

ORIGINAL RESEARCH

Understanding the effects of seasonal variation in prey availability on prey switching by large carnivores

M. Vettorazzi^{1,*}, N. Mogensen², B. Kaelo² & F. Broekhuis^{1,*} ¹Wildlife Ecology and Conservation Group, Wageningen University and Research, Wageningen, The Netherlands²Mara Predator Conservation Programme, Kenya Wildlife Trust, Nairobi, Kenya

Keywords

diet; large carnivore; prey availability; prey switching; migration; predator–prey interactions; *Panthera leo*; *Acinonyx jubatus*.

Correspondence

Femke Broekhuis, Wildlife Ecology and Conservation Group, Wageningen University and Research, Droevendaalsesteeg 3a, 6708 PB Wageningen, The Netherlands.
Email: femke.broekhuis@wur.nl

*Equal contribution

Editor: Matthew Hayward

Associate Editor: Stéphanie Périquet

Received 28 January 2022; revised 17 June 2022; accepted 18 August 2022

doi:10.1111/jzo.13013

Abstract

Optimal foraging theory predicts that carnivores select prey species based on intrinsic factors, such as body size, vulnerability, and abundance. Prey abundance can vary significantly, especially when prey species move in and out of an area *en masse* in search of food. However, little is known about how these resource pulses influence the prey profiles of large carnivores. Using data on lion (*Panthera leo*) and cheetah (*Acinonyx jubatus*) kills in the Maasai Mara in Kenya, we investigate whether changes in prey abundance, as a result of a mass annual migration of herbivores, influence the prey profiles of these two carnivore species. Furthermore, for cheetah we investigate whether there are sex-specific differences in prey profiles in response to changes in prey abundance. Using data from 387 lion kills and 220 cheetah kills (160 female and 60 male), we found that changes in prey abundance had a strong influence on prey profiles, but that for cheetahs this varied by sex and social grouping. More specifically, during the migration, when there is an influx of wildebeest (*Connochaetes taurinus*), lions and male cheetah (particularly those in coalitions) were more likely to feed on wildebeest than out of the migration. In addition, when wildebeest were less abundant, lions switched to buffalo (*Syncerus caffer*). Overall, the breadth of the prey profiles was narrower during the migration compared to out of the migration but this was most significant for lions and coalitions of male cheetahs. These changes in prey profiles could have an impact on herbivore dynamics, human-wildlife conflict and ecological interactions more broadly. Through the detailed characterisation of prey profiles, we contribute to the understanding of predator–prey dynamics and trophic interactions in complex, multi-species ecosystems and illustrate the importance of taking into account inter- and intraspecific variations in predators when modelling predator–prey dynamics.

Introduction

What animals consume is an integral part of animal ecology and food web dynamics as it can influence morphology (Van Valkenburgh & Wayne, 2010), body condition (Moorhouse-Gann et al., 2020), growth rate (Hooker et al., 2017), disease transmission (Gakuya et al., 2012), space-use (Broekhuis et al., 2021), intraguild predation (Palomares & Caro, 1999), competition (Helldin & Danielsson, 2007), predator–prey dynamics, and community composition (Ripple & Beschta, 2004). The optimal foraging theory predicts that predator species will prefer prey that yields the most energy per unit handling time, which can be influenced by the intrinsic factors of both predator and prey (e.g. size, defence mechanisms and health status) and abundance (less time is needed to find more abundant prey; MacArthur &

Pianka, 1966; Pyke et al., 1977). Therefore, as the abundance of preferred prey increases, the breadth of the prey profile should decrease as less profitable prey items are no longer of interest. Alternatively, if the abundance of preferred prey decreases, then there will be a switch to nonpreferred prey, a behaviour referred to as prey switching. Several studies have explored the drivers of prey switching (e.g. Kjellander & Nordström, 2003; van Leeuwen et al., 2013) but observational studies on prey switching in large carnivores in systems where they can choose between multiple different prey species are relatively scarce (e.g. Davidson et al., 2013; Elbroch et al., 2013; Owen-Smith & Mills, 2008). In addition, the effect that prey switching can have on the breadth of prey profiles, especially in complex, multi-species systems, is still unclear. Dietary breadth is however key in our mechanistic understanding of food web structure as it

provides an indication of the number of connections within a food web (Beckerman *et al.*, 2006). Furthermore, responses to changes in prey abundance could vary according to intraspecific factors, such as sex or social grouping (Moorhouse-Gann *et al.*, 2020), potentially adding additional complexity to food web dynamics.

Changes in prey abundance can be influenced by environmental conditions such as increased rainfall or periods of drought. For example, herbivores can time their births to coincide with increased food availability brought on by the rains (Ogutu *et al.*, 2011), whereas drought can increase their mortality as body conditions decrease due to a decrease in food availability (Abraham *et al.*, 2019). Indeed, it has been shown that carnivores, such as lions (*Panthera leo*), switch prey as a result of both these factors (Davidson *et al.*, 2013). However, changes in prey abundance can also come about through movement of individuals in and out of an area as animals migrate. This movement, often triggered by an increase in rainfall and plant productivity, can cause resource pulses where a hyperabundance of an ephemeral resource is followed by depletion through time. While research has shown that these resource pulses can have significant effects on food web dynamics (Yang *et al.*, 2010), there is paucity in our knowledge in terms of the effect that migratory prey can have on the prey profiles of large carnivores, especially in Africa.

