Evaluating the effect of ecological and anthropogenic variables on site use by sympatric large carnivores in Gir protected area, Gujarat, India

Authors: Chaudhary, Rohit, Zehra, Nazneen, Musavi, Azra, and Khan, Jamal A.

Source: Wildlife Biology, 2020(4)

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.00696

Wildlife Biology 2020: wlb.00696
doi: 10.2981/wlb.00696
© 2020 The Authors. This is an Open Access article
Subject Editor: John Ball. Editor-in-Chief: Ilse Storch. Accepted 30 September 2020

Evaluating the effect of ecological and anthropogenic variables on site use by sympatric large carnivores in Gir protected area, Gujarat, India

Rohit Chaudhary, Nazneen Zehra, Azra Musavi and Jamal A. Khan

R. Chaudhary (https://orcid.org/0000-0003-4616-5057) ✉ (rchaudhary259@gmail.com), N. Zehra and J. A. Khan, Dept of Wildlife Sciences, Aligarh Muslim Univ., IN-202002 Uttar Pradesh, India. – A. Musavi, Centre for Women Studies, Aligarh Muslim Univ., Aligarh, Uttar Pradesh, India.

Habitat destruction is one of the major causes of large carnivore decline worldwide. The present study assesses the ecological and anthropogenic determinants of site use by leopard and lion in the Gir forest. Data on leopard and lion site use was collected through camera traps and modeled using prey availability, proximity to water, woody cover, proximity to human habitation and grazing intensity as the predictor variable. A generalized linear model was used to find the effect of a predictor variable on leopard and lion site use intensity. Leopard site use intensity was positively associated with chital, nilgai, and sambar availability, and grazing intensity while negatively associated with proximity to water. Lion site use intensity was positively associated with nilgai availability, woody cover and grazing intensity while negatively associated with sambar availability, and proximity to water. The present study indicated that habitat might have a substantial role in determining prey–predator spatial relationships. Also, humans provide resources such as artificial water holes could potentially affect the distribution of both the predators in our study area. The present study could be useful while making management decisions in Gir.

Keywords: Gir, habitat, large carnivore, prey, space use

Large carnivores can affect the structure and functioning of the ecosystem disproportionately due to their predatory behavior (Ford et al. 2014, Boyce 2018). Also, large carnivores provide ecosystem services (Gilbert et al. 2017) and livelihood options for local communities through ecotourism (Verma et al. 2017). Despite having such importance for ecosystem functioning and human wellbeing, large carnivores are facing a conservation crisis due to the collapse in their population worldwide (Ripple et al. 2014). For instance, more than half of the world's large carnivores have lost more than half of their historical range (Wolf and Ripple 2018). Large body size and predatory habitat results in specific habitat requirements of large carnivores, which make them susceptible to habitat loss and change (Woodroffe 2000), and hence loss of habitat is among one of the major causes of their population decline across the globe (Ripple et al. 2014). Anthropogenic use of lands in the form of activities such as farming, raising cattle and urban development has led to the loss and fragmentation of large carnivore habitat worldwide (Wolf and Ripple 2018). Protected areas around the globe are the only safe habitats available for persistent large carnivore populations (Yackulic et al. 2011, Le Saout et al. 2013). Despite having significant importance for large carnivore conservation, protected areas are also not free from human disturbances (Geldmann et al. 2019). Studies have found that human disturbance can potentially affect space use of large carnivores negatively inside the protected area which includes change in their spatial distribution, disruption in prey–predator relationship and restriction in movement (Ngoprasert et al. 2007, Muhly et al. 2011, Valeix et al. 2012, Tucker et al. 2018, Broekhuis et al. 2019). Therefore, assessing the space use of large carnivores in the protected area and understanding their resource use while living in sympatry with a human could be beneficial for their conservation and management.

Leopards *Panthera pardus fusca* and Asiatic lion *Panthera leo leo* (henceforth lion) are two threatened large carnivores that inhibit the Gir wildlife sanctuary and national park, Gujarat, India (henceforth Gir). Once they roamed from Persia to eastern India, but the Asiatic lion has faced a drastic decline in most of its range and has remained in a single population in Gir forest, Gujarat, India (Jhala et al. 2019). While leopards, despite their ecological plasticity and broad habitat requirements has witnessed a 70–90% population decline in India (Bhatt et al. 2020). Both the predators coexist with the semi-nomadic pastoralist community inside Gir called 'maldharis', which inhabitants live in bomas called 'ness' (Jhala et al. 2019). The Maldharis depend upon milk products for their livelihood and they used to graze cattle in Gir (Banerjee et al. 2013). Also, due to intense management and protection in Gir, there are high densities of both lion and leopards and also of their ungulate prey (Jhala et al. 2019, Khan et al. 2019). Despite being a significant area for large carnivore conservation, there is a paucity of information regarding fine-scale spatial relations between anthropogenic disturbances and crucial ecological variables such as grazing intensity and prey in Gir with two threatened predators. Lack of this information may hinder the proper conservation planning of these two threatened predators. Therefore, in the present study, we aimed to understand the site use of leopard and lion in Gir in relation to ecological and anthropogenic factors.

