Title: Coping with transition: offspring risk and maternal behavioral changes at the end of the hiding phase

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1 Hiding is a cooperative mother-infant behavioral strategy used by many ungulate species to
2 mitigate infant predation risk. During the late stages of the hiding phase, infants begin a
3 transition out of the strategy and exhibit behavioral changes that increase their exposure to
4 predators. Mothers in many hider species are known to exhibit potentially costly changes in
5 habitat use, gregariousness, and vigilance behavior at the onset of the hiding phase. However,
6 the effects of infant transitional behavior on maternal behavioral patterns are understudied. In
7 this study, we compare the behavioral patterns of Thomson's gazelle (*Eudorcas thomsonii*)
8 females with young and transitioning fawns to determine the effect of fawn behavioral changes
9 on maternal behavior. We find that, although transitioning fawns are at greater risk than younger
10 fawns while hidden, mothers of transitioning fawns are less vigilant than mothers of younger
11 fawns during hiding periods. Mothers and fawns rely on group membership rather than
12 heightened maternal vigilance to mitigate fawn risk during the transition. Group membership is
13 apparently made possible by the shorter hiding bouts of transitioning fawns relative to younger
14 fawns: more frequent activity bouts likely enable mothers to relocate their fawns more
15 frequently, which helps the mother and fawn to keep up with group movements.

16
17 Keywords: hiding strategy, Thomson's gazelle, maternal behavior, risk, antipredation behavior,
18 ungulate, transition, group size, activity

19
20 Across ungulate species, infant survival and juvenile recruitment rates are highly
21 variable and play a key role in population dynamics (Gaillard et al. 1998). Infant mortality rates
22 of 50% or more are common in ungulate populations, and where predators are present,
23 predation is usually the primary cause of infant death (Estes & Estes 1979; Epstein et al. 1983;
24 Festa-Bianchet et al. 1994; Adams et al. 1995; Linnell et al. 1995; Jarnemo 2004; Lomas &
25 Bender 2007; Bercovitch & Berry 2009). Relative to adults, ungulate infants are particularly
26 vulnerable to predation due to their smaller size and lesser escape ability (Bleich 1999; Barber-
27 Meyer & Mech 2008). To mitigate infant risk, ungulate species have evolved a range of
28 cooperative mother-infant behavioral strategies that fall on a spectrum between “following” and
29 “hiding” (Walther 1965; Walther 1969; Lent 1974). Follower species include all perissodactyls
30 and camelids, most caprines, and a few bovid and cervid species, such as wildebeest
31 (*Connochaetes* spp.) and caribou (*Rangifer tarandus*). In contrast, most cervids and bovids are
32 classified as hidiers (Lent 1974; Fisher et al. 2002). In follower species, the young accompany
33 their mothers more or less continuously from birth until independence and rely on maternal
34 defense, flight, and/or the safety of groups for protection against predators. This strategy is
35 usually associated with large adult body size, gregariousness, and open habitat (Lent 1974;
36 Fisher et al. 2002). In hider species, the infant conceals itself in vegetation shortly after birth and
37 spends long periods separated from its mother. The mother returns and retrieves the infant
38 several times per day to feed and care for it. During these active periods, the mother may lead
39 her offspring to a new hiding area where the infant selects a specific hiding spot (Lent 1974;
40 Byers 1997; Jarnemo et al. 2004). The alternation of short active periods and long hiding
41 periods continues for the duration of the hiding phase, which varies in duration among species
42 from several days to several months (Lent 1974). While concealed, the infant is at lower risk of
43 being detected and killed by a predator (Barrett 1978; Fitzgibbon 1990b). Hiding is typically
44 associated with small-bodied species living solitarily or in small groups and in closed habitats
45 (Lent 1974; Fisher et al. 2002).

46 Antipredator strategies improve the survival prospects of infants (Barrett 1978; Fitzgibbon
47 1990b; Gaillard et al. 2000), but sometimes necessitate changes to mothers’ behavior that can