In East Africa, approximately 1.4 million wildebeest (*Connochaetes taurinus*) and other ungulates, including plains zebra (*Equus quagga*) and Thomson's gazelle (*Gazella thomsoni*), migrate every year between their wet season range in the Serengeti, Tanzania, and their dry season range in the Maasai Mara, Kenya (Holdo *et al.*, 2009). This temporal hyperabundance of prey provides an opportunity to empirically test the impact of changes in prey availability on the prey profiles of large carnivores, in this case lion and cheetah (*Acinonyx jubatus*). In the Serengeti ecosystem in Tanzania, it has been shown that lion predation patterns vary as a result of this migration (Scheel & Packer, 1995). We build on this research by explicitly characterising lion prey profiles and comparing these between the migration and the period out of the migration. In addition, we incorporated cheetahs in the study to understand how responses between carnivore species may differ.

In general, lions prefer prey within the body mass range of 92–632 kg (Clements *et al.*, 2014), such as wildebeest and buffalo (*Syncerus caffer*), but occasionally kill smaller species (Hayward & Kerley, 2005), while cheetahs prefer prey within the body mass range of 14–40 kg (Clements *et al.*, 2014). However, cheetah prey profiles can vary according to sex (Broekhuis *et al.*, 2018; Clements *et al.*, 2016; Radloff & Du Toit, 2004; Rostro-García *et al.*, 2015), which is likely due to differences in sexual dimorphism and social structure. Female cheetahs tend to be smaller than males (Boast *et al.*, 2013; Caro, 1994) and are solitary, unless they are accompanied by dependent cubs. Male cheetahs, on the other hand, can either be solitary or form groups, known as coalitions, consisting of 2–5 individuals (Broekhuis *et al.*, 2019; Caro, 1994).

Using data on kills by lion and cheetah during and out of the annual wildebeest migration, we test the hypothesis that sudden differences in prey availability results in changes of large carnivore prey profiles. Based on the optimal foraging theory (MacArthur & Pianka, 1966; Pyke *et al.*, 1977), we predict that lion and cheetah will kill proportionally more wildebeest during the migration, when they are more abundant, compared to out of the migration. If this is the case, then we predict that the prey breadth during the migration will be narrower (less diverse) than out of the migration as other prey items might become less profitable due to a decrease in their relative abundance. As a result, we predict that, within each species/social group, the similarities in prey profiles between the two periods will differ, indicated by a low degree of overlap. However, because female cheetah tend to refrain from killing large prey such as wildebeest (Broekhuis *et al.*, 2018), we predict that differences in prey profiles will be more pronounced for male cheetahs, especially those in coalitions, than females.

Materials and methods

Study area

The study was conducted in the Greater Mara Ecosystem in south-west Kenya (1°S, 35°E; elevation c. 1700 m) where, to the south, it borders the Serengeti National Park in Tanzania. The study area experiences a bimodal rainfall pattern, with the wet season spanning November–June and the dry season July–October. The wet season is characterised by two distinct periods: the short rains (November–December) and the long rains (March–June; Ogutu *et al.*, 2008). The long rains attract the migrating wildebeest, plains zebra and Thomson's gazelle from the Serengeti. Generally, the migration peaks in the Maasai Mara in July after which the numbers slowly decline until most of the migrating individuals have returned to Tanzania in November (Stelfox *et al.*, 1986). Independent of the migration, substantial populations of wildebeest and Thomson's gazelle are resident year-round, along with other prey species such as buffalo, topi (*Damaliscus lunatus jimela*), Grant's gazelle (*G. granti*), impala (*Aepyceros melampus*), warthog (*Phacochoerus africanus*) and hares (*Lepus spp.*).

Data collection and processing

Between June 2013 and October 2020, vehicle-based data collection teams covered the ~2400 km² study area as uniformly as possible in search of lion and cheetah (see Broekhuis & Gopalaswamy, 2016 for details). When a lion or cheetah was sighted, and a feeding event was observed, the number of individuals present, date and time were recorded in addition to the prey species and whether the feeding event was due to predation or scavenging. Scavenging was either directly observed or inferred based on circumstantial evidence including the condition of the carcass and the presence of other predators. All scavenging and livestock predation events were removed prior to analysis. While both lion and cheetah kill livestock, this

rarely occurs within the wildlife areas, where the fieldwork occurred (Broekhuis *et al.*, 2018; Thuo *et al.*, 2020). For cheetahs, the data were split into the following categories: females, single males and male coalitions. No differentiation was made between females with or without cubs as their prey profiles are comparable (Broekhuis *et al.*, 2018). The kill data were classified into two distinct periods: one out of the wildebeest migration (January–May) and one during the wildebeest migration (July–November) with a 1-month gap between these two seasons (June and December).

Data analyses

To test whether lion and cheetah prey profiles were influenced by changes in prey availability, the composition and breadth of prey profiles were calculated for the two periods: during the migration and out of the migration. In addition, to determine whether there were any differences between the two periods, we quantified the overlap of the prey profiles, with a greater overlap indicating greater similarity. These metrics were calculated for lion and each cheetah social group.

Prey composition

The number of different prey species and the frequencies at which they were killed were quantified for lions and each cheetah social group for the two periods of varying prey availability: during the migration and out of the migration. In addition, we tested whether the frequency of the most commonly killed prey species differed between the two time periods using a chi-squared goodness-of-fit test or a Fisher's exact test if the expected frequency in a group was >5 . If a significant difference between the two periods was found, then post hoc tests with Bonferroni correction were conducted per prey species. Commonly killed prey species were classified as those that, per carnivore social group, had a total observed frequency ≥ 10 . Prey species below this threshold were grouped together in a category called 'Other'.

Prey profile breadth

For both periods (during and out of the migration), the breadth of each of the prey profiles (B_{pp}) was calculated using the Levin's index (Krebs, 1999):

$$B_{pp} = \frac{\left(\frac{1}{\sum p_i^2}\right) - 1}{n - 1}$$

where p_i is the proportion of prey species i killed by carnivore species p during a particular period and n is the number of observed prey species. In this study, n equals the number of prey species that were killed by each carnivore species during this study. Values close to 0 indicate that only a few different prey species were killed, whereas values close to 1 indicate that a wide variety of prey species were killed. To test whether there was a difference in the breadth of the carnivore prey profiles, a paired t-test was conducted.

