Dietary niche differentiation facilitates coexistence of two large carnivores

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ABSTRACT

An animal's diet is an important attribute of its niche, and affects the role that it plays in the ecosystem. Comparing the diets of sympatric species reveals the level of dietary niche overlap between them, which can be used to gauge the potential for competition, as well as each species' vulnerability to competitive exclusion. Because of a morphology adapted to predation, sympatric carnivores can have particularly aggressive and dangerous competitive interactions; the intensity of which may be directly related to the amount of overlap in prey species consumed. Using predator scat analysis and prey survey techniques, we analyse and compare the underlying mechanisms of prey selection – prey body size and group size – between sympatric populations of leopard *Panthera pardus* and lion *Panthera leo*, to test for possible means of competitive avoidance between them. Because leopard and lion differ in both size and social structure, we controlled for the differing prey handling ability of each species, and found that there was still a significant difference in mean prey body size preference between the two carnivores ($P = 0.050$), despite a relatively high level of dietary niche overlap (0.717). Both species avoid prey in larger groups, but the tendency is more pronounced for leopards. Where intraguild competitors overlap spatiotemporally, dietary niche segregation such as this may be a mechanism through which competition is avoided and, in the case of carnivores, could reduce the frequency of potentially costly interactions.

KEYWORDS:
competition; intraguild; leopard; lion; predation; scat

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INTRODUCTION

The average carnivore in Africa overlaps in range with 26 other members of the order Carnivora, and feeds on the same prey as 22 of them (Caro and Stoner 2003). The leopard *Panthera pardus* has the largest natural range of any wild felid (Henschel et al. 2008; Nowell and Jackson 1996), and overlaps spatially with more intraguild competitors (N = 66) than any other predator (Caro and Stoner 2003). Comparable to their relationship with the larger tiger *Panthera tigris* in Asia (Harihar et al. 2011), leopard are competitively subordinate to lion *Panthera leo* in Africa (Macdonald et al. 2010; Palomares and Caro 1999). Competition may be reduced through temporal, spatial and dietary niche segregation (Pianka 1973), and here we investigate whether the level of dietary overlap could influence the competitive relationship between leopard and lion.

Among the large carnivores, the leopard consumes the widest range of prey, with 92 species reported in Africa, from mice to adult eland (Bailey 1993; Hayward et al. 2006). This dietary breadth, and prey size variation, could in part reflect the level of intraguild competition that leopards face throughout their range, and may be a means by which to relieve the potential effects of this competition. Caro and Stoner (2003) report that the leopard is the most vulnerable carnivore to exploitative competition, with 13 potential kleptoparasitic competitors in Africa – as many as 10% of their kills lost just to lion (Bertram 1979). In India, leopard were found to switch from a diet dominated by rodents to consumption of larger prey following extirpation of the local tiger population (Mondal et al. 2011), suggesting that leopard alter their behavioural ecology in relation to the level of intraguild competition.

Competition within the predator guild may force species into niches within which they are less efficient, impacting on their survival. This niche deviation may include habitat restricted hunting behaviour and limited prey accessibility (Harihar et al. 2011). The available prey within the ecosystem may be largely responsible for determining the carnivore guild component densities (Andheria et al. 2007; Karanth and Sunquist 1995), and selective killing could potentially facilitate their coexistence through ecological separation (Karanth and Sunquist 2000). Prey selection may in fact be more dependent on the level of intraguild competition than on the relationship between predator and prey body size (Radloff and Du Toit 2004).

Here we compare the diets of sympatric lion and leopard to investigate the level of dietary niche overlap between them. By considering only the prey species accessible to direct predation by both carnivores, we test for the mechanisms by which the level of dietary competition (as a proxy for general competitive potential) between lion and leopard may be alleviated. Specifically, we investigate the patterns of prey group size and prey body size utilisation between the carnivores to test for differences that may reduce competition. Knowledge of dietary overlap between sympatric carnivores may be particularly important in situations of asymmetric conservation attention, such as there is currently on the lion (e.g. Macdonald et al. 2016), which may increase the risk of competitive exclusion of sensitive or endangered species (e.g. Harihar et al. 2011).

We aimed to establish whether individual characteristics of prey selection, as a proxy for intraguild competition, potentially facilitate coexistence or exacerbate conflict between sympatric lion and leopard. We therefore hypothesize, firstly, that the differing social organisation and levels of intraspecies cooperation between leopard and lion would lead to different patterns in prey group size utilisation; and, secondly, that to reduce dietary competition between leopard and lion there would be a difference in prey body size selection after controlling for differences in each predator's prey handling ability.

METHODS

Study site

Between August 2010 and November 2012, carnivore scats were collected opportunistically on the 3,230 km^2 Bubye Valley Conservancy (BVC) in southern Zimbabwe (centred at 21°33.3ˈS, 30°06.0ˈE; 550 m elevation). BVC is a wildlife conservancy boasting the full complement of historically endemic species. The mean annual rainfall between 2007 and 2012 was 351 ± 76 mm, falling mostly during November through March with May through August being the driest months. Artificial water points are abundantly available throughout the conservancy, and help to sustain the wildlife in drought years. The vegetation on BVC is dominated by mopane *Colophospermum mopane* and acacia *Acacia* spp. scrub and woodland, traversed by seasonal drainage-lines and associated riparian vegetation, with dispersed patches of open grassland.