negatively impact maternal survival or fecundity. For example, mothers in many follower and hider species exhibit changes in habitat preference during parturition and early lactation. Mothers in these species leave their normally preferred habitats in favor of areas with greater visibility (Bangs et al. 2005; Poole et al. 2007; Rearden et al. 2011; Pinard et al. 2012), lower predator density (Bergerud et al. 1984; Alados & Escos 1988; Festa-Bianchet 1988; Bergerud et al. 1990), or more concealing vegetation (Gosling 1969; Jarman 1976; Leuthold 1977; Fitzgibbon 1990a; Bongi et al. 2008; Ciuti et al. 2009; Roberts & Rubenstein 2014). Although safer for infants, these habitats often offer poorer foraging conditions for mothers than their normally preferred habitats (White & Berger 2001; Ciuti et al. 2009; Panzacchi et al. 2010), and can also increase maternal predation risk if they conceal approaching predators (Fitzgibbon 1990a). Habitat changes vary in duration. In some follower species, these changes encompass only parturition and the few hours or days necessary for the mother and offspring to bond and for the infant to develop the motor skills and speed necessary to keep up with a group of adults or evade predators (Bergerud et al. 1984; Langbein et al. 1998; Daleszczyk 2004; Bangs et al. 2005); in other species, females may exhibit some degree of habitat preference alteration until weaning is completed (Bon et al. 1995; Grignolio et al. 2007). Because their young depend strongly on vegetation cover for protection, hider mothers typically remain in these habitats for the duration of the hiding phase (Clutton-Brock & Guinness 1975; Ozoga et al. 1982; Schwede et al. 1993; Byers 1997; Bongi et al. 2008).

Habitat change is often accompanied by social isolation. Isolation may be a side effect of mothers leaving normally-preferred habitats, or may result from mothers intentionally isolating from conspecifics in order to avoid aggression (Fischhoff et al. 2010; Roberts & Rubenstein 2014) or to space out vulnerable infants (Tinbergen et al. 1967; Clutton-Brock & Guinness 1975; Bergerud & Page 1987; Schwede et al. 1993; Byers 1997). Hider mothers tend to be spatially tethered to their offspring, typically remaining within several hundred meters or less of its hiding location (Lent 1974; Schwede et al. 1994; Byers 1997; Bongi et al. 2008). They may therefore find themselves isolated when groups move beyond this radius (Brooks 1961; Walther 1969; O'Brien 1984). Compared to individuals in large groups, solitary individuals and those in smaller groups are at greater risk of predation due to a smaller dilution effect or preferential hunting by

77 predators (Hamilton 1971; Foster & Treherne 1981; Fitzgibbon 1990a).

78 In addition to these grouping and habitat changes, ungulate mothers may suffer reduced
79 foraging time or efficiency due to heightened vigilance. Ungulates, along with many other
80 animals, use vigilance to detect approaching predators and enable effective escape or defense
81 responses (Dehn 1990; Fitzgibbon 1990b; Creel et al. 2014). Vigilance tends to increase when
82 perceived risk is higher (Pöysä 1987; Lima & Bednekoff 1999; Devereux et al. 2006) and
83 mothers with dependent young tend to be more vigilant than non-mothers due to the greater
84 vulnerability of their offspring (Clutton-Brock & Guinness 1975; Alados & Escos 1988;
85 Fitzgibbon 1993; Hunter & Skinner 1998; Roberts 2014). For many species, vigilance is
86 incompatible with other activities such as foraging and resting (Lima & Dill 1990; Lima 1998;
87 Toïgo 1999; Hamel & Côté 2008; Creel et al. 2014). Reduced foraging time, in combination with
88 the high energetic requirements of lactation, may reduce fecundity and prevent mothers from
89 capitalizing on their next reproductive opportunity (Benton et al. 1995; Cook et al. 2004).

90 The severity of these various maternal costs likely change as infants mature and become
91 less vulnerable to predation, but research on this topic is lacking. As follower infants develop
92 speed and agility, isolation in protective habitats likely becomes less necessary, allowing
93 mothers to return to preferred habitats, rejoin groups, and possibly reduce their investment in
94 vigilance. For hider species, the relationship between maternal costs and offspring age may be
95 less linear. Toward the end of the hiding phase, the infant begins a transition out of the hiding
96 strategy. It emerges from hiding more often, resulting in fewer, shorter hiding periods and more
97 time spent out of hiding (Fitzgibbon 1990b; Olazábal et al. 2013). Additionally, the infant initiates
98 the end of hiding periods independently by standing up on its own more frequently, without
99 waiting for its mother to retrieve it (Alados & Escos 1988; Fitzgibbon 1990b; Byers 1997). It
100 appears that this transition typically occurs before the infant has developed sufficient speed and
101 agility to escape predators (Fitzgibbon 1990b; Byers 1997); therefore, this period of transition is
102 particularly risky for ungulate infants. Hider infants that survive the transition no longer conceal
103 themselves but instead remain constantly active and in the same social group as their mothers
104 (Lent 1974). That is, they behave as followers. These transitional changes in offspring behavior
105 likely alter maternal investment trade-offs and affect the behavioral constraints experienced by

106 mothers. The shorter hiding bouts and more frequent active periods of transitioning infants may
107 allow mothers to relocate their offspring more often and track group movements more
108 effectively, thereby increasing mothers' time spent in social groups and reducing maternal risk.
109 However, increased infant risk during the transition may necessitate greater maternal vigilance.