Prey profile overlap

The percentage of overlap (O_{pp}) between the prey profiles during the migration and out of the migration was calculated following (Krebs, 1999):

$$O_{pp} = \left[\sum_{i=1}^n \left(\text{minimum } p_{ij}, p_{ik} \right) \right] 100$$

where p_{ij} is the proportion of prey species i in the prey profile during the migration and p_{ik} is the proportion of the same prey species i in the prey profile out of the migration. The overlap ranges from 0, when there are no common prey between the two periods, to 1, when the same prey are consumed in identical proportions between the two periods.

Results

In total, 607 kills were observed spanning 17 different prey species. Cheetah were observed killing a larger variety of prey species out of the migration compared to during the migration, but the opposite was observed for lions (Table 1). However, for both cheetahs and lions the frequency of observed kills across prey species was more evenly distributed out of the migration compared to during the migration resulting in differences in the breadths of the prey profiles (Table 1, Fig. 1). More specifically, the prey profiles were larger out of the migration compared to during the migration ($t = -3.11$, d.f. = 3, P -value = 0.05) indicating that during the migration cheetahs and lions disproportionately killed a smaller number of species. However, the effect of the migration on prey profiles differed for lions and the different cheetah social groups.

A total of 387 lion kills were observed (262 during the migration and 125 out of the migration) of 12 different prey species (Table 1). During the migration, lions were observed killing 11 different prey species and 10 different prey species out of the migration. Overall, the most commonly killed ($n_{\text{total}} \geq 10$) prey species for lions were wildebeest ($n_{\text{total}} = 245$, 63.31%), zebra ($n_{\text{total}} = 41$, 10.49%), buffalo ($n_{\text{total}} = 37$, 9.56%), warthog ($n_{\text{total}} = 22$, 5.68%) and topi ($n_{\text{total}} = 18$, 4.65%, Table 1). However, the proportions of the most commonly killed prey species differed between the two periods ($\chi^2 = 52.50$, d.f. = 5, P -value < 0.001 , Fig. 2). More specifically, the proportion of wildebeest kills was significantly higher during the migration compared to out of the migration (P -value < 0.001) but for buffalo the opposite was observed, with a significantly higher proportion of buffalo being killed out of the migration compared to during the migration (P -value < 0.001). These differences in the number of different species killed and the proportions at which they were killed resulted in differences in the breadth of the prey profiles between the two periods, with a greater breadth out of the migration ($B_{pp} = 0.28$) compared to during the migration ($B_{pp} = 0.07$, Fig. 1). As a result, the similarity between lion prey profiles between the two periods was 64.5%.

For cheetahs, a total of 220 kills were recorded (Table 1); 160 for females (95 during the migration and 65 out of the

migration), 32 for single males (22 during the migration and 10 out of the migration) and 28 for male coalitions (13 during the migration and 15 out of the migration). Female cheetah were observed feeding on 10 different prey species with the most commonly killed prey species being Thomson's gazelle ($n = 80$; 50%) and impala ($n = 44$; 27.5%), followed by Grant's gazelle ($n = 12$; 7.5%). When comparing the proportion of kills that were made of these three prey species during and out of the migration, no significant difference was found ($\chi^2 = 3.87$, d.f. = 3, P -value = 0.27, Fig. 3). However, there was a slight difference in the overall number of prey species that were killed as females were observed killing seven different prey species during the migration and 10 out of the migration. This resulted in the prey profile being slightly broader out of the migration ($B_{pp} = 0.17$) compared to during the migration ($B_{pp} = 0.14$, Fig. 1). However, the difference between the two prey profiles was small, as indicated by the large degree of overlap ($O_{pp} = 87.4\%$).

Of the 60 kills that were made by male cheetah, 32 were from single males and 28 from male coalitions. The number of different prey species that were consumed by single males barely differed between the two periods with five different species killed during the migration and six out of the migration. However, the proportion of each prey species did vary between the two periods which resulted in a much narrower prey profile breadth during the migration ($B_{pp} = 0.09$) compared to out of the migration ($B_{pp} = 0.24$, Fig. 4) which also meant that there was a lower degree of similarity in the prey profiles between the two periods ($O_{pp} = 76.40\%$) compared to female cheetahs. Most notably, single males preferred wildebeest but, while wildebeest were killed proportionally more during the migration (63.64%) compared to out of the migration (40.00%), this difference was not significant (Fisher's exact test; P -value = 0.27, Fig. 4).

The prey profiles of male coalitions, on the other hand, differed significantly between the two periods. Most notably, male coalitions killed a smaller variety of prey species during the migration ($n = 4$) compared to out of the migration ($n = 7$) and at varying proportions. Indeed, wildebeest, which were the most commonly killed prey species by male coalitions, comprised only 26.67% of their prey profile out of the migration but this increased significantly to 76.92% during the migration ($\chi^2 = 5.17$, d.f. = 1, P -value = 0.02, Fig. 4). As a result, the breadth of the prey profile of male coalitions was considerably smaller during the migration ($B_{pp} = 0.05$) compared to out of the migration ($B_{pp} = 0.33$, Fig. 1). Consequently, there was only a 33.30% similarity between the prey profiles during the migration and out of the migration.

