

Geographic variation in jungle cat (*Felis chaus* Schreber, 1777) (Mammalia, Carnivora, Felidae) body size: is competition responsible?

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There is a striking difference in body size of jungle cats (*Felis chaus*) in the west and the east of their distribution, with Israeli cats being 43% heavier than Indian cats. We tested the hypothesis that increasing competition from other small felids towards the east is responsible for the difference in body size. We measured jungle cat skulls for eight cranial and dental variables and related these to independent variables such as species richness (local and regional), latitude, longitude, temperature, and precipitation. Data from a narrow band between latitudes 24.0°N and 33.9°N, where Bergmann's rule was largely not observed, showed that the western population ($\leq 50.0^\circ\text{E}$ longitude) of jungle cats is larger than the eastern ($> 60.0^\circ\text{E}$ longitude) population with the size difference being most evident in the upper carnassials (P⁴L). Species richness at the regional level showed a significant negative relation to P⁴L. An even spacing in condylobasal length for a small-cat guild from India through null model analysis indicated the occurrence of character displacement. The results support the hypothesis that competition is responsible for geographical variation in jungle cat body size in the region where Bergmann's rule does not apply. © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, **92**, 163–172.

ADDITIONAL KEYWORDS: Bergmann's rule – character displacement – character release – felids – skull morphometry – sympatry.

INTRODUCTION

Intraspecific geographical variation in body size has been documented in several wide ranging species from varied taxa and has been the subject of much debate, with several theories and ideas being propounded for its cause (Mayr, 1963; James, 1970; McNab, 1971; Gould & Johnston, 1972; Boyce, 1979; Abrams, 1983; Dayan & Simberloff, 1996). Bergmann's rule has been a frequently cited trend and has been documented for several species, including some felids (Wigginton & Dobson, 1999; Ashton, Tracy & de

Queiroz, 2000; Meiri & Dayan, 2003; Meiri, Dayan & Simberloff, 2004). Explanations for the geographical variation include climatic factors, habitat structure, varied prey body size patterns and availability (abundance), and competition with sympatric species (James, 1970; Dayan *et al.*, 1990; Bakker & Kelt, 2000; Simberloff *et al.*, 2000).

Among these factors, competition has been extensively reviewed (Connor & Simberloff, 1986; Peters, 1991; Huston, 1994). Following the description by Brown & Wilson (1956) of character displacement as the process facilitating coexistence, and the definition by Grant (1972) of its complement, character release, several studies addressed competition through these mechanisms and studied their role in structuring communities and generating geographical variation

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Table 1. Felid species richness in 10° longitude classes between latitudes 24.0°N and 33.9°N

Longitude classes	Number of felid species (< 20 kg mean body mass)	Felid species
30–40	4	<i>Felis chaus</i> , <i>Caracal caracal</i> , <i>Felis lybica</i> , <i>Felis margarita</i>
40–50	5	<i>Felis chaus</i> , <i>Caracal caracal</i> , <i>Felis lybica/ornata</i> , <i>Felis margarita</i> , <i>Otocolobus manul</i> (Pallas, 1776)
50–60	4	<i>Felis chaus</i> , <i>Caracal caracal</i> , <i>Felis ornata</i> , <i>Felis margarita</i>
60–70	5	<i>Felis chaus</i> , <i>Caracal caracal</i> , <i>Felis ornata</i> , <i>Felis margarita</i> , <i>Prionailurus viverrinus</i>
70–80	6	<i>Felis chaus</i> , <i>Caracal caracal</i> , <i>Felis sylvestris ornata</i> , <i>Prionailurus viverrinus</i> , <i>Prionailurus bengalensis</i> , <i>Prionailurus rubiginosus</i>
80–90	7	<i>Felis chaus</i> , <i>Prionailurus viverrinus</i> , <i>Prionailurus bengalensis</i> , <i>Prionailurus rubiginosus*</i> , <i>Catopuma temmincki</i> , <i>Pardofelis marmorata</i> , <i>Neofelis nebulosa</i>
90–100	6	<i>Felis chaus</i> , <i>Prionailurus viverrinus</i> , <i>Prionailurus bengalensis</i> , <i>Catopuma temmincki</i> , <i>pardofelis marmorata</i> , <i>Neofelis nebulosa</i>

*Probable occurrence.