Lion and leopard dietary data

The most commonly used technique employed to determine predator dietary composition is identification and analysis of the undigested prey matter detected in a sample of their scats (Andheria et al. 2007; Klare et al. 2011). The volume, mass and frequency of each prey type detected may be modelled to define a species' diet, and allow determination of dietary overlap and niche partitioning between species (Klare et al. 2011). If a prey species is consumed in a greater proportion than it naturally occurs relative to other species, then this indicates that it is preferentially taken (Hayward et al. 2006), possibly because it is easier to kill (Schaller 1972). Klare et al. (2011) review and describe the most common methods of modelling carnivore diets from scat analyses, and conclude that biomass calculations tend to produce the most accurate depiction of actual predation and consumption.

Here we used samples of sympatric leopard and lion scats to determine and compare their diets; only fresh scats that were identifiable by the visible spoor of the carnivore that left them were collected. The majority of the scats were collected along roads and game trails (e.g. Figure 1).

Figure 1: Camera-trap image of a leopard and recently deposited scat (indicated by the arrow) *on a high-traffic game trail in the study site.*

Scat component identification and analysis

Identification of consumed prey was done almost solely on identification of hairs present in the scats (see Appendix 1). We classified scat prey remains to the highest taxonomic level possible (e.g. Klare et al. 2011) based on hair length, width, colour, cross-sectional shape and structure (Keogh 1985), as well as microscopy of their external scale patterns (Demarinis and Agnelli 1993; Mukherjee et al. 1994).

To avoid problems associated with regional variation, hair identification was based on a reference sample of 29 mammal species' collected from carcasses opportunistically encountered at the study site. Non-mammalian prey was identified using whatever undigested matter detectable in the scat, such feathers and claws.

Statistical analyses

All statistical analyses were done in R (R 3.2.1; R Core Team 2015).

Diet stabilisation curves of leopard and lion

To remove a potential source of error, strict criteria for including scats in the sample required that the scat had to be both fresh and accompanied by the spoor of the animal that left it. This led to many unusable scats, resulting in an accurate sample of 64 (wet season: 10; dry season: 54) leopard and 89 (wet season: 24; dry season: 65) lion scats (Supplementary Information 1a and 1b). A Fisher's exact test of prey species proportionality per season was non-significant for both leopard ($P = 0.895$) and lion ($P = 0.776$), and the seasonal samples were thus pooled for each predator.

Trites and Joy (2005) used Fisher's exact test on Monte Carlo simulations of frequency of occurrence methods to investigate the effect of sample size in scat analyses, calculating that a minimum of 59 scats is required to broadly describe a site specific species' diet (but see Mukherjee et al. 1994). Similarly, we undertook a diet stabilisation analysis to test whether our sample sizes were adequate. Using a *for* loop in R, for each number of subsequently collected scats since the first, we took 1,000 random samples from the analysed data set of both lion and leopard, and calculated the mean and standard deviation of the number of prey species present in each sample. This indicated that there were no significant additional prey species to be detected in our sample after analysing 55 leopard and 65 lion scats (Figure 2; but see Supplementary Information 2).

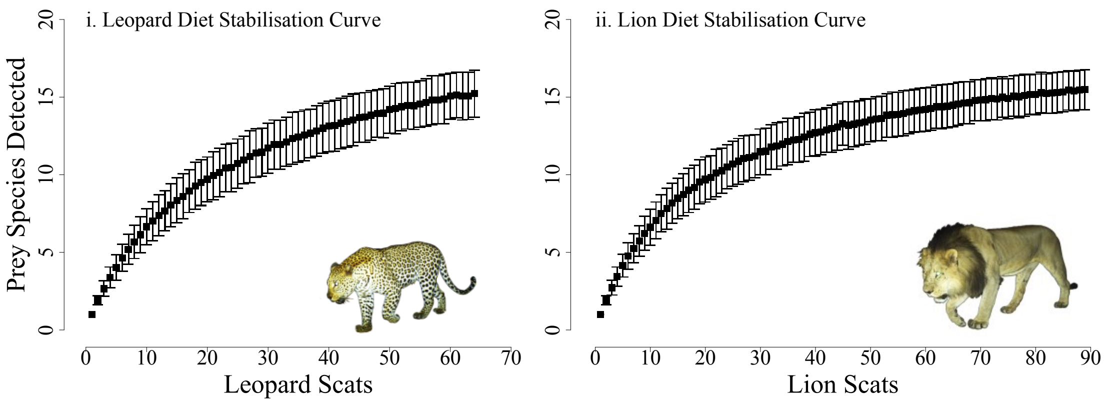

Figure 2: Diet stabilisation curves for leopard (Fig. 2i) and lion (Fig. 2ii). Points represent the mean number of prey species detected in increasing numbers of scats. Bars represent the standard deviation of the mean.

While scat analyses are inherently biased, this affects equally the results for both lion and leopard, and is not a confounding factor in their comparison (see Appendix 2). Increased sample sizes would probably reveal additional prey species (e.g. Bodendorfer et al. 2006; Trites and Joy 2005), however the aim of this research was not to exhaustively list each predator's menu, but to investigate the dietary niche overlap between them. For comparative purposes, categorising species by body size and social grouping behaviour was therefore sufficient.