Discussion

Our results show that ephemeral changes in prey abundance can have a significant impact on large carnivore prey profiles, but that responses between, and even within, carnivore species can differ. In line with the optimal foraging theory, the proportion of wildebeest kills by lions and male cheetah (especially those in coalitions) was positively associated with wildebeest abundance, higher during the migration compared to out of

the migration. In addition, the breadth of lion and male cheetah prey profiles was narrower during the migration compared to out of the migration. Our results suggest that prey switching does occur especially for lions who, out of the migration, made a distinct switch from wildebeest to buffalo. The occurrence of prey switching has been observed in various carnivore species, including Arctic foxes (*Vulpes lagopus*) who switch to preying on goose eggs when lemming (*Lemmus trimucronatus* and *Dicrostonyx groenlandicus*) densities are low (McKinnon et al., 2013). Similarly, other studies have found that lions switch between primary and alternative prey depending on their vulnerability and availability (Bissett et al., 2012; Davidson et al., 2013). Prey availability in these previous studies varied as a result of fluctuations in births and deaths, but our results indicate that similar responses occur when changes in prey availability are driven by changes in prey space use.

Similarly, out of the migration impala made up a significant proportion of the prey profiles of male cheetahs in a coalition, but not during the migration. However, our sample size for kills that were made by male cheetahs in coalitions was too small to test its significance. So, while the results show that the proportion of wildebeest consumed by males increases with increased availability, the impact that this might have on prey profiles might not be fully captured in our study. A study on lions in arid areas found that a sample size of more than 52 kills is needed to make robust inferences about lion prey profiles (Beukes et al., 2017). The same might be the case for male cheetahs; however, collecting data on male cheetahs is challenging not only because cheetah generally reside at low densities but also because males form coalitions thereby reducing the number of sampling units (Broekhuis et al., 2019; Broekhuis & Gopalaswamy, 2016). Despite the low sample size, our results corroborate those of Clements et al. (2016) who found that male coalitions killed larger prey species than female cheetahs.

Additionally, our results indicate that the impact of changes in prey abundance on prey profiles not only differs between carnivore species but also within. More specifically, we found that female cheetahs did not exhibit prey switching, indicating that wildebeest are not optimal prey for female cheetahs possibly due to factors related to morphology and increased risk of kleptoparasitism (Hayward et al., 2006). These results suggest that prey switching does not always occur when prey abundance changes as access to prey can be influenced by size, vulnerability and defence mechanism of both predator and prey (Tallian et al., 2017). However, female cheetahs, like lions and male cheetahs, did kill an increased number of prey species out of the migration resulting in a wider prey profile breadth. Numerous studies have shown that cheetah prey profiles can vary according to sex and group composition (Broekhuis et al., 2018; Clements et al., 2016; Radloff & Du Toit, 2004; Rostro-García et al., 2015), and by showing that carnivores may additionally respond differently to changes in prey abundance, we highlight additional complexities of predator-prey dynamics.

It has been widely shown that prey switching is a dynamically important feature of food webs as it can have significant direct

Table 1 A summary of the prey composition of the prey profiles of lions (*Panthera leo*) and each cheetah (*Acinonyx jubatus*) social group both during and out of the annual wildebeest migration

Prey species	Lion						Cheetah					
	Migration		No Migration		Total		Migration		No Migration		Total	
	n	%	n	%	n	%	n	%	n	%	n	%
Buffalo	10	(3.8%)	27	(21.6%)	37	(10%)	1	(10%)	1	(10%)	2	(6.7%)
Bushbuck												
Coke's hartebeest												
Eland	3	(1.1%)	3	(2.4%)	6	(1.5%)	1	(1.5%)	1	(10%)	2	(6.7%)
Giraffe	5	(1.9%)	2	(1.6%)	7	(1.9%)	1	(4.5%)	1	(10%)	2	(6.7%)
Grant's gazelle												
Hare												
Hippo	2	(0.7%)	1	(0.8%)	3	(0.8%)	9	(9.5%)	3	(4.6%)	12	(3.3%)
Impala	1	(0.4%)	4	(3.2%)	5	(1.4%)	2	(2.1%)	3	(4.6%)	5	(1.4%)
Ostrich	1	(0.4%)			1	(0.3%)	28	(29.5%)	16	(24.6%)	44	(12.2%)
Reedbuck	1	(0.4%)			1	(0.3%)	3	(3.2%)	1	(1.5%)	4	(1.1%)
Thomson's gazelle												
Topi	10	(3.8%)	1	(0.8%)	11	(3.0%)	48	(50.5%)	32	(49.2%)	80	(22.2%)
Warthog	12	(4.6%)	8	(6.4%)	20	(5.4%)	1	(1.1%)	2	(3.1%)	3	(0.8%)
Waterbuck												
Wildebeest	195	(74.4%)	50	(40.0%)	245	(66.6%)	4	(4.2%)	5	(7.7%)	9	(2.5%)
Zebra	22	(8.4%)	19	(15.2%)	41	(11.1%)	14	(63.6%)	4	(40%)	18	(5.0%)
Total kills	262		125		387		95		65		160	
Total species	11		10		21		7		10		17	

