Behavioral Ecology and Sociobiology (2018) 72:74
https://doi.org/10.1007/s00265-018-2481-y

ORIGINAL ARTICLE

Cheetahs modify their prey handling behavior depending on risks from top predators

Anne Hilborn[1,2] · **Nathalie Pettorelli**[2] · **Tim Caro**[3] · **Marcella J. Kelly**[1] · **M. Karen Laurenson**[4] · **Sarah M. Durant**[2]

Received: 19 December 2017 / Revised: 6 March 2018 / Accepted: 12 March 2018

Abstract

While handling large kills, mesocarnivores are particularly vulnerable to kleptoparasitism and predation from larger predators. We used 35 years of observational data on cheetah (*Acinonyx jubatus*) hunts in Serengeti National Park to investigate whether cheetahs' prey handling behavior varied in response to threats from lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*). Male cheetahs and single females, whose main threat was kleptoparasitism, minimized time on the kill by being less vigilant and eating quickly, thereby shortening their handling times. Mothers with cubs showed a different strategy that prioritized vigilance over speed of eating, which increased time spent handling prey. Vigilance allowed them to minimize the risk of their cubs being killed while giving cubs the time they need to eat at the carcass. Flexible behavioral strategies that minimize individual risk while handling prey likely allow mesocarnivores to coexist with numerous and widespread apex predators.

Significance statement

Medium-sized carnivores like cheetahs face the challenge of coexisting with larger carnivores that steal their kills and kill their cubs. We investigated how cheetahs modify their behavior on kills to minimize risks from larger predators. Using 35 years of data on 400+ cheetah hunts across 159 individuals, we found that cheetahs without cubs whose primary danger is having their kill stolen spent little time engaged in vigilance and instead ate quickly, reducing the risk of theft. Mothers with cubs, however, took a slower approach and were more vigilant while handling prey to avoid cub predation by lions and spotted hyenas. The ability of cheetahs to modify their prey handling behavior depending on the type of risk they face likely allows them to coexist with numerous larger carnivores.

Keywords Predator-prey interactions · Foraging behavior · Behavioral flexibility · Carnivore coexistence

Introduction

Predation is a key factor in shaping ecological communities (Sih 1985), and the direct impact of apex carnivores goes beyond their primary prey species, extending to mesocarnivores, i.e., carnivores that are mid-ranking in a food web (Prugh et al. 2009). Apex carnivores can negatively affect mesocarnivores through direct predation, kleptoparasitism, and harassment (Prugh et al. 2009; Ritchie and Johnson 2009); yet, smaller carnivores do manage to coexist with numerous apex carnivores. For example, in Serengeti National Park in Tanzania where lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) live at high densities, there are eight species of mesocarnivores in the felid and canid families alone (Estes 1991). This raises a question about carnivore coexistence: what behaviors do mesocarnivores use to minimize negative interactions with dangerous larger predators? Illuminating coexistence strategies can expand our knowledge

---

Communicated by P. A. Bednekoff

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00265-018-2481-y) contains supplementary material, which is available to authorized users.

✉ Anne Hilborn
ahilborn@vt.edu

[1] Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, Virginia, USA

[2] Institute of Zoology, Zoological Society of London, London, UK

[3] Department of Wildlife, Fish and Conservation Biology, University of California, Davis, California, USA

[4] Frankfurt Zoological Society, PO Box 450189, Musakanya Drive, Mpika, Zambia

of how diverse communities of carnivores are structured and maintained (Vanak et al. 2013), and potentially aid in our understanding of how top-down pressures affect relationships between mesopredators and their prey (Dunphy-Daly et al. 2010; Suraci et al. 2016).

Many of the known strategies mesocarnivores use to minimize risk from apex predators rely on spatial avoidance. For example, wild dogs (*Lycaon pictus*) can coexist with lions by shifting their core areas to places lions do not use (Darnell et al. 2014). In the presence of wolves (*Canis lupus*) and coyote (*Canis latrans*), home ranges tend to occur in between, or on the edges of, wolf pack territories (Fuller and Keith 1981; Arjo and Pletscher 1999). However, in systems where apex predator densities are high and their habitat use is broad, avoiding them completely may not be possible, and more fine scale strategies are likely to come into play. For example, in both the Okavango Delta of Botswana and Serengeti National Park in Tanzania, cheetahs (*Acinonyx jubatus*) avoid lions and spotted hyenas on short temporal and spatial scales (Durant 1998, 2000a; Broekhuis et al. 2013; Swanson et al. 2016), which allows them to coexist within the larger landscape. However, fine-scale avoidance requires the ability to react appropriately and rapidly to changes in current risk, which can negatively affect foraging behavior. For example, the proximity of larger carnivores lowers the chances that cheetahs will initiate a hunt (Durant 1998, 2000a; Cooper et al. 2007). Once a hunt has begun, moving to avoid larger carnivores would involve abandoning a kill or losing opportunities to hunt prey, and therefore may not be the optimal reaction to short-term changes in risk. Thus, it is probable that mesocarnivores will choose less costly modifications of their foraging behavior in order to hunt and retain sufficient prey while avoiding potentially dangerous interactions with larger predators.

Foraging in the presence of predators is inherently risky, and the tradeoffs between time spent foraging and safety have been extensively studied (Brown 1988; Verdolin 2006). Vigilance is a common strategy used by a wide variety of taxa to lower predation risk (Bøving and Post 1997; Toïgo 1999; Randall and Boltas King 2001; Favreau et al. 2010). Mesocarnivores are no exception, for example, captured wild stoats (*Mustela ermine*) were more vigilant while feeding in patches closer to caged ferrets (*Mustela furo*) or feral cats (*Felis catus*) (Garvey et al. 2015); and coyotes scavenging carcasses in Yellowstone National Park became more vigilant once wolves were reintroduced (Switalski 2003). Larger mesocarnivores like cheetahs and wild dogs may face lower predation risk than smaller species, but since they hunt relatively large prey that cannot be consumed rapidly, they may increase the risk of losing their kills to apex predators (kleptoparasitism) (Gorman et al. 1998; Hunter et al. 2007a). One strategy to lessen kleptoparasitism is to spend less time with the carcass, lowering the chances of detection by predators. For example, wild dogs, who pay a steep metabolic cost when kills are stolen (Gorman et al. 1998), eat the majority of the carcass within 15 min (Carbone et al. 2005).