(Connor & Simberloff, 1986; Losos, 2000; Schluter, 2000; Simberloff *et al.*, 2000). One such study by Dayan *et al.* (1990) found character displacement occurring in a felid guild in Israel including caracal *Caracal caracal* (Schreber, 1776), jungle cat *Felis chaus*, African wildcat *Felis* [cf. *sylvestris*] *lybica* Forster, 1770 and the sand cat *Felis margarita* Loche, 1858. Most of these felids occur in sympatry from the Nile, eastward along a narrow strip through Israel, Iraq, Iran, Pakistan, and western India (IUCN, 1996).

India has the largest number of felid species in the world. Of the 15 species of cats that occur here, 11 are small- to medium-sized in the weight range 1–20 kg (IUCN, 1996) (Table 1). The jungle cat is the most common small cat in India and, although largely Oriental in distribution, has a wide global spread from Egypt to the west, through south-west Asia, parts of Europe (Georgia, Russia, and Azerbaijan), China, South and South-east Asia to Vietnam to the east. Its global distribution is centred in India (IUCN, 1996). Based largely on variation in external morphology, ten subspecies have been proposed: *Felis chaus nilotica* (Egypt), *Felis chaus furax* (Israel and Iraq), *Felis chaus chaus* (Caucasus), *Felis chaus*

oxiana (Syr Darya and Amu Darya), *Felis chaus prateri* (Thar desert in the Indo-Pak region), *Felis chaus affinis* (Himalayan region), *Felis chaus kutas* (northern India), *Felis chaus valballala* (Southern India), *Felis chaus kelaarti* (Sri Lanka), and *Felis chaus fulvidina* (South-east Asia) (Pocock, 1939; Heptner & Sludskii, 1972).

If body size were influenced by competition, jungle cats would be expected to be smaller eastwards as the number of other felid species increases. In the present study, the hypothesis that the decrease in body size of jungle cats eastward is related to increasing competition from other sympatric felids was tested. The importance of environmental factors such as temperature and precipitation in explaining the east–west pattern in body size of jungle cats was also tested. Finally, the role of competition in the structuring of a small cat guild from India was examined.

MATERIAL AND METHODS

Body mass measures of jungle cats from Israel were obtained from Dayan *et al.* (1990), and from India from Pocock (1939) and the Natural History Museum,

London. Measurements were taken on 251 jungle cat skulls (131 males and 120 females) from collections at the Natural History Museum (London), the Powell–Cotton Museum (Birchington), the Bombay Natural History Society (Mumbai), the Zoological Survey of India (Calcutta), the University of Tel Aviv Zoology Museum, the Zoologisches Museum Alexander Humboldt (Berlin), the University Zoological Museum (Hamburg), the Museum für Naturkunde (Stuttgart), the Thai Zoological Reference Collection (Bangkok), the National Zoological Reference Collection (Singapore), and the Museum of Comparative Zoology (Harvard). Skulls were measured to 0.01 mm precision using Vernier callipers. Some skull measures were obtained from Dayan *et al.* (1990). The variables measured were total length of skull (TL), zygomatic breadth (ZB), condylobasal length (CBL), mandibular length (ManL), maxillary length (MaxL), interorbital width (IO), postorbital constriction width (PO), upper canine diameter ($C^{\text{sup}}D$), and upper carnassial length (P^4L).

Latitudinal and longitudinal coordinates of the area of collection for each skull were obtained from several atlases and the mean annual precipitation and the mean maximum and minimum temperatures for each location of collection (available at: <http://www.diva-gis.org>; accessed 1 May 2004). Average temperature and the temperature range were calculated from the mean minimum and maximum temperatures. Information on felid species richness at a regional level (every 10° longitudinal class from longitudes 30.0°E to 100.0°E), as well as at a local level (nearest area or region), where the jungle cat skulls were collected, were obtained from IUCN (1996). The various skull measures were subjected to a Spearman's correlation test using the program STATISTICA, version 6 (StatSoft Inc., 2001) to determine the degree of relation among them.