Dietary analysis

Prey biomass consumption was calculated using Ackerman's equation, $Y = 1.980 + 0.035X$ [*where* X *is the prey species' mean female weight (kg), and* Y *is the weight of prey consumed per scat (kg)*], which was derived from feeding trials of captive cougars *Puma concolor* (see Ackerman et al. 1984). Comparative studies on leopard and lion digestion are not available, but assumed equivalent (e.g. Andheria et al. 2007; Henschel et al. 2005; Karanth and Sunquist 1995).

Prey species' body weights were taken from Kingdon and Hoffmann (2013a & b). There were breaks in the distribution of the mean female body mass of prey consumed (e.g. Packer 1983; Caro and Stoner 2003), and prey was therefore divided into the body size classes '*small*' (<5 kg), '*medium*' (5 – 100 kg), '*large*' (101 – 500 kg) and '*mega*' (>501 kg) based on these breaks (Figure 3).

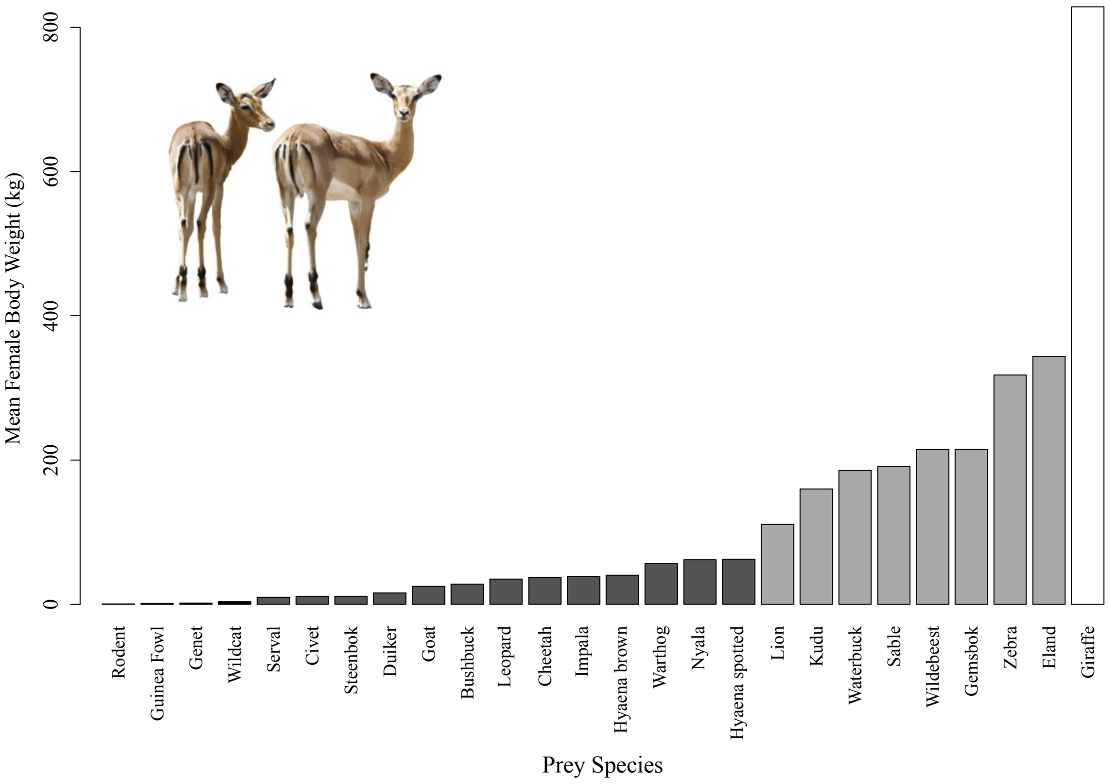

Figure 3: Distribution of the mean female body mass of prey species recorded in the scat samples of lion and leopard in this survey. Colour of the bars indicates the body size classification of each species (black = 'small'*, dark grey =* 'medium'*, light grey =* 'large'*, white =* 'mega'*). Only prey in the* 'mega' *body size class was inaccessible to leopard, and all prey in the* 'small', 'medium' *and* 'large' *body classes were considered available for consumption by both leopard and lion. [Inset top left: impala* Aepyceros melampus *ewes. Mean impala ewe body mass lies approximately at the median position in the body mass spectrum of the prey consumed by leopard and lion].*

Although the actual size of the animals killed cannot readily be determined from scat samples, it is likely that larger prey species detected in the leopard diet were juveniles (e.g. Radloff and Du Toit 2004); and we therefore recognise the potential limitation of direct prey body size inference due to the uncertainty of the actual size of prey consumed. However, intraspecific prey size variation is not important with respect to investigating niche segregation between the carnivores, as juveniles and adults of the same prey species are likely to associate spatiotemporally (see Estes 1991; Kingdon and Hoffmann 2013b). Therefore, even though there may be separation in the age/size class selection of the same prey species by each carnivore, there may be little spatial separation in actual predation behaviour and events when consuming the same prey species. Hunting different size classes of the same species could therefore still lead to incidents of predator interaction and conflict; and the potential ecological separation between the carnivores to reduce competition may still be tested without including data on the size of individuals consumed.

