

Feeding ecology of cheetahs in the Maasai Mara, Kenya and the potential for intra- and interspecific competition

Journal:	<i>Journal of Zoology</i>
Manuscript ID	JZO-05-17-OM-129.R1
Manuscript Type:	Original Manuscript
Date Submitted by the Author:	n/a
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Keywords:	Cheetah, Lion, Competition, Prey profiles, Prey selection, Feeding ecology

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1 **Feeding ecology of cheetahs in the Maasai Mara, Kenya and the potential for intra- and**
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5 **interspecific competition**
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35 14 Short title: Cheetah feeding ecology and potential competition
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Abstract

Competition is an important ecological factor influencing the population dynamics of carnivores especially as shifts in prey selection could have negative consequences for other members of the carnivore guild. It is therefore important to determine a species' resource requirements to help understand the potential degree and consequences of competition. Cheetahs (*Acinonyx jubatus*) compete over resources with larger carnivores, such as lions (*Panthera leo*). While cheetahs generally favour smaller prey than lions, male cheetahs frequently occur in coalitions and are larger than solitary females. This could result in male cheetahs killing larger prey and potentially competing more directly with lions than female cheetahs. To determine the potential for both intra- and interspecific competition, we analysed data on 194 cheetah and 214 lion kills, and compared the feeding ecology of four cheetah social groups; single females, female with cubs, single males and male coalitions to that of lions in the Maasai Mara, Kenya. The results show that the greatest potential for interspecific competition is between male cheetahs, especially those in coalitions, and lions. Intraspecific competition is most likely to occur between singleton females and females with cubs. Understanding these ecological relationships is key, especially as prey is declining.

Keywords: cheetah, competition, feeding ecology, lion, prey profiles, prey selection

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32 **Introduction**

33 Competition is an important ecological factor influencing the population dynamics of carnivores
34 (Caro & Stoner 2003, Linnell & Strand 2000, Palomares & Caro 1999). Determining resource
35 requirements to help understand the degree of competition is important, especially in light of
36 increased anthropogenic effects, such as habitat loss and prey depletion, which could increase
37 competition (Caro & Stoner 2003, Creel 2001). Food is one resource where both indirect and direct
38 competition can occur between sympatric carnivore species. Indirect competition occurs when
39 common food resources are exploited by one competitor, reducing resource abundance and hence
40 constraining availability to other competitors (Pianka 1974, Wootton 1994). Competition over
41 resources can be minimised through resource partitioning, for example, by selecting different prey
42 types (Schoener 1974). Whilst there is a positive relationship between predator body mass and their
43 preferred prey body mass (Carbone *et al.* 1999), this does not necessarily mean that the larger
44 species specialise on bigger prey (Radloff & Du Toit 2004). Carnivore species within the same guild
45 are therefore likely to compete, to some degree, over similar food resources (Hayward & Kerley
46 2008, Mills & Biggs 1993) and as a result occupy similar areas based on the spatial distribution of
47 prey (Karanth & Sunquist 1995).

48 A high degree of dietary overlap is positively linked to direct, negative interactions, such as
49 kleptoparasitism, where one carnivore species steals another carnivores' kill, and intraguild
50 predation, where one carnivore species kills another (Donadio & Buskirk 2006, Palomares & Caro
51 1999). As the outcome of direct competition tends to favour the larger species, it is the smaller
52 species that will be affected adversely and will therefore be at bigger risk of being extirpated if
53 competition is severe. However, prey preference within a species is not necessarily uniform as it
54 could vary according to group composition or sex, especially considering that most carnivores exhibit
55 some degree of sexual dimorphism, possibly to minimise intraguild competition (Meiri, Dayan &
56 Simberloff 2005, Moors 1980). Amongst felids for example, males are generally bigger than females
57 and can therefore kill larger prey (Radloff & Du Toit 2004). These differences could play a role in

both intra- and interspecific competition. However, the potential for competition in terms of resource breadth and overlap, are often investigated without taking into account intraspecific variation (e.g. Hayward & Kerley 2008). This pooling of data could mask important differences among demographics.

