Tigers and leopards coexist despite similarities in space use and habitat selection

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Tigers and leopards coexist despite similarities in space use and habitat selection

We assessed the roles of space use and habitat selection in fostering coexistence of large felids using sympatric radio-collared tigers *Panthera tigris* and leopards *P. pardus*. We found that intraspecific spatial overlap was 2 to 17 times lower than interspecific overlap and variation in habitat preference was greater between individuals than between species. These results imply that in certain contexts tigers and leopard coexist despite interspecific similarities in space use and habitat selection.

Ecologically similar species may compete for limited resources, but resource partitioning via space use (MacArthur 1958, Durant 1998) or foraging differences (Johnsingh 1992, Karanth & Sunquist 2000, Lovari et al. 2014) may facilitate their coexistence. In carnivores, space use differences may result from differential habitat selection (Murray & Boutin 1991, Lendrum et al. 2014) sometimes driven by interspecific interactions including interspecific killing (Caro & Stoner 2003). In addition, intraspecific competition for prey and mating opportunities can influence space use and habitat selection (Rich et al. 2012, Pilfold et al. 2014). Greater interspecific differences in space use and/or habitat selection relative to intraspecific differences may contribute to reduced interspecific competition allowing for coexistence.

Tigers, an endangered large felid, overlap extensively with another large felid, leopards. Both species are solitary ambush predators of ungulate prey (Karanth & Sunquist 2000). However, the much smaller leopard is competitively subordinate as tigers displace (Odden et al. 2010, Harihar et al. 2011) and occasionally kill leopards (Seidensticker 1976, Karanth & Sunquist 2000). In the Western Ghats of southern India, these two species co-occur at high densities (Karanth & Sunquist 1995, 2000).

Interactions between these species are largely examined using diet analyses (Johnsingh 1992, Lovari et al. 2014) and occupancy models (Ramesh et al. 2012, Steinmetz et al. 2013, Karanth et al. 2017). Few studies have explicitly examined space use differences between sympatric tigers and leopards using radio-collared animals likely due to the difficulties with capture and immobilization (Miller et al. 2010). Using telemetry data from sympatric tigers and leopards, we examined the role of habitat selection and space use in promoting their coexistence. We first compared interspecific and intraspecific differences in space use overlap. We then determined individual habitat selection and evaluated interspecific and intraspecific differences. Finally, we synthesized the results to help elucidate drivers of tiger and leopard coexistence.

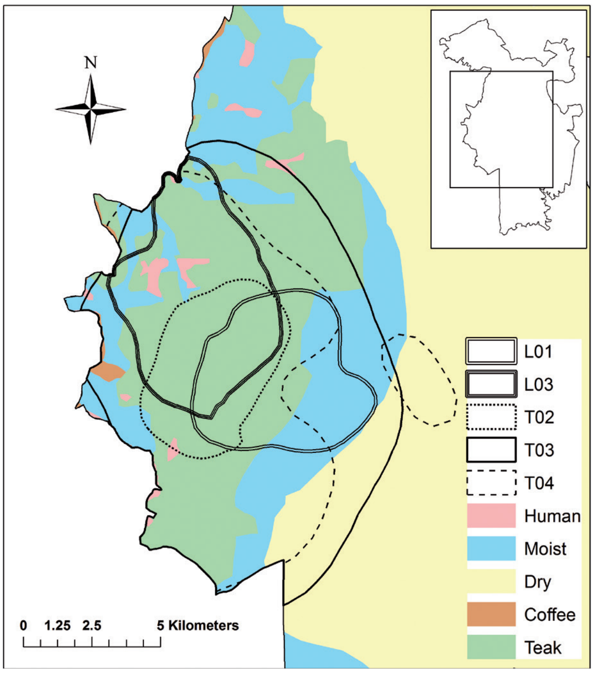

Fig. 1. Home ranges (95% utilization distributions) and habitat selection of both tigers and leopards in Nagarahole National Park, India over a six-month period. Human = human-dominated, Moist = moist deciduous forest, Dry = dry deciduous forest, Coffee = coffee plantation, Teak = teak plantation.

Methods

The study area covered ~200 km^2 within Nagarahole National Park, Karnataka, India (11°55'12''–12°15'0'' N / 76°0'0''–76°15'0'' E) as described by Karanth & Sunquist (2000). Within the study area we identified five distinct habitat types: human-dominated (open agriculture, settlements), moist deciduous forest (*Lagerstroemia microcarpa, Terminalia tomentosa, Dillenia pentagyna*; Pascal 1982), dry deciduous forests (*Anogeissus latifolia, Tectona grandis, Terminalia tomentosa*; Pascal 1982), coffee plantations and teak plantations (interspersed with moist deciduous and secondary forests, swampy fallows and clearings; Pascal 1982, Karanth & Sunquist 1992). Principal prey species present included guar *Bos gaurus*, sambar *Rusa unicolor*, chital *Axis axis*, wild pig *Sus scrofa*, muntjac *Muntiacus vaginalis* and hanuman langur *Semnopithecus entellus* (Karanth & Sunquist 2000).