Predator prey preference

Prey selection preference was determined by comparing the proportional abundance of each species recorded in the scat samples to the proportional density of the species in the study site (e.g. Karanth and Sunquist 1995; Ramesh et al. 2009) (see Appendix 3), using Jacobs' index (Jacobs 1974), $D = r-p/((r+p)-(2rp))$ [*where* r *is the proportion of total kills containing a particular prey species, and* p *is the proportional abundance of that species detected in the ecosystem's prey population*].

To compare the similarity of the diet between lion and leopard, and their overlapping consumption of the same species, we used Pianka's multiplicative measure of niche overlap (Pianka 1973), $P = \sum p_{ij}p_{ik}/\sqrt{(\sum_i p_{ij}^2 \sum_i p_{ik}^2)}$ [*where* p_{ij} *is the percentage of prey* i *of* *predator* j*, and* p_{ik} *is the percentage of prey* i *of predator* k]. This index is a value between '*0*', indicating no dietary overlap, and '*1*', suggesting complete overlap.

Potential for dietary niche segregation between leopard and lion

The potential for dietary segregation between leopard and lion was considered separately in two different respects: prey group size, and prey body size.

The effect of prey group and body size on predation by each carnivore was first investigated with all prey for both species included. However, group and body size differences between the predators themselves means that lion are able to kill prey larger than is possible for leopard. Therefore, if a significant difference was detected either in group or body size selection, the data would be reanalysed including only those prey species accessible to both carnivores. By considering only those species available to predation by both leopard and lion means that any differences in the patterns of predation between them may be directly due to dietary niche segregation.

RESULTS

Jacobs' Indices of individual prey species

In total, 19 prey species were identified from 64 leopard scats, and 18 species from 89 lion scats. A Jacobs' Index value was calculated for each prey species to determine its comparative preference (relative to abundance) by each carnivore (see Supplementary Information 3).

Pianka's Index of niche overlap

In total there were 11 prey species common to leopard and lion, while eight species were preyed on exclusively by leopard, and seven by lion (see Supplementary Information 4). The Pianka Index of dietary overlap was calculated as 0.717 between the two carnivore species.

Prey group size preference

A linear model was used to regress the Jacobs' Index values of prey selection preference against prey group size, and was compared between the carnivores. This analysis revealed no significant difference in prey group size utilisation between lion and leopard (model: *lm(JacobsIndex~GroupSize*CarnivoreSpecies)*, $F_{3,48} = 0.793$, $P = 0.504$, $R^2 = 0.047$).

The mean Jacobs' Index values for each prey group size class were compared for the influence of group size on selection by each carnivore (Figure 4). Leopard and lion both displayed a decreasing trend of prey selection preference with increased group size; and although there was no significant difference in the trend of group size preference between the carnivores, this was more exaggerated for leopard than lion.

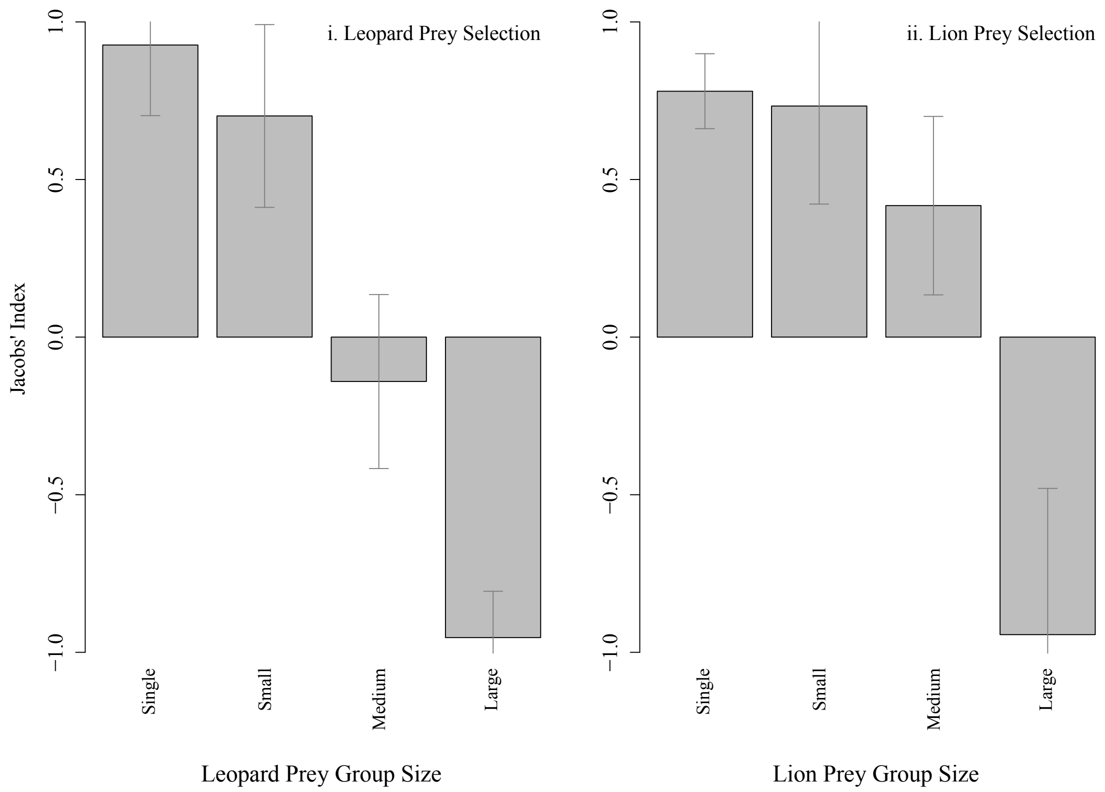

Figure 4: Jacobs' Indices indicating the mean and standard error leopard (Fig. 4i) and lion (Fig. 4ii) prey group size class preference.

