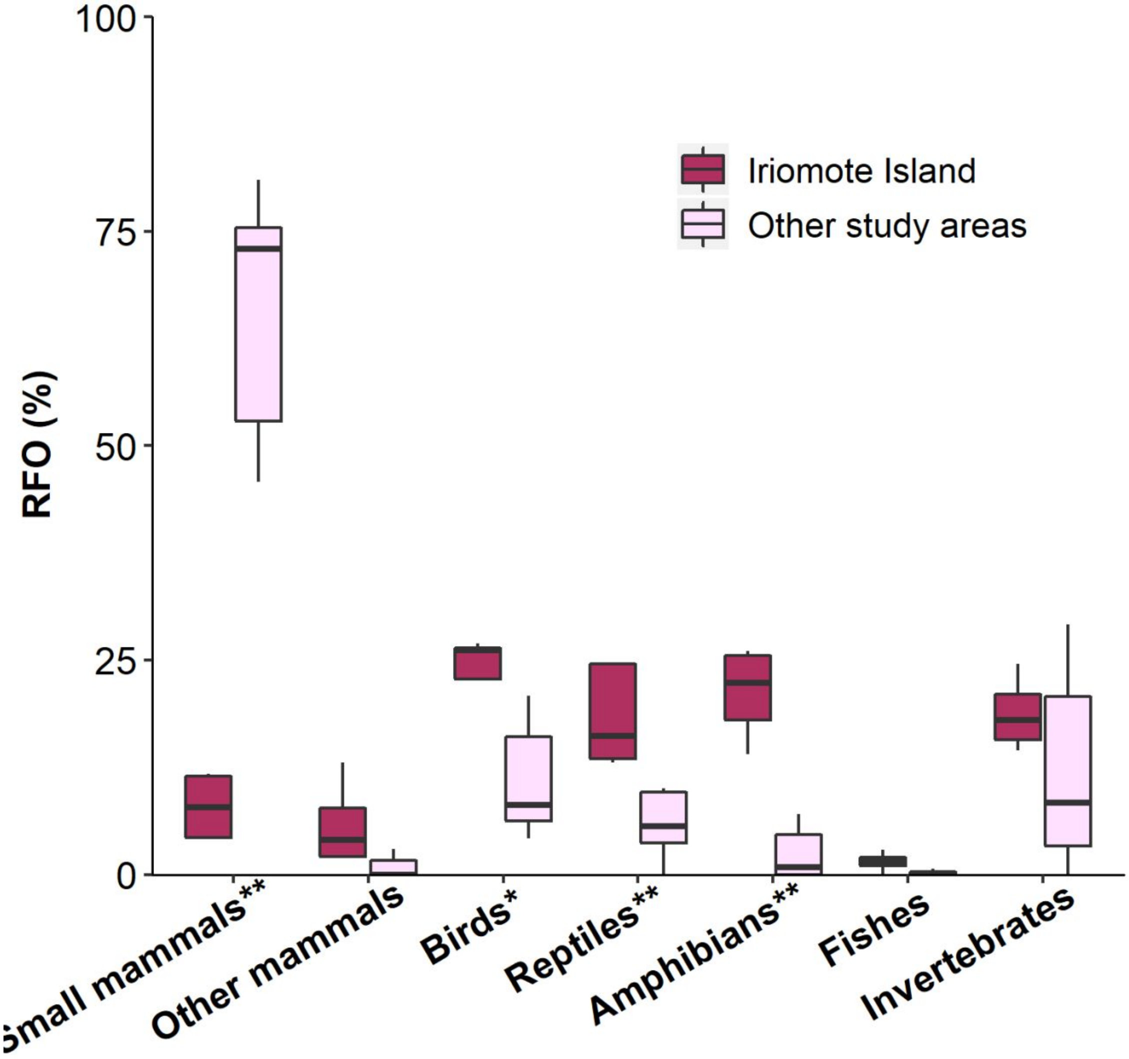