To test for Bergmann's rule, the data was divided into 10° longitudinal classes and, within each class, the Spearman's correlation (one-tailed) was conducted with CBL and P^4L (selected as indicators of body size) against latitude (StatSoft Inc., 2001). Bergmann's rule did not apply through most of the region between 24.0°N and 33.9°N latitudes and, consequently, the data ($N = 146$, 83 males and 63 females) were able to be used to examine differences in body size along the longitudinal gradient (30.0°E to 100.0°E longitudes). Craniodental measures were subjected to discriminant canonical function (DCF) analysis (StatSoft Inc., 2001), treating males and females separately, to look for patterns of variation among the various subspecies.

To test for differences among populations, the skull variables CBL and P^4L were selected as indicators of body size, and the sample was divided into 10° lon-

gitude classes. The data were subjected to a bootstrap simulation with 5000 iterations of subsamples that equalled sample size using the computer program SIMSTAT (Peladeau, 2000). Comparisons between jungle cat populations were made from 95% bootstrap confidence intervals. Measures of canine diameters could not be obtained across the entire jungle cat distributional range, and the data of Dayan *et al.* (1990) for that region were used and means and ranges of this variable were plotted for each 10° longitude class.

To relate variation in body size to environmental factors and competition, a partial correlation was conducted with species richness locally and regionally, average temperature, temperature range, and mean annual precipitation versus roots 1 and 2 from the DCF analysis, where each independent factor was tested while controlling for the others (StatSoft Inc., 2001).

Finally, to test the hypothesis that the morphological structure observed in a small cat guild in India is shaped by competition, resulting in character displacement, a null model analysis was conducted using the software EcoSim (Gotelli & Entsminger, 2000). Skull measures were available for only one of the various small felid guilds within the latitudinal range 24.0°N and 33.9°N within India. This included the rusty spotted cat *Prionailurus rubiginosus* (I. Geoffroy Saint-Hillaire, 1831), leopard cat *Prionailurus bengalensis* (Kerr, 1792), jungle cat, and fishing cat *Prionailurus viverrinus* (Bennett, 1833). Measurements on ZB and CBL of the small felids (excluding the jungle cat) within this guild between 24.0°N and 33.9°N within India were taken from Pocock (1939). The minimum and maximum records of each of the skull measurements were used to define the boundaries of segments and log-transformed data were used to conduct tests on variance of segment lengths, with 1000 iterations.

RESULTS

The jungle cat skulls were from populations in the region between latitudes 7.10°N and 43.0°N and longitudes 30.0°E and 100.0°E. Male and female jungle cats in Israel weighed (mean \pm SD) 10 ± 1.40 kg ($N = 10$) and 7 ± 1.73 kg ($N = 3$), respectively, and were 43% heavier than Indian males (5.75 ± 1.41 kg, $N = 21$) and females (4 ± 1.97 kg, $N = 12$). All skull variables were significantly ($P < 0.05$) correlated with each other. The relation of the dental measure P^4L with skull measures, although significant, was not as strong (with TL: $r_s = 0.60$, $N = 209$; with CBL: $r_s = 0.65$, $N = 227$; with ZB: $r_s = 0.55$, $N = 241$); this could reflect the fact that skulls in which P^4 was in occlusion represent different degrees of adult growth.

Table 2. The correlation of jungle cat skull and dental measures with latitude, within 10° longitude classes across its global range

Longitude class	Latitudinal range (°)	Gender	Feature	r_s	P	N
30–40	9.2 (24.0–33.2)	Male	CBL	0.28	0.13	18
			P ⁴ L	0.06	0.41	18
	5.7 (26.5–32.2)	Female	CBL	-0.19	0.31	9
			P ⁴ L	0.17	0.30	12
40.01–50	12 (31.0–43.0)	Male	CBL	0.19	0.30	9
			P ⁴ L	-0.53	0.04	12
	21 (32.0–53.0)	Female	CBL	0.16	0.31	12
			P ⁴ L	-0.46	0.05	14
60.01–70	14 (24.0–38.0)	Male	CBL	0.47	0.04	14
			P ⁴ L	0.26	0.16	16
	8.5 (22.5–31.0)	Female	CBL	0.33	0.19	9
			P ⁴ L	-0.11	0.38	10
70.01–80	25.4 (8.6–34.0)	Male	CBL	0.45	0.00	45
			P ⁴ L	0.17	0.12	46
	30.6 (8.4–39.0)	Female	CBL	0.39	0.00	50
			P ⁴ L	0.33	0.01	51
80.01–90	20.9 (7.1–28.0)	Male	CBL	0.53	0.00	28
			P ⁴ L	0.47	0.00	27
	4 (24.0–28.0)	Female	CBL	0.36	0.09	15
			P ⁴ L	0.39	0.07	15
90.01–100	7.4 (18.6–26.0)	Male	CBL	-0.15	0.39	6
			P ⁴ L	-0.74	0.02	7
	15 (11.5–26.5)	Female	CBL	0.55	0.06	9
			P ⁴ L	0.44	0.10	10