Prey body size preference

A linear model was used to regress the Jacobs' Index values of lion and leopard prey selection preference against prey body weight, and compared between carnivores. This analysis revealed a significant difference in prey body size utilisation between lion and leopard (model: *lm(JacobsIndex~PreyMass*CarnivoreSpecies)*, $F_{3,48} = 4.126$, $P = 0.011$, $R^2 = 0.205$). The mean Jacobs' Index values for each prey body size class were compared as to the influence of prey body size on selection by each carnivore (Figure 5).

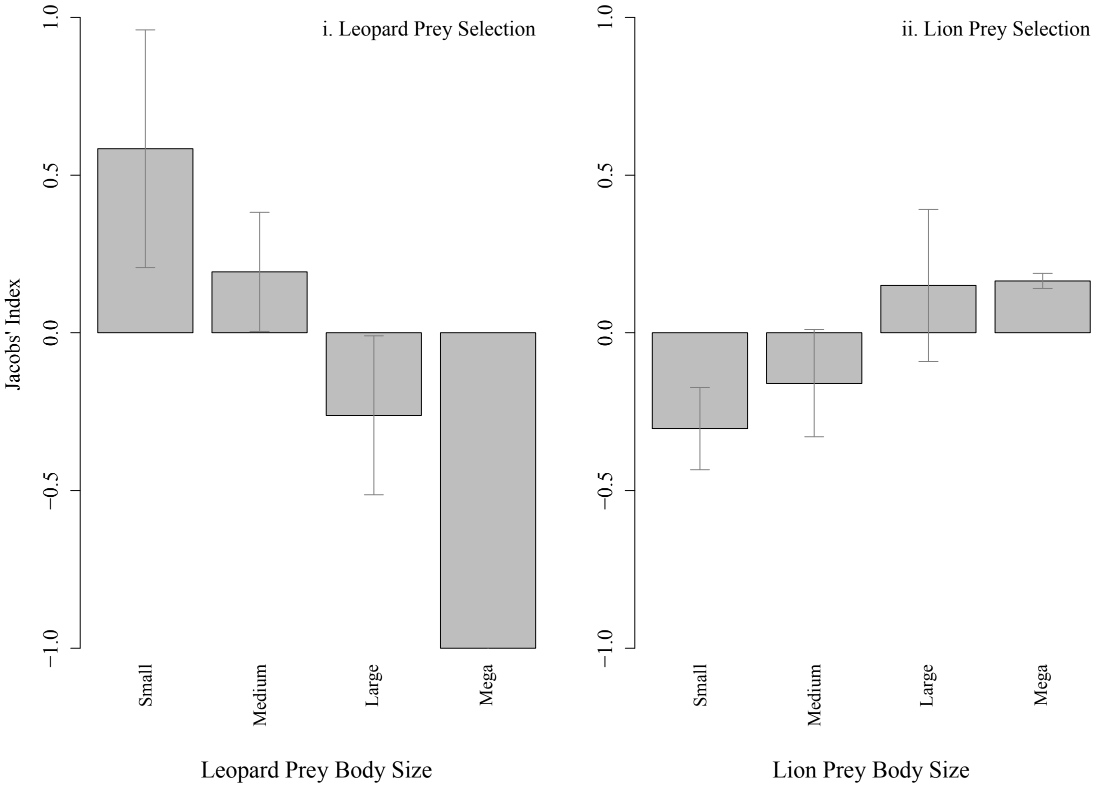

Figure 5: Jacobs' Indices indicating the mean and standard error leopard (Fig. 5i) and lion (Fig. 5ii) prey body size class selection preferences.

Potential dietary niche segregation between leopard and lion

Prey characterised by each group size ('*single*', '*small*', '*medium*' and '*large*') were represented in the scat samples of both leopard and lion, and there was no significant difference in the selection patterns of any of the classes between the carnivore species.

Prey of all the body size classes ('*small*', '*medium*', '*large*' and '*mega*') were detected in the lion scat samples; however, only three prey body size classes ('*small*', '*medium*' and '*large*') were detected in the leopard diet, with notable absence of the '*mega*' body size class. The overall comparison between leopard and lion diet revealed a significant difference in prey body size preference when all prey was included; however this analysis alone was not enough to determine whether this difference was due to dietary niche segregation, or whether it was just because of the physical disparity between the carnivores in terms of the maximum size of prey they could each handle.

Therefore, to test whether the difference in the prey body size utilisation between leopard and lion was due to selection by the individual carnivore, as opposed to differential ability to subdue large prey species, only those prey within the body size range consumed by both carnivores in this study were compared. This analysis revealed that there was still a significant difference in prey body size selection preference between the carnivores – despite the exclusion of prey accessible to only lion (model: *lm(JacobsIndex~PreyMass*CarnivoreSpecies)*, $F_{3,46} = 2.794$, $P = 0.050$, $R^2 = 0.099$). All of the prey considered in this analysis, including those preferentially selected for by lion, were within the body size range accessible to predation by leopard.