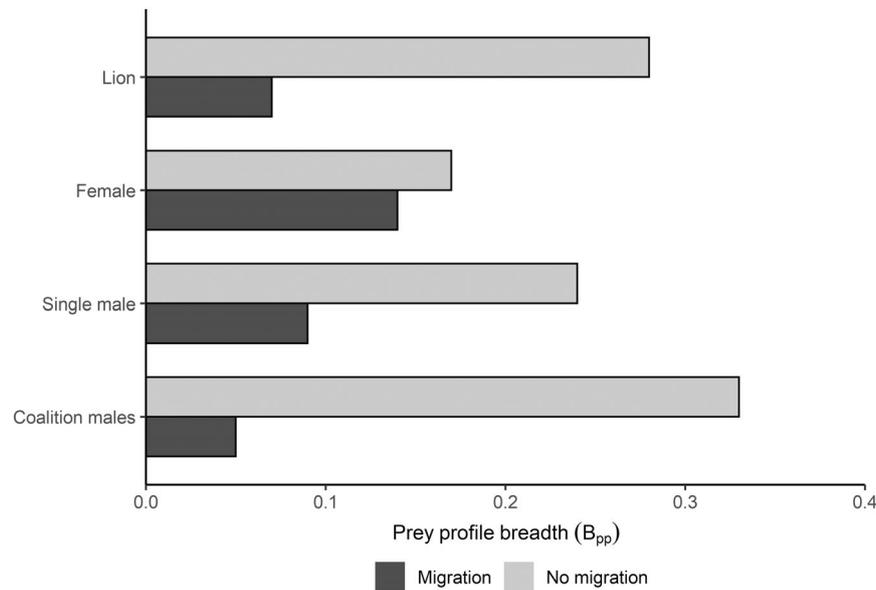


Figure 1 Prey profile breadths for lions (*Panthera leo*) and cheetah (*Acinonyx jubatus*) in the Maasai Mara, Kenya, during and out of the annual wildebeest migration.

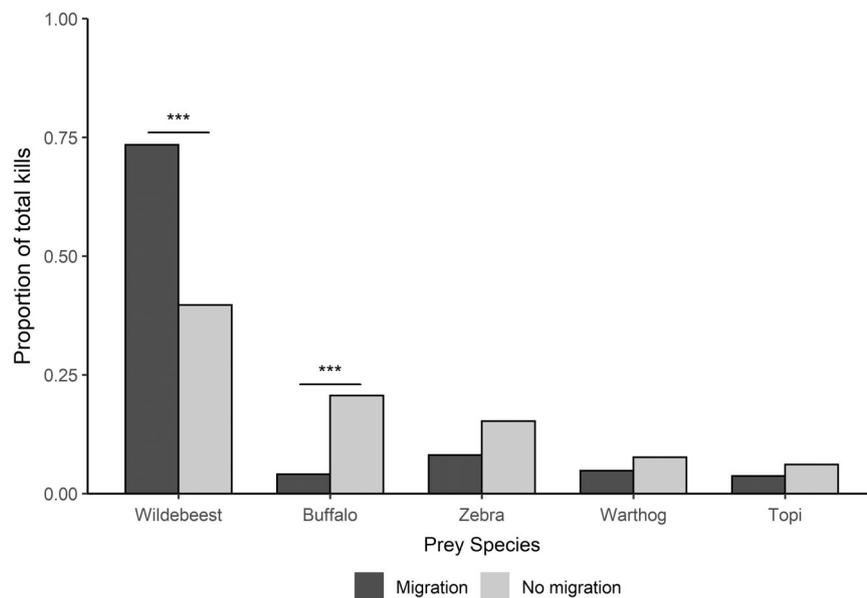


Figure 2 The proportion of kills by lions (*Panthera leo*) in the Maasai Mara, Kenya, during and out of the annual wildebeest migration. The category 'Other' is not shown in this graph. ***Bonferroni-corrected P -values <0.001 .

and indirect effects (Abrams *et al.*, 1998). For example, when primary prey is abundant it gives alternative prey a chance to recover in what is called *apparent mutualism*. This has been observed in Tarangire, Tanzania, where during the wildebeest migration lion predation on giraffe (*Giraffa camelopardalis*) calves decreased and hence survival increased (Lee *et al.*, 2016). But prey switching can also have the opposite effect on the population of alternative prey through what is called *apparent*

competition. Predators can respond to resource pulses not just functionally but also numerically, either demographically through reproductive change (Chevallier *et al.*, 2020; Giroux *et al.*, 2012) or spatially through movement-induced aggregation (Broekhuis *et al.*, 2021). This increase in predator abundance, caused by an increase in abundance of primary prey, can consequently result in increased predation of alternative prey (Abrams *et al.*, 1998; Holt, 1977). As a result, resource pulses, such as large-scale

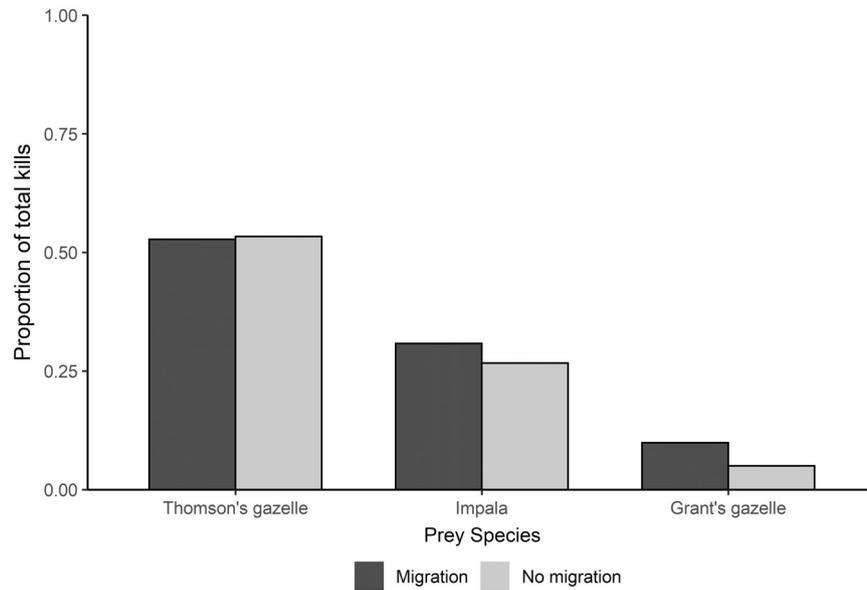


Figure 3 The proportion of kills made by female cheetah (*Acinonyx jubatus*) in the Maasai Mara, Kenya, during and out of the annual wildebeest migration. The category 'Other' is not shown in this graph.