Cheetahs (*Acinonyx jubatus*) occupy the African large carnivore guild alongside leopards (*Panthera pardus*), wild dogs (*Lycaon pictus*), lions (*P. leo*) and spotted hyaenas (*Crocuta crocuta*). Cheetahs are one of the smaller members of this guild and are therefore often used as a model species to investigate competition and interactions with larger guild members, particularly lions (e.g. Broekhuis *et al.* 2013, Cozzi *et al.* 2012, Durant 1998, Swanson *et al.* 2014). Cheetahs weigh around 35-45 kg (Caro 1994) and are thereby considerably smaller than lions (83 - 225kg; Smuts, Robinson & Whyte 1980). Lions are generally found in fission-fusion groups (Schaller 1972), while cheetahs are mainly solitary apart from females with cubs and males in coalitions (Caro 1994). Their smaller body size and solitary nature renders cheetahs prone to negative, direct interactions with other predators that steal their kills (Caro 1994, Hunter, Durant & Caro 2007b) and occasionally kill adult cheetahs and their cubs (Broekhuis 2015, Laurenson 1995). In terms of indirect competition with other predators over prey resources, cheetahs prefer prey within the body mass range of 14-40 kg (Clements *et al.* 2014), whereas lions preferentially select larger prey within the body mass range of 92-632 kg (Clements *et al.* 2014), but do occasionally eat smaller prey (Hayward & Kerley 2005).

Using data from different regions across Africa, Hayward and Kerley (2008) investigated the overlap of prey profiles between these species, regardless of sex or social structure, and found that the overlap between lions and cheetahs was minimal. Cheetahs, however, exhibit slight sexual size dimorphism where male cheetahs are generally larger than females (Caro 1994). In Namibia, males weigh 45.6 ± 5.99 kg and females weigh 37.2 ± 5.14 kg with the heaviest male weighing 64 kg and the heaviest female weighing 51 kg (mean \pm SD; Marker & Dickman 2003). Similar differences exist in Botswana where males weigh 46.7 ± 8.7 kg and females weigh 38.6 ± 3.5 kg (mean \pm SD; Boast *et al.*

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3 83 2013). Male cheetahs, especially those in coalitions, kill large prey such as wildebeest (*Connochaetes*
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5 84 *taurinus*) and kudu (*Tragelaphus strepsiceros*), which lie in the same weight category as some of the
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7 85 prey species killed by lions (Radloff & Du Toit 2004, Rostro-García, Kamler & Hunter 2015).
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9 86 Therefore, although both sex and social grouping of cheetahs impact their prey selection (Rostro-
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11 87 García, Kamler & Hunter 2015), it is unclear how this could influence resource partitioning and hence
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13 88 the potential for intra- and interspecific competition to occur.

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17 89 The presence of indirect competition is most conclusively determined by experimental
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19 90 manipulations through removal or introduction of species (Schoener 1983). However, when
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21 91 manipulative experiments are not possible, the potential for indirect competition can be inferred
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23 92 from species prey profiles (composition and breadth), prey selection and overlap (Barrientos &
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25 93 Virgós 2006, Kitchen, Gese & Schauster 1999). Here, we compare the feeding ecology of four
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27 94 cheetah social groups; single females, female with cubs, single males and male coalitions to that of
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29 95 lions in the Maasai Mara, Kenya, to determine the degree of resource partitioning to infer the
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31 96 potential for both intra- and interspecific competition. In addition, we quantify direct competition by
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33 97 investigating the number of cheetah kills that were stolen by other predators.

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37 98 **Methods**

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39 99 *Study area*

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42 100 The study was conducted in the Maasai Mara in the south-west of Kenya. The study area (°1 S, 35 °
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44 101 E; elevation c. 1700 m) covers approximately 2400km² and includes the Maasai Mara National
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46 102 Reserve (MMNR) and the adjacent conservancies; Mara Triangle, Mara North, Ol Chorro, Lemek,
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48 103 Olare-Motorogi, Naboisho and Ol Kinyei. Hereafter, the conservancies and the MMNR will
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50 104 collectively be referred to as the Maasai Mara. To the south, the Maasai Mara borders the Serengeti
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52 105 National Park in Tanzania, to the north and west it borders intensive agricultural land and east of the
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54 106 Maasai Mara is largely pastoralist settlement (Ogutu *et al.* 2009).