This range of responses by mesocarnivores to different threats from larger predators suggests that the strategies used to minimize risk while handling prey could follow a continuum. At one end are behaviors that maximize amount of food consumed before the kill is potentially stolen. However, eating quickly usually requires spending extended periods with a lowered head, which is risky since it prevents scanning for incoming threats. A larger predator could approach a feeding mesocarnivore undetected, creating the possibility of a dangerous encounter. Therefore when predation is the primary concern and an encounter is potentially extremely dangerous, we would expect to see behaviors from the other end of the continuum, i.e., behaviors that prioritize vigilance and safety over speed in eating.

Not all individuals are equally vulnerable to predation (Pettorelli et al. 2011), and their reactions to threats from predators may vary as well. To examine whether individual cheetahs use different prey handling behaviors to cope with risks from large predators, we used a long-term data set from Serengeti National Park (SNP). Predation risk varies by age for cheetahs, as larger predators are the leading cause of cheetah cub death in SNP (Laurenson 1994), but adults are relatively safe from predation (Caro 1994). In SNP, cheetahs lose ~ 11% of their kills to lions and spotted hyenas (Hunter et al. 2007a). Some of the behaviors cheetahs use such as moving kills to longer grass and leaving immediately after eating can lower the probability of detection by larger carnivores, and therefore decrease the chances of kleptoparasitism and/or cub predation (Hunter et al. 2007a). However, a more detailed examination of how much time a cheetah spends on a carcass may reveal a tradeoff between avoiding kleptoparasitism and cub predation. Our study builds on Hunter et al. (2007a) work on the environmental and ecological factors that affect specific cheetah behaviors at the kill, to uncover whether cheetahs vary the speed at which they handle prey depending on whether cub predation or kleptoparasitism is the primary threat. In general, the more time spent handling prey, the greater chance of detection by larger carnivores. Therefore, we hypothesized that cheetahs without cubs (i.e., single females, single males, and male groups), whose main threat is kleptoparasitism, would adapt their behavior to minimize time spent handling prey. Losing a kill to larger predators has less effect on fitness than losing a cub; therefore, we expected that mothers with cubs would prioritize cub safety over quick nutritional gain and use prey handling behaviors at the safer end of the continuum. Mother cheetahs are vigilant at kills primarily to be able to protect cubs from incoming predators rather than to scan for prey (Caro 1987). Thus, we hypothesized that mothers would be more vigilant than cheetahs without cubs, primarily to minimize the risk of their cubs encountering predators.

The time cheetahs spend handling prey is made up of three major behaviors which are hunting, pausing before eating (during which cheetahs can recover breath, move the kill, and/or scan for predators), and eating. We predicted that to shorten handling time, cheetahs without cubs whose main threat is kleptoparasitism would spend less time pausing and/or eating than mothers with cubs. If cheetahs without cubs spent less time handling prey, we predicted that they would lose a lower percentage of their kills to lions and hyenas than mothers with cubs. To account for the contribution of time spent hunting to overall handling time, we also investigate whether time spent hunting differed between mothers and cheetahs without cubs.

Vigilance lengthens time spent handling prey but increases the chance that mothers will see approaching lions and spotted hyenas and be able to lead their cubs to safety. Therefore, we predicted that mothers would be more vigilant while eating, leading to longer eating times when compared to cheetahs without cubs. We also expected mothers to spend more time pausing to scan for predators before eating, which combined with longer eat times would lead to longer handling times.

We also test whether there was variation in prey handling strategy between mothers depending on cub age. Cubs younger than 4 months of age cannot run at full speed and are especially vulnerable to predation (Caro 1987). Therefore, we predicted that mothers with young cubs would prioritize behaviors that emphasize cub safety, such as being more vigilant while eating, which would lead to more time spent eating and handling prey than mothers with older cubs.

Material and methods

Study system

The Serengeti Cheetah Project (SCP) study site covers an area of 2200 km^2 of open plains and woodland edge in the Serengeti National Park and Ngorongoro Conservation Area in Tanzania. Serengeti cheetahs are highly mobile and many follow the seasonal migration of Thomson's gazelles (*Eudorcas thomsonii*), their main prey (Durant et al. 1988; Caro 1994). Detailed descriptions of the study site and ecosystem can be found in Sinclair and Arcese (1995).

Cheetah social system

Cheetahs have a unique social structure among cats, with multiple types of social groups (Caro 1994). Adult females are solitary unless they have dependent cubs. From birth until they are about 2 months old, cubs stay in the den and are not with their mother when she is hunting. Adult males can either be solitary or in lifelong coalitions with other males. We divided cheetahs into the following social groups: (i) mothers with following cubs up to 4 months of age, (ii) mothers with cubs older than 4 months, (iii) single females, (iv) single males, and (v) males in groups. Note that mothers with cubs in the den were classified as single females since cubs were not present while they handled prey.