Based on earlier literature, we consider three ecological variables that can potentially affect the site use of leopard and lion. These include prey availability (Ramesh et al. 2012a, Davidson et al. 2014, Abade et al. 2019, Everatt et al. 2019), proximity to water (Mondal et al. 2013, Oriol-Cotterill et al. 2015) and woody cover (Bailey 1993, Karanth and Sunquist 2000, Van Cleave et al. 2018). Among anthropogenic variables, we consider grazing intensity (Everatt et al. 2019) and proximity to human habitation (Ngoprasert et al. 2007, Mondal et al. 2013, Abade et al. 2019). We hypothesize that both the predators will use sites more with high prey availability, closer proximity to water and considerable woody cover while using sites less with high grazing intensity and close proximity to human habitation. In relation to data analysis we further hypothesized that both the predators will show positive relationships with prey availability and woody cover while showing negative relationships with distance from ness and distance from water and grazing intensity.

Material and methods

Study area

The present study was carried out in Gir National Park and Sanctuary (Fig. 1) situated in semi-arid biogeographic zones (Rodgers and Panwar 1988) in Gujarat, India. Gir protected (20°57′–21°20′N, 70°27′–71°13′E) area consists of a wildlife sanctuary with an area of 1153 km^2 and national park with an area of 259 km^2. The forest type is very dry deciduous, and teak dominated (Champion and Seth 1968). There is a cool dry winter in Gir from December to March (average minimum 9°C) followed by a hot dry season (average maximum 42°C) which lasts until mid-June. Nearly 70% of the Gir in western and central part is dominated by *Tectona grandis* while eastern part of Gir is dominated with *Anogeissus latifolia*. Gir is divided into three management units: Sanctuary West (SW), National Park (NP) and Sanctuary East (SE). These units differ in terms of vegetation, rainfall, topography, human settlement density and, hence, habitat degradation. SW is moderately wooded; NP is more densely wooded while SE has open wooded grassland vegetation with undulating topography (Khan et al. 1996).

Data collection

Large carnivores due to their shy and nocturnal behavior hard to study in forested landscapes (Wang and Macdonald 2009). Camera traps have been proved a useful tool to study large carnivores due to their 24-h functioning. We select an intensive study area (ISA) representing major habitat types of 200 km^2 and deploy camera traps in this ISA. We follow systematic sampling while deploying the camera traps since it provides equal coverage to the sampled area (Ramesh et al. 2012a). We divided ISA in 50 grids of 4 km^2 and placed a camera trap in centroid or within 300 m of the centroid of each grid with an inter trap distance of 1.8–2 km. Large carnivores prefer to use trails and roads (Gogoi et al. 2020); therefore, in each grid camera traps were placed along trails and roads to maximize the captures of leopard and lion.

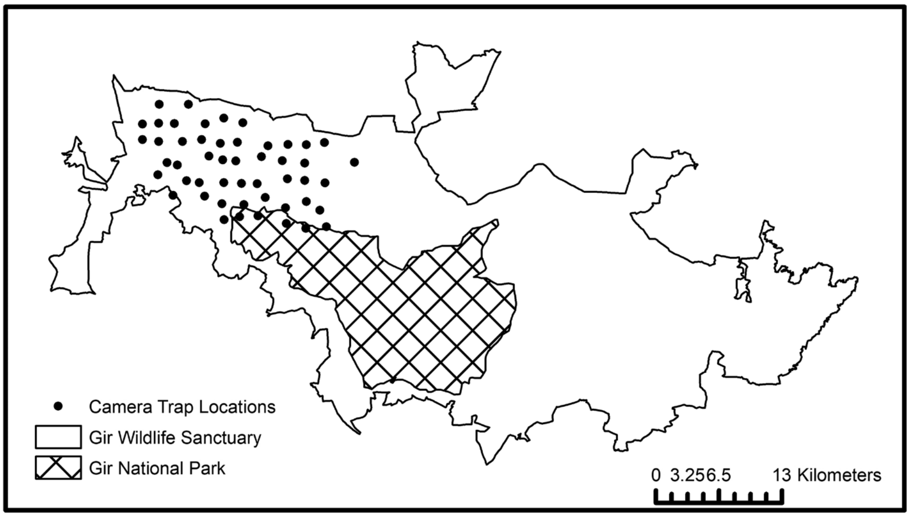

Figure 1. Map of study area along with camera trap locations.

