

Temporal structuring of vigilance behavior by female Thomson's gazelles with hidden fawns

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Peer reviewed manuscript accepted for publication in *Animal Behaviour*.

<https://doi.org/10.1016/j.anbehav.2018.09.007>

Prey animals often face a trade-off between investing time in antipredator behavior and performing self-maintenance activities, such as foraging. Parents face particularly high stakes as they must protect highly valuable offspring while also meeting elevated energetic demands. To optimize this trade-off, the risk allocation hypothesis predicts that prey should adjust their antipredator behavior to reflect temporal fluctuations in risk. That is, they should invest more in antipredator behavior when risk is high and prioritize other activities when risk is low. Here we investigate whether changes in risk level resulting from periodic fawn exposure drive maternal vigilance patterns in Thomson's gazelle, *Eudorcas thomsonii*. We find that maternal vigilance patterns match the predictions of the risk allocation hypothesis. Mothers are highly vigilant prior to fawn retrieval, when risk of fawn detection by predators is high. They exhibit low levels of vigilance after fawns resume hiding, when certainty of predator absence is high and, therefore, risk is low. We suggest that fawn active periods may function secondarily as a form of predator sampling and that mothers may adjust their vigilance levels in response to information yielded by this sampling.

Key words: antipredator behaviour, gazelle, hiding, maternal behaviour, predation risk, risk allocation hypothesis, Thomson's gazelle, ungulate, vigilance

Introduction

Predation is a major threat to survival and reproductive success and therefore exerts a powerful selective force on the physical and behavioral phenotypes of prey species (Lima & Dill, 1990). Vigilance is a common behavioral means by which prey animals preempt capture by predators and thereby mitigate predation risk: generally, more vigilant individuals are less likely to fall victim to predation than less vigilant individuals (FitzGibbon, 1990c; Godin & Smith, 1988; Quinn & Cresswell, 2004). However, vigilance also comes at a cost. In some cases, it is mutually exclusive to other behaviors such that engaging in vigilance reduces time available for other activities (Lima, 1998), such as foraging (Metcalf & Furness, 1984) and resting (Switalski, 2003; Toïgo, 1999). In other cases, vigilance can be performed in

conjunction with other behaviors, but negatively affects the efficiency of these activities (Abramsky et al., 2002; Barnier et al., 2016; Beauchamp & Livoreil, 1997). For example, increased vigilance during foraging is associated with lower bite rates in bighorn sheep, *Ovis canadensis* (Ruckstuhl et al., 2003). Thus, prey species commonly face a trade-off between mitigating risk through vigilance and investing in other social or self-maintenance activities (Krause & Godin, 1996). Mismanaging this trade-off can be costly: individuals that are not vigilant enough or not vigilant at the right time risk death from predation, while those that are overly vigilant may suffer loss of body condition, lower fecundity, or missed opportunities for social interactions (Cords, 1995; Creel et al., 2011; Maestriperi, 1993).

The risk allocation hypothesis predicts that animals should manage the trade-off be-

tween vigilance and other activities by changing their behavior in response to temporal fluctuations in risk (Lima & Bednekoff, 1999). That is, they should prioritize vigilance when risk of predation is high and invest more in other activities when risk subsides, with the relative levels of vigilance during high- and low-risk states depending on the frequency and duration of each state type. The capacity for an animal to structure its vigilance behavior as predicted by the risk allocation hypothesis depends on its ability to accurately gauge current risk levels or detect changes in risk (Lima & Bednekoff, 1999; Sih, 1992). There is abundant evidence across animal taxa that individuals exhibit “proactive” responses to predation risk (Creel et al., 2014). That is, they set their vigilance rates to reflect *average* levels of vulnerability mediated by general cues such as social context and habitat type (Avilés & Bednekoff, 2007; Barnier et al., 2016; Lima, 1995; Roberts, 1996; Underwood, 1982). For example, animals are typically less vigilant when in groups than when alone because group membership reduces individual vulnerability via various mechanisms, including risk dilution and enhanced predation detection (Beauchamp, 2008; Bertram, 1980; Dehn, 1990; FitzGibbon, 1990c, 1990b; Hamilton, 1971; Lehtonen & Jaatinen, 2016). Likewise, animals tend to be more vigilant when utilizing habitats that, on average, confer greater risk of predator encounter and attack (Altendorf et al., 2001; Burger et al., 2000; FitzGibbon, 1988; Frid, 1997; Sansom et al., 2009; Underwood, 1982).

In addition to accounting for general risk factors, prey animals can further fine-tune their antipredator behavior by responding to indicators of real-time changes in risk level. Individuals across taxa are sensitive to numerous visual, chemical and auditory cues that signal acute high risk due to predator presence (Blumstein et al., 2008; Creel et al., 2014; Kats & Dill, 1998; Périquet et al., 2012; Templeton & Greene, 2007; Wisenden et al., 2004). These specific cues override general risk factors: clearly, if a predator is actually present, a prey

animal should exhibit an appropriate anti-predator response to avoid detection, attack, or capture, regardless of its current habitat or social setting. Plains zebras, *Equus quagga*, offer a clear illustration of this concept: in general, zebras use grassland habitat patches during daylight hours but shift to woodland patches at night in order to avoid lions, *Panthera leo*, that emerge from the woodland at night to hunt in grasslands. However, zebras abandon patches of any type in response to actual lion presence on that patch (Fischhoff et al., 2007).

Just as prey prioritize antipredator behavior in the presence of predators, they should forgo it when predators are absent. However, it may be difficult for prey to recognize acute low-risk conditions because there are few cues that reliably signal predator absence (Lima & Bednekoff, 1999; Sih, 1992). Predators exhibit numerous behaviors and physical traits that help them avoid detection or recognition by their prey prior to attack (Dettner & Liepert, 1994; Downes & Shine, 1998; Heithaus et al., 2002; Hilborn et al., 2012; Théry & Casas, 2002). Therefore, lack of evidence of predator presence does not necessarily indicate predator absence. Uncertainty regarding predator absence can cause prey animals to over-invest in antipredator responses at the expense of foraging or other activities (Bouskila & Blumstein, 1992; Sih, 1992).