Data collected

It was not possible to use a blinded methodology because our study involved focal animals in the field. We used observations of cheetah hunts by members of the Serengeti Cheetah Project (including TC, MKL, SMD, and AH) collected between 1980 and 2014. Serengeti cheetahs are mainly diurnal hunters and are usually habituated to vehicles, making it possible to directly observe and record their hunting behavior. We observed hunting behavior with binoculars to minimize disturbance and recorded the amount of time spent hunting, pausing, and eating in seconds (see Caro 1994). Handling time was defined as the time from when a cheetah started hunting (took two or more steps in an alert stalking gait towards prey), through the the chase and the kill, and ended when the cheetah was finished eating. Protocols for data collection on hunts used a standardized checksheet, and hence were standard across observers. Hunt time began at the start of the hunt and finished when the prey was immobilized (i.e., the cheetah has applied a stranglehold). Pause time started when the prey was dead (i.e., the cheetah dropped the stranglehold) to when the cheetah started to eat. Eat time was from the first bite taken to when the last bite was taken. If a cheetah stopped eating for an hour or more, we considered them to be finished eating. When we observed single females or single males, they were the focal animal. For mothers with cubs, the mother was always the focal animal, and the amount of time spent hunting, pausing, and eating represents her behavior. Males in groups usually hunt and eat together, and times recorded were for how long the group took to do a particular activity. Thus, handling time was from when the first male initiated a hunt to when the last male finished eating. Likewise, hunt time was from when a male initiated a hunt until he or another male applied the stranglehold to prey. Pause time was from when the stranglehold was dropped to when any of the males started to eat. Eat time was from when any male started eating until the last one had finished. We were not always able to collect data on all stages of handling time at every successful hunt; therefore, the number of observations for each stage varies (see supplementary Table S1).

For time spent vigilant, we used 3 years of data from MKL and 7 months of data from AH. MKL focused on females, while AH followed cheetahs opportunistically. Thus, the sample sizes for single females are larger than those for other social groups (see supplementary Table S1). Time spent vigilant (looking up from the carcass either while standing, sitting, or crouching) was recorded to the second for each individual except for mothers with cubs, when vigilance was only recorded for mothers. Vigilance was then calculated as a percentage of total time spent eating. For males in groups, we randomly chose data from one individual in the group to use in the analysis.

Statistics and modeling

Handling time was log transformed to achieve normality and used as the dependent variable in the models. Since there were multiple hunts by the same cheetah, we used linear mixed models with a coefficient representing the identity of cheetah as the random effect to avoid problems of pseudoreplication and to account for variation in hunting behavior among individual cheetahs. We included the following fixed effects in the models to account for the factors previously found to influence time spent handling prey in a variety of species including cheetahs (Croy and Hughes 1991; Bindoo and Aravindan 1992; Hilborn et al. 2012): social group, age of hunting cheetah (adolescent = 18 months to 2 years, young = 2–4 years, adult = 4 + years), hunger state, whether the kill was stolen, social and reproductive grouping, and the amount of meat available per cheetah. Short-term hunger state was determined by estimating belly size by eye on a 14 point scale (Caro 1994) and treated as a continuous variable. Whether the kill was stolen was a bivariate (yes/no) variable. We calculated the amount of meat available per cheetah by dividing the expected amount of meat from the carcass (estimated following Blumenschine and Caro (1986)) by the number of cheetahs present, except in the case of mothers with cubs. For mothers with cubs, we calculated the number of adult cheetah equivalents present at the kill. Following Caro (1994) and Laurenson (1995), we assumed that cubs' food intake was proportional to their body height relative to that of their mother (for values used, see supplementary Table S2). Thus, if a mother and two half sized cubs ate at a kill, we considered the two cubs as one additional cheetah, and therefore, the food consumed was equivalent to two adult cheetahs. We log-transformed meat available per cheetah to achieve normality.

After modeling handling time as a whole, we further broke it into its consecutive behaviors to determine if the differences in handling time among social groups could be accounted for by differences in amount of time spent on the hunt, the pause before eating, or the time spent eating. The amounts of time spent hunting and pausing were not normally distributed; therefore, we used non-parametric Wilcoxon sum rank tests to check for significant differences in the median amount of time mothers with cubs spent in those activities compared to other social groups. We pooled mothers with cubs together and compared amount of time they spent in an activity to time spent by all other cheetahs grouped together. We then separately compared mothers with cubs to single females, single males, and male groups to test if time spent in the activity varied significantly among social groups.

To determine if mothers with cubs spent more time eating than other cheetahs, we used a mixed effects model with log transformed time spent eating as the dependent variable. We included a coefficient representing the identity of cheetah as the random effect, and our fixed effects were the factors identified as important in the handling time model, i.e., social group, meat available per cheetah, and whether or not the kill was stolen. In the model, we separated mothers into those with old versus young cubs. As with the handling time models, the variability explained by the fixed effects and the model as a whole was calculated using the method outlined in Nakagawa and Schielzeth (2013). We used a Chi-squared test to see if there were differences in rates of kleptoparasitism among social groups.

We log-transformed our data on proportion of time on a kill spent vigilant and used it as the dependent variable in mixed effects models. To test our a priori expectation that mothers with young cubs are more vigilant on a kill than those with old cubs, we first examined only kills made by mothers with cubs. In the model, we included a coefficient representing the identity of cheetah as the random effect, and our two fixed effects were a factor representing mothers with old versus young cubs, and prey size. Previous work shows that cheetahs are more vigilant on kills larger than 10 kg (Hunter et al. 2007a); therefore, we included a two-level factor for prey size (greater or less than 10 kg) according to Blumenschine and Caro (1986). We also combined all mothers with cubs together and used another mixed effects model with the same random and fixed effects, except that social group was a four-level factor with mothers with cubs compared to single males, single females, and males in groups.

Data availability The datasets used and/or analyzed during the current study are available from the appropriate author on reasonable request.