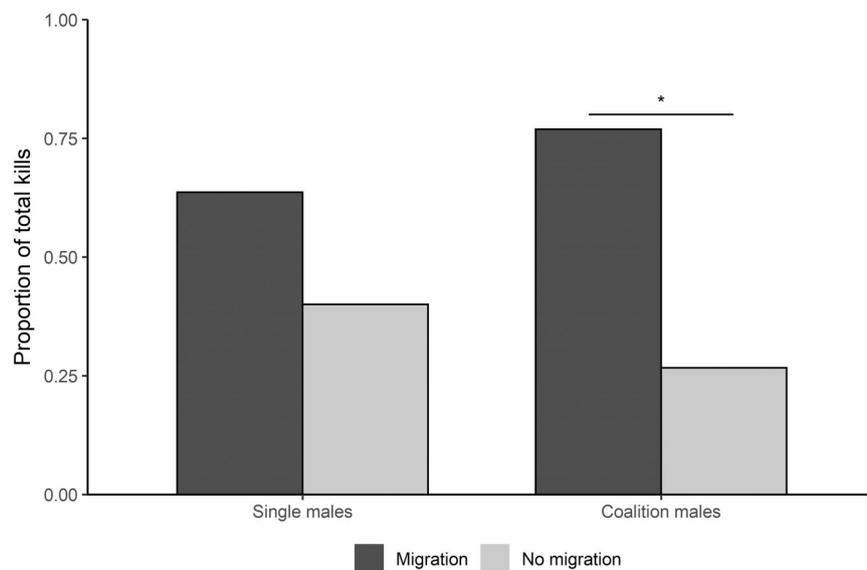


Figure 4 The proportion of wildebeest kills made by male cheetah (*Acinonyx jubatus*) in the Maasai Mara, Kenya, during and out of the annual wildebeest migration. *Bonferroni-corrected P -values <0.05 .

migrations, can have significant ecosystem impacts, by changing a system that is bottom-up driven, through increased prey abundance during the migration, to one that is driven by top-down predator effects out of the migration (Jaksic *et al.*, 1997). In the Maasai Mara, carnivores are likely to have a substantial impact on herbivore populations as the densities of lion and cheetah are high (lion density = 17.08 lions >1 year old/100 km², cheetah density = 0.66–1.39 independent cheetahs/100 km²), possibly one of the highest of any unfenced system (Broekhuis

et al., 2021; Elliot & Gopalaswamy, 2017), and thus their impacts, especially that of lions, can be significant.

While there may have been interannual variation in environmental conditions, such as rainfall (Bartzke *et al.*, 2018), we did not observe changes in the migration and we assumed that environmental conditions did not influence our sampling effort, supported by the fact that our findings are in line with previous research. Estimating seasonal herbivore abundance would provide insights into potential interannual variation in

predator–prey dynamics. While this is a challenging undertaking for a large study area with high densities of wildlife, this may be possible in the future with technological and computational advancements (Marchowski, 2021).

Our findings, which are supported by ecological theory, could have wider conservation implications (Bagchi, 2019). For example, the fact that carnivore prey profiles are influenced by changes in prey abundance could have an impact on the presence and prevalence of human-wildlife conflict. Indeed, large carnivores such as wolves (*Canis lupus*) are more likely to prey on livestock when the abundance of primary wild prey is low (Sidorovich *et al.*, 2003). In the case of the Maasai Mara, human-wildlife conflict is more likely to occur out of the migration when lions and male cheetahs look for alternative prey species (Mukeka *et al.*, 2019). In this study, we excluded data on livestock predation as livestock predation is most likely to occur outside protected areas where detection of predators can be difficult. As such, we would suggest that scats, in combination with molecular techniques (Thuo *et al.*, 2020), are used to quantify livestock predation between these two periods to test whether human-wildlife conflict is more likely to occur out of migration as a result of prey switching.

Prey switching can have a significant effect on predator–prey dynamics and community dynamics more broadly and is thought to have a stabilizing effect on food web dynamics (Tallian *et al.*, 2017). Understanding the impact of changes in prey abundance on carnivore populations provides key insights into their ecology and food web functioning. This is especially crucial as ecosystems are being transformed by anthropogenic pressures. For example, migration events across the globe are being negatively impacted by factors such as climate change and human-induced habitat loss and fragmentation (Kauffman *et al.*, 2021). Through the detailed characterisation of prey profiles, we contribute to the understanding of predator–prey dynamics and trophic interactions in complex, multi-species ecosystems and illustrate the importance of taking into account inter- and intraspecific variations when modelling predator–prey dynamics.

Acknowledgements

Permissions for this study were granted by the National Commission for Science, Technology and Innovation (permit no.: NACOSTI/P/16/69633/10821), the Kenya Wildlife Service (permit no.: KWS/BRM/5001), Narok County Government and the management of the conservancies. This study was funded by the African Wildlife Foundation, BAND Foundation, Vidda Foundation, WWF-UK, WWF-Kenya and numerous private donors. We would like to thank the research team in the Mara for assisting with data collection and Dennis Sonkoi for helping translate the abstract into Swahili.