As a result of their maternal care strategy, female Thomson’s gazelles, *Eudorcas thomsonii*, with dependent fawns have periodic access to reliable cues indicating predator absence; thus, they offer a rare opportunity to examine whether or not prey animals take advantage of such information and adjust their vigilance behavior accordingly. In this study, we examine whether female Thomson’s gazelles with fawns exhibit temporal vigilance patterns consistent with the predictions of the risk allocation hypothesis. Thomson’s gazelles are preyed upon by a wide variety of predator species and rely heavily on vigilance to mitigate this risk (FitzGibbon, 1988, 1989, 1990c). Females with young fawns are generally more vigilant

than non-mothers because they must manage their own risk as well as that of their highly vulnerable fawn (Fitzgibbon, 1990a, 1993a; Roberts, 2014). Mothers also face heightened energetic demands arising from the simultaneous lactation and gestation that is common in this species (Brooks, 1961; Hvideberg-Hansen, 1970). Therefore, we expect maternal vigilance patterns to be very sensitive to information regarding probabilistic and actual risk. Female gazelles and their fawns engage in a cooperative strategy of maternal care, known as hiding, that results in discrete periods of high and low fawn risk and generates reliable information regarding predator absence. The hiding strategy is characterized by long periods of separation of the mother and offspring during which the fawn lies hidden in vegetation (Lent, 1974; Walther, 1965). The mother retrieves her fawn from hiding several times per day. During these brief active periods, the mother grooms the fawn and the infant nurses and plays. At the end of the active period, the fawn selects a hiding spot and lies down to begin the next hiding period. Hiding periods typically last at least two hours, while active periods last approximately half an hour on average (FitzGibbon, 1990a). This alternation of brief active periods and long hiding periods persists for the duration of the hiding phase, which lasts for the first two months of life in Thomson's gazelle (Fitzgibbon, 1990a; Walther, 1973).

Hiding and active periods constitute states of low and high fawn risk, respectively. Fawns are relatively safe while hidden, when their cryptic coloration, small body size and near immobility protect them from detection by nearby predators. However, risk of detection and attack is higher during active periods, when the fawn is exposed and engages in conspicuous behaviors such as play. Previous studies have found that infant predation risk in hider species increases with time spent out of hiding (Barrett, 1978; FitzGibbon, 1990a). Therefore, according to the risk allocation hypothesis, mothers should be more vigilant

during active periods than during hiding periods. This pattern has been previously reported in Thomson's gazelle (Costelloe & Rubenstein, 2015) and other hiding species (Clutton-Brock & Guinness, 1975; White & Berger, 2001). Fitzgibbon (1990a) found that heightened maternal vigilance increases the likelihood that an exposed gazelle fawn will survive a cheetah, *Acinonyx jubatus*, attack: more vigilant mothers were able to alert their fawns to the cheetah sooner, enabling the fawn to drop down and hide while the cheetah was still far away.

In this study, we test a further two predictions stemming from the risk allocation hypothesis. First, we predict that mothers should exhibit heightened vigilance behavior prior to retrieving the fawn from hiding. We expect intense maternal vigilance prior to retrieval because this is a period of elevated fawn risk relative to the rest of the hiding period. Although mothers with hidden fawns are identifiable because they tend to be more vigilant than non-mother females, they typically give away little information regarding their fawn's location during the majority of the hiding period (FitzGibbon, 1993a). However, when a female retrieves her offspring, she must approach to within several meters of the hiding spot to prompt the fawn to emerge. As she approaches, she provides increasingly specific information regarding the fawn's hiding area, and of course once the fawn stands up its exact location is revealed and it is readily detectable by predators. We expect that mothers mitigate this risk by elevating their vigilance levels prior to and during the approach to increase their chances of detecting lurking predators. This behavioral pattern has been described in other hiding species (Blank et al., 2015; Byers, 1997; Clutton-Brock & Guinness, 1975).

Our second prediction is that females will exhibit very low vigilance rates immediately after the fawn resumes hiding, provided that no predator attack or sighting occurred during the previous active period. We argue that the non-occurrence of a predator encounter dur-

ing an active period constitutes a reliable cue indicating predator absence. When predators detect an active Thomson's gazelle fawn they readily attack regardless of maternal presence (FitzGibbon, 1993a; BRC, personal observation) rather than waiting for the fawn to resume hiding and for the female to move away, as has been described for predators hunting larger hiding ungulate species (Byers, 1997; Byers & Byers, 1983; Jarnemo, 2004). Thus, if a predator does not attack during a given active period, it is very likely that there are actually no predators active nearby. If female gazelles take advantage of this cue, they should have a high degree of certainty regarding the temporary safety of themselves and their fawn and therefore should invest minimally in vigilance. As time elapses, the information regarding predator absence becomes older and less reliable, and we expect maternal vigilance to increase accordingly.

Here we test our predictions by examining changes in maternal vigilance levels relative to time until and since fawn active periods. We also test for effects of fawn age and females' group membership and habitat type, as these factors are known to affect predation risk of adult gazelle (FitzGibbon, 1990c).

Methods

Field Site

We conducted all fieldwork from March to June 2011, August to November 2011, and June to September 2012 at Ol Pejeta Conservancy in Laikipia, Kenya. Ol Pejeta is a fenced, 360 km² conservancy consisting of discrete grassy plains divided by *Acacia drepanolobium* and *Euclea divinorum* woodlands. In 2012, Ol Pejeta had a population of approximately 1300 Thomson's gazelles. The conservancy also has high densities of predators. Species that prey on adult gazelles include lions, cheetahs, leopards, *Panthera pardus*, African wild dogs, *Lycaon pictus*, and spotted hyenas, *Crocuta crocuta* (Borner et al., 1987; Brooks, 1961; Estes & Goddard, 1967; Walther, 1969). Fawn predators include

all predators of adult gazelle as well as black-backed jackals, *Canis mesomelas*, olive baboons, *Papio anubis*, and warthogs, *Phacochoerus africanus* (Roberts, 2012; Roberts & Rubenstein, 2014; Walther, 1969; Wyman, 1967).

Behavioral Observations

Animals at Ol Pejeta are well-habituated to vehicles, allowing approaches to within 100 m. At this distance we were able to observe gazelles through binoculars without disturbing them or eliciting vigilance reactions. In order to further minimize disturbance of the subject during observations, we waited to begin observations until the vehicle had been stationary for five minutes, and thereafter moved the vehicle only as necessary to keep the subject in sight.

We observed female gazelles with hiding-aged fawns. We identified mothers either by their swollen udders or the presence of a fawn. Hiding-aged fawns can be identified and roughly aged by their size relative to their mothers and their coloration (FitzGibbon, 1990a; Walther, 1973). Using these cues, we designated each fawn as either "young" (less than one month old) or "old" (between one and two months old). Observations lasted for two hours unless the female's fawn was not active in this time, in which case we observed the female for an additional two hours or until the fawn emerged from hiding, whichever occurred first. If the fawn had not emerged after four hours, we excluded the observation from this study. We photographed females head-on with a 500 mm lens and used unique, natural horn shapes and facial markings to differentiate individuals after observation (Walther, 1973).