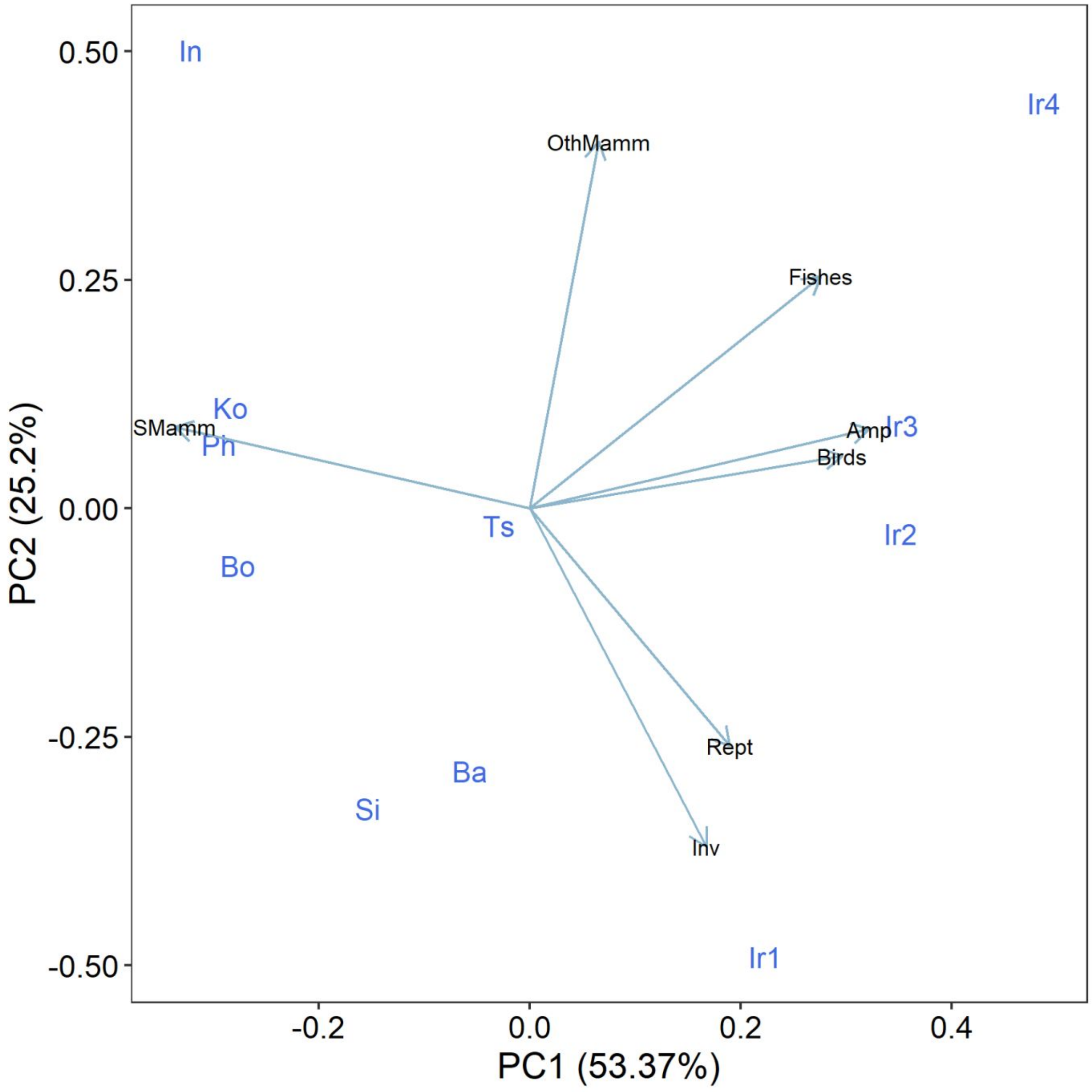