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108 The study area experiences a bimodal rainfall pattern, with the wet season spanning November–
 109 June and the dry season July–October. The wet season is characterised by two distinct periods; the
 110 short rains (November–December) and the long rains (March–June) (Ogutu *et al.* 2008). The long
 111 rains attract the migrating wildebeest, plains zebra (*Equus quagga*) and Thomson’s gazelle (*Gazella*
 112 *thomsoni*) from the Serengeti. Generally the migration peaks in the Maasai Mara in July after which
 113 the numbers slowly decline until most of the migrating individuals have returned to Tanzania in
 114 November (Stelfox *et al.* 1986). Independent of the migration, substantial populations of wildebeest
 115 and Thomson’s gazelle are resident year round, along with other prey species such as Cape buffalo
 116 (*Syncerus caffer*), Grant’s gazelle (*G. granti*), impala (*Aepyceros melampus*) and hares (*Lepus spp.*).
 117 The most abundant large carnivore species present across the study area are cheetah, lion, leopard
 118 and spotted hyaena. Wild dogs also occur in the study area but their distribution is localised and
 119 sightings are extremely rare.

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121 *Data collection*

122 Between 1st July 2013 and 31st October 2016 (40 months) cheetahs and lions were located on an *ad*
 123 *hoc* basis using the search-encounter method described in Broekhuis & Gopalaswamy (2016). When
 124 a feeding event was observed at a sighting, the date, time, species, sex and age of prey species were
 125 recorded. Lions, and occasionally cheetahs (Broekhuis & Irungu 2017, Schaller 1972), scavenge so
 126 any events that were believed to be scavenged were excluded from the analysis. If a scavenging
 127 event was not directly observed then the possibility of a scavenging event having taken place was
 128 based on circumstantial evidence including the condition of the carcass and the presence of other
 129 predators. For cheetahs, whenever possible, we would stay with an individual until it finished
 130 feeding or the kill was stolen.

131 *Analyses*

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132 To quantify intraspecific competition in cheetahs and to determine which cheetah social group is
133 potentially most affected by competition with lions, the data on cheetah kills were categorised
134 according to four social groups; single females (SF, 24 individuals), female with cubs (FwC, 14
135 individuals), single males (SM, 16 individuals) and male coalitions (MC, four different two-male
136 coalitions). To determine the potential for both intra- and interspecific competition, we calculated
137 the prey profile (composition and breadth), prey selection and overlap of the four different social
138 groups and compared these to the same metrics for lions (44 different prides or groups). For the
139 analyses, prey species, rather than prey type (sex and age), was used as the sample size was too
140 small to categorise each species into a prey type.

141 *Prey profiles (composition and breadth)* – Prey profiles were created for lions and the four cheetah
142 social groups (hereafter referred to as predator groups) by calculating the composition and breadth
143 of the prey species that were killed. The composition was determined by calculating the proportion
144 of each prey species in the diet in relation to the total number of prey species that were killed for
145 each predator group. The differences in composition for each of the predator groups were tested
146 using the Fisher’s Exact Test as some of the counts for the prey species killed were <5 (Crawley
147 2007). The breadth of the individual prey profiles was calculated to determine whether a predator
148 group was a generalist (equal distribution amongst the available prey species) or a specialist
149 (focused on a limited number of prey species) by investigating the range of species that were killed.
150 The breadth of each of the prey profiles (B_{pp}) was calculated using the Levin’s index (Krebs, 1999):

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

151 Where p_i is the proportion of prey species i killed by predator group p and n are the number of prey
152 items that are available. In this case, n is taken as the sum of all the prey species consumed by both
153 cheetah and lions during the study period. Values close to 1 indicate that a predator group is a
154 generalist whereas values close to 0 indicate that a predator group is a specialist.