Every 30 minutes during each observation, we collected two-minute continuous focal samples of the female's vigilance behavior, noting when she began and ended vigilance bouts (Altmann, 1974). Following Fitzgibbon (1990a), we considered a subject vigilant if her head was above shoulder level and not vigilant if her head was below shoulder level. We did not take samples when the female was lying down, and

terminated samples if she lied down before two minutes were finished. We discarded terminated samples shorter than 60 s in duration. Every 15 minutes we used a laser rangefinder to measure the distance from our vehicle to the subject, and noted whether the subject was in a group or alone and whether the grass surrounding the subject was tall (above the subject's hock) or short (below the subject's hock). We considered the subject to be in a group if she was within 50 m of an adult conspecific (FitzGibbon, 1990c). We also noted when the fawn emerged from or began hiding and any predators sighted during observations. We excluded observations with predator sightings from our analyses, unless the predator in question was a warthog. Warthogs only threaten gazelle less than two hours old and do not elicit antipredator reactions from mothers (Roberts, 2012; Roberts & Rubenstein, 2014). Therefore, we only excluded observations with warthog sightings if the warthog behaved aggressively toward the subject or her fawn.

Our observations were non-invasive, did not cause harm to our subjects and did not entail the manipulation of the animals or their behavior. Therefore, ethical review of our methods was not required under the guidelines of Princeton University's Institutional Animal Care and Use Committee.

Analyses

We performed all analyses in R version 3.3.2 (R Core Team, 2016). We classified each vigilance sample as having occurred while the fawn was active or while it was hiding. We assigned each sample that occurred during a hiding period a time value corresponding to the number of minutes (rounded to the nearest five) until or since an active period. We assigned negative values to sample taken before the fawn emerged from hiding, and positive values to samples taken after the fawn resumed hiding. If a sample fell between two observed active periods, we assigned it the number with the lowest absolute value. For example, if the

sample was taken 45 minutes after one active period and 10 minutes before the next active period, we assigned the sample a value of -10. An exception to this rule occurred when the later active period was initiated by the fawn rather than by the mother. In these cases, we assigned the sample a time value relative to the first active period, because the mother's behavior cannot be expected to anticipate an emergence that she does not initiate.

We used linear mixed-effects models to explore the effects of grass height, group membership, fawn age, and time until or since fawn activity on maternal vigilance. We analyzed vigilance samples preceding and following fawn activity separately. In both models, the response variable was the proportion of seconds in the sample that the mother spent vigilant, transformed as follows:

$$\ln[(0.5 + n)/(0.5 + N - n)]$$

where n is the number of seconds that the mother spent vigilant and N is the total number of seconds in the sample. We sampled each female multiple times and therefore included female ID as a random effect.

Our full model of maternal vigilance prior to fawn retrieval included group membership (scored as 1 if the female was in a group, 0 if not), grass height (scored as 1 for tall grass, 0 for short grass), observation distance, and minutes until fawn retrieval as fixed effects, in addition to subject ID as a random effect. Adult gazelle are at higher risk of predation when alone and in tall grass (Fitzgibbon, 1990c), so we expected vigilance to be elevated under these circumstances. We also included the interaction between grass height and minutes until fawn retrieval as a fixed effect, reasoning that females may need to spend more time searching for fawn predators in tall grass and therefore should increase their vigilance rates earlier relative to fawn retrieval in tall grass habitats compared to short grass habitats. We also included the observation distance (distance from the observation vehicle to the subject) as a fixed effect in order to verify that our proxim-

ity did not affect maternal vigilance behavior. For this model, we only used data from mothers with young fawns and thus did not include fawn age as a fixed effect. Old fawns tend to terminate hiding periods by standing up on their own rather than waiting for their mothers to retrieve them (Costelloe & Rubenstein, 2015). We therefore excluded data from mothers with old fawns on the grounds that they do not control the timing of retrieval and therefore are not expected to exhibit heightened vigilance in anticipation of this event.

In our full model of maternal vigilance following the end of an active period, we included minutes since fawn activity, fawn age (scored as 0 if young, 1 if old), maternal group membership, grass height and observation distance as fixed effects, in addition to subject ID as a random effect. As before, we expect group membership and short grass to reduce maternal predation risk and therefore be associated with lower maternal vigilance. Based on previous findings (Costelloe & Rubenstein, 2015), we expect females with old fawns to be less vigilant than females with young fawns. We also included interactions between minutes since fawn activity and group membership, and minutes since fawn activity and grass height. We expect that certainty regarding predator absence should decline more quickly in tall grass than in short grass, because mothers may be less likely to notice predators entering the area if they are concealed by tall grass. Thus, we predict that maternal vigilance will increase more rapidly in tall grass habitats than in short

grass habitats after the fawn resumes hiding. In contrast, we expect that certainty of predator absence will decay more slowly when females are in groups than when they are alone because groups of gazelles have a higher probability of detecting predators than do solitary individuals (FitzGibbon, 1993b). Thus, when females are in a group predators are less likely to approach undetected, and maternal vigilance should increase more slowly in groups compared to when females are alone.

We used the lme4 package (Bates et al., 2015) to fit the full models described above and then used the dredge() function in the MuMIn package (Bartón, 2016) to examine all possible submodels. We ranked submodels based on AIC_c values (Appendix 1). For both the pre- and post-activity models, the AIC_c score of the top-ranked model differed from the next-best model by >2 . However, in both cases the weight of the top model was <0.9 , so we elected to conduct model averaging (Grueber et al., 2011). We averaged all models with a ΔAIC_c of less than four relative to the best model. This threshold yielded a set of four out of a possible 20 models of vigilance prior to fawn active periods, and a set of seven out of a possible 52 models of vigilance following fawn active periods (Appendix 1). We also tested thresholds of $\Delta AIC_c < 6$ and $\Delta AIC_c < 10$, but results were similar across all three thresholds and the higher thresholds resulted in relatively large model sets given our sample sizes. Therefore, we proceeded with the lower threshold of $\Delta AIC_c < 4$ (Grueber et al., 2011).

Table 1. Distribution of vigilance samples before and after fawn active periods across fawn age classes and social and environmental conditions. Old fawns were excluded from analyses of maternal vigilance prior to fawn retrieval (see Methods for justification).