110 In this study, we seek to understand how relevant maternal costs change as the hiding
111 phase progresses. We examine maternal and fawn behavior during the hiding phase in
112 Thomson's gazelle (*Eudorcas thomsonii*), a small-bodied East African antelope species. We first
113 investigate how fawn risk changes throughout the hiding phase by comparing the hiding
114 behavior of transitioning fawns to younger fawns. Following the findings of previous studies
115 (Fitzgibbon 1988, 1990b), we expect older, transitioning fawns to emerge from hiding more
116 often than young fawns and to initiate emergence on their own more often, without waiting for
117 their mothers to retrieve them. We hypothesize that these behaviors increase fawn risk by
118 preventing mothers from increasing their vigilance in anticipation of emergence.

119 We next examine changes in maternal vigilance, maternal grouping behavior, and maternal
120 and fawn habitat use throughout the hiding phase. Since fawn risk is expected to be higher
121 during the transition, we expect mothers of transitioning fawns to be more vigilant than mothers
122 of younger fawns. Adult Thomson's gazelles are normally gregarious and strongly prefer open,
123 short grass habitats (Brooks 1961). However, in previous studies, females with young fawns
124 have often been found alone and in tall grass habitats (Brooks 1961; Walther 1969; Fitzgibbon
125 1988). We hypothesize that greater fawn mobility resulting from more frequent active periods
126 will enable transitional mothers to more closely match non-maternal grouping and habitat use
127 patterns. Therefore, we predict that mothers with transitioning fawns will spend more time in
128 short grass, more time in groups, and more time in larger groups than mothers with young
129 fawns. Hiding is likely to be more effective in tall grass habitats compared to short grass
130 habitats. We therefore expect all fawns to prefer tall grass habitats, but for this preference to be
131 weaker in transitioning fawns, which rely less heavily on the hiding strategy.

132 Finally, to understand the relative impact of these behavioral changes to mothers' risk
133 perception, we construct a series of multivariate models to examine the effects of fawn age,
134 fawn and maternal habitat type, and maternal social setting on maternal vigilance.

METHODS

Field Site and Study Species

We conducted all fieldwork from March to June 2011, August to November 2011, and June to September 2012 at Ol Pejeta Conservancy (OPC) in Laikipia, Kenya. OPC is a fenced, 360 km² conservancy consisting of discrete grassy plains divided by *Acacia drepanolobium* and *Euclea divinorum* woodlands. In 2012, OPC had a population of approximately 1300 Thomson's gazelles. The conservancy has high densities of gazelle predators including lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*), black-backed jackals (*Canis mesomelas*), spotted hyenas (*Crocuta crocuta*), warthogs (*Phacochoerus africanus*) and olive baboons (*Papio anubis*). Human hunting of wildlife is illegal in Kenya and to our knowledge this population of Thomson's gazelle is not subject to poaching.

Female Thomson's gazelles form open-membership groups with sizes varying from two to several hundred individuals (Brooks 1961). They reproduce aseasonally and give birth to singleton fawns after a 5.5 month gestation (Brooks 1961; Walther 1969; Hvideberg-Hansen 1970). Fawns hide intensively for the first month of life before beginning the transition out of hiding. The transition is complete by the time the fawn is two months old (Fitzgibbon 1990b).

Behavioral Observations

Animals at OPC are well-habituated to vehicles, allowing slow approaches to within 100 meters. At this distance, we were able to observe gazelle through binoculars without disturbing them or eliciting vigilance reactions. In order to further minimize disturbance of the subject, 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 identified mothers by their swollen udders or the presence of a hiding-aged fawn. We grouped hiding-aged fawns into two age groups according to their size and coloration (Walther 1973; Fitzgibbon 1990b): fawns less than four weeks old are considered "pure" hidiers and referred to here as "young" fawns, while fawns between five and eight weeks old are

163 transitioning fawns. Observations lasted two hours unless the fawn had not yet emerged from
164 hiding. In this case, we observed the subject for an additional two hours or until the fawn
165 emerged, whichever occurred first. If the fawn did not emerge after four hours, we excluded the
166 observation from this study. We photographed females head-on with a 500 mm lens and used
167 unique, natural horn shapes and facial markings to differentiate individuals after observation
168 (Walther 1973).