Prey profile overlap – The overlap between the prey profiles (O_{pp}) was calculated to determine whether lions and the different cheetah social groups utilise a common prey base. The percentage overlap between the prey profiles of lions and each pair of cheetah social groups was calculated following (Krebs 1999):

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

Where p_{ij} is the proportion of prey species i in the prey profile of predator j and p_{ik} is the proportion of the same prey species i in the prey profile of predator k .

Prey selection – Prey preference was calculated to determine whether certain prey species were preferred or avoided depending on their abundance (availability). Species availability was based on the average figures for 2013-2016 from Ogutu et al. (2016) for both medium and large prey species (Table 1). No differentiation was made according to age and sex as abundance was only available for a species as a whole. Prey selection was calculated based on the Jacob's Index (Jacobs 1974):

$$\text{Prey selection} = \frac{c_i - p}{c_i + p - 2c_i p}$$

Where p is the proportion of each prey species in relation to its total abundance and where c_i is the proportion of prey species i killed by predator group c . Values for whether a prey is selected or avoided based on its availability range from -1 to +1 where -1 indicates maximum avoidance and +1 indicates maximum preference.

Results

Based on 194 cheetah kills and 214 lion kills, the results indicate that there are distinct differences in the prey profiles between the different cheetah social groups, which are likely to influence intra- and interspecific competition. The largest overlap, and hence potential for competition, was between singleton females and females with cubs ($O_{pp} = 90.9\%$, Fig. 1). The prey profiles of singleton females

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176 and females with cubs did not differ significantly in terms of composition (Fisher's Exact Test; p-
177 value = 0.696) and breadth, with the most dominant prey item being Thomson's gazelle, 51% and
178 54% respectively (Table 1). In addition to Thomson's gazelle, female cheetahs also selected for
179 impala and Grant's gazelle but avoided larger prey species (Table 1, Fig. 2). In relation to male
180 cheetahs, females (both with and without cubs) overlapped more with singleton males than with
181 male coalitions (Fig. 1). The two male groups showed a high degree of overlap ($O_{pp} = 61.1\%$), as both
182 predominantly killed wildebeest (SM = 54%, MC = 84%), but the composition of their prey profiles
183 differed significantly (Fisher's Exact Test; $p < 0.00$). Singleton males did not select for wildebeest
184 based on their availability (selectivity index = -0.18), whilst the male coalitions strongly selected for
185 wildebeest (selectivity index= 0.61, Fig. 2). While both groups are considered to be specialists (B_{pp}
186 values close to 0), singleton males had a larger prey profile breadth ($B_{pp} = 0.17$, Table 1) and their
187 prey profile included more prey species than male coalitions who had the lowest prey profile
188 breadth ($B_{pp} = 0.02$, Table 1) of the cheetah social groups and were seen feeding on only three
189 species.

190 Lions had the most diverse prey profile in terms of number of different species consumed ($n=11$). In
191 addition to the smaller prey species, such as Thomson's gazelle, they also fed on larger species such
192 as wildebeest, zebra and giraffe (*Giraffa camelopardalis*; Table 1). Wildebeest made up 57% of the
193 lion's prey profile which in part resulted in the large degree of overlap (Fig. 1) with male cheetahs,
194 both singletons (57.6%) and male coalitions (59.9%), but little overlap with single females (11.2%)
195 and females with cubs (11.7%).

196 On 108 occasions, feeding events were observed until a cheetah finished feeding or abandoned its
197 kill. Of these, 14 kills (13%) were stolen by other predators; of which 11 (10%) were by spotted
198 hyaenas, two (2%) by lions and one by a black-backed jackal (Table 2). There was also one case
199 where a cheetah was chased off her kill by tourists, and on two occasions cheetahs were seen

200 'surplus killing' where they killed more than they could eat (Kruuk 1972). The likelihood that a kill
 201 was stolen by another predator did not differ per cheetah social group ($\chi^2 = 4.833$, $df = 3$, $p = 0.18$).