	Prior to fawn retrieval			After fawn has resumed hiding		
	Alone	In group	Total	Alone (young, old)	In group (young, old)	Total
Short grass	11	11	22	4 (4, 0)	29 (22, 7)	33 (26, 7)
Tall grass	1	3	4	2 (2, 0)	9 (6, 3)	11 (8, 3)
Total	12	14	26	6 (6, 0)	38 (28, 10)	44 (34, 10)

Results

We analyzed data from 33 observations of 30 different females, which yielded a total of 70

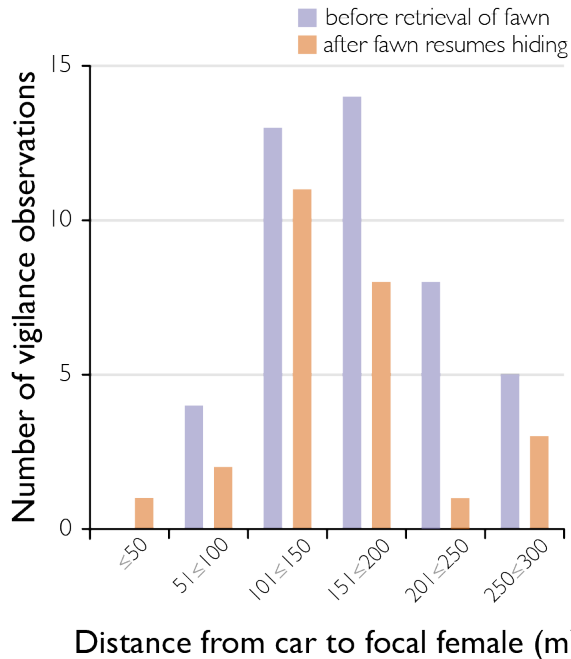


Figure 1. Distributions of observation distances from which vigilance samples were taken. Purple bars indicate samples taken prior to fawn retrieval; orange bars indicate samples taken after the fawn resumed hiding.

vigilance samples taken during fawn hiding periods. Twenty-six samples occurred prior to fawn retrieval and 44 occurred after the fawn resumed hiding. All samples were two minutes in length except for one sample occurring before fawn retrieval (116 s) and two occurring after the fawn resumed hiding (97 and 110 s). The distribution of samples across fawn age and social and environmental contexts is given in Table 1. The distributions of observation distances for each dataset are shown in Figure 1.

The averaged model for maternal vigilance prior to fawn retrieval included time until fawn retrieval, grass height, maternal group membership and observation distance as fixed effects (Table 2). Time until fawn retrieval was the only significant effect, with maternal vigilance levels increasing in anticipation of fawn retrieval (Figure 2A). In the case of grass height, the lack of an effect may be due to our low number of samples from females in tall grass ($N = 4$) (Table 1).

The averaged model for maternal vigilance following fawn active periods included grass height, time since fawn activity, mater-

Parameter	Estimate	Adjusted standard error	Relative importance	Z	p
Intercept	3.0018	1.0141	NA	2.96	<0.01
Minutes until fawn retrieval	0.0250	0.0078	1.00	3.22	<0.01
Grass height	-1.5752	1.5710	0.20	1.00	0.32
Observation distance	-0.0020	0.0100	0.12	0.21	0.84
Group membership	-0.0585	1.0254	0.12	0.06	0.96

Table 2. Summary of the averaged model of maternal vigilance prior to fawn retrieval.

Parameter	Estimate	Adjusted standard error	Relative importance	Z	p
Intercept	-3.2041	0.7008	NA	4.57	<0.001
Grass height	1.3874	0.6372	0.92	2.18	<0.05
Minutes since fawn activity	0.0244	0.0109	0.91	2.23	<0.05
Observation distance	-0.0036	0.0054	0.12	0.66	0.51
Group membership	0.4286	0.7837	0.12	0.55	0.59
Grass height * minutes since fawn activity	0.0098	0.0275	0.11	0.36	0.72
Fawn age	-0.1001	0.7877	0.10	0.13	0.90

Table 3. Summary of the averaged model of maternal vigilance following fawn active periods.

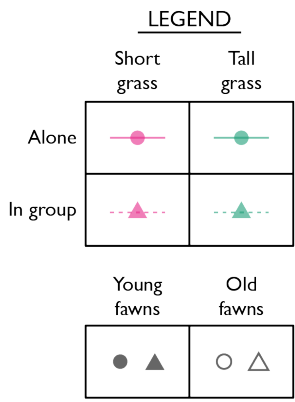
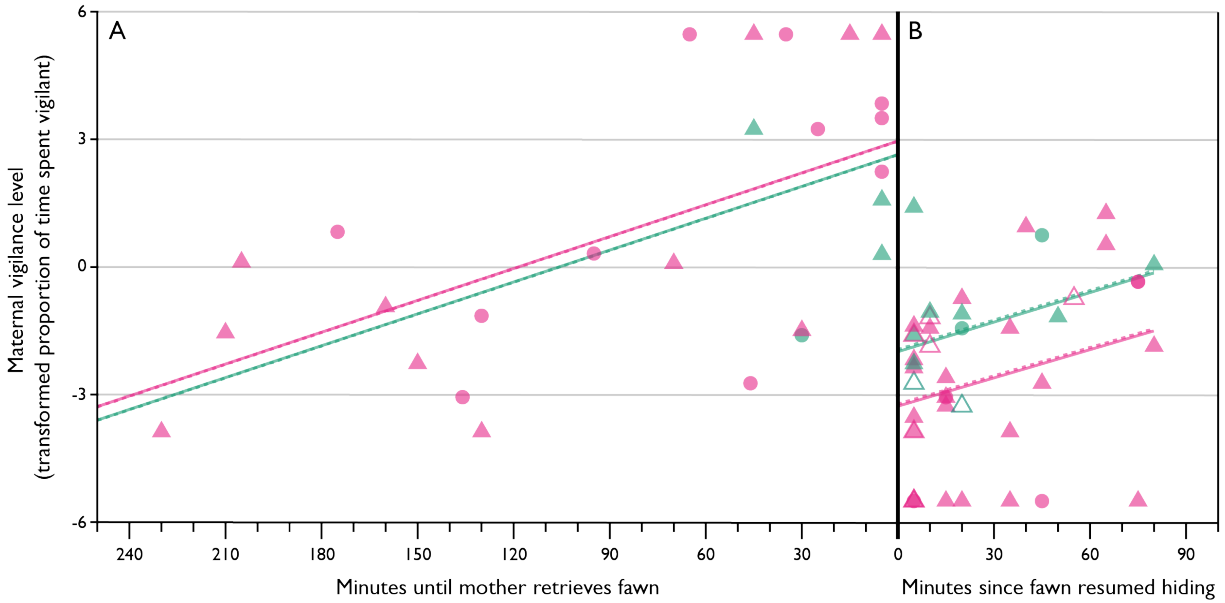


Figure 2. Changes in maternal vigilance levels over time (A) prior to fawn retrieval and (B) after the fawn resumes hiding. Lines were generated using the averaged models summarized in Tables 2 and 3. For visualization purposes, observation distance was held constant at the mean value (164.4 m) when generating fit lines. A. Females with old fawns were not included in this analysis (see Methods for justification). B. We show only the fit lines for young fawns because the effect of fawn age is so small that the fit lines for separate age classes cannot be visually distinguished.

nal group membership, observation distance, fawn age, and the interaction between group membership and minutes since fawn activity was fixed effects (Table 3). However, only grass height and time since fawn activity were significant. Maternal vigilance levels were low following fawn activer periods, but increased over time (Figure 2B). On average, females in tall grass were more vigilant than those in short grass. The lack of a significant effect of maternal group membership may be due to our low number of samples from solitary females ($N = 6$) (Table 1). Likewise, given that previous work has demonstrated stark differences in vigilance levels between mothers of young and old fawns during hiding periods (Costelloe & Rubenstein, 2015), we suspect that the lack of a significant effect of fawn age is due to our small sample

size for females with old fawn ($N = 10$) (Table 1). Old fawns are rare at our field site due to high infant predation rates (Roberts & Rubenstein, 2014).