Table 1. Summary of generalized linear model (GLM) use to assess site use of leopard and lion. Only parameters for the best set of models with ΔAICc < 2 are reported. Int. = intersection; df = degrees of freedom; log lik = log likelihood function; ΔAICc = difference in value of Akaike's information criterion between the focal model and the top-ranked model; Est. = estimator for the GLM average model. Variables are described in materials and methods.

Model	Int.	CA	SA	NA	DW	TA	GI	DN	df	log lik	ΔAICc	Weight
Leopard site use												
1	1.60	–	0.04	0.10	–0.56	–	0.001	–	5	–175.38	0.00	0.519
2	1.58	0.002	0.04	0.09	–0.5352	–	–	–	5	–176.014	1.25	0.27
3	1.68	–	0.04	0.10	–0.6057	–	–	–	4	–177.551	1.88	0.20
Est.	1.61	0.0005	0.04	0.10	–0.56	–	0.001	–				
SE	0.12	0.001	0.008	0.03	0.15	–	0.001	–				
Lion site use												
1	1.66	–	–0.04	0.07	–0.67	–	0.006	–	5	–189.21	0.00	0.35
2	1.42	–	–0.04	0.07	–0.65	0.01	0.005	–	6	–188.05	0.21	0.32
3	1.49	–	–0.04	–	–0.66	0.01	0.005	–	5	–190.008	1.58	0.16
4	1.74	–	–0.04	–	–0.68	–	0.006	–	4	–191.255	1.63	0.15
Est.	1.54	–	–0.04	0.06	–0.66	0.007	0.005	–				
SE	0.21	–	0.02	0.04	0.17	0.009	0.006					

Camera traps were operated for 24 h with a 5-s interval between photographs and monitored three times a week to check functioning and retrieve pictures. The camera traps were placed at the height of 35 cm above the ground and 3–4 m away from the trails and roads (Ramesh et al. 2012a), from March 2017 to June 2017 and November to January 2017–2018, resulting in a total effort of effort of 2246 trap nights (one trap night is equal to 24 h) (42 ± 3.5; mean ± SE trap nights each site).

Ecological variable and anthropogenic variable

We consider the availability of chital *Axis axis* (CA), sambar *Rusa unicolor* (SA), nilgai *Boselaphus tragocamelus* (NA) since all three species contribute more than 60% of the diet of both the carnivores (Zehra et al. 2017). Prey availability was obtained by counting independent pictures (camera trap capture > 30 min) from camera trap data (Guerisoli et al. 2019). Distance from water (DW) was quantified using euclidean distance from a digitized map of Gir using ArcGis (ver. 10.3). We used tree abundance (TA) around each camera trap as a proxy for woody cover. Tree abundance was assessed by counting tree numbers in a camera trap centered circular plot of 20-m radius (Ramesh et al. 2012b). Among anthropogenic variables, we consider the distance from ness (DN) and grazing intensity (GI). Distance from ness was also quantified using euclidean distance from digitized map of Gir using ArcGis (ver. 10.3), while cattle independent pictures were used as a proxy for grazing intensity.

Data analysis

We used the generalized linear model (hereafter GLM) to test our hypothesis (Guisan et al. 2002, Zhao et al. 2017). Prior to run analysis, we reduce multicollinearity and remove highly correlated predictor variables (r > 70%) using the spearman rank correlation test (Nath et al. 2019). Leopard and lion independent captures at each site were used as response variable while variables defined in section ecological and anthropological variables were used as a predictor variables. Since our response variable includes count variables; therefore, we used the Poisson distribution with log link distribution (Guisan et al. 2002). We created a list of all possible models given a list of predictor variables considering additive effects only using the 'dredge' function of package MuMIn in program R and model with ΔAIC < 2 were considered as the final model (Guerisoli et al. 2019). Models were ranked using the Akaike information criterion adjusted for small sample size (AICc), while to evaluate the relative importance of each model among final models, we used ΔAIC and AIC weight (Burnham and Anderson 2002). Models with ΔAICc < 2 were averaged following Burnham and Anderson (2002). All analysis was carried out in program R ver. 4.0.2 (<www.r-project.org>).