202 Discussion

203 The results show that differences in feeding ecology within a species can influence the potential for
 204 both intra- and interspecific competition to occur. For competition between cheetahs and lions the
 205 prey profiles, breadth and selection of male cheetahs were the most noteworthy which, unlike the
 206 female cheetahs, were dominated by large prey, especially wildebeest. While our sample size for
 207 male cheetahs (SM = 16 individuals; MC = four different two-male coalitions) was smaller than for
 208 female cheetahs (SF = 24 individuals; FwC = 14 individuals), other studies support our finding that
 209 male cheetahs prefer killing larger prey (Rostro-García, Kamler & Hunter 2015, Tambling *et al.* 2014).
 210 These differences in prey profiles reduce the overlap between these two sexes, thereby reducing the
 211 potential for intraspecific competition to occur. This potential for intraspecific competition could be
 212 further reduced as female cheetahs generally kill juveniles and sub-adults of bigger prey species,
 213 whereas males tend to kill sub-adults and adults (Tambling *et al.* 2014). However, with the current
 214 sample size we were unable to break down prey species into age and sex classes.

215 Between the two male social groups there was a high degree of overlap but their prey profiles
 216 differed significantly in that singletons were slightly less specialised in their prey selection than
 217 coalition males whose prey profile almost solely consisted of wildebeest. Similarly, lions
 218 predominantly killed wildebeest resulting in substantial overlap with the prey profiles of male
 219 cheetahs, especially male coalitions, suggesting that there is a high potential for interspecific
 220 competition to occur. This is in contrast to Hayward and Kerley's (2008) results who, based on
 221 pooled cheetah data that did not take into account sex and social structure, found that the overlap
 222 in prey profiles between lions and cheetahs was minimal.

223 Even though there is a high degree of overlap between male cheetahs and lions, simple ecological
 224 niche theory suggests that species can coexist if segregation takes place along the other dimensions

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3 225 of the ecological niche; such as space or time (e.g. Kronfeld-Schor & Dayan 2003, Schoener 1974).
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5 226 However, on a broad scale cheetahs do not avoid lions in space (Broekhuis *et al.* 2013, but see
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7 227 Durant 1998) possibly because both are attracted to areas where suitable prey is available. Similarly,
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9 228 although lions are predominately nocturnal and cheetahs diurnal (Cozzi *et al.* 2012), cheetahs,
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11 229 especially males, are active at night (Grünewälder *et al.* 2012). This high degree of overlap in prey,
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13 230 space and time, especially for males, suggests that there is a high likelihood for them to have direct,
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15 231 negative encounters with lions. In addition, larger carcasses are more likely to attract scavengers so
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17 232 there is a higher chance that male cheetahs will have a direct encounter with lions compared to
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19 233 female cheetahs. The level of kleptoparasitism found in this study (13%) is similar to those found in
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21 234 Serengeti National Park (12.9%; Hunter, Durant & Caro 2007a) and Kruger National Park (12%; Mills,
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23 235 Broomhall & du Toit 2004), but as in the Serengeti National Park, no differences in kleptoparasitism
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25 236 were observed between the different cheetah social groups (Hunter, Durant & Caro 2007b). Despite
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27 237 the presence of both indirect and direct competition, lions have little effect on cheetah numbers
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29 238 (Swanson *et al.* 2014). This suggests that resource partitioning is complex and that these competing
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31 239 species can co-exist through finer scale spatio-temporal avoidance (Broekhuis *et al.* 2013). This is
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33 240 illustrated by the fact that, even though male cheetahs are more likely to compete with lions than
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35 241 female cheetahs, it is the male cheetahs who avoid direct interactions with other predators by
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37 242 adjusting their behaviour i.e. by moving their kill into thicker vegetation to avoid detection (Hunter,
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39 243 Durant & Caro 2007b).
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44 244 Singleton females and females with cubs showed a strong potential for intraspecific competition as
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46 245 their prey profiles were very similar and hence the degree of overlap was large. This is not surprising
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48 246 since cubs that are younger than 11 months will not assist their mother in hunts (Caro 1994) and
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50 247 therefore a female with cubs is likely to kill similar prey to a female without cubs. This intraspecific
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52 248 competition between female cheetahs could be considerable as there is a great deal of overlap
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54 249 between female home-ranges (Caro 1994). Despite this high degree of overlap, and the fact that
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female cheetahs do occasionally scavenge (Broekhuis & Irungu 2017), no direct interactions were observed between female cheetahs at kills.