P⁴L, upper carnassial length; CBL, condylobasal length.

Bergmann's rule applied between longitudes 60.0°E and 90.0°E (Table 2), but not in most of the region between latitudes 24.0°N and 33.9°N (Table 3). The only place where Bergmann's rule was clearly observed for this region was between longitudes 80.01°E to 90.00°E, in a latitudinal range of 4°, for P⁴L measures of male jungle cat (Table 3). The region between latitudes 24.0°N and 33.9°N has six described subspecies of jungle cat. Results from natural-log-transformed data and untransformed data for the DCF analysis were similar and hence the results from untransformed data are presented here.

The DCF analysis with the six subspecies of jungle cat plotted against the first two canonical variates showed a separation by size of P⁴L between the eastern (*F. c. prateri*, *F. c. affinis* and *F. c. kutas*), and western populations (*F. c. nilotica* and *F. c. furax*) on the first axis for both males (Fig. 1) and females (Fig. 2). Specimens from within the areas of distribution of *F. c. chaus* and *F. c. oxiana* were positioned between the eastern (longitudes > 60.0°E) and western (longitudes ≤ 50.0°E) populations; the males were close to the western population whereas the

females were closer to the eastern population. The second and subsequent axes did not show any further separation for females. *Felis c. nilotica* males were segregated to a small extent from *F. c. furax* on the second axis (Fig. 1). The highest factor loading on the first axis for both males and females was for the variable P⁴L (males = -0.72; females = 0.83) whereas, on the second axis, for females, it was MaxL (-0.64) and, for males, ManL (0.48), ZB (0.36), and TL (0.35). In females, the two roots resolved 93% of the total variation (first root = 89%; second root = 4%) whereas, in males, the two roots resolved 98% of the total variation (first root = 94%; second root = 4%).

Bootstrapping supported results from the DCF analysis and showed three distinct populations, a western population at longitudes ≤ 50.0°E, an intermediate one between longitudes 50.01°E to 60.00°E, and an eastern population at longitudes > 60.0°E (Fig. 3). Eastern males and females were smaller than their western counterparts by 11% for CBL, 19% for P⁴L, and 23% in males and 25% in females for C^{sup}D. The bootstrap 95% confidence intervals showed an overlap in size between the western females and eastern males (Fig. 3).

Table 3. The correlation of jungle cat skull and dental measures with latitude, within 10° longitude classes between latitudes 24.0°N and 33.9°N

Longitude class	Latitudinal range (°)	Gender	Feature	r_s	P	n
30–40	8.9 (24.0–32.9)	Male	CBL	0.18	0.24	17
			P ⁴ L	–0.12	0.32	17
	5.7 (26.5–32.2)	Female	CBL	–0.19	0.31	9
			P ⁴ L	0.17	0.30	12
40.01–50	1.12 (31.0–32.32)	Male	CBL	0.32	0.34	4
			P ⁴ L	–0.80	0.05	5
	1 (32.0–33.0)	Female	CBL	0.41	0.21	6
			P ⁴ L	0.14	0.38	7
60.01–70	7 (24.0–31.0)	Male	CBL	0.56*	0.02	13
			P ⁴ L	0.13	0.32	15
	6 (25.0–31.0)	Female	CBL	0.13	0.39	7
			P ⁴ L	0.40	0.19	7
70.01–80	8.3 (24.0–32.3)	Male	CBL	–0.22	0.14	24
			P ⁴ L	–0.31	0.07	24
	6.6 (26.0–32.36)	Female	CBL	0.09	0.36	16
			P ⁴ L	–0.56	0.01	19
80.01–90	4 (24.0–28.0)	Male	CBL	0.13	0.09	20
			P ⁴ L	0.49	0.01	20
	4 (24.0–28.0)	Female	CBL	0.36	0.18	15
			P ⁴ L	0.39	0.14	15