Results

Handling time

Total handling time for 351 successful hunts ranged from 6 to 530 min. The majority of handling time was spent eating prey, with the rest taken up by hunting and pausing before eating (Fig. 1). In our handling time model, significant factors were cheetah social group, meat available per cheetah, and whether or not the kill was stolen (Table 1). Age of cheetah and short-term hunger state did not significantly affect how much time cheetahs spend handling prey. Cheetahs without cubs had shorter handling times than mothers. Single males had the

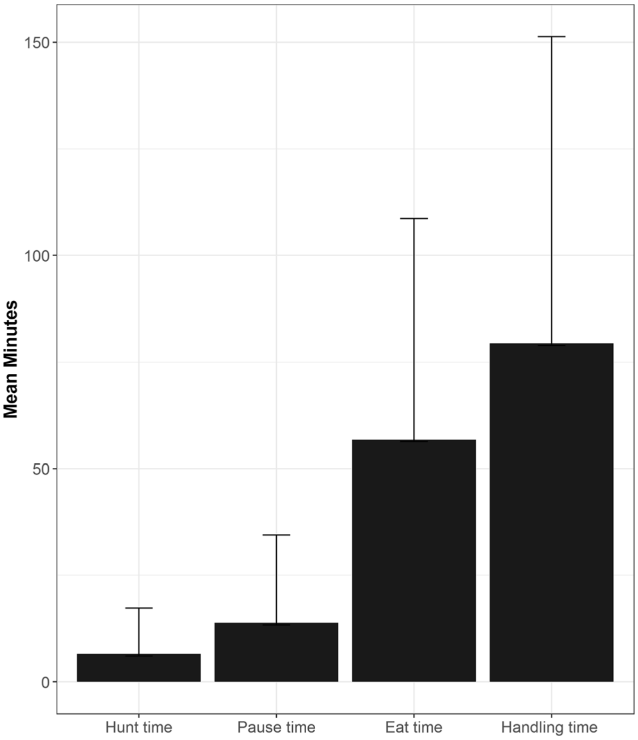

Fig. 1 Mean time (untransformed) cheetahs spent on activities making up handling time, and handling time as a whole in Serengeti National Park in 1980–2014. Bars are standard deviation

shortest handling time followed by male groups, than single females (Table 1). Mothers with young cubs spent significantly longer handling prey than mothers with old cubs (Table 1). The larger the kill, the longer the handling time, and if the kill was stolen, handling time was necessarily shortened (Table 1; Fig. 2). The fixed effects (i.e., amount of meat available per cheetah, social group, and whether the kill was stolen) explained 41.9% of the variation in the data, while the model as a whole (fixed effects plus the random effect of identity of cheetah) explained 56.8% of the variation, indicating that identity of individual cheetahs influenced model results.

Table 1 Effect size and significance of fixed effects in the handling time model. Log-transformed handling time is the dependent variable, ID of hunting cheetah is the random effect. Note: females with young cubs, male groups, single females, and single males are in comparison to females with old cubs (older than 4 months). Adult and young cheetahs are in comparison to adolescent cheetahs (18 months to 2 years old)

Parameter	Value	Std. error	*t* value	*p* value
Intercept	3.528	0.230	15.307	< 0.001
KG meat per cheetah	0.478	0.037	12.982	< 0.001
Females with young cubs	0.437	0.097	4.513	< 0.001
Male groups	− 0.353	0.188	− 1.878	0.062
Single females	− 0.141	0.098	− 1.442	0.151
Single males	− 0.473	0.181	− 2.618	**0.010**
Belly size	0.017	0.024	0.697	0.486
Adult	− 0.157	0.141	− 1.120	0.264
Young	− 0.154	0.148	− 1.035	0.302
Kill Stolen	− 0.794	0.112	− 7.102	< 0.001

Hunting

Once we broke handling time into its constituent parts (i.e., hunting, pausing, eating), we found that the median amount of time mothers with cubs spent hunting was not significantly different than all other cheetahs combined. When we compared mothers to the different social groups separately, the only significant difference was that mothers had shorter hunts than male groups (Fig. 3a).

Pausing

Pause time ranged from − 8 min to over 2.5 h. The negative pause times were usually the result of one male in a group starting to eat before his brother had finished strangling the prey. However, some negative numbers came from single cheetahs who were ineffective at strangling and started to eat before prey were dead. Cheetahs without cubs (single females and males combined) paused for significantly less time (median = 3.9 min) than mothers with cubs (median = 11.4 min, $p = 0.004$, Fig. 3b). When comparing mothers with cubs to other social groups individually, mothers paused significantly longer than single males (median = 3.2 min, $p = 0.012$) and male groups (median = 0 min, $p = < 0.001$), but not single females (median = 8.1 min, $p = 0.163$).

Eating

Out of the 447 observations of time spent eating, 84% were of Thomson's gazelle, ~ 10% were hares (*Lepus* spp.), with reedbuck (*Redunca redunca*), impala (*Aepyceros melampus*), and wildebeest (*Connochaetes taurinus*) making up the rest. Mothers with young cubs did not spent significantly longer eating than those with older cubs; however, single males, male groups, and single females spent less time eating than both mothers with young and old cubs (Table 2), though the difference between mothers with old cubs and male groups was not significant. The more meat that was available per cheetah, the longer they took to eat. The three fixed effects we included in our eat time model (social group, meat available per cheetah, and whether the kill was stolen) explained 37.7% of variability in the data, while the full model including identity of cheetah explained 48.4% of the variability. There were no significant differences in rates of kleptoparasitism among social groups ($\chi^2 = 4.15$, $df = 4$, $p = 0.38$).