We relied on a subset of telemetry data from tigers and leopards previously described by Karanth & Sunquist (2000). We only included individuals with ≥50 locations (Seaman et al. 1999) during a time period when all individuals were collared and present in the study area (January–June 1990). This data subset yielded information from five individuals: two resident male leopards (L01 and L03), two transient male tigers (T03 and T04) and one resident female tiger (T02).

We calculated spatial overlap using the utilisation distribution overlap index UDOI (Fieberg & Kochanny 2005) at the home range (95% UD) and core area (50% UD) levels (Robert et al. 2012) with the "adehabitat" package (Calenge 2006) in Program R.

We assessed 3rd order (vegetation types within home range) habitat selection (Johnson 1980) by tigers and leopards among the five habitat types using layers digitized from Pascal (1982). Available habitat was compared to used habitat with Fisher's exact test (Custer & Galli 2002). If a habitat was never used, then 0.0001 was entered as the observed proportion used and 0.9999 was entered if one habitat was used exclusively (Aebischer et al. 1993). If Fisher's exact test was significant (p<0.1), we determined which habitats were preferred, avoided, or used in proportion to availability using confidence intervals with Bonferroni corrections for multiple comparisons (Neu et al. 1974). All statistical analyses were conducted using Program R version 3.0.2 (R Core Development Team 2014).

Table 1. Spatial overlap between individual tigers and leopards in Nagarahole National Park, India. Overlap between individual home ranges (95% utilization distribution) as well as overlap between individual core area (50% utilization distribution) shown with core area overlap in parentheses. Bold indicates interspecific overlap while non-bold indicates intraspecific overlap.

	L01	L03	T02	T03	T04
L01	-	0.03 (0.00)	**0.24 (0.00)**	**0.24 (0.01)**	**0.06 (0.00)**
L03	0.03 (0.00)	-	**0.45 (0.04)**	**0.33 (0.02)**	**0.26 (0.00)**
T02	**0.24 (0.00)**	**0.45 (0.04)**	-	0.20 (0.01)	0.21 (0.00)
T03	**0.24 (0.01)**	**0.33 (0.02)**	0.20 (0.01)	-	0.52 (0.00)
T04	**0.06 (0.00)**	**0.26 (0.00)**	0.21 (0.00)	0.52 (0.00)	-

Results

At the within home range level, the UDOI for leopards × leopards was lower than the UDOI for both tigers × tigers and leopards × tigers (Table 1). The average UDOI between leopards was 0.04, between tigers 0.31 and between both tigers and leopards 0.26. This yielded leopard spatial overlap 2 to 17 times lower than that between tigers and between leopards and tigers (Fig. 1).

At the core area level, the UDOI for leopards × leopards and tigers × tigers were lower than leopards × tigers (Table 1). The average UDOI between leopards was 0, between tigers was 0.004 and between both tigers and leopards was 0.01 amounting to at least 2.5 times more interspecific spatial overlap relative to intraspecific spatial overlap (Table 1).

Differences in habitat preferences were greater between individuals than between species (Table 2). Of the two leopards, L03 used all available habitats proportional to availability while L01 exhibited significant selection for or against each available habitat type. Similarly, one tiger (T02) used each available habitat in proportion to its availability while the other two tigers exhibited significant selection for four out of the five available habitats. Both these tigers (T03 & T04) avoided dry deciduous forests and human-dominated areas, but T03 selected for teak plantations while T04 selected against it. They also had differing preferences for moist deciduous forests and coffee plantations. Leopards did not use coffee plantations or dry deciduous forests and only L03 used human-dominated areas. Tigers generally avoided these habitats.

Discussion

Intraspecific differences in both space use and habitat selection overwhelmed interspecific differences. Intraspecific spatial overlap was less than interspecific overlap implying that individuals avoid conspecifics more than heterospecifics. Furthermore, as leopards showed similar selection as tigers,

Table 2. Third order habitat selection for tigers and leopards in Nagarahole National Park, India. Human = human-dominated, Moist = moist deciduous forest, Dry = dry deciduous forest, Coffee = coffee plantation, Teak = teak plantation. * indicates significant preference.