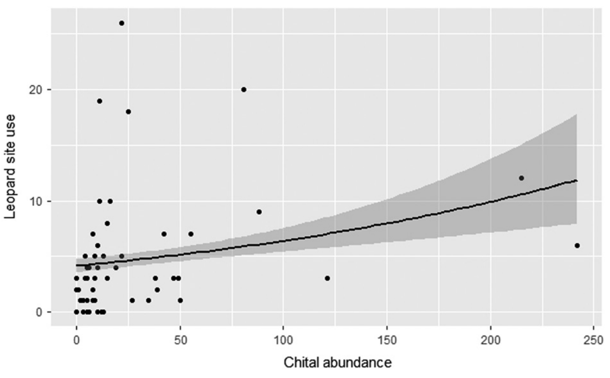

Figure 2. Relationship between leopard site use and chital abundance.

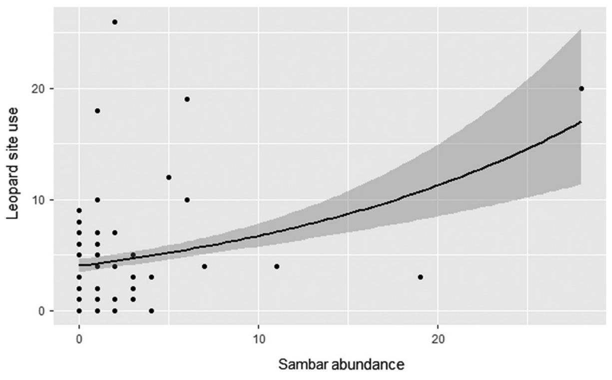

Figure 3. Relationship between leopard site use and sambar abundance.

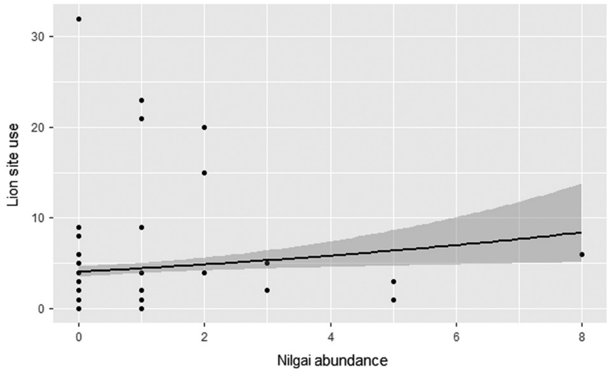

Figure 4. Relationship between leopard site use and nilgai abundance.

Results

We did not find any strong correlations among our predictor variables; so we retained all predictor variables (Supplementary material Appendix 1). We got 254 independent captures of leopards followed by 232 of lions. Among prey, we got 1479 pictures of chital followed by 133 of sambar and 38 of nilgai while we got 1119 captures of cattle. The average tree number per trap site was 17.3 ± 1.1 (mean ± SE). In the case of leopards, three models performed best with less than an ΔAIC < 2, while in the case of the lion, four models performed best with ΔAIC < 2 (Table 1). Predictor variables included in the case of leopards were chital, sambar and nilgai availability, distance from water and grazing intensity. Availability of chital (0.0005 ± (SE) 0.001) (Fig. 2), sambar (0.047 ± (SE) 0.008) (Fig. 3), nilgai (0.105 ± (SE) 0.033) (Fig. 4) and grazing intensity (0.001 ± (SE) 0.001) (Fig. 5) were associated positively with site use of leopard while the distance from the water was negatively associated (–0.56 ± (SE) 0.15) (Fig. 6) with site use of leopards. In the case of the lion, predictor variables included in the best models were sambar and nilgai availability, distance from water, grazing intensity and tree abundance. Nilgai abundance (0.061 ± (SE) 0.04) (Fig. 7), tree abundance (0.007 ± (SE) 0.009) (Fig. 8) and grazing intensity (0.005 ± (SE) 0.0006) (Fig. 9) were positively associated with lion site use while sambar availability (−0.04 ± (SE) 0.02) (Fig. 10) and distance from water was negatively associated with lion site use (−0.662 ± (SE) 0.171) (Fig. 11).