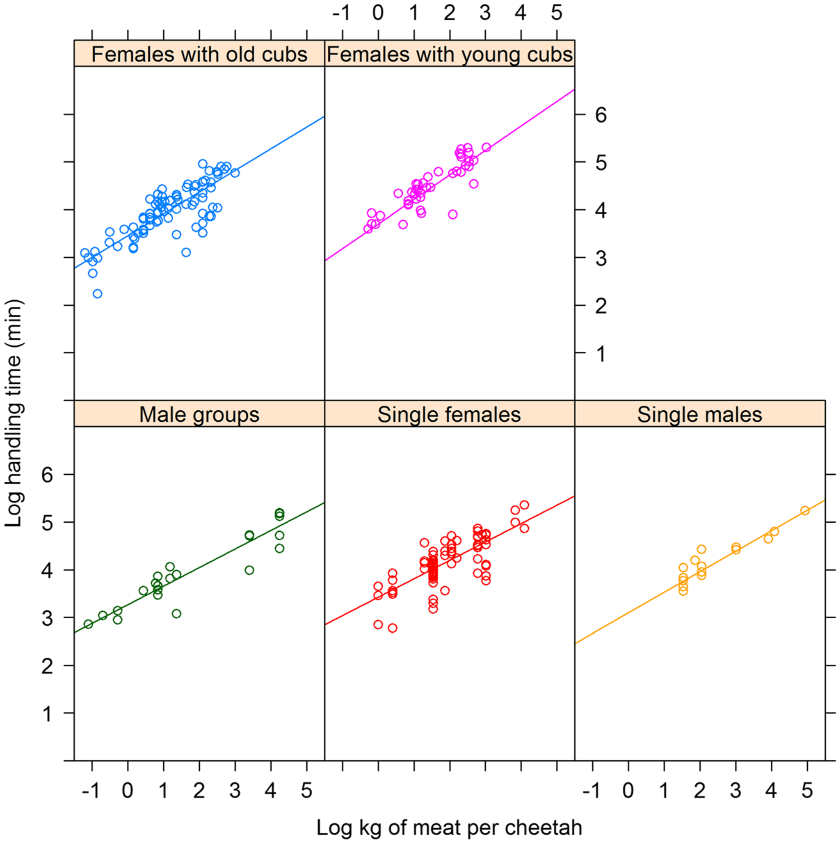

Fig. 2 Model predictions from handling time model. Shows minutes spent handling (log - transformed) by social group and meat available per cheetah (log-transformed)

Vigilance while eating

Cheetahs were less vigilant on small kills than large ones though the difference was only marginally significant (Table 3). When prey size was accounted for, there was no significant difference in amount of time on a kill spent being vigilant between mothers with young versus old cubs (supplementary Table S3). When we grouped all mothers with cubs together, they spent significantly more time being vigilant than single males and single females, but not male groups (Table 3).

Discussion

Our research reveals that aspects of cheetah prey handling behavior depend on risk from larger carnivores. Males and single females whose primary risk is kleptoparasitism have comparatively short overall handling times because they spend less time paused before eating and they eat relatively quickly. Mothers take a different approach since their primary threat is larger carnivores killing their cubs. Instead of speed, they use vigilance to minimize risk. They spend more time paused before eating and are more vigilant, increasing the amount of time they spend eating, which increases their overall handling time.

In order to reduce the chances of encountering large predators while hunting, mesopredators can avoid hunting when predators are nearby (Durant 1998; Cooper et al. 2007), or they can preferentially forage when the predators are less active (Harrington et al. 2009; Mukherjee et al. 2009). However, once prey are caught, there are other behaviors a mesopredator can use to lower the risks of predation and kleptoparasitism. When hunting large prey, maximizing nutritional gain requires spending substantial time handling the carcass, which increases the time spent in a risky situation. Moving the kill to a refuge is a strategy used by leopards (*Panthera pardus*) to lower rates of kleptoparasitism (Balme et al. 2017), while pumas (*Puma concolor*) cache large carcasses making their kills less likely to be detected by bears (*Ursus americanus* and *arctos*) (Murphy et al. 1998). Cheetahs cannot conceal their prey nor can they reliably defend their kills against larger predators and therefore they must employ different strategies, wile lions and hyenas are more likely to find and steal larger kills (Hunter et al. 2007b). Hayward et al. (2006) show that cheetahs do not preferentially select smaller prey to avoid kleptoparastism. Irrespective of size, to minimize the risk of their kill being stolen, they need to lower the chances of being detected by predators. Moving the kill to where it is better hidden by vegetation can extend the amount of time before it is discovered by hyenas (Hunter et al. 2007b), but regardless of habitat, decreasing handling time gives other predators less

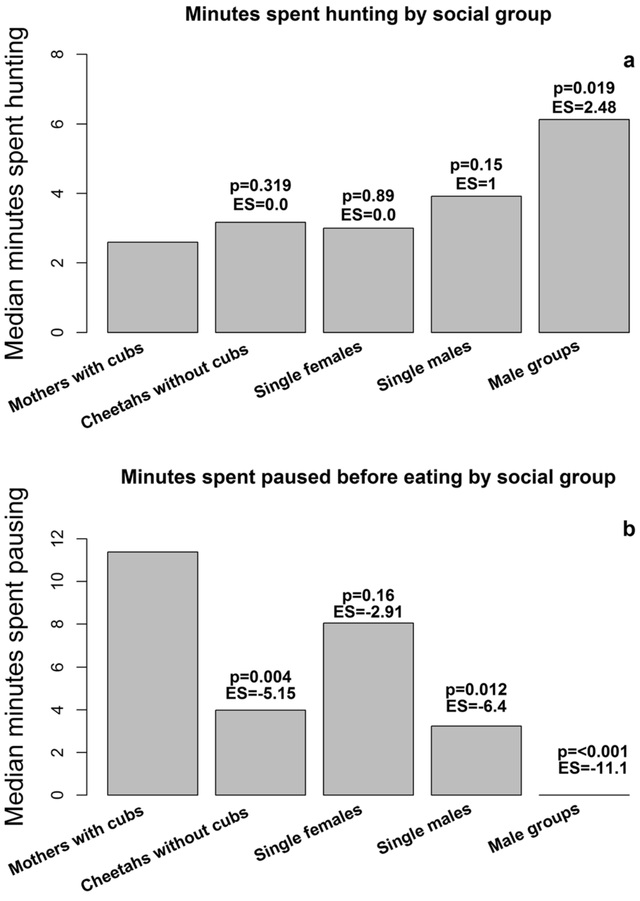

Fig. 3 Median time spent hunting (**a**), pausing (**b**) between cheetah social groups. ES = Effect size and *p* value refer to the test of that social group against mothers with cubs. Cheetahs without cubs refer to pooling the data from single females, single males, and male groups. Values are from raw data