Here we show that, in sexually dimorphic species, it is important to take into account intraspecific differences when investigating resource partitioning especially with the increasing evidence that resources, such as prey, are declining (Ogutu *et al.* 2016). As indirect competition over resources tends to be strongest when the common resource is limited (Pianka 1974, Wootton 1994), there is a strong possibility that these changes in prey availability can cause shifts in prey selection (Owen-Smith & Mills 2008). For example, it is believed that the leopard density in Nalkeri Reserved Forest in India decreased because tigers switched to medium-sized prey thereby increasing the indirect competition with leopards (Karanth & Sunquist 1995). Furthermore, carnivores are more likely to select for domestic animals, rather than wild, as natural prey resources diminish (Farhadinia *et al.* 2012). It is therefore important to understand the resource requirements and the impact of competition to help predict the consequences of environmental change.

Acknowledgements

We are grateful to the National Council for Science and Technology, Kenya Wildlife Service, Narok County Government, the Maasai Mara Wildlife Conservancies Association and the Mara Conservancy for granting permission to conduct research in the Maasai Mara. We would like to thank the Mara Lion Project (MLP) for allowing us to use their lion data. The Mara Cheetah Project (MCP) and MLP received funding from the African Wildlife Foundation, the Vidda Foundation, WWF and private donations made through the Kenya Wildlife Trust. We would like to thank the MCP and MLP teams for assisting with data collection and Nic Elliot and three anonymous reviewers for their useful comments.

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Tables

Table 1: A summary of the species abundance and prey profiles (composition and breadth) of four different cheetah social groups and lions in the Maasai Mara, Kenya. Prey abundance and proportions were based on the average figures for 2013-2016 from Ogutu et al. (2016) for both medium and large prey species. Only those species where figures were available were used to calculate the predator prey profiles. The composition was determined by calculating the proportion of each prey species in the diet in relation to the total number of prey species that were killed for each predator group. For each predator group the whole count and the percentage (in parenthesis) that a prey species contributed to each predator prey profile are given for each predator group. The breadth (B_{pp}) of the individual prey profiles was calculated to determine whether a predator group was a generalist (equal distribution amongst the available prey species) or a specialist (focused on a limited number of prey species) by investigating the range of species that were killed.

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Prey			Cheetah				Lion (N=44)
Species	Abundance	Proportion	Single female (N=24)	Female with cubs (N=14)	Single male (N=16)	Male coalition (N=4)	
Hare (<i>Lepus spp.</i>)	-	-	1 (2%)	4 (5%)			
Thomson’s gazelle (<i>Gazella thomsoni</i>)	29 317	0.07	32 (51%)	45 (54%)	7 (20%)	1 (8%)	3 (1%)
Warthog (<i>Phacochoerus africanus</i>)	1 938	< 0.01		1 (1%)	1 (3%)		15 (7%)
Impala (<i>Aepyceros melampus</i>)	23 890	0.06	15 (24%)	21 (25%)	5 (14%)	1 (8%)	4 (2%)
Sheep (<i>Ovis aries</i>)	-	-			2 (6%)		
Grant’s gazelle (<i>G. granti</i>)	8 774	0.02	8 (13%)	4 (5%)	2 (6%)		
Reedbuck (<i>Redunca redunca</i>)	-	-	1 (2%)	1 (1%)			
Wildebeest (<i>Connochaetes taurinus</i>)	228 054	0.57	4 (6%)	5 (6%)	16 (46%)	11 (85%)	120 (56%)
Topi (<i>Damaliscus lunatus topi</i>)	10 214	0.03	1 (2%)	1 (1%)	1 (3%)		11 (5%)
Coke’s Hartebeest (<i>Alcelaphus buselaphus cokii</i>)	1 562	< 0.01		1 (1%)			
Waterbuck (<i>Kobus ellipsirygnus</i>)	1 042	< 0.01	1 (2%)				
Zebra (<i>Equus burchelli</i>)	71 920	0.18					27 (13%)
Cattle (<i>Bos taurus</i>)	-	-					2 (1%)
Cape buffalo (<i>Syncerus caffer</i>)	15 418	0.04			1 (3%)		16 (7%)
Eland (<i>Tragelaphus oryx</i>)	2 038	0.01					2 (1%)
Giraffe (<i>Giraffa camelopardalis tippelskirchi</i>)	1 562	< 0.01					7 (3%)
Hippopotamus (<i>Hippopotamus amphibius</i>)	-	-					7 (3%)
Elephant (<i>Loxodonta africana</i>)	2 434	0.01					
Total kills			63	83	35	13	214
Total species			8	9	8	3	11
Prey profile breadth (B_{pp})			0.13	0.12	0.17	0.02	0.12