*This figure was skewed by the presence of a particularly large individual with high values for all skull measures except the P⁴L. When this individual was removed, the values for CBL versus latitude were: $r_s = 0.43$, $P = 0.07$.

P⁴L, upper carnassial length; CBL, condylobasal length.

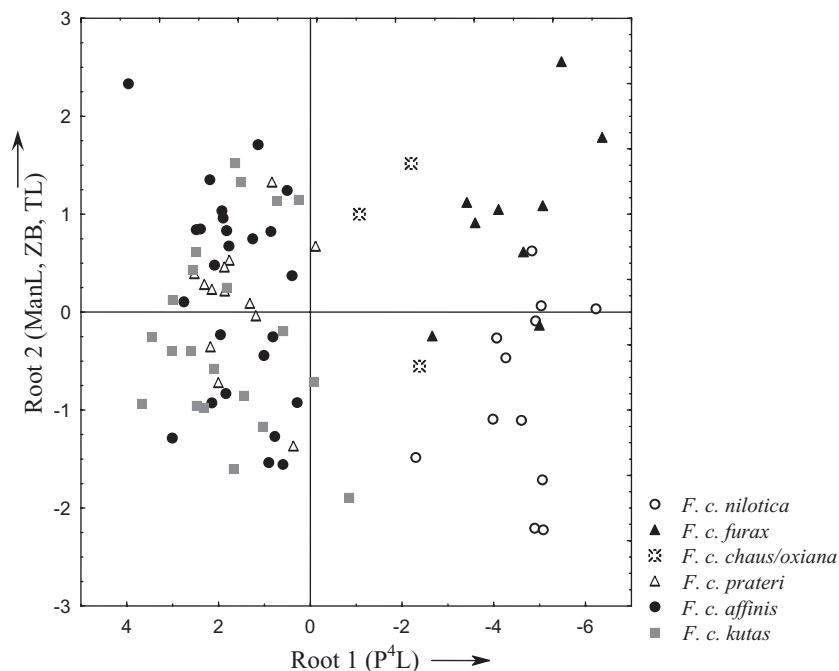
Partial correlation with environmental variables and species richness locally and regionally showed a negative relation between root 1 of the DCF analysis and species richness regionally for both males (partial $r = -0.61$; $\beta = -0.95$; $P = 0.00$; $N = 83$) and females (partial $r = -0.60$; $\beta = -0.76$; $P = 0.00$; $N = 62$) (Table 4). Root 1 for females was also related negatively to temperature difference (partial $r = -0.34$; $\beta = -0.37$; $P = 0.01$; $N = 62$) (Table 4). Root 2 of the DCF analysis showed no relation with environmental variables and species richness locally and regionally in both males and females.

In the small felid guild from India, there was no overlap in CBL (Fig. 4) and ZB of rusty-spotted cat, leopard cat, and jungle cat. Rusty spotted cat males and females were smaller than leopard cat males and females, and leopard cat males and females were in turn smaller than jungle cat males and females in CBL and ZB. Male jungle cats, however, overlapped with female fishing cats in CBL (Fig. 4) and ZB. Sexual dimorphism (male/female) from CBL (Fig. 4) and ZB measurements was highest in the fishing cat followed by the jungle cat. Null model analysis showed an even spacing in CBL of small cats in India. The observed index for variance in segment length was 0.00034, which was smaller than the mean vari-

ance of the simulated index of 0.00158, 983 times out of the 1000 iterations, generating a tail probability of $P = 0.02$. The ZB of small felids did not show significant evenness in spacing of small cats on a size gradient, with a tail probability of $P = 0.15$.