169 During each observation, we instantaneously sampled the mother's behavior every five
170 minutes, recording her behavior as either vigilant, feeding, lying down, self-grooming, or
171 grooming the fawn (Altmann 1974). Every fifteen minutes we used a laser rangefinder and
172 compass to measure the distance and bearing from our vehicle to the mother and her fawn.
173 With these measurements we used the law of cosines to calculate mother-fawn distances.
174 Every fifteen minutes we also noted the mother's group size (excluding her fawn), and whether
175 she and her fawn were in short (below the mother's hock) or tall grass (above the mother's
176 hock). Following Fitzgibbon (1990a), subjects were considered to be in a group if they were less
177 than 50 meters from their nearest neighbor. We noted when fawn hiding periods began and
178 ended, as well as whether each hiding period was terminated by the mother retrieving the fawn
179 or by the fawn standing up on its own. Finally, we noted any predator sightings that occurred
180 during the observation. We excluded observations during which predators were sighted from all
181 analyses.

182 Our methods were non-invasive, did not entail behavioral manipulation and did not cause
183 harm or disturbance to our subjects or other animals. Therefore, ethical review and approval of
184 this study was not required under the guidelines of Princeton University's Institutional Animal
185 Care and Use Committee.

186 187 *Analyses*

188 We performed all statistical analyses in R 3.1.2 using the base (R Core Team 2014), lme4
189 (Bates et al. 2014), MuMIn (Bartón 2015), and plotrix (Lemon 2006) packages. We tested data
190 for normalcy using the Shapiro-Wilk W test. All data were non-normal and therefore subjected to
191 nonparametric tests in our analyses where appropriate. In all tests, significance was accepted at

$P = 0.05$.

We observed two mother-fawn pairs twice, and all other pairs only once. In both cases, duplicate observations occurred within five days of one another, the fawn's age class did not change between observations, and the mother's grouping patterns and habitat use were very similar between the first and second observations. Therefore, to avoid pseudoreplication we combined data from repeat observations for each mother-fawn pair.

Changes in mother-fawn behavior during the hiding phase

We counted the number of times each fawn emerged from hiding and whether the fawn emerged on its own or waited for its mother to retrieve it. For each mother-fawn pair we calculated the rate of emergence events per hour of observation and compared the mean rates across fawn age groups using a Wilcoxon test, which is valid for non-parametric data. We used Fisher's exact test, which is valid for small sample sizes, to measure the difference in relative frequency with which fawns of different ages initiated the end of hiding bouts. For each fawn emergence event, we calculated the proportion of the two preceding maternal behavior samples that were scored as vigilance, and compared the mean proportions across fawn age groups using a Wilcoxon test. Finally, we used Wilcoxon tests to compare the mean mother-fawn distances of young and transitioning fawns during active and hiding periods.

Changes in vigilance, habitat use, and grouping behavior during the hiding phase

We quantified maternal vigilance levels as the percent of behavior samples for each mother that we scored as vigilant. Maternal behavior patterns differ when the fawn is hidden compared to when it is active (Fitzgibbon 1988; Roberts 2014). Therefore, we divided maternal behavior samples into those taken while the fawn was active and while the fawn was hiding, and from these datasets calculated separate vigilance percentages for hiding and active periods. We excluded from our analyses any vigilance percentages based on fewer than four behavior samples. We used Wilcoxon tests to compare mean vigilance percentages across female types and across fawn active and hiding periods.

We calculated the percent time each mother and each fawn spent in short grass by

dividing the number of grass height samples scored as short grass by the total number of samples for that individual. We compared mean percent time spent in short grass between mothers and fawns in different fawn age groups using Wilcoxon tests.

To characterize maternal grouping patterns, we first calculated the percent time that each subject spent alone by dividing the number of group size samples where the mother was the only member of her group by the total number of samples. We used a Wilcoxon test to compare the mean percent time that mothers of young and transitioning fawns spent alone. To understand mothers' grouping patterns when they were not alone, we calculated the percent time that mothers were found in pairs and in small (3 to 4 animals), medium (5 to 19 animals) and large (20 or more animals) groups by dividing the number of samples that fell into each of these group size classifications by the total number of group size samples in which the mother was not scored as solitary. We used Wilcoxon tests to compare the mean percent time spent in each group type by mothers of transitioning and young fawns.

Factors influencing maternal vigilance

We examined the relative effects of fawn age and activity, maternal social context, and habitat type on maternal vigilance behavior using a generalized linear mixed modeling approach. We used the R package lme4 (Bates et al. 2014) to construct generalized linear mixed models (GLMMs) with binomial distributions and logit link functions. In all models, our response variable, maternal vigilance, was binary and consisted of our five-minute behavior samples coded as either vigilant (1) or non-vigilant (0). We included maternal identity as a random effect in each model to account for the fact that we have multiple samples per mother-fawn pair.