Table 2: Number of kleptoparasitism events (N=14) based on the number of kills that were observed until the cheetah was finished feeding or the kill was stolen (N=108).

Cheetah	Total feeding events	Spotted hyaena	Lion	Jackal	Total kills stolen
Single female	31	4	2	1	7
Female with cubs	55	6	-	-	6
Single male	14	-	-	-	0
Male coalition	8	1	-	-	1
Total	108	11	2	1	14

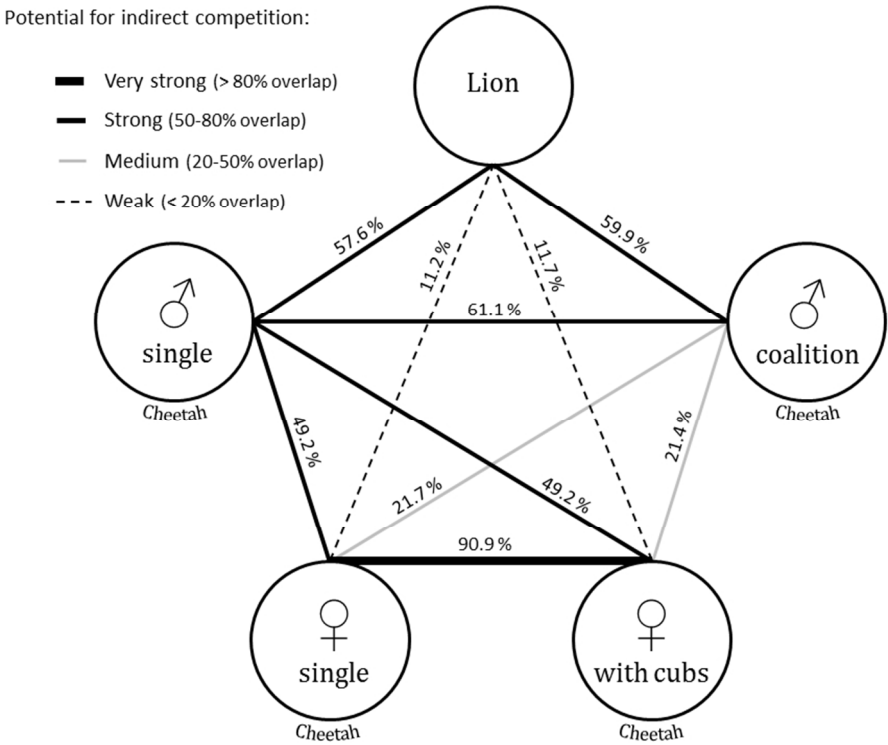
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400 **Figures**

401 **Figure 1:** The potential for indirect competition based on the amount of overlap (O_{pp} displayed as
402 percentages) of the prey profiles of four different cheetah social groups (single females, female with
403 cubs, single males and male coalitions) and lions in the Maasai Mara, Kenya.