DISCUSSION

Bergmann's rule has been demonstrated in both sexes of jungle cats in the Palaearctic region in a latitudinal range of 25.0° (Meiri *et al.*, 2004). The results of the present study showed that this rule applied even in the Oriental region at latitudinal ranges greater than 10°, although not always in both sexes (Table 2). Apart from the north–south cline, however, we found that competition from sympatric felids at a regional level is the variable responsible for an east–west cline between latitudes 24.0°N and 33.9°N. Species richness at a local level did not show a strong or significant result with size (Table 4). Most of the skulls were collected in the late 19th and early 20th century. Recent reports have demonstrated the presence of some species, such as the rusty spotted cat and the Asiatic wild cat, in areas where they were not known to occur previously (IUCN, 1996; Mukherjee, 1998); either they have extended their ranges



Arrow indicates direction of increase

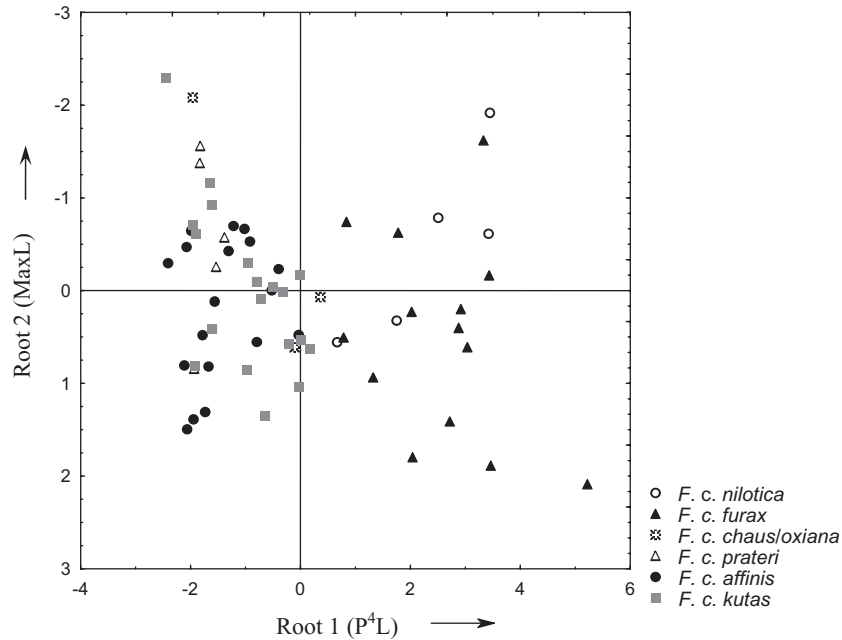
Figure 1. Discriminant canonical function analysis of skull and dental variables of male jungle cats between the latitudes 24.0°N to 33.9°N. ManL, mandibular length; TL, total length of skull; ZB, zygomatic breadth; P⁴L, upper carnassial length.

within India in the past few decades or, more likely, they went unnoticed previously. On the other hand, the caracal is reported to have had a much wider range in the past than is presently observed (Prater, 1948). Although the regional species richness (Table 1) of small felids included combinations of species that are currently not known to be sympatric in any part of their range, it is possible that these species have interacted in the past when climatic patterns in the Indian subcontinent were different; the present size patterns of jungle cats observed could be a result of that past interaction.

The east–west jungle cat size variation was not strictly clinal but showed the presence of three groups (Fig. 3). No variation was observed within each group. The observation that the size difference between the western and eastern populations was manifested to a greater degree in a dental (P⁴) rather than a cranial feature in the DCF analysis is interesting. Meiri & Dayan (2003) cautioned against using dental measures as surrogates for body size because selection may act differentially on them, leading to low correlations between the two measures; dental characters are more likely to be influenced by factors associated

with feeding, such as prey size and competition from sympatric species, whereas body size and skull measures are more often related to environmental factors (Dayan & Simberloff, 1996). Moreover, teeth erupt and their size thereafter does not change in response to continued bone growth. Among dental features, the maximal diameter of the upper canines has been reported to be the best measure for establishing the role of competition in structuring felid guilds because canines function explicitly as prey-killing tools in felids (Leyhausen, 1979; Dayan & Simberloff, 1996). An increase in all measures (body mass, cranial measures, as well as dental characters) was seen westwards, although not proportionally. The greatest increase was in body mass, which was not surprising; being a cubic measure, it is expected to increase faster than linear measures. Compared to the CBL, the dental measures (P⁴L and C^{sup}D) showed a higher percentage of difference between the eastern and western populations.