time to find the kill. When size of prey is taken into account, cheetahs without cubs decrease handling time by reducing time spent pausing after hunting, and reducing vigilance, which allows them to eat more quickly. Vigilance may enable a cheetah to see an approaching lion or spotted hyena, but it does not prevent the kill from being stolen. Although like Broekhuis et al. (2018), we found no significant differences in rates of kill loss by different cheetah social groups, out of 22 kills by single males in our dataset, none were lost to lions or hyenas. Habitat affects rates of kill loss (Hunter et al. 2007b); however, it is likely that spending the lowest amount of time eating and handling prey contributed to single males' low rate of kleptoparasitism.

Table 2 Effect size and significance of fixed effects in model of social grouping and meat available per cheetah on time spent eating (log-transformed). Note: females with young cubs, male groups, single males, single females are in comparison to mothers with old cubs (cubs > 4 months)

Parameter	Value	Std. error	*t* value	*p* value
Intercept	3.176	0.070	45.517	< 0.001
KG meat per cheetah	0.469	0.033	14.298	< 0.001
Females with young cubs	0.124	0.090	1.373	0.171
Male groups	− 0.252	0.152	− 1.656	0.099
Single females	− 0.188	0.086	− 2.196	0.029
Single males	− 0.393	0.162	− 2.432	0.016
Kill stolen	− 1.067	0.110	− 9.686	< 0.001

Table 3 Effect size and significance of fixed effects in model of social grouping and prey size on proportion of time on a kill spent vigilant. Note: male groups, single males, single females are in comparison to mothers with cubs (all ages). Small prey (< 10 kg flesh weight) is in comparison with prey > 10 kg flesh weight

Parameter	Value	Std. error	*t* value	*p* value
(Intercept)	− 1.131	0.216	− 5.242	< 0.001
Male groups	− 0.490	0.442	− 1.109	0.276
Single females	− 0.399	0.178	− 2.242	0.027
Single males	− 0.892	0.421	− 2.118	0.042
Small prey	− 0.347	0.177	− 1.961	0.053

Since mothers with cubs on a kill face the risk of both predation and kleptoparasitism (Caro 1987), we might expect that they would also try to minimize time spent handling the carcass. A short handling time would reduce the chances of being discovered by lions and hyenas, lowering both risks. However, having cubs at the kill puts constraints on the ability of mothers to shorten their handling time. First, they have to make sure their cubs get enough to eat. Young cubs potentially slow down their mothers considerably since they have small mouths and are unfocused eaters, taking frequent breaks to rest and/or play (Caro 1994). Second, starting at ~ 4.5 months, the cubs practice chasing and killing live gazelle fawns brought to them by their mother (Caro 1995), which increases the time spent handling prey. However, it does not increase hunt time or pause time as it occurs after the prey is captured but before the prey is dead. A short handling time might minimize the time the cubs spend being vulnerable to predators, but it could compromise the cubs' ability to eat to completion and to practice hunting. Contrary to our expectations, there were no significant differences in the amount of time mothers with young versus old cubs spent eating, pausing, or being vigilant. However, there were differences between mothers and cheetahs without cubs. In general, mothers were more vigilant, paused for longer before eating, and spent more time eating, which led to longer handling times than for cheetahs without cubs. The longer pauses shown by mothers may allow them to simultaneously take time for breath recovery while scanning for predators before starting to eat. Cheetahs without cubs do not pause as long, likely because predation is not a major threat and starting to eat quickly reduces the chance of kleptoparasitism. This suggests that mothers favor behaviors that slow down their handling time but keep them and their cubs safer, using vigilance to lessen the primary threat to the cubs while allowing them the time they need with prey.

Group size can affect the amount of time animals spend handling and eating prey through group vigilance (Lima 1995; Roberts 1996) and intragroup competition for food (Lamprecht 1978). Theoretically, group vigilance means each individual can be less vigilant while maintaining similar levels of safety, while intragroup competition for food favors those who eat quickly. Both of these factors should push males in groups to shorten their handling time. Yet, we found they eat more slowly and are more vigilant than single males, resulting in longer handling times. The explanation may lie in the multiple uses of vigilance, as Caro (1994) found that males use vigilance not as an anti-predator strategy but mainly to look out for potential mates. Thus, intragroup competition for mates may cause males to favor behaviors that result in a slower and more vigilant prey handling strategy. For male cheetahs, group living does not lead to reduced individual vigilance or less time spent eating as seen in many other species (Lima and Dill 1990).

The variety of risks cheetahs face from larger predators and the tradeoffs imposed by having cubs creates two broad prey handling strategies. A short handling time is favored by those primarily facing kleptoparasitism, while mothers slow down, taking time to be vigilant in order to lessen predation risk to their cubs. How cheetahs shorten their handling times varies by social group. For example, single males ate the fastest and were the least vigilant, while males in groups shorten their pauses instead of the time they spend eating. Individual identity also played a role in determining how long cheetahs spent eating and handling prey, suggesting that cheetahs display a continuum of prey handling and vigilance behaviors that individuals adapt depending on the risks and pressures they face at the kill. Therefore, we expect that these behaviors would vary in areas where the pressures on cheetahs are different. For example in Kgalagadi (Kalahari) Transfrontier Park (KTP) in South Africa and Botswana, lion densities are three times lower and spotted hyena densities are one hundred times lower than in SNP, and cheetah cub survival is eight times higher (Mills and Mills 2014). Thus, we might expect that lower risks to cubs from lions and hyenas at the kill in KTP will result in different prey handling behaviors by mothers compared to those in Serengeti, though this remains to be investigated. These flexible and individual strategies to minimize risk from apex predators likely contribute to successful coexistence of cheetahs with lions and spotted hyenas across a steep gradient of large carnivore densities.