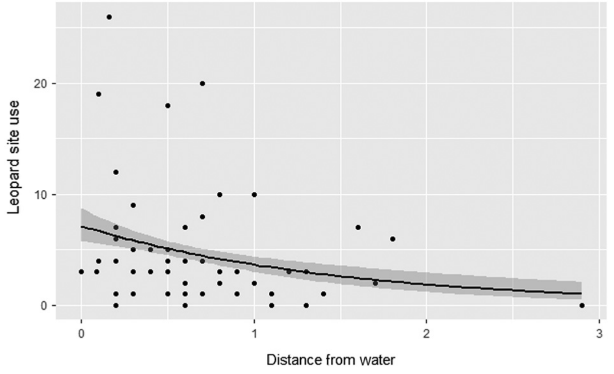

Figure 6. Relationship between leopard site use and distance from water.

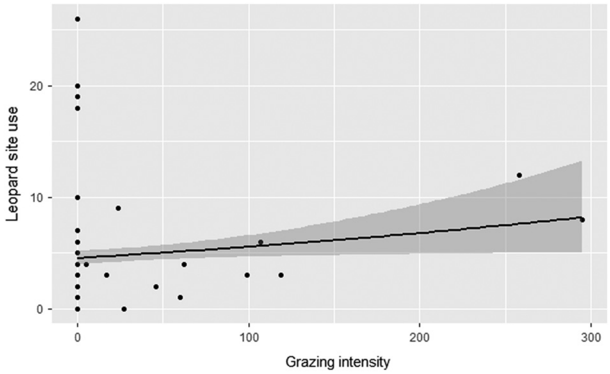

Figure 5. Relationship between leopard site use and grazing intensity.

Discussion

As we hypothesized, the availability of all three prey species showed a positive association with site use by leopards, which was also reported by earlier studies of leopards (Ramesh et al. 2012a, Mondal et al. 2013). All three species are high in biomass consumption of leopards, while sambar and nilgai are preferred prey species of leopards (Zehra et al. 2017). This positive association can be discussed in the light of foraging theory and habitat preferences of leopard and its prey. Foraging theory predicts that predators will use areas of high prey availability, which can result in high encounter rates and enhance their foraging success (MacArthur and Pianka 1966). Chital is within the preferred killing weight range of leopards (Hayward et al. 2006), small size of chital make handling process easy. Therefore, by using sites with high chital abundance leopards might increase their encounter rates with chital and hence foraging success. Positive association of leopard site use with sambar abundance may be the result of similar habitat preference and terrain use. Both sambar and leopard have strong preferences for dense habitat and undulating terrain (Khan et al. 1996, Chaudhary et al. 2019), consequently there is a strong positive association between leopard site use and sambar abundance. Nilgai in our study area have wide distribution and use diverse habitat (Chaudhary et al. 2019). This might result in a positive association between leopard site use. In the case of the lion, our analysis revealed more limited support since the lion showed a positive association with one prey i.e. nilgai and a negative

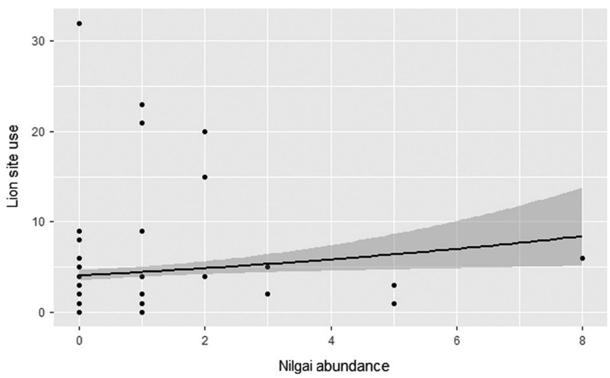

Figure 7. Relationship between lion site use and nilgai abundance.

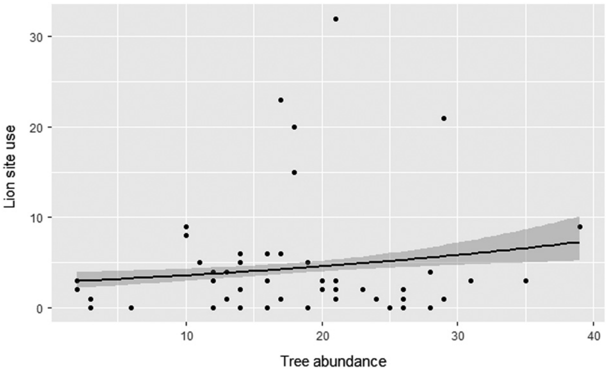

Figure 8. Relationship between lion site use and tree abundance.

association with sambar availability. Sambar and nilgai are preferred prey species for lion in Gir (Zehra et al. 2017). Earlier studies in the African ecosystem found that large prey affects lion space use positively (Everatt et al. 2019, Abade et al. 2020). Therefore, by using sites with high nilgai abundance lion seem to increase their hunting success. Negative site use relationships with sambar might be a result of their different terrain use. Sambar uses hilly and rugged terrain (Khan et al. 1996) while the lion used to prefer the area in flat valleys (Gogoi et al. 2020). This different use of terrain might result in a negative site use relationship between lion and sambar. Gogoi et al. (2020), while creating a density surface model for lion, also found that the lion density surface was negatively associated with the sambar density surface in Gir. However, sambar is among the preferred prey species of lions, and looking at the negative spatial relationship at a fine scale (present study) as well at the broad-scale (Gogoi et al. 2020) it would be an interesting question for further research into what spatial conditions favour lions killing sambar.