DISCUSSION

The difference in the body sizes of leopard and lion may largely be the result of long-term evolutionary adaptation, by one or both species, to reduce competition through allowing each carnivore to maximise the cost-benefit trade-off of preying on different sized animals. However, here we show that leopard and lion further reduce dietary competition with each other in the short-term by still selecting for different prey even within the body-size range accessible to predation by both carnivores.

Relative to their body and group sizes, leopards may kill proportionally larger prey than do lion – but that they are not selecting some prey within the limits of what they can handle suggests a trade-off in effort regarding killing versus consumption. Whilst leopard preferentially killed smaller prey species, this may be less due to their inability to kill large prey than their inability to defend it from kleptoparasitism; smaller prey items may either be instantly consumed, or are easier to cache. If lion density was reduced, and hence the level of kleptoparasitism lowered, the balance of predation risk/reward would be different, and under less competitive conditions leopard may select for larger prey, as has been found for cheetah (McVittie 1979), wild dog (Carbone et al. 1997), and insectivorous mammals (Dickman 1988).

The Pianka Index of dietary overlap between leopard and lion calculated here, at 0.717, was lower than reported between sympatric leopard and tiger, of 0.940 by Mondal et al. (2012a), 0.840 by Andheria et al. (2007) and 0.777 – 0.897 by Harihar et al. (2011). Where the dietary niches of sympatric competitors are identical, the species that can survive at the lowest resource density will outcompete and exclude the other (Odden et al. 2010). Preying on the same species increases the level of competition; but the ability to hunt a wider variety of prey may allow for dietary niche partitioning, and reduce the risk of encounters between carnivores (Andheria et al. 2007; Karanth and Sunquist 1995). Where leopard and tiger have high dietary overlap they may reduce competition by selecting different age and sex classes of prey (Mondal et al. 2012a), although increasing tiger density still resulted in a significant decline in leopard density (Mondal et al. 2012b).

That there was no significant difference in the prey group size utilisation between leopard and lion is not surprising. Despite any differences in leopard and lion social organisation that may result in different hunting strategies (e.g. Hayward et al. 2006), the success of the hunt may still depend on the predator being able to approach undetected to within a critical distance of the prey. Both carnivores favoured preying on smaller group sizes, which is likely due to a reduced level of vigilance and a greater chance of hunt success than there is in larger groups with higher levels of vigilance (e.g. Pays et al. 2012; Periquet et al. 2012).

CONCLUSION

Increased competition for prey may in turn lead to increased incidents of direct interaction and a greater level of interference competition between predators (Harihar et al. 2011). Competition between species may be directly related to their resultant density and, ultimately, their survival (e.g. Mondal et al. 2012b).

Sympatric carnivores, with similar predatory morphology, and that utilise the same prey resources, have the potential for both exploitative and interference competition (Caro and Stoner 2003; Durant 2000), which may include intraguild predation. In fact, more than a third of the prey species identified in this study were other carnivores (9/26). We found that differential prey selection may facilitate sympatry between lion and leopard by reducing the potential for competition between them.

ETHICS STATEMENT

No live animals were handled or disturbed during this study.

DATA ACCESSIBILITY

Supplementary Information 1: Tables 1 and 2
Supplementary Information 4: Table 3

COMPETING INTERESTS STATEMENT

The authors declare no competing interests.

AUTHORS' CONTRIBUTIONS

Collected the scats: BdP and PT. Processed the scats: JP. Conducted the sighted-transects: PT. Analysed the data: BdP. Produced first manuscript: BdP. Contributed to revisions: BdP, JP, PT, AJL and DWM. Oversaw the project: AJL and DWM

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REFERENCES

Ackerman, B.B., Lindzey, F.G., Hemker, T.P., 1984. Cougar Food-Habits in Southern Utah. Journal of Wildlife Management 48, 147-155.

Andheria, A.P., Karanth, K.U., Kumar, N.S., 2007. Diet and prey profiles of three sympatric large carnivores in Bandipur Tiger Reserve, India. Journal of Zoology 273, 169-175.

Bailey, T.N., 1993. The African leopard: Ecology and behavior of a solitary felid. Columbia University Press, New York.

Bertram, B.C.R., 1979. Serengeti Predators and Their Social Systems, In Serengeti: Dynamics of an Ecosystem. eds A.R.E. Sinclair, M. Norton-Griffiths, pp. 221-285. The University of Chicago Press, United States of America.

Bodendorfer, T., Hoppe-Dominik, B., Fischer, F., Linsenmair, K.E., 2006. Prey of the leopard (*Panthera pardus*) and the lion (*Panthera leo*) in the Comoe and Marahoue National Parks, Cote d'lvoire, West Africa. Mammalia 70, 231-246.

Breuer, T., 2005. Diet choice of large carnivores in northern Cameroon. African Journal of Ecology 43, 181-190.

Buckland, S.T., Anderson, D.R., Burnham, K.P., 1993. Distance Sampling: Estimating Abundance of Biological Populations. Chapman & Hall, London.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, Second edn. Springer Science, New York.