404 **Figure 2:** Prey selection of four different cheetah social groups and lions in the Maasai Mara, Kenya
405 using the Jacob's index for preference/avoidance. Values >0 indicate that a prey species was killed more
406 than its availability (preference) and values <0 indicate that a prey species was killed less than
407 availability (avoidance).

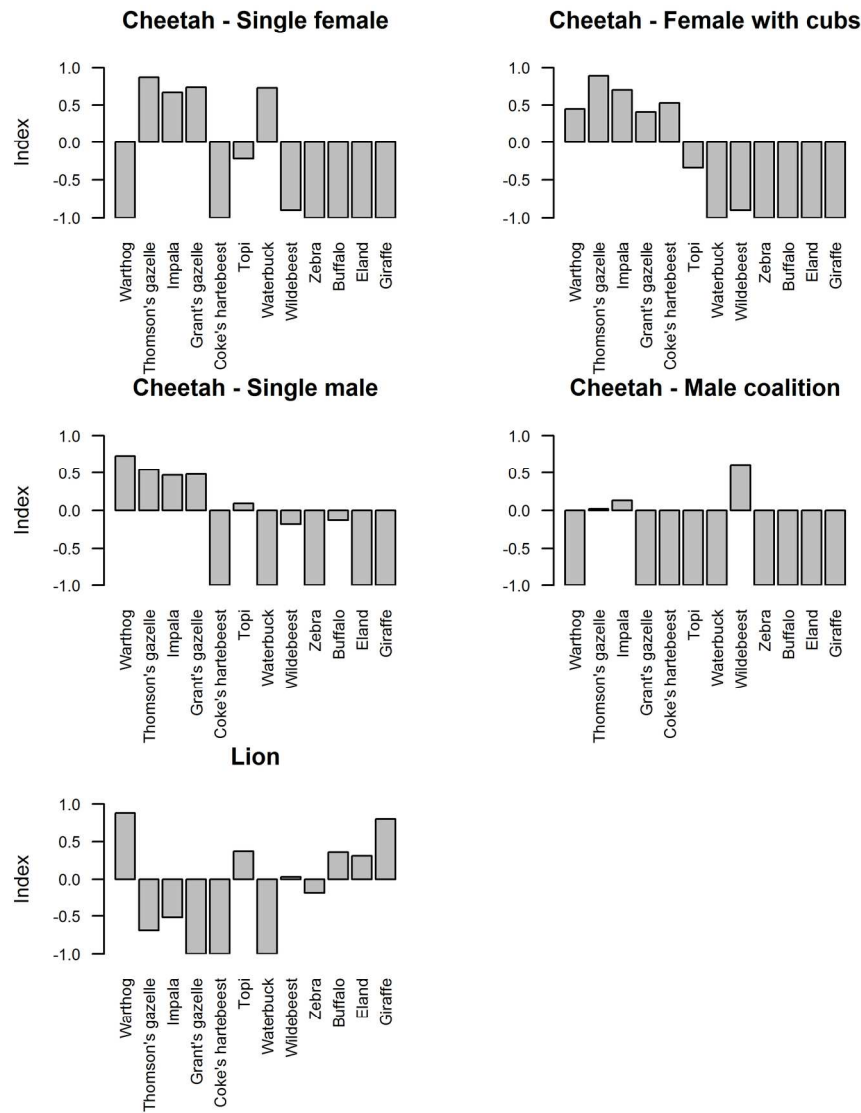
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The potential for indirect competition based on the amount of overlap (Opp displayed as percentages) of the prey profiles of four different cheetah social groups (single females, female with cubs, single males and male coalitions) and lions in the Maasai Mara, Kenya.

254x190mm (96 x 96 DPI)

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Prey selection of four different cheetah social groups and lions in the Maasai Mara, Kenya using the Jacob's index for preference/avoidance. Values >0 indicate that a prey species was killed more than its availability (preference) and values <0 indicate that a prey species was killed less than availability (avoidance).

169x225mm (300 x 300 DPI)



Male cheetah feeding on a wildebeest in the Maasai Mara, Kenya

877x588mm (96 x 96 DPI)