How apex predators affect mesocarnivore prey handling behavior has implications beyond coexistence. Studies of mesopredator release have provided detail on how the reduction or extirpation of apex predator populations leads to mesopredators increasing predation pressure on prey species (Ritchie and Johnson 2009). Functional response models quantify how changes in predator foraging behaviors, such as handling time, affect the number of prey they kill (Beddington et al. 1976; Messier 1994; Murdoch et al. 2003). This provides a framework to help understand how mesopredator release can operate on a behavioral level. The role that apex predators play in shaping the functional response parameters of mesopredators indicates a mechanism for understanding the interactions among carnivores on multiple trophic levels together with their prey. Our work adds to the evidence that not only do other predators influence the functional response parameters of carnivores, but that the influence is not equal across individuals. Smith et al. (2015) found female pumas in California increased their kill rates to compensate for abandoning kills in areas with higher human housing density, while males did not. In this case, female pumas reacted to the increased pressure from a human ‘predator’ by having shorter handling times, leading to an increase in prey killed. Altering prey handling strategies along a continuum based on individual risk levels may aid mesocarnivores in coexisting with multiple apex predators, and be key to mesocarnivore survival, especially when spatial avoidance of predators is not possible (Durant 2000a, b).

Acknowledgments We are grateful to Tanzania National Parks and Tanzania Wildlife Research Institute for permission to collect data. The Howard G. Buffett Foundation, Wildlife Conservation Society, Frankfurt Zoological Society (FZS), and National Geographic Society provided funds. AH’s dissertation was funded by a National Science Foundation Graduate Research Fellowship under Grant No. DGE-1048542, a National Science Foundation Doctoral Dissertation Improvement Grant Award Number 1405491, P.E.O, and Virginia Tech. We are very grateful to Dennis Minja, Helen O’Neill, Laura Simpson, Sultana Bashir, John Shemakunde, and all other research assistants on the Serengeti Cheetah Project who helped collect data. Logistical support was provided by G. and M. Russell, B. Allen, O. Newman, A. Barrett, J. Jackson, J. Dreissen, A. Geertsma, P. and L. White, C. MacConnell and the staff at Ndutu Safari Lodge, M. Borner and others at FZS, as well as T. Mariki. AH thanks Ulrike Hilborn for data entry and general support and Ray Hilborn for help with R. We also thank Dr. Matt Hayward and an anonymous reviewer for their helpful comments.

Funding AH’s dissertation was funded by a National Science Foundation Graduate Research Fellowship under Grant No. DGE-1048542, a National Science Foundation Doctoral Dissertation Improvement Grant Award Number 1405491, P.E.O, and GTAships from Virginia Tech.

Compliance with ethical standards

Conflict of interest The authors declare that they do not have conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

References

Arjo WM, Pletscher DH (1999) Behavioral responses of coyotes to wolf recolonization in northwestern Montana. Can J Zool 77:1919–1927

Balme GA, Miller JRB, Pitman RT, Hunter LTB (2017) Caching reduces kleptoparasitism in a solitary, large felid. J Anim Ecol 86:634–644

Beddington JR, Hassell MP, Lawton JH (1976) The components of arthropod predation: II. The predator rate of increase. J Anim Ecol 45: 165–185

Bindoo M, Aravindan CM (1992) Influence of size and level of satiation on prey handling time in *Channa striata* (Bloch). J Fish Biol 40: 497–502

Blumenschine RJ, Caro TM (1986) Unit flesh weights of some east African bovids. Afr J Ecol 24:273–286

Bøving PS, Post E (1997) Vigilance and foraging behaviour of female caribou in relation to predation risk. Rangifer 17:55–64

Broekhuis F, Cozzi G, Valeix M, McNutt JW, Macdonald DW (2013) Risk avoidance in sympatric large carnivores: reactive or predictive? J Anim Ecol 82:1098–1105

Broekhuis F, Thuo D, Hayward MW (2018) Feeding ecology of cheetahs in the Maasai Mara, Kenya and the potential for intra- and interspecific competition. J Zool 304:65–72

Brown JS (1988) Patch use as an indicator of habitat preference, predation risk, and competition. Behav Ecol Sociobiol 22:37–47

Carbone C, Frame L, Frame G, Malcolm J, Fanshawe J, FitzGibbon C, Schaller G, Gordon IJ, Rowcliffe JM, du Toit JT (2005) Feeding success of African wild dogs (*Lycaon pictus*) in the Serengeti: the effects of group size and kleptoparasitism. J Zool 266:153–161

Caro TM (1987) Cheetah mothers' vigilance: looking out for prey or for predators ? Behav Ecol Sociobiol 20:351–361

Caro TM (1994) Cheetahs of the Serengeti Plains: group living in an asocial species. University of Chicago Press, Chicago

Caro TM (1995) Short-term costs and correlates of play in cheetahs. Anim Behav 49:333–345

Cooper AB, Pettorelli N, Durant SM (2007) Large carnivore menus: factors affecting hunting decisions by cheetahs in the Serengeti. Anim Behav 73:651–659

Croy MI, Hughes RN (1991) The influence of hunger on feeding-behavior and on the acquisition of learned foraging skills by the 15-spined stickleback, *Spinachia spinachia* L. Anim Behav 41: 161–170

Darnell AM, Graf JA, Somers MJ, Slotow R, Szykman Gunther M (2014) Space use of African wild dogs in relation to other large carnivores. PLoS One 9:e98846

Dunphy-Daly MM, Heithaus MR, Wirsing AJ, Mardon JSF, Burkholder DA (2010) Predation risk influences the diving behavior of a marine mesopredator. Open Ecol J 3:8–15