Fig. 2


RFO (%)
100
75
50
25
0
Iriomote Island
Other study areas
Small mammals**
Other mammals
Birds*
Reptiles**
Amphibians**
Fishes
Invertebrates

9 **Fig. 3**


0.50
0.25
0.00
-0.25
-0.50
PC2 (25.2%)
-0.2
0.0
0.2
0.4
PC1 (53.37%)
In
Ir4
OthMamm
Fishes
Ko
SMamm
Ph
Amp
Ir3
Birds
Ts
Ir2
Bo
Rept
Ba
Si
Inv
Ir1

10

Supplementary Information for

Adaptations to prey base in the hypercarnivorous leopard cat *Prionailurus bengalensis*

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This file includes:

- Supplementary Methods
- Tables S1 and S2
- References for Supplementary Information

Supplementary Methods

Assessing possible methodological problems

1. The dataset compiled included inconsistent sampling methodologies [one study (Nakanishi and Izawa 2016) examined stomach contents, while all the others were based upon faecal analysis], sample sizes (number of analysed faeces or stomachs, n), and sampling durations (months). To check if these artefacts caused bias in interpreting leopard cat diet bias (Putman, 1984: *cf*. Lozano et al., 2006; Zhou et al., 2011), we performed a permutational multivariate analysis of variance (PERMANOVA) using the R package vegan (Oksanen et al., 2015). We defined sampling as sample size per month (n / month) for each study to avoid multicollinearity (Dormann et al., 2013) between the sample size and duration (r = 0.77). Across studies, there was no significant influence arising from sampling effort variation (PERMANOVA: $F = 0.88$, $R^2 = 0.08$, $P = 0.450$) and methodology ($F = 1.64$, $R^2 = 0.16$, $P = 0.244$) on RFO per food category. Alternatively, we excluded the study employed stomach contents analysis (Nakanishi & Izawa 2016) and repeated the PERMANOVA and subsequent *post-hoc* tests to assess differences in diet composition between Iriomote and the mainland (see the main analysis described in *Materials and methods* in the main text). This approach produced similar results: PERMANOVA ($F = 10.72$, $R^2 = 0.57$, $P = 0.055$), Chi-squared tests (P <0.001 for small mammals, P <0.001 for reptiles, $P = 0.002$ for amphibians). Consequently, all the 11 studies were used for subsequent analyses (Table S2; Fig. 1).
2. In one study from India, the leopard cat consumed a considerable amount of carrion (16.7% RFO vs 0-5% elsewhere). To investigate whether our results were influenced or biased by dietary intake resulting from consumption of carrion against hunted prey, we also repeated

the main PERMANOVA analysis (see Materials and methods in the main text) to compare leopard cat food composition between Iriomote and the mainland by removing the food items being considered as carrion (i.e., ungulates). This approach yielded consistently similar results (PERMANOVA: $F = 26.51$, $R^2 = 0.75$, $P = 0.016$), and thereby we discuss the results based on the main results including both hunted prey and carrion.

3. To compare RFO of each food category specifically between mainland sites vs Iriomote, in addition to the Chi-squared test, we also employed likelihood ratio test [*G*-test, a more conservative approach, which can reduce the potential for type I error (Malo et al., 2004; Lozano et al. 2006)] and a rank-based method (Mann-Whitney *U* test) to confirm the robustness of the analysis. Alternative approaches also showed that this lack of small mammals on Iriomote (*G*-test: $P < 0.001$, Mann-Whitney *U* test: $P = 0.016$) was compensated by consuming more reptiles (*G*-test: $P = 0.001$, Mann-Whitney *U* test: $P = 0.028$), and amphibians (*G*-test: $P < 0.001$, Mann-Whitney *U* test: $P = 0.021$); with mixed support for a greater consumption of birds (Mann-Witney *U* test: $P = 0.024$; *versus G* test: $P = 0.070$).

50 **Table S1.** A list of 24 dietary studies reviewed on the leopard cat.

Source	Geographical location
Studies that met the screening criteria and were included in the analysis	
Bashir et al. (2014)	Sikkim, Northern India
Chua et al. (2016)	Pulau Tekong, Singapore
Khan (2004)	Ganges Delta, Eastern India/Southern Bangladesh
Lorica and Heaney (2013)	Hacienda Dos Marias, Phillippines
Lee et al. (2014)	Gangwon, Gyeongsangbuk, South Korea
Nakanishi and Izawa (2016)	Iriomote Island, Southern Japan
Rajaratnam et al. (2007)	Sabah, Northern Borneo, Malaysia
Sakaguchi and Ono (1994)	Iriomote Island, Southern Japan
Watanabe (2012)	Iriomote Island, Southern Japan
Tatara and Doi (1994)	Tsushima Island, Western Japan
Watanabe et al. (2003)	Iriomote Island, Southern Japan
Studies that did not meet the screening criteria	
Bao et al. (2005)	Beijing, Northern China
Inoue (1972)	Tsushima Island, Western Japan
Fernandez and De Guia (2011)	La Carlota, Central Philippines
Grassman (2000)	Kaeng Krachan, Central Thailand
Grassman et al. (2005)	Phu Khieo, Northern Thailand
Lee et al. (2013)	Samcheok, Goheung, Gwangju, South Korea
Rabinowitz (1990)	Huai Kha Khaeng, Central Thailand
Díaz-Sacco and Izawa (2013)	Iriomote Island, Southern Japan
Sakaguchi (1994)	Tsushima Island, Western Japan
Japan Wildlife Research Center (1998)	Tsushima Island, Western Japan
Watanabe and Izawa (2005)	Iriomote Island, Southern Japan
Izawa et al. (2000)	NA
Watanabe (2015)	Iriomote Island, Southern Japan

51 See *Materials and methods* in the main text for the inclusion criteria.

Table S2. Results from the principal components analysis (PCA) of using the seven food categories.

Variables	Factor 1	Factor 2	Factor 3	Factor 4
Small mammals	-0.50	0.13	0.14	0.15
Other mammals	0.10	0.60	-0.39	-0.67
Birds	0.44	0.09	0.47	-0.05
Reptiles	0.28	-0.39	-0.69	0.15
Amphibians	0.48	0.13	-0.12	0.35
Fishes	0.41	0.38	0.20	0.23
Invertebrates	0.25	-0.55	0.28	-0.57

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