The null model analysis of the felid guild from India showed even spacing and hence character displacement operating in CBL but not in ZB measures. Dayan *et al.* (1990) reported character displacement



Arrow indicates direction of increase

Figure 2. Discriminant canonical function analysis of skull and dental variables of female jungle cats between the latitudes 24.0°N to 33.9°N. MaxL, maxillary length; P⁴L, upper carnassial length.

Table 4. Partial correlation of root 1 from the discriminant canonical function analysis with environmental variables and species richness between the latitudes 24.0°N and 33.9°N for male ($N = 83$) and female ($N = 62$) jungle cats

Effect	Gender	R^2	β	Partial r	t	P
Species richness locally	Male	0.18	-0.03	-0.04	-0.37	0.71
	Female	0.16	0.04	0.05	0.40	0.69
Species richness regionally	Male	0.73	-0.95	-0.61	-6.79	0.00
	Female	0.56	-0.76	-0.60	-5.79	0.00
Mean precipitation	Male	0.79	0.22	0.15	1.37	0.17
	Female	0.71	-0.17	-0.14	-1.07	0.29
Average temperature	Male	0.55	0.04	0.04	0.35	0.73
	Female	0.26	0.03	0.04	0.29	0.77
Temperature range	Male	0.40	-0.08	-0.09	-0.87	0.39
	Female	0.58	-0.37	-0.34	-2.79	0.01

only in canine diameters and not in CBL for the Israeli felid guild; in the Sindh felid guild, they observed character displacement even in CBL measures. When the CBL and ZB measures of the western population of jungle cat were superimposed on the Indian felid guild, the western measures overlapped with the fishing cat CBL (Fig. 4) and ZB. This supported the idea of character displacement/release

operating in jungle cats, leading to the prevalent body size patterns. Both the fishing cat and the jungle cat are restricted in their distribution by the availability of water. Their habitats overlap considerably, especially in the dry western regions of India and the eastern parts of Pakistan (IUCN, 1996).

Might the jungle cat have become larger as it went westward where there were fewer felid competitors, a