Discussion

The temporal patterns of maternal vigilance exhibited by Thomson’s gazelle females with hidden fawns align with our predictions, which we based on the principles outlined in the risk allocation hypothesis (Lima & Bednekoff, 1999). Specifically, mothers become highly vigilant prior to retrieving their fawns from hiding, when risk of revealing the fawn to nearby predators is high, and they exhibit low levels of vigilance after fawns resume hiding, when they can be reasonably certain that predators are absent.

Vigilance prior to fawn retrieval

Pre-retrieval peaks in maternal vigilance have been described in pronghorn, *Antilocapra americana* (Byers, 1997), goitered gazelles, *Gazella subgutturosa* (Blank et al., 2015), and red deer, *Cervus elaphus* (Clutton-Brock & Guinness, 1975). This behavior is conspicuous. Females all but cease other activities in favor of vigilance. They move slowly in the direction of the fawn's hiding spot, stopping frequently to scan the environment. Several females in our observations engaged in "sham" feeding behavior, in which they lowered their heads to the ground as if to feed before quickly raising them back up to scan. In one instance, a female appeared to actively search for predators by climbing to the top of a slight hill to scan prior to approaching her fawn's hiding spot. These tactics have been described previously in pronghorn (Byers, 1997).

By engaging in these distinctive pre-retrieval behaviors, females risk alerting nearby predators to the presence of the fawn and its imminent exposure (Byers, 1997; Byers & Byers, 1983). However, this risk is effectively mitigated if these tactics enable females to detect nearby predators prior to revealing the fawn's location. When a female detects a predator she immediately aborts retrieval of the fawn, at which point the predator can either search for the fawn or wait for the female to attempt retrieval again. Searching may not be fruitful due to the difficulty of locating hidden fawns. Multiple authors have reported instances of predators passing within a few meters of hidden fawns without detecting them (FitzGibbon, 1990a; Kruuk, 1972; Walther, 1969). Waiting is also unlikely to be worthwhile as females can delay retrieval for hours after detecting a predator, making it more profitable for predators to seek alternative prey (FitzGibbon, 1993a). Thus, although pre-retrieval vigilance peaks can reveal the presence of a fawn to waiting predators, they also enable mothers to detect these predators and abort retrieval before the infant's location is revealed (Byers,

1997).

Although adult gazelle are more vulnerable when they are alone than when they are in a group (FitzGibbon, 1990c), we found no effect of group membership on maternal vigilance levels prior to fawn active periods. This is likely because maternal vigilance during the retrieval stage is driven by elevated fawn risk rather than maternal risk, and fawn risk is not modulated by the mother's group membership status. Adult gazelle in groups benefit from risk dilution and early detection of predators (FitzGibbon, 1988). Groups of gazelle are better at detecting predators than singletons due to the "many eyes" effect (FitzGibbon, 1988; Powell, 1974). However, many fawn predators, including baboons and jackals, pose little or no threat to fully-grown gazelle and therefore do not elicit antipredator reactions from non-mother adults. Due to the aseasonal reproduction of Thomson's gazelle and the very high predation rates on gazelle fawns at OPC (Roberts & Rubenstein, 2014), mothers were not typically found in groups with other mothers (only 32% of mothers observed in groups were with at least one other mother [BRC, unpublished data]). Therefore, if other group members detect a fawn predator, they are unlikely to react in a way that alerts the mother to its presence. Thus, group membership should not improve the mother's chances of detecting predators that prey only on fawns. Group membership is also unlikely to dilute predation risk to young fawns, which are conspicuous in groups of adults due to stark differences in size and coloration (Walther, 1973). Fawns are also easier to capture than adults (FitzGibbon, 1988, 1990a), and therefore likely to be targeted by predators regardless of the number of adults present. Thus, maternal group membership is unlikely to mitigate fawn risk and therefore does not affect maternal vigilance prior to fawn retrieval.

An alternative explanation for heightened maternal vigilance prior to fawn retrieval is that mothers are attempting to visually locate

their fawns, whose hiding spots they have forgotten. Studies of pronghorn (Autenreith & Fichter, 1975) and captive sable antelope, *Hippotragus niger* (Thompson, 1996), indicate that mothers sometimes have difficulty locating their hidden fawns, especially if the mother did not watch the fawn while it selected its hiding spot or if the fawn moved while the mother was away. In other instances, mothers are reported to walk directly toward their hidden young, indicating knowledge of their precise location (Leuthold, 1977; Murdock et al., 1983). Byers and Byers (1983) found that pronghorn mothers modulate their distance to their hidden fawns according to fawn risk and orient their heads and bodies towards their hidden fawns more often than expected by chance. Likewise, in a previous study of Thomson's gazelles, FitzGibbon (1993a) found that mothers' behavior varies with distance to their hidden fawns. These findings suggest that mothers typically remember where their young are hidden. However, we cannot rule out the possibility that heightened maternal vigilance sometimes serves to help the mother locate her fawn instead of or in addition to detecting predators.

Vigilance following active periods

Mothers exhibit very low vigilance rates immediately after their fawns resume hiding. This is consistent with our hypothesis that the non-occurrence of a predator attack on the fawn during an active period constitutes a reliable indicator of predator absence, and with the risk allocation hypothesis (Lima & Bednekoff, 1999), which predicts that female gazelle should lower their vigilance rates in response to this information. The subsequent rise in vigilance rates following the initial drop is also predicted: vigilance should increase over time as the information regarding predator absence grows older and its reliability decays.

For many hiding ungulate species, the non-occurrence of a predator attack during an active period is not indicative of actual pred-

ator absence because predators of these species sometimes wait to attack until the infant resumes hiding and the mother moves away. This "watch and wait" behavior has been described in coyotes, *Canis latrans*, hunting pronghorn, mule deer, *Odocoileus hemionus*, and white-tailed deer fawns, *O. virginianus* (Byers, 1997; Byers & Byers, 1983; Michael, 1967; Truett, 1979); in dingoes, *Canis lupus*, hunting domestic cattle calves, *Bos taurus* (Rankine & Donaldson, 1968); and in red foxes, *Vulpes vulpes*, hunting roe deer fawns, *Capreolus capreolus* (Jarnemo, 2004). Attacking after rather than during an active period may constitute a counter-strategy to maternal defense: after the mother has moved away from her fawn the predator has a chance to seize its prey quickly, before the mother can intervene to defend her offspring (Byers, 1997). In each of the above examples, maternal defense is an effective means of preventing infant predation and can even result in injury to the attacking predator (Grovenburg et al., 2012; Lingle et al., 2005; Reynolds, 1983; Thomson, 1992; Wilkinson & Douglass, 2002). Waiting to attack until the mother leaves may thus increase the probability of prey capture and reduce the predator's risk of injury from maternal defense.