Carbone, C., DuToit, J.T., Gordon, I.J., 1997. Feeding success in African wild dogs: Does kleptoparasitism by spotted hyenas influence hunting group size? Journal of Animal Ecology 66, 318-326.

Carbone, C., Turvey, S.T., Bielby, J., 2011. Intra-guild competition and its implications for one of the biggest terrestrial predators, Tyrannosaurus rex. Proceedings of the Royal Society B-Biological Sciences 278, 2682-2690.

Caro, T.M., Stoner, C., 2003. The potential for interspecific competition among African carnivores. Biological Conservation 110, 67-75.

Demarinis, A.M., Agnelli, P., 1993. Guide to the Microscope Analysis of Italian Mammals Hairs - Insectivora, Rodentia and Lagomorpha. Bollettino Di Zoologia 60, 225-232.

Dickman, C.R., 1988. Body Size, Prey Size, and Community Structure in Insectivorous Mammals. Ecology 69, 569-580.

Durant, S.M., 2000. Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. Behavioral Ecology 11, 624-632.

Estes, R.D., 1991. The Behavior Guide to African Mammals: Including Hoofed Mammals, Carnivores, Primates. Russel Friedman Books CC, Halfway House, South Africa.

Floyd, T.J., Mech, L.D., Jordan, P.A., 1978. Relating Wolf Scat Content to Prey Consumed. Journal of Wildlife Management 42, 528-532.

Funston, P.J., Mills, M.G.L., Biggs, H.C., 2001. Factors affecting the hunting success of male and female lions in the Kruger National Park. Journal of Zoology 253, 419-431.

Harihar, A., Pandav, B., Goyal, S.P., 2011. Responses of leopard *Panthera pardus* to the recovery of a tiger *Panthera tigris* population. Journal of Applied Ecology 48, 806-814.

Hayward, M.W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G., Kerley, G.I.H., 2006. Prey preferences of the leopard (Panthera pardus). Journal of Zoology 270, 298-313.

Hayward, M.W., Kerley, G.I.H., 2005. Prey preferences of the lion (Panthera leo). Journal of Zoology 267, 309-322.

Hayward, M.W., Slotow, R., 2009. Temporal partitioning of activity in large African carnivores: tests of multiple hypotheses. South African Journal of Wildlife Research 39, 109-125.

Henschel, P., Abernethy, K.A., White, L.J.T., 2005. Leopard food habits in the Lope National Park, Gabon, Central Africa. African Journal of Ecology 43, 21-28.

Henschel, P., Hunter, L.T.B., Breitenmoser, U., Purchase, N., Packer, C., Khorozyan, I., Bauer, H., Marker, L., Sogbohossou, E., Breitenmoser-Wursten, C., 2008. *Panthera pardus.* IUCN Red List of Threatened Species. Version 2013-2. IUCN 2013.

Jacobs, J., 1974. Quantitative Measurement of Food Selection - Modification of Forage Ratio and Ivlevs Electivity Index. Oecologia 14, 413-417.

Johnson, K.G., Wang, W., Reid, D.G., Hu, J.C., 1993. Food-Habits of Asiatic Leopards (Panthera-Pardus Fusea) in Wolong Reserve, Sichuan, China. Journal of Mammalogy 74, 646-650.

Karanth, K.U., Sunquist, M.E., 1995. Prey Selection by Tiger, Leopard and Dhole in Tropical Forests. Journal of Animal Ecology 64, 439-450.

Karanth, K.U., Sunquist, M.E., 2000. Behavioural correlates of predation by tiger (*Panthera tigris*), leopard (*Panthera pardus*) and dhole (*Cuon alpinus*) in Nagarahole, India. Journal of Zoology 250, 255-265.

Karanth, K.U., Thomas, L., Kumar, N.S., 2002. Field Surveys: Estimating Absolute Densities of Prey Species Using Line Transect Sampling, In Monitoring Tigers and their Prey: A Manual for Researchers, Managers and Conservationists in Tropical Asia. eds K.U. Karanth, J.D. Nichols, pp. 111-120. Centre for Wildlife Studies, Bangalore, India.

Keogh, H.J., 1979. An atlas of hair from southern African species with reference to its taxonomic and ecological significance. University of Pretoria, Pretoria.

Keogh, H.J., 1985. A Photographic Reference System Based on the Cuticular Scale Patterns and Groove of the Hair of 44 Species of Southern African Cricetidae and Muridae. South African Journal of Wildlife Research 15, 109-159.

Kingdon, J., Hoffmann, M., 2013a. Carnivores, Pangolins, Equids and Rhinoceroses, In Mammals of Africa. eds J. Kingdon, D.C.D. Happold, T.M. Butynski, M. Hoffmann, M. Happold, J. Kalina, p. 560. Bloomsbury Publishing, London.

Kingdon, J., Hoffmann, M., 2013b. Pigs, Hippopotamuses, Chevrotain, Giraffes, Deer and Bovids, In Mammals of Africa. eds J. Kingdon, D.C.D. Happold, T.M. Butynski, M. Hoffmann, M. Happold, J. Kalina, p. 704. Bloomsbury Publishing, London.

Klare, U., Kamler, J.F., Macdonald, D.W., 2011. A comparison and critique of different scat-analysis methods for determining carnivore diet. Mammal Review 41, 294-312.