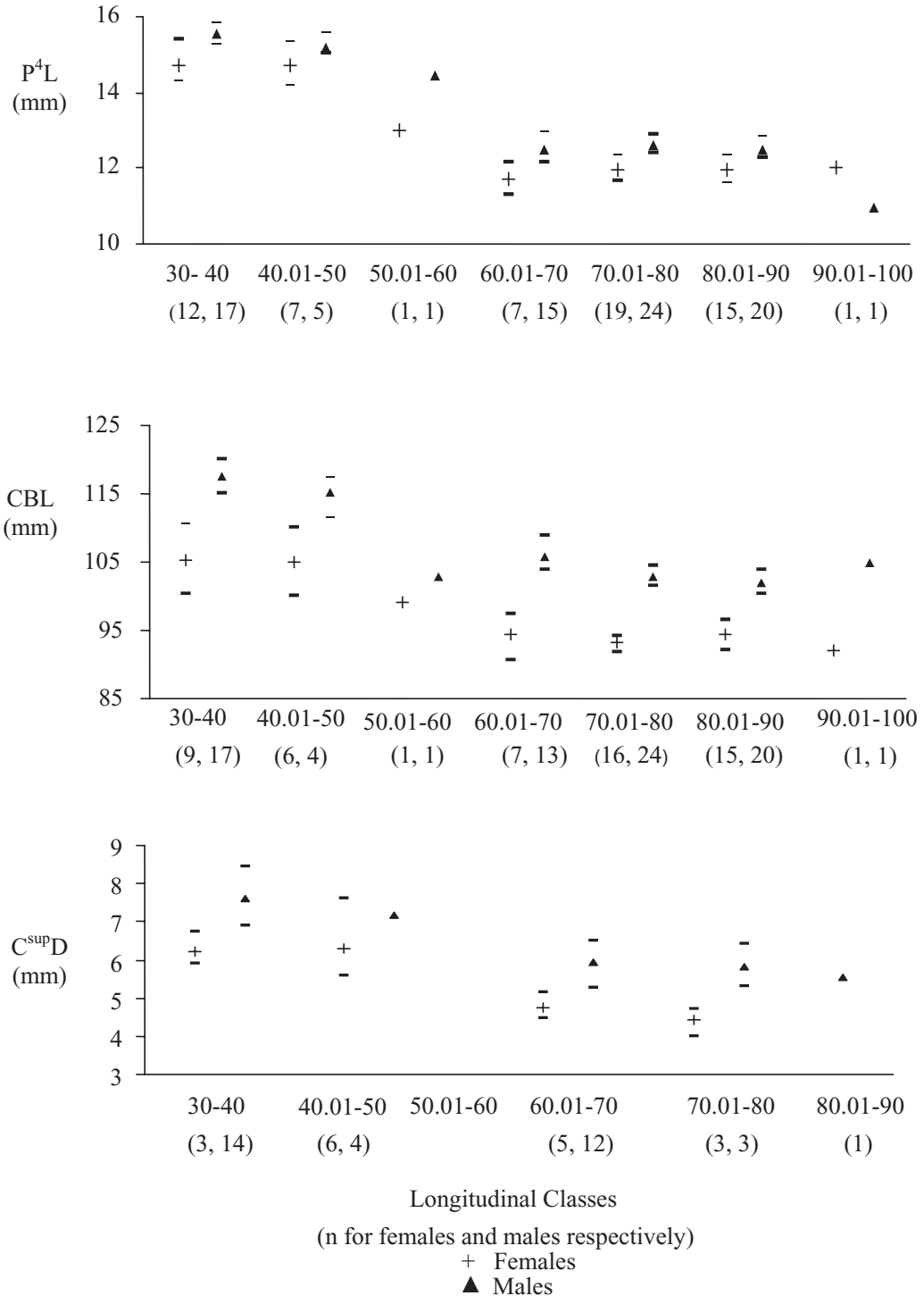


Figure 3. Means and 95% confidence intervals from bootstrap simulation (5000 iterations with subsamples equaling sample size) for upper carnassial length (P⁴L) and condylobasal length (CBL) measures, and means and ranges of upper canine diameter (C^{sup}D) of male and female jungle cats in 10° longitude classes between latitudes 24.0°N and 33.9°N.

case of character release, or did it move eastward from the west and become smaller on encountering more felid competitors, especially the fishing cat (character displacement)? Molecular studies on jungle

cats would help to identify the location of evolutionary origin of the species as well as resolve the taxonomic ambiguity, which may possibly result in a reevaluation of current taxonomic knowledge at the

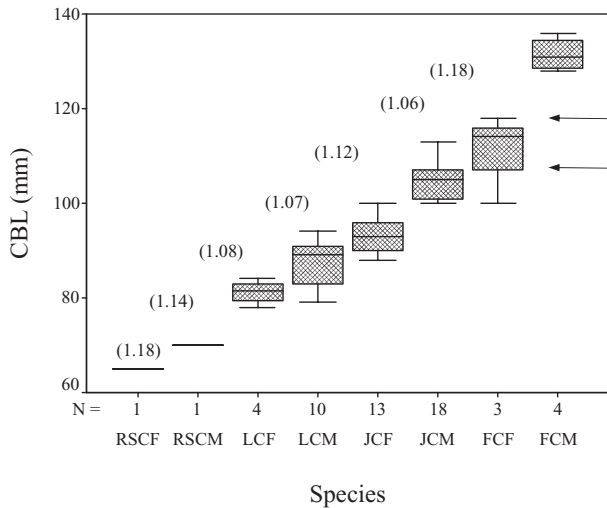


Figure 4. Condylbasal lengths of small felid species from a guild in India with size ratios between adjacent species. RSCF, rusty spotted cat female; RSCM, rusty spotted cat male; LCF, leopard cat female; LCM, leopard cat male; JCF, jungle cat female; JCM, jungle cat male; FCF, fishing cat female; FCM, fishing cat male. Arrows indicate position of females and males in the western population of jungle cats.

subspecific or even specific level. A taxonomic study is currently in preparation by us.

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