In case of human disturbance, our analyses we did not support our hypothesis since both leopard and lion site use was positively associated with grazing intensity, and distance from ness had no effect on leopard and lion site use, which is contrary to some earlier studies (Ngoprasert et al. 2007, Mondal et al. 2013, Everatt et al. 2019). Grazing in Gir is diurnal, while lion and leopards show crepuscular to nocturnal inactivity (Dave and Jhala 2011, Chaudhary et al. 2020). Therefore, there seems to be a temporal partitioning between cattle grazing and both the predators, with both the predators may use sites during night time when cattle are inside the ness.

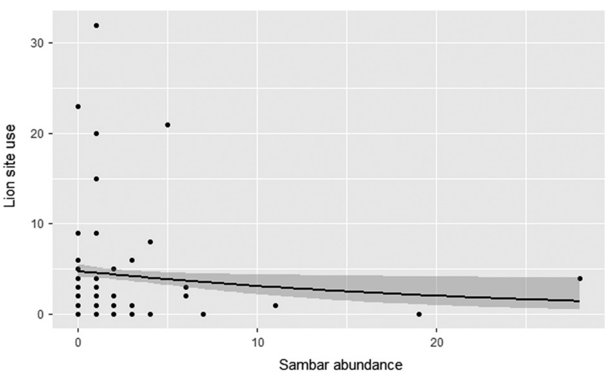

Figure 10. Relationship between lion site use and sambar abundance.

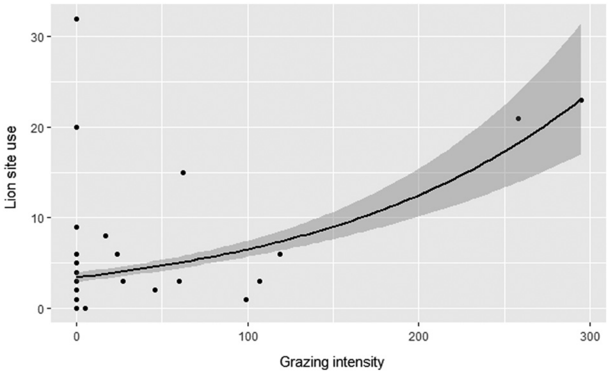

Figure 9. Relationship between lion site use and grazing intensity.

This topic of spatial association between leopard, lion and cattle grazing needs further research because, despite temporal partitioning, how both the predators respond to cattle grazing while their concurrent activity is not clear and our data set is not large enough to answer this question. Further, our hypothesis regarding the use of sites near water holes is supported in the case of both leopard and lion since both show a negative association with distance from water holes. Some earlier studies also found that water is a critical physiological requirement, especially in the arid ecosystem like ours (Mondal et al. 2013, Davidson et al. 2014), where water remains present in artificial water holes during most of the part of the year. Therefore, to fulfil their fundamental requirement for water, both the predators use sites near the water holes intensively. The tree abundance hypothesis was supported for lions site use since they were positively associated with tree abundance and did not have any association with leopards. Lions in Gir use flat areas extensively (Gogoi et al. 2020) which have less ground cover. Since lions are ambush predators (Hopcraft et al. 2005), sites with high tree abundance may provide woody cover for concealment of prey, consequently, there is a positive association between tree abundance and lion site use. Leopards prefer habitat in undulating and hilly terrain (Chaudhary et al. 2019) where shrub cover is high and therefore does not have to rely much on woody cover compared to lions.