Author contributions

FB conceived the ideas; NM, BK and FB collected the data; MV, NM and FB analysed the data; MV and FB led the

writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

References

- Abraham, J. O., Hempson, G. P., & Staver, A. C. (2019). Drought-response strategies of savanna herbivores. *Ecology and Evolution*, **9**, 7047–7056.
- Abrams, P. A., Holt, R. D., & Roth, J. D. (1998). Apparent competition or apparent mutualism? Shared predation when populations cycle. *Ecology*, **79**, 201–212.
- Bagchi, S. (2019). Conserving large carnivores amidst human-wildlife conflict: The scope of ecological theory to guide conservation practice. *Food Webs*, **18**, e00108.
- Bartzke, G. S., Ogotu, J. O., Mukhopadhyay, S., Mtui, D., Dublin, H. T., & Piepho, H.-P. (2018). Rainfall trends and variation in the Maasai Mara ecosystem and their implications for animal population and biodiversity dynamics. *PLoS One*, **13**, e0202814.
- Beckerman, A. P., Petchey, O. L., & Warren, P. H. (2006). Foraging biology predicts food web complexity. *Proceedings of the National Academy of Sciences*, **103**, 13745–13749.
- Beukes, M., Radloff, F. G. T., & Ferreira, S. (2017). Estimating lion's prey species profile in an arid environment. *Journal of Zoology*, **303**, 136–144.
- Bissett, C., Bernard, R. T., & Parker, D. M. (2012). The response of lions (*Panthera leo*) to changes in prey abundance on an enclosed reserve in South Africa. *Acta Theriologica*, **57**, 225–231.
- Boast, L. K., Houser, A. M., Good, K., & Gusset, M. (2013). Regional variation in body size of the cheetah (*Acinonyx jubatus*). *Journal of Mammalogy*, **94**, 1293–1297.
- Broekhuis, F., Elliot, N. B., Keiwua, K., Koinet, K., Macdonald, D. W., Mogensen, N., Thuo, D., & Gopalaswamy, A. M. (2021). Resource pulses influence the spatio-temporal dynamics of a large carnivore population. *Ecography*, **44**, 358–369.
- Broekhuis, F., & Gopalaswamy, A. M. (2016). Counting cats: Spatially explicit population estimates of cheetah (*Acinonyx jubatus*) using unstructured sampling data. *PLoS One*, **11**, e0153875.
- Broekhuis, F., Madsen, E. K., Keiwua, K., & Macdonald, D. W. (2019). Using GPS collars to investigate the frequency and behavioural outcomes of intraspecific interactions among carnivores: A case study of male cheetahs in the Maasai Mara, Kenya. *PLOS ONE*, **14**, e0213910.
- Broekhuis, F., Thuo, D., & Hayward, M. W. (2018). Feeding ecology of cheetahs in the Maasai Mara, Kenya and the potential for intra- and interspecific competition. *Journal of Zoology*, **304**, 65–72.
- Caro, T. M. (1994). *Cheetahs of the Serengeti: Group living in an asocial species*. The University of Chicago Press.
- Chevallier, C., Gauthier, G., Lai, S., & Berteaux, D. (2020). Pulsed food resources affect reproduction but not adult apparent survival in arctic foxes. *Oecologia*, **193**, 557–569.