In contrast to the above examples, predators of Thomson's gazelles do not delay their attacks. FitzGibbon (1988, 1990a) reports attacks by cheetahs, wild dogs, spotted hyenas, and golden jackals, *Canis aureus*, on active fawns. During our study we documented 10 attacks by black-backed jackals and three attacks by warthogs (BRC, unpublished data). All of these began when the predator(s) spotted an active fawn or discovered a fawn that had been hidden for some time; none occurred at the beginning of a hiding period.

A combination of two factors could account for gazelle predators' tendency to eschew the "watch and wait" strategy. First, defense by Thomson's gazelle females appears to be relatively ineffective at preventing fawn predation or injuring the predator. Gazelle moth-

ers only engage in aggressive defense against small predators, such as jackals, and never defend against larger, more threatening species (FitzGibbon, 1988; Walther, 1969). Mothers are often successful at preventing fawn predation by single jackals, but usually unsuccessful against multiple jackals (FitzGibbon, 1988; Lamprecht, 1978; Walther, 1969; Wyman, 1967). We suspect that the majority of jackal attacks experienced by gazelle at OPC involve multiple jackals. Black-backed jackals typically hunt in pairs or small groups, especially when hunting ungulate fawns and other large prey (Estes, 1967; Lamprecht, 1978; Wyman, 1967). Indeed, of the 10 jackal attacks we documented, nine involved two or more jackals. The attack by a solitary jackal occurred when a gazelle and her fawn inadvertently approached a sleeping jackal. The resulting attack was unsuccessful. The other 9 attacks involved pairs or small groups of actively foraging jackals, and all resulted in the death of the fawn despite maternal defense efforts. In addition to its limited effectiveness in preventing fawn predation, maternal defense poses little risk of injury to attackers because females rarely make contact with predators (Walther, 1969; Wyman, 1967).

Predators may also attack fawns immediately rather than watching and waiting because fawns are difficult to locate once they hide, due in part to the lack of visual landmarks in open grassland habitat. Hunting cheetahs often lose track of fawns if they drop down and hide, especially if they drop down while the cheetah is far away (FitzGibbon, 1990a). The lack of cover in open grasslands may prevent predators from remaining undetected by females unless they maintain a large distance from the mother and active fawn. Once the predator has lost sight of the hidden fawn but revealed itself, mothers can impede the predator's search for the fawn by repeatedly driving it away from the fawn's hiding area (in the case of small predators) or by moving away from the hiding spot, thereby removing herself

as a usable landmark and drawing the predator away from the fawn, as has been described for pronghorn (Byers & Byers, 1983). Thus, there appears to be little reason to delay attacking an active fawn while its mother is present, and waiting to attack may result in prey loss.

We thus argue that active periods, which are driven by the necessity of caring for hidden fawns, may also secondarily function as a form of "predator sampling" (Sih, 1992) in this system where predators attack immediately upon detecting an exposed fawn. This is similar to sampling behavior described in Atlantic salmon (*Salmo salar*) and various flocking bird species where, following a simulated predator attack at a feeding station, competitively dominant or less food-stressed individuals wait to return to the feeding station until other group members have resumed foraging (de Laet, 1985; Gotceitas & Godin, 1991; Hegner, 1985; Hogstad, 1988; Roth et al., 2008; Waite & Grubb Jr., 1987). Individuals that can afford to wait to eat appear to use their presumably more desperate group mates to test for the continued presence of the predator before assuming the risk of foraging themselves. Similarly, the behavior of gazelle mothers following active periods suggests that they may take advantage of the predator sampling information generated by fawn exposure.

According to the risk allocation hypothesis, periods of low vigilance can occur either in response to low risk levels, as we propose here, or as a result of heightened foraging motivation (Lima & Bednekoff, 1999). An alternative explanation for the pattern we have described, then, is that females lower their vigilance following active periods because their resources are so depleted that they must feed to meet their energetic demands, regardless of their risk level. The steady increase in vigilance following the initial drop would then be explained by the female becoming gradually satiated. Although heightened maternal vigilance during active periods is associated with a decrease in time spent foraging, females still

spend, on average, about a third of their time foraging while their fawns are active and most vulnerable (Appendix 2). Given that active periods are relatively brief and infrequent compared to hiding periods (FitzGibbon, 1990a) and that females spend a considerable portion of active periods foraging, we find this alternative explanation unlikely.

Maternal vigilance following fawn active periods is also affected by habitat type (Figure 2B), with females in tall grass exhibiting higher vigilance levels than those in short grass. This suggests that maternal vigilance during this time serves at least in part to mitigate the mother's own risk, since tall grass is known to increase maternal risk but mitigate fawn vulnerability (FitzGibbon, 1988, 1990c). This pattern may also reflect the quality of the information regarding predator absence, or, put another way, the female's level of certainty that predators are still absent at any given point in time following the end of an active period. Adult and fawn predators are more likely to enter the area undetected in tall grass, which provides more cover than short grass (FitzGibbon, 1988). Thus, females should be less certain of predator absence (and therefore more vigilant) in tall grass than in short grass. Following this logic, we expected the reliability of the information regarding predator absence to decay more quickly when females were in tall grass. Contrary to our expectations, we did not find support for an interaction between grass height and time since fawn activity, but this may be because our sample size for females in tall grass ($N = 11$) was insufficient to demonstrate an interaction (Table 1).

Conclusions

The ability to recognize changes in risk level and adjust antipredator behavior accordingly is crucial to the optimization of prey behavioral patterns, especially for parents that must protect vulnerable offspring while meeting elevated energetic demands. Models of optimal prey behavior often assume that prey have perfect

knowledge of their own level of vulnerability, but risk estimation is likely imperfect in actuality. Situations in which prey can achieve a high degree of certainty regarding predator absence may be particularly rare (Lima & Bednekoff, 1999; Sih, 1992). Female Thomson's gazelles with hiding-aged fawns engage in a maternal care strategy that generates reliable information regarding predator absence and also features predictable periods of elevated fawn risk. Here we have demonstrated that female gazelle exhibit temporal patterns in their vigilance behavior that are consistent with the risk allocation hypothesis, suggesting that mothers may anticipate impending increases in fawn risk and that they may take advantage of fawn exposure as an opportunity for predator sampling. Further study of vigilance behavior in hiding ungulates may help to clarify if females are actually responding to a drop in risk after the activity period: species whose predators frequently adopt a watch and wait strategy should not exhibit a sharp drop in vigilance after the fawn resumes hiding, while those whose predators tend to attack active fawns immediately should exhibit the same pattern we describe for Thomson's gazelles.