Macdonald, D.W., Jacobsen, K.S., Burnham, D., Johnson, P.J., Loveridge, A.J., 2016. Cecil: A Moment or a Movement? Analysis of Media Coverage of the Death of a Lion, Panthera leo. Animals 6.

Macdonald, D.W., Loveridge, A.J., Nowell, K., 2010. *Dramatis personae*: an introduction to the wild felids, In Biology and Conservation of Wild Felids. eds D.W. Macdonald, A.J. Loveridge, pp. 3-58. Oxford University Press Inc., New York, United States.

McVittie, R., 1979. Changes in the social behaviour of south west African cheetah. Madoqua 11, 171–184.

Mondal, K., Gupta, S., Bhattacharjee, S., Qureshi, Q., Sankar, K., 2012a. Prey selection, food habits and dietary overlap between leopard Panthera pardus (Mammalia: Carnivora) and re-introduced tiger Panthera tigris (Mammalia: Carnivora) in a semi-arid forest of Sariska Tiger Reserve, Western India. Italian Journal of Zoology 79, 607-616.

Mondal, K., Gupta, S., Bhattacharjee, S., Qureshi, Q., Sankar, K., 2012b. Response of leopards to re-introduced tigers in Sariska Tiger Reserve, Western India. international Journal of Biodiversity and Conservation 4, 228-236.

Mondal, K., Gupta, S., Qureshi, Q., Sankar, K., 2011. Prey selection and food habits of leopard (Panthera pardus fusca) in Sariska Tiger Reserve, Rajasthan, India. Mammalia 75, 201-205.

Mukherjee, S., Goyal, S.P., Chellam, R., 1994. Standardization of Scat Analysis Techniques for Leopard (Panthera-Pardus) in Gir-National-Park, Western India. Mammalia 58, 139-143.

Nowell, K., Jackson, P., 1996. Leopard, *Panthera pardus*, In Wild Cats: Status Survey and Conservation Action Plan. p. 406. IUCN, Switzerland.

Odden, M., Wegge, P., Fredriksen, T., 2010. Do tigers displace leopards? If so, why? Ecological Research 25, 875-881.

Palomares, F., Caro, T.M., 1999. Interspecific killing among mammalian carnivores. American Naturalist 153, 492-508.

Pays, O., Blanchard, P., Valeix, M., Chamaille-Jammes, S., Duncan, P., Periquet, S., Lombard, M., Ncube, G., Tarakini, T., Makuwe, E., Fritz, H., 2012. Detecting predators and locating competitors while foraging: an experimental study of a medium-sized herbivore in an African savanna. Oecologia 169, 419-430.

Periquet, S., Todd-Jones, L., Valeix, M., Stapelkamp, B., Elliot, N., Wijers, M., Pays, O., Fortin, D., Madzikanda, H., Fritz, H., Macdonald, D.W., Loveridge, A.J., 2012. Influence of immediate predation risk by lions on the vigilance of prey of different body size. Behavioral Ecology 23, 970-976.

Pianka, E.R., 1973. The Structure of Lizard Communities. Annual Review of Ecology and Systematics, 53-74.

Radloff, F.G.T., Du Toit, J.T., 2004. Large predators and their prey in a southern African savanna: a predator's size determines its prey size range. Journal of Animal Ecology 73, 410-423.

Ramakrishnan, U., Coss, R.G., Pelkey, N.W., 1999. Tiger decline caused by the reduction of large ungulate prey: evidence from a study of leopard diets in southern India. Biological Conservation 89, 113-120.

Ramesh, T., Kalle, R., Sankar, K., Qureshi, Q., 2012. Dietary partitioning in sympatric large carnivores in a tropical forest of Western Ghats, India. Mammal Study 37, 313-321.

Ramesh, T., Snehalatha, V., Sankar, K., Qureshi, Q., 2009. Food habits and prey selection of tiger and leopard in Mudumalai Tiger Reserve, Tamil Nadu, India. J. Sci. Trans. Environ. Technov. 2, 170-181.

Reynolds, J.C., Aebischer, N.J., 1991. Comparison and Quantification of Carnivore Diet by Fecal Analysis - a Critique, with Recommendations, Based on a Study of the Fox Vulpes-Vulpes. Mammal Review 21, 97-122.

Schaller, G.B., 1972. The Serengeti Lion: A Study of Predator-Prey Relations. University of Chicago Press.

Stander, P.E., 1998. Spoor counts as indices of large carnivore populations: the relationship between spoor frequency, sampling effort and true density. Journal of Applied Ecology 35, 378-385.

Thomas, L., Karanth, K.U., 2002. Statistical Concept: Estimating Absolute Densities of Prey Species Using Line Transect Sampling, In Monitoring Tigers and their Prey: A Manual for Researchers, Managers and Conservationists in Tropical Asia. eds K.U. Karanth, J.D. Nichols, pp. 87-109. Centre for Wildlife Studies, Bangalore, India.

Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Borchers, D.L., Buckland, S.T., Anderson, D.R., Burnham, K.P., Hedley, S.L., Pollard, J.H., 2001. DISTANCE 4.0 Beta 3. Research Unit for Wildlife Population Assessment, University of St. Andrews, Scotland, UK.

Trites, A.W., Joy, R., 2005. Dietary analysis from fecal samples: How many scats are enough? Journal of Mammalogy 86, 704-712.