Our study is among the first in Gir to reveal the site use of leopards and lions, which could have ecological and management implications. We found that habitat has a role in determining the prey–predator site-specific relationship, at least at the scale of our analysis. Change in habitat structure,

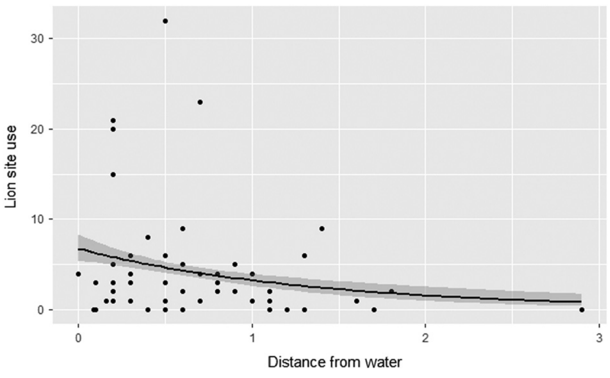

Figure 11. Relationship between lion site use and distance from water.

therefore, could have critical implications for the predator–prey spatial relationships in Gir. We also found that lion and leopard site use was not affected by grazing in Gir, which needs further investigation of predator space use with respect to grazing intensity since this is potentially very important to predator conservation. Proper planning is also needed while making artificial water holes since they seem to be one of the critical factors that have the potential for affecting the distribution of both predators.

Acknowledgements – Authors are thankful to chief wildlife warden of Gujarat state to provide permission for field work and Chief conservator of forest (Junagadh Circle) for facilitating the work. Authors are also thankful to deputy conservator of forest, Wildlife division Sasan and Gir west for providing necessary support in field work. We are also thankful to our field assistants Usmaan and Fatteh Mohamad who support us during our field work.

References

Abade, L. et al. 2019. The relative effects of prey availability, anthropogenic pressure and environmental variables on lion (*Panthera leo*) site use in Tanzania's Ruaha landscape during the dry season. – J. Zool. 310: 135–144.

Bailey, T. N. 1993. The African leopard: a study of the ecology and behaviour of a solitary felid. – Columbia Univ. Press.

Banerjee, K. et al. 2013. Living with lions: the economics of coexistence in the Gir forests, India. – PLoS One 8: e49457.

Bhatt, S. et al. 2020. Genetic analyses reveal population structure and recent decline in leopards (*Panthera pardus fusca*) across the Indian subcontinent. – Peer J. 8: e8482.

Boyce, M. S. 2018. Wolves for Yellowstone: dynamics in time and space. – J. Mamm. 99: 1021–1031.

Broekhuis, F. et al. 2019. Predators and pastoralists: how anthropogenic pressures inside wildlife areas influence carnivore space use and movement behaviour. – Anim. Conserv. 22: 404–416.

Burnham, K. P. and Anderson, D. R. (eds) 2002. Model selection and multimodel inference: a practical information–theoretic approach. – Springer.

Champion, H. G. and Seth, S. K. 1968. A revised survey of the forest types of India. – Govt. of India Press.

Chaudhary, R. et al. 2019. Status and habitat use of large mammals in Gir National Park and Sanctuary, Gujarat, India. – Int. J. Ecol. Environ. Sci. – 45: 257–266.

Chaudhary, R. et al. 2020. Spatio–temporal partitioning and coexistence between leopard (*Panthera pardus fusca*) and Asiatic lion (*Panthera leo persica*) in Gir protected area, Gujarat, India. – PLoS One 15: e0229045.

Dave, C. and Jhala, Y. V. 2011. Is competition with livestock detrimental for native wild ungulates? A case study of chital (*Axis axis*) in Gir Forest, India. – J. Trop. Ecol. 27: 239–247.

Davidson, Z. et al. 2014. Seasonal diet and prey preference of the African lion in a waterhole-driven semi-arid savanna. – PLoS One 8: e55182.

Everatt, K. T. et al. 2019. Africa's apex predator, the lion, is limited by interference and exploitative competition with humans. – Global Ecol. Conserv. 20: e00758.

Ford, A. T. et al. 2014. Large carnivores make savanna tree communities less thorny. – Science 346: 346–349.

Geldmann, J. et al. 2019. A global-level assessment of the effectiveness of protected areas at resisting anthropogenic pressures. – Proc. Natl Acad. Sci. USA 116: 23209–23215.

Gilbert, S. L. et al. 2017. Socioeconomic benefits of large carnivore recolonization through reduced wildlife–vehicle collisions. – Conserv. Lett. 10: 431–439.

Gogoi, K. et al. 2020. Spatially explicit density and its determinants for Asiatic lion in the Gir forest. – PLoS One 15: e0228374.

Guerisoli, M. M. et al. 2019. Habitat use and activity pattern of *Puma concolor* in a human dominated landscape of central Argentina. – J. Mamm. 100: 202–211.

Guisan, A. et al. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. – Ecol. Model. 157: 89–100.

Hayward, M. W. et al. 2006. Prey preferences of the leopards (*Panthera pardus*). – J. Zool. 270: 298–313.