Understanding the capacity of prey animals to utilize available information to accurately gauge risk and respond accordingly is important to our understanding of the indirect effects that predators can have on prey populations (Creel et al., 2011; Creel et al., 2007; Creel et al., 2014). In ungulates, which face high infant mortality rates from predation (Linnell et al., 1995), understanding the dynamics of predator-prey relationships during infancy and the factors that affect offspring survival probability can facilitate the effective management of ungulate populations.

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APPENDIX 1: Model selection and averaging

Tables A1-1 and A1-2 give the full set of models for maternal vigilance prior to and following fawn active periods, respectively. We included all models with $\Delta AIC_c < 4$ in the final averaged models. We also tried model averaging with thresholds of $\Delta AIC_c < 6$ and $\Delta AIC_c < 10$. Results for these different thresholds are compared in Tables A1-3 and A1-4. Changing the thresholds did not affect the qualitative conclusions of the models.

Table A1-1. Full set of models for maternal vigilance prior to fawn retrieval. Shaded rows denote models that were included in the final model averaging.

Model rank	Fixed effects						df	AIC _c	ΔAIC _c	Weight
	Intercept	Minutes until fawn retrieval	Group membership	Grass height	Observation distance	Grass height * minutes until fawn retrieval				
1	2.867	0.02451					4	125.5	0.00	0.463
2	3.342	0.02698		+			5	127.5	2.03	0.167
3	3.161	0.02418			-0.00204		5	128.5	3.05	0.101
4	2.895	0.02446	+				5	128.6	3.09	0.099
5	3.395	0.02761		+		+	6	130.6	5.15	0.035
6	3.738	0.02658		+	-0.00269		6	130.8	5.37	0.032
7	3.246	0.02747	+	+			6	130.9	5.38	0.031
8	3.199	0.02412	+		-0.00207		6	131.9	6.46	0.018
9	1.154						3	132.0	6.49	0.018
10	3.239	0.02858	+	+		+	7	134.2	8.73	0.006
11	2.380				-0.00786		4	134.3	8.80	0.006
12	3.882	0.02715		+	-0.00330	+	7	134.3	8.82	0.006
13	3.631	0.02705	+	+	-0.00261		7	134.6	9.10	0.005
14	1.411		+				4	134.6	9.14	0.005
15	1.132			+			4	134.8	9.30	0.004
16	2.633		+		-0.00785		5	137.2	11.73	0.001
17	2.398			+	-0.00791		5	137.4	11.89	0.001
18	1.375		+	+			5	137.7	12.21	0.001
19	3.721	0.02809	+	+	-0.00328	+	8	138.3	12.84	0.001
20	2.607		+	+	-0.00777		6	140.6	15.15	0.000

Table A1-2. Full set of models for maternal vigilance following fawn activity periods. Shaded rows denote models that were included in the final model averaging

Model rank	Intercept	Fixed effects							df	AIC _c	ΔAIC _c	Weight
		Minutes since fawn activity	Group membership	Grass height	Fawn age	Observation distance	Group membership * minutes since fawn activity	Grass height * minutes since fawn activity				
1	-3.335	0.02473		+					5	182.1	0.00	0.231
2	-2.705	0.02448		+		-0.00355			6	184.3	2.24	0.075
3	-3.749	0.02595	+	+					6	184.5	2.38	0.071
4	-3.292	0.02283		+			+		6	184.6	2.56	0.064
5	-3.307	0.02451		+	+				6	184.7	2.67	0.061
6	-2.694			+					4	184.9	2.83	0.056
7	-2.897	0.02204							4	185.3	3.18	0.047
8	-4.640	0.05261	+	+				+	7	186.1	4.05	0.030
9	-1.906	0.02194				-0.00585			5	186.7	4.62	0.023
10	-2.355								3	186.7	4.67	0.022
11	-2.018			+		-0.00385			5	187.0	4.92	0.020
12	-2.665	0.02263		+		-0.00355	+		7	187.0	4.96	0.019
13	-3.099	0.02533	+	+		-0.00288			7	187.0	4.96	0.019
14	-2.658	0.02419		+	+	-0.00361			7	187.1	5.05	0.018
15	-3.697	0.02414	+	+			+		7	187.2	5.10	0.018
16	-2.606			+	+				5	187.2	5.14	0.018
17	-3.726	0.02565	+	+	+				7	187.2	5.17	0.017
18	-2.743		+	+					5	187.5	5.38	0.016
19	-3.269	0.02269		+	+		+		7	187.5	5.39	0.016
20	-3.034	0.02245	+						5	187.8	5.70	0.013
21	-2.863	0.02179			+				5	187.8	5.72	0.013
22	-1.351					-0.00594			4	188.1	6.04	0.011
23	-3.921	0.05279	+	+		-0.00334		+	8	188.8	6.70	0.008
24	-4.138	0.05497	+					+	6	188.9	6.83	0.008
25	-4.604	0.05117	+	+			+	+	8	188.9	6.86	0.008

Model rank	Fixed effects								df	AIC _c	ΔAIC _c	Weight
	Intercept	Minutes since fawn activity	Group membership	Grass height	Fawn age	Observation distance	Group membership * minutes since fawn activity	Grass height * minutes since fawn activity				
26	-2.269				+				4	189.0	6.91	0.007
27	-4.626	0.05269	+	+	+			+	8	189.0	6.97	0.007
28	-2.205		+						4	189.1	7.05	0.007
29	-1.846	0.02159			+	-0.00591			6	189.3	7.27	0.006
30	-1.770	0.02165	+			-0.00606			6	189.4	7.29	0.006
31	-1.901			+	+	-0.00398			6	189.4	7.33	0.006
32	-1.832		+	+		-0.00419			6	189.7	7.58	0.005
33	-2.725		+	+	+				6	189.9	7.81	0.005
34	-3.044	0.02351	+	+		-0.00290	+		8	189.9	7.85	0.005
35	-3.073	0.02503	+	+	+	-0.00288			8	190.0	7.91	0.004
36	-2.625	0.02244		+	+	-0.00359	+		8	190.0	7.94	0.004
37	-3.679	0.02396	+	+	+		+		8	190.1	8.07	0.004
38	-0.831		+			-0.00679			5	190.4	8.33	0.004
39	-1.227				+	-0.00609			5	190.4	8.35	0.004
40	-3.013	0.02221	+		+				6	190.4	8.37	0.004
41	-2.862	0.05499	+			-0.00633		+	7	190.5	8.43	0.003
42	-2.177		+		+				5	191.5	9.44	0.002
43	-4.120	0.05503	+		+			+	7	191.7	9.61	0.002
44	-3.884	0.05129	+	+		-0.00335	+	+	9	191.8	9.68	0.002
45	-3.901	0.05287	+	+	+	-0.00335		+	9	191.9	9.79	0.002
46	-4.592	0.05131	+	+	+		+	+	9	192.0	9.97	0.002
47	-1.742	0.02138	+		+	-0.00608			7	192.2	10.10	0.001
48	-1.821		+	+	+	-0.00413			7	192.2	10.17	0.001
49	-0.796		+		+	-0.00681			6	192.9	10.85	0.001
50	-3.023	0.02333	+	+	+	-0.00291	+		9	193.1	10.99	0.001
51	-2.835	0.05506	+		+	-0.00634		+	8	193.4	11.36	0.001
52	-3.867	0.05143	+	+	+	-0.00336	+	+	10	195.1	12.98	0.000