Individual	Habitat	Number of Telemetry Points and Observed Proportion Used	95% Confidence Interval for Proportion Used	Expected Number of Points and Proportion Available	Preference
L01	Moist	18 (0.21)	0.11 – 0.31	30.35 (0.36)	less*
p=0.06	Teak	67 (0.79)	0.69 – 0.89	54.65 (0.64)	more*
L03	Human	4 (0.05)	-	2.89 (0.04)	-
p=0.89	Moist	9 (0.11)	-	7.77 (0.10)	-
	Teak	67 (0.84)	-	69.33 (0.87)	-
T02	Human	0 (0.0001)	-	0.40 (0.004)	-
p=1	Moist	0 (0.0001)	-	0.77 (0.008)	-
	Teak	100 (0.9999)	-	98.83 (0.99)	-
T03	Human	0 (0.0001)	-0.003 – 0.003	1.01 (0.02)	less*
p=0.04	Moist	15 (0.24)	0.10 – 0.38	18.01 (0.29)	-
	Dry	1 (0.02)	-0.03 – 0.06	7.18 (0.12)	less*
	Coffee	0 (0.0001)	-0.003 – 0.003	0.35 (0.01)	less*
	Teak	46 (0.74)	0.60 – 0.89	35.45(0.57)	more*
T04	Human	0 (0.0001)	-0.003 – 0.003	1.61 (0.02)	less*
p<0.01	Moist	40 (0.51)	0.37 – 0.66	18.69 (0.24)	more*
	Dry	1 (0.01)	-0.02 – 0.05	7.42 (0.10)	less*
	Coffee	4 (0.05)	-0.01 – 0.12	0.65 (0.01)	-
	Teak	33 (0.42)	0.28 – 0.57	49.64 (0.64)	less*

negative interspecific interactions with tigers may not strongly influence leopard habitat selection.

Intraspecific space use overlap was relatively minimal. The two resident male leopards exhibited minimal intraspecific spatial overlap consistent with solitary male carnivores defending their territories from other males (Sandell 1989). The three tigers, however, exhibited more overlap partly due to considering both female and non-resident tigers which may have different space use than residents (Karanth & Sunquist 2000). Therefore, intraspecific spacing patterns of the tigers and leopards likely influenced spatial overlap more than interspecific interactions.

Interspecific spatial overlap between tigers and leopards generally overwhelmed intraspecific spatial overlap especially for leopards. Leopard home ranges overlapped with tigers by on average 7 and as much as 17 times more than they overlapped with each other. At core areas, tigers were 2.5 times more likely to overlap with leopards than with other tigers.

Intraspecific differences and interspecific similarities also shaped habitat use. Within species, both leopards and tigers selected for different habitat. However, L03 and T02 used habitat in the same way and L01 used habitat most similarly to T03. All cats seemed to use moist deciduous forests and/or teak plantations more than other habitats, likely due to their higher ungulate biomass (Karanth & Sunquist 1992) which is consistent with prey driven habitat selection in other carnivores (Lendrum et al. 2014, Pilfold et al. 2014). The similar selection of leopards and tigers implies that tigers do not strongly influence leopard habitat selection.

In the Western Ghats of India both space use patterns and habitat selection suggest high overlap between competing felid species. How, then, are they able to coexist? Felids in this area generally show high temporal overlap (Karanth & Sunquist 2000, Karanth et al. 2017) but exhibit some fine-scale spatio-temporal differences (Karanth et al. 2017). In addition, prey partitioning by size is influential in their coexistence in the Western Ghats (Karanth & Sunquist 1995, 2000). In areas with lower prey density and lower availability of the large prey preferred by tigers (Karanth & Sunquist 1995, 2000), tigers can displace leopards (Odden et al. 2010, Harihar et al. 2011, Steinmetz et al. 2013). However, in Russia, leopards and tigers co-exist despite the lack of large prey and low prey biomass (Sugimoto et al. 2016).

Intraspecific interactions may dominate in this system, as leopards can avoid tigers by climbing trees (Karanth & Sunquist 2000). Additionally, intraspecific killing amongst African leopards is likely their greatest mortality source (Vanak et al. 2013). Thus, at least in some contexts, leopards may seek to minimise encounters with conspecifics more than with tigers implying that for some carnivores intraspecific encounters can be more dangerous than interspecific encounters.

Our finding of interspecific similarities and intraspecific differences was consistent across spatial scales (core area and home range), species (tigers and leopards) and analyses (space use overlap and habitat preference) emphasizing the robustness of our findings. Although we were not able to include all sympatric tigers and leopards possibly introducing some bias, we relied on detailed spatial telemetry data rather than felid signs or photographs to infer interspecific interactions. We also recognize that our infer-ence is limited by sample size; however, our five individuals are on par with other telemetry studies of tiger-leopard interactions (N=2, Seidensticker 1976; N=3, Rabinowitz 1989).

Our data suggest that in areas with high prey densities (91 animals/km^2, Karanth & Sunquist 1995) and adequate escape cover, tigers and leopards coexist despite selecting for similar habitats with high prey availability. In this context, intraspecific interactions, particularly negative ones, may overwhelm interspecific interactions.

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