Hopcraft, J. G. C. et al. 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. – J. Appl. Ecol. 74: 559–566.

Jhala, Y. V. et al. 2019 Asiatic lion: ecology, economics and politics of conservation. – Front. Ecol. Evol. 7: 1–21.

Karanth, K. U. and Sunquist, M. E. 2000. Behavioral correlates of predation by tiger (*Panthera tigris*) leopard (*Panthera pardus*) and dhole (*Cuon alpinus*) in Nagarahole, India. – J. Zool. 250: 255–265.

Khan, J. A. et al. 1996. Ungulate densities and biomass in the tropical dry deciduous forests of Gir, Gujarat, India. – J. Trop. Ecol. 12: 149–162.

Khan, J. A. et al. 2019. Monitoring structure, functioning and ecosystem services of a dry tropical forest ecosystem of Gir for conservation and management of ecosystem, prey population and predator. – Dept of Wildlife Sciences, Aligarh Muslim Univ., Aligarh. General Technical Report, pp. 1–120.

Le Saout, S. et al. 2013. Protected areas and effective biodiversity conservation. – Science 342: 803–805.

MacArthur, R. W. and Pianka, E. R. 1966. On optimal use of a patchy environment. – Am. Nat. 100: 603–609.

Mondal, K. et al. 2013. Factors influencing the distribution of leopard in a semiarid landscape of western India. – Acta Theriol. 58: 179–187.

Muhly, T. B. et al. 2011. Human activity helps prey win the predator–prey space race. – PLoS One 6: e17050.

Nath, A. et al. 2019. Sparrows in urban complexity: macro and micro-scale habitat use of sympatric sparrows in Guwahati City, India. – Urban Ecosyst. 22: 1047–1060.

Ngoprasert, D. et al. 2007. Human disturbance affects habitat use and behaviour of Asiatic leopard *Panthera pardus* in Kaeng Krachan National Park, Thailand. – Oryx 41: 343–351.

Oriol-Cotterill, A. et al. 2015. Spatio–temporal pattern of lion space use in a human dominated landscape. – Anim. Behav. 101: 27–39.

Ramesh, T. et al. 2012a. Spatio–temporal partitioning among large carnivores in relation to major prey species in Western Ghats. – J. Zool. 287: 269–275.

Ramesh, T. et al. 2012b. Factors affecting habitat patch use by sloth bears in Mudumalai Tiger Reserve, Western Ghats, India. – Ursus 23: 78–85.

Ripple, W. J. et al. 2014. Status and ecological effects of world's largest carnivores. – Science 343: 1241484.

Rodgers, W. A. and Panwar, S. H. 1988. Biogeographical classification of India. – New Forest Publication.

Tucker, M. A. et al. 2018. Moving in the Anthropocene: global reductions in terrestrial mammalian movements. – Science 359: 466–469.

Valeix, M. et al. 2012. Influence of prey dispersion on territory and group size of African lions: a test of resource dispersion hypothesis. – Ecology 93: 2490–2496.

Van Cleave, E. K. et al. 2018. Diel patterns of movement activity and habitat use by leopards (*Panthera pardus pardus*) living in a human-dominated landscape in central Kenya. – Biol. Conserv. 226: 224–237.

Verma, M. et al. 2017. Making the hidden visible: ECONOMIC valuation of tiger reserves in India. – Ecosyst. Serv. 26: 236–244.

Wang, S. W. and Macdonald, D. W. 2009. The use of camera traps for estimating tiger and leopard populations in the high-altitude mountains of Bhutan. – Biol. Conserv. 142: 606–613.

Wolf, C. and Ripple, W. J. 2018. Rewilding the world's large carnivores. – R. Soc. Open Sci. 5: 172235.

Woodroffe, R. 2000. Predators and people: using human densities to interpret declines of large carnivores. – Anim. Conserv. 3: 165–173.

Yackulic, C. B. et al. 2011. Anthropogenic and environmental drivers of modern range loss in large mammals. – Proc. Natl Acad. Sci. USA 108: 4024–4029.

Zehra, N. et al. 2017. Food habits of large carnivores in Gir national park and sanctuary, Gujarat, India. – World J. Zool. 12: 67–81.

Zhao, C. et al. 2017. Relationship between human disturbance and Endangered giant panda *Ailuropoda melanoleuca* habitat use in the Daxiangling Mountains. – Oryx 51: 146–152.

Supplementary material (available online as Appendix wlb-00696 at <www.wildlifebiology.org/appendix/wlb-00696>). Appendix 1.