Table A1-3. Comparison of averaged models of maternal vigilance prior to fawn retrieval using different thresholds for model inclusion. All models included female ID as a random effect. For fixed effects, asterisks indicate significant level of effects (** for $P < 0.01$, * for $P < 0.05$, • for $P < 0.1$, NS for not significant). The direction of the relationship (+ or -) is given for significant effects. Blank cells indicate that the effect was not included in the model.

Averaging threshold	Number of models included	Fixed effects				
		Minutes until fawn retrieval	Group membership	Grass height	Observation distance	Grass height * minutes until fawn retrieval
$\Delta AIC_c < 4$	4	**+	NS	NS	NS	
$\Delta AIC_c < 6$	7	**+	NS	NS	NS	NS
$\Delta AIC_c < 10$	15	**+	NS	NS	NS	NS

Table A1-4. Comparison of averaged models of maternal vigilance following fawn active periods using different thresholds for model inclusion. All models included female ID as a random effect. For fixed effects, asterisks indicate significant level of effects (** for $P < 0.01$, * for $P < 0.05$, • for $P < 0.1$, NS for not significant). The direction of the relationship (+ or -) is given for significant effects. Blank cells indicate that the effect was not included in the model.

Averaging threshold	Number of models included	Fixed effects						
		Minutes since fawn activity	Group membership	Grass height	Fawn age	Observation distance	Group membership * minutes since fawn activity	Grass height * minutes since fawn activity
$\Delta AIC_c < 4$	7	*+	NS	*+	NS	NS		NS
$\Delta AIC_c < 6$	21	•+	NS	*+	NS	NS	NS	NS
$\Delta AIC_c < 10$	46	•+	NS	*+	NS	NS	NS	NS

APPENDIX 2: Maternal activity budgets before, during and after hiding periods

To construct activity budgets, we instantaneously sampled maternal behavior every five minutes during our observations of female gazelles and their fawns (Altmann, 1974). We recorded the mother's behavior as vigilant, grazing, lying down, or other according to the ethogram in Table A2-1. For each observation, we divided the behavior samples into three groups: those recorded during fawn active periods, those recorded in the 30 minutes prior to fawn activity, and those recorded in the 30 minutes following fawn activity. We constructed separate maternal activity budgets for each of these groups by dividing the number of samples scored as a given behavior by the total number of samples taken during the observation. We excluded any budgets based on fewer than three samples from all analyses, yielding sample sizes of 16 activity budgets for the 30 minutes before fawn retrieval, 26 during fawn active periods, and 26 for the 30 minutes after the fawn resumed hiding. We compared the proportion of time subjects devoted to vigilance, grazing, and lying down in each period using Wilcoxon rank sum tests. Many observations started or ended during fawn active periods, resulting in few observations with both "before" and "after" activity budgets. For this reason we were unable to perform paired tests.

Table A2-1. Ethogram used for instantaneous scan sampling of maternal behavior.

Behavior	Description
Vigilant	Subject is walking or standing with head raised above shoulder level.
Grazing	Subject is walking with head below shoulder level, either actively biting/chewing vegetation (i.e. feeding) or with gaze oriented toward the ground/surrounding grass (i.e. searching).
Lying down	Subject is lying down
Other	Subject's behavior is not described by above categories. Includes self-grooming behaviors, fawn grooming behaviors, and social interactions.

Figure A2-1 shows the percentages of time mothers spent vigilant, grazing, and lying down before, during, and after fawn active periods. These three behaviors accounted for 97% of samples taken before active periods, 91% of samples taken during active periods, and 99% of samples taken after active periods. Mothers were significantly more vigilant in the 30 minutes before and during fawn active periods than in the 30 minutes after the fawn resumed hiding (before: 0.44 ± 0.10 ; during: 0.52 ± 0.06 ; after: 0.18 ± 0.04 ; Wilcoxon test_(before, after) $W = 292, P < 0.05$; Wilcoxon test_(during, after) $W = 575.5, P < 0.001$). Although heightened vigilance was associated with a decrease in time spent grazing (before: 0.35 ± 0.09 ; during: 0.37 ± 0.06 ; after: 0.73 ± 0.05 ; Wilcoxon test_(before, after) $W = 94, P < 0.01$; Wilcoxon test_(during, after) $W = 123, P < 0.001$), mothers still spent approximately a third of their time grazing prior to and during fawn active periods. Time spent lying down did not differ significantly across the three time periods.

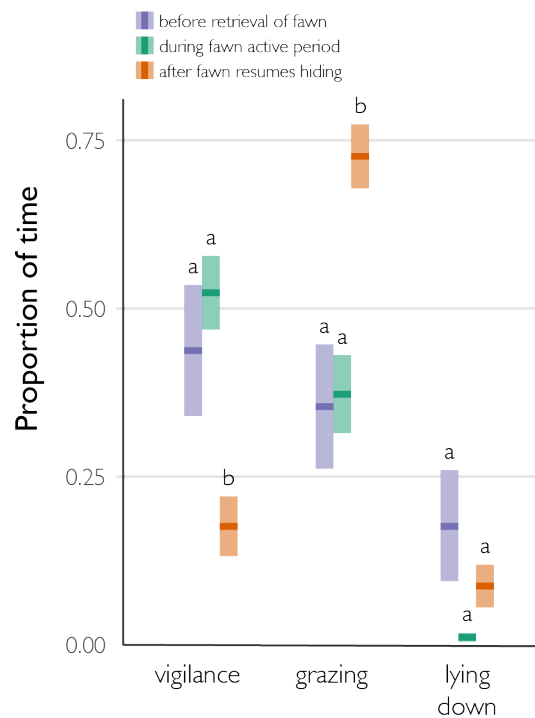


Figure A2-1. Activity budgets of female gazelles in the 30 minutes before the fawn is retrieved from hiding, during fawn active periods, and in the 30 minutes after the fawn resumes hiding. Within each behavior, bars with the same letter are not significantly different ($P > 0.05$).