Durant SM (1998) Competition refuges and coexistence: an example from Serengeti carnivores. J Anim Ecol 67:370–386

Durant SM (2000a) Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. Behav Ecol 11:624–632

Durant SM (2000b) Predator avoidance, breeding experience and reproductive success in endangered cheetahs, *Acinonyx jubatus*. Anim Behav 60:121–130

Durant SM, Caro TM, Collins DA, Alawi RM, Fitzgibbon CD (1988) Migration patterns of Thomson's gazelles and cheetahs on the Serengeti plains. Afr J Ecol 26:257–268

Estes R (1991) The behavior guide to African mammals. University of California Press, Berkeley

Favreau FR, Goldizen AW, Pays O (2010) Interactions among social monitoring, anti-predator vigilance and group size in eastern grey kangaroos. Proc R Soc Lond B 277:2089–2095

Fuller TK, Keith LB (1981) Non-overlapping ranges of coyotes and wolves in northeastern Alberta. J Mammal 62:403–405

Garvey PM, Glen AS, Pech RP (2015) Foraging ermine avoid risk: behavioural responses of a mesopredator to its interspecific competitors in a mammalian guild. Biol Invasions 17:1771–1783

Gorman ML, Mills MG, Raath JP, Speakman JR (1998) High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. Nature 852:1992–1994

Harrington LA, Harrington AL, Yamaguchi N, Thom MD, Ferreras P, Windham TR, Macdonald DW (2009) The impact of native competitors on an alien invasive : temporal niche shifts to avoid interspecific aggression. Ecology 90:1207–1216

Hayward MW, Hofmeyr M, O'Brien J, Kerley GIH (2006) Prey preferences of the cheetah (*Acinonyx jubatus*) (Felidae: Carnivora): morphological limitations or the need to capture rapidly consumable prey before kleptoparasites arrive? J Zool 270:615–627

Hilborn A, Pettorelli N, Orme CDL, Durant SM (2012) Stalk and chase: how hunt stages affect hunting success in Serengeti cheetah. Anim Behav 84:701–706

Hunter JS, Durant SM, Caro TM (2007a) To flee or not to flee: predator avoidance by cheetahs at kills. Behav Ecol Sociobiol 61:1033–1042

Hunter JS, Durant SM, Caro TM (2007b) Patterns of scavenger arrival at cheetah kills in Serengeti National Park Tanzania. Afr J Ecol 45: 275–281

Lamprecht J (1978) The relationship between food competition and foraging group size in some larger carnivores. Ethology 46:337–343

Laurenson MK (1994) High juvenile mortality in cheetahs (*Acinonyx jubatus*) and its consequences for maternal care. J Zool 234:387–408

Laurenson MK (1995) Behavioral costs and constraints of lactation in free-living cheetahs. Anim Behav 50:815–826

Lima SL (1995) Back to the basics of anti-predatory vigilance: the group-size effect. Anim Behav 49:11–20

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640

Messier F (1994) Ungulate population models with predation: a case study with the north American moose. Ecology 75:478–488

Mills MGL, Mills MEJ (2014) Cheetah cub survival revisited: a re-evaluation of the role of predation, especially by lions, and implications for conservation. J Zool 292:136–141

Mukherjee S, Zelcer M, Kotler BP (2009) Patch use in time and space for a meso-predator in a risky world. Oecologia 159:661–668

Murdoch W, Briggs C, Nisbet R (2003) Consumer-resource dynamics. Princeton University Press, Princeton

Murphy KM, Felzien GS, Hornocker MG, Ruth TK (1998) Encounter competition between bears and cougars: some ecological implications. Ursus 10:55–60

Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol Evol 4:133–142

Pettorelli N, Coulson T, Durant SM, Gaillard J-M (2011) Predation, individual variability and vertebrate population dynamics. Oecologia 167:305–314

Prugh LR, Stoner CJ, Epps CW, Bean WT, Ripple WJ, Laliberte AS, Brashares JS (2009) The rise of the mesopredator. Bioscience 59: 779–791

Randall JA, Boltas King DK (2001) Assessment and defence of solitary kangaroo rats under risk of predation by snakes. Anim Behav 61: 579–587

Ritchie EG, Johnson CN (2009) Predator interactions, mesopredator release and biodiversity conservation. Ecol Lett 12:982–998

Roberts G (1996) Why individual vigilance declines as group size increases. Anim Behav 51:1077–1086

Sih A (1985) Predation, competition, and prey communities: a review of field experiments. Annu Rev Ecol Syst 16:269–311

Sinclair ARE, Arcese P (1995) Serengeti II: dynamics, management, and conservation of an ecosystem, vol 2. University of Chicago Press, Chicago

Smith JA, Wang Y, Wilmers CC (2015) Top carnivores increase their kill rates on prey as a response to human-induced fear. Proc R Soc B 282:20142711

Suraci JP, Clinchy M, Dill LM, Roberts D, Zanette LY (2016) Fear of large carnivores causes a trophic cascade. Nat Commun 7:10698

Swanson A, Arnold T, Kosmala M, Forester J, Packer C (2016) In the absence of a “landscape of fear”: how lions, hyenas, and cheetahs coexist. Ecol Evol 6:8534–8545

Switalski TA (2003) Coyote foraging ecology and vigilance in response to gray wolf reintroduction in Yellowstone National Park. Can J Zool 81:985–993

Toïgo C (1999) Vigilance behavior in lactating female alpine ibex. Can J Zool 77:1060–1063

Vanak AT, Fortin D, Thaker M, Ogden M, Owen C, Greatwood L, Slotow R (2013) Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. Ecology 94:2619–2631

Verdolin JL (2006) Meta-analysis of foraging and predation risk tradeoffs in terrestrial systems. Behav Ecol Sociobiol 60:457–464