- Clements, H. S., Tambling, C. J., Hayward, M. W., & Kerley, G. I. (2014). An objective approach to determining the weight ranges of prey preferred by and accessible to the five large African carnivores. *PLoS One*, **9**, e101054.
- Clements, H. S., Tambling, C. J., & Kerley, G. I. H. (2016). Prey morphology and predator sociality drive predator prey preferences. *Journal of Mammalogy*, **97**, 919–927.
- Davidson, Z., Valeix, M., Van Kesteren, F., Loveridge, A. J., Hunt, J. E., Murindagomo, F., & Macdonald, D. W. (2013). Seasonal diet and prey preference of the African Lion in a waterhole-driven semi-arid savanna. *PLoS One*, **8**, e55182.
- Elbroch, L. M., Lendrum, P. E., Newby, J., Quigley, H., & Craighead, D. (2013). Seasonal foraging ecology of non-migratory cougars in a system with migrating prey. *PLoS One*, **8**, e83375.
- Elliot, N. B., & Gopalaswamy, A. M. (2017). Toward accurate and precise estimates of lion density. *Conservation Biology*, **31**, 934–943.
- Gakuya, F., Ombui, J., Maingi, N., Muchemi, G., Ogara, W., Soriguer, R. C., & Alasaad, S. (2012). Sarcoptic mange and cheetah conservation in Masai Mara (Kenya): epidemiological study in a wildlife/livestock system. *Parasitology*, **139**, 1587–1595.
- Giroux, M.-A., Berteaux, D., Lecomte, N., Gauthier, G., Szor, G., & Bêty, J. (2012). Benefiting from a migratory prey: Spatio-temporal patterns in allochthonous subsidization of an arctic predator. *Journal of Animal Ecology*, **81**, 533–542.
- Hayward, M. W., Hofmeyr, M., O'Brien, J., & Kerley, G. I. H. (2006). Prey preferences of the cheetah (*Acinonyx jubatus*) (Felidae: Carnivora): Morphological limitations or the need to capture rapidly consumable prey before kleptoparasites arrive? *Journal of Zoology*, **270**, 615–627.
- Hayward, M. W., & Kerley, G. I. H. (2005). Prey preference of the lion (*Panthera leo*). *Journal of Zoology*, **267**, 309–322.
- Heldin, J.-O., and A. V. Danielsson. 2007. Changes in red fox *Vulpes vulpes* diet due to colonisation by lynx *Lynx lynx*. *Wildlife Biology* **13**:475–480, 476.
- Holdo, R. M., Holt, R. D., & Fryxell, J. M. (2009). Opposing rainfall and plant nutritional gradients best explain the wildebeest migration in the Serengeti. *The American Naturalist*, **173**, 431–445.
- Holt, R. D. (1977). Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology*, **12**, 197–229.
- Hooker, O. E., Van Leeuwen, T. E., & Adams, C. E. (2017). The physiological costs of prey switching reinforce foraging specialization. *Journal of Animal Ecology*, **86**, 605–614.
- Jaksic, F. M., Silva, S. I., Meserve, P. L., & Gutiérrez, J. R. (1997). A long-term study of vertebrate predator responses to an El Niño (ENSO) disturbance in Western South America. *Oikos*, **78**, 341–354.
- Kauffman, M. J., Aikens, E. O., Esmaili, S., Kaczensky, P., Middleton, A., Monteith, K. L., Morrison, T. A., Mueller, T., Sawyer, H., & Goheen, J. R. (2021). Causes, consequences, and conservation of ungulate migration. *Annual Review of Ecology, Evolution, and Systematics*, **52**, 453–478.
- Kjellander, P., & Nordström, J. (2003). Cyclic voles, prey switching in red fox, and roe deer dynamics—a test of the alternative prey hypothesis. *Oikos*, **101**, 338–344.
- Krebs, C. J. (1999). *Ecological methodology*. Addison-Wesley Educational Publishers, Inc.
- Lee, D. E., Kissui, B. M., Kiwango, Y. A., & Bond, M. L. (2016). Migratory herds of wildebeests and zebras indirectly affect calf survival of giraffes. *Ecology and Evolution*, **6**, 8402–8411.
- MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. *The American Naturalist*, **100**, 603–609.
- Marchowski, D. (2021). Drones, automatic counting tools, and artificial neural networks in wildlife population censusing. *Ecology and Evolution*, **11**, 16214–16227.
- McKinnon, L., Berteaux, D., Gauthier, G., & Bêty, J. (2013). Predator-mediated interactions between preferred, alternative and incidental prey in the arctic tundra. *Oikos*, **122**, 1042–1048.
- Moorhouse-Gann, R. J., Kean, E. F., Parry, G., Valladares, S., & Chadwick, E. A. (2020). Dietary complexity and hidden costs of prey switching in a generalist top predator. *Ecology and Evolution*, **10**, 6395–6408.
- Mukeka, J. M., Ogutu, J. O., Kanga, E., & Røskoft, E. (2019). Human-wildlife conflicts and their correlates in Narok County, Kenya. *Global Ecology and Conservation*, **18**, e00620.
- Ogutu, J., Piepho, H.-P., Dublin, H., Bhola, N., & Reid, R. (2011). Dynamics of births and juvenile recruitment in Mara–Serengeti ungulates in relation to climatic and land use changes. *Population Ecology*, **53**, 195–213.
- Ogutu, J. O., Piepho, H. P., Dublin, H. T., Bhola, N., & Reid, R. S. (2008). Rainfall influences on ungulate population abundance in the Mara–Serengeti ecosystem. *Journal of Animal Ecology*, **77**, 814–829.
- Owen-Smith, N., & Mills, M. G. (2008). Shifting prey selection generates contrasting herbivore dynamics within a large-mammal predator-prey web. *Ecology*, **89**, 1120–1133.
- Palomares, F., & Caro, T. M. (1999). Interspecific killing among mammalian carnivores. *The American Naturalist*, **153**, 492–508.
- Pyke, G. H., Pulliam, H. R., & Charnov, E. L. (1977). Optimal foraging: A selective review of theory and tests. *The Quarterly Review of Biology*, **52**, 137–154.
- 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.
- Ripple, W. J., & Beschta, R. L. (2004). Wolves and the ecology of fear: Can predation risk structure ecosystems? *Bioscience*, **54**, 755–766.
- Rostro-García, S., Kamler, J. F., & Hunter, L. T. B. (2015). To kill, stay or flee: The effects of lions and landscape factors on habitat and kill site selection of Cheetahs in South Africa. *PLoS One*, **10**, e0117743.

- Scheel, D., & Packer, C. (1995). Variation in predation by lions: Tracking a movable feast. In A. R. E. Sinclair & P. Arcese (Eds.), *Serengeti II: dynamics, management, and conservation of an ecosystem*. The University of Chicago Press.
- Sidorovich, V. E., L. L. Tikhomirova, & B. Jędrzejewska. 2003. Wolf *Canis lupus* numbers, diet and damage to livestock in relation to hunting and ungulate abundance in northeastern Belarus during 1990–2000. *Wildlife Biology* **9**, 103–111, 109.
- Stelfox, J. G., Peden, D. G., Epp, H., Hudson, R. J., Mbugua, S. W., Agatsiva, J. L., & Amuyunzu, C. L. (1986). Herbivore dynamics in Southern Narok, Kenya. *The Journal of Wildlife Management*, **50**, 339–347.
- Tallian, A., Smith, D. W., Stahler, D. R., Metz, M. C., Wallen, R. L., Geremia, C., Ruprecht, J., Wyman, C. T., & MacNulty, D. R. (2017). Predator foraging response to a resurgent dangerous prey. *Functional Ecology*, **31**, 1418–1429.
- Thuo, D., Broekhuis, F., Furlan, E., Bertola, L. D., Kamau, J., & Gleeson, D. M. (2020). An insight into the prey spectra and livestock predation by cheetahs in Kenya using faecal DNA metabarcoding. *Zoology*, **143**, 125853.
- van Leeuwen, E., Brännström, Å., Jansen, V. A. A., Dieckmann, U., & Rossberg, A. G. (2013). A generalized functional response for predators that switch between multiple prey species. *Journal of Theoretical Biology*, **328**, 89–98.
- Van Valkenburgh, B., & Wayne, R. K. (2010). Carnivores. *Current Biology*, **20**, R915–R919.
- Yang, L. H., Edwards, K. F., Byrnes, J. E., Bastow, J. L., Wright, A. N., & Spence, K. O. (2010). A meta-analysis of resource pulse–consumer interactions. *Ecological Monographs*, **80**, 125–151.