We first created an overall model with fawn age group (young = 0, transitioning = 1), fawn activity status (hiding = 0, active = 1), fawn habitat type (tall grass = 0, short grass = 1), and maternal habitat type (tall grass = 0, short grass = 1) as fixed effects. We also included one of two measures of maternal social context: group size (the actual group sizes recorded in the field) or a binary variable (henceforth referred to as "solitary") indicating whether the mother was (0) or was not in a group (1). We elected to explore both of these alternative variables because

while we expected vigilance to decline with increasing group size, we expected the largest decline in vigilance to occur between solitary mothers and mothers that were in a group with at least one other adult animal. However, because these variables were highly correlated, we did not include them both in the model simultaneously, but rather ran the model analysis on two versions of the model, one with the group size variable and one with solitary. Because we found significant differences in fawn hiding behavior and maternal grouping patterns between transitioning and non-transitioning mother-fawn pairs, we also included two-way interactions between fawn age and activity, and fawn age and group size or solitary. Finally, we included an interaction between fawn activity and group size or solitary because we anticipated that fawn risk while active may depend on the social setting in which the active period occurs.

Both versions of the overall model revealed strong significant effects of fawn age and all of its interactions (see Results); therefore, we created two additional models, one for each fawn age class, to investigate the different factors influencing the vigilance behavior of mothers with young and transitioning fawns. Each of these models was run twice, once with the group size variable and once with the solitary variable and also included fawn activity, fawn and maternal habitat type, and the interaction between maternal group size or solitary and fawn activity as fixed effects.

For the overall model and each of the fawn age class models, we refined the initial model by systematically removing terms and interactions to find the submodel with the lowest Akaike's information criteria (AIC) value. We used the R package MuMIn (Bartón 2015) to calculate the marginal and conditional R^2 values (R^2_m and R^2_c , respectively) for each model as recommended by Nakagawa and Schielzeth (2013). We also report the difference in AIC value between the best and second-best submodels examined (ΔAIC) and the degrees of freedom for the best submodel.

RESULTS

We analyzed data from 42 observations of 40 mother-fawn pairs. Nine observed mothers had transitioning fawns, and the remaining 31 had young fawns. Mothers with transitioning fawns were relatively scarce due to high rates of predation on gazelle fawns at our field site

(Roberts & Rubenstein 2014). Fawns were hiding for at least part of every observation, and were active during 34 observations.

Changes in Mother-Fawn Behavior During the Hiding Phase

There was a non-significant trend for transitioning fawns to emerge from hiding more frequently than young fawns. Young fawns ($N = 31$) stood up 0.48 ± 0.09 times per hour on average. This is approximately half as frequently as transitioning fawns ($N = 9$), which stood up 0.95 ± 0.26 times per hour (Wilcoxon test: $W = 84.5$, $P = 0.07$).

Transitioning fawns tended to terminate hiding bouts independently, while young fawns were more likely to wait for their mothers to retrieve them (Table 1; two-tailed Fisher's exact test: $P = 0.001$). In instances where the mother terminated hiding bouts, the fawn's emergence was significantly more likely to be preceded by maternal vigilance behavior. On average, when they retrieved fawns ($N = 24$), mothers were vigilant in 1.04 out of the two behavior samples preceding fawn emergence. When fawns emerged on their own ($N = 22$), mothers were only vigilant in 0.47 of the two previous behavior samples (Wilcoxon test, $W = 361.5$, $P = 0.02$).

On average, mothers of young fawns ($N = 31$) were further away from their hiding offspring than were mothers of transitioning fawns ($N = 8$; $X_{\text{young}} + \text{SE} = 102.2 + 10.5$ m, $X_{\text{transitioning}} + \text{SE} = 57.9 + 15.0$ m; Wilcoxon test: $W = 184$, $P = 0.037$). However, when fawns were active, mothers of young fawns ($N = 25$) were closer to their offspring than were mothers of transitioning fawns ($N = 8$; $X_{\text{young}} + \text{SE} = 3.5 + 1.3$ m; $X_{\text{transitioning}} + \text{SE} = 13.8 + 5.8$ m; Wilcoxon test: $W = 167$, $P = 0.004$).

	Initiator		
	Mother	Fawn	Total
Fawn Age			
Young	21	8	29
Old	4	14	18
Total	25	22	47

Table 1. Contingency table showing the frequencies with which fawns of different ages initiate the end of their own hiding periods versus waiting for their mothers to retrieve them.

Changes in Vigilance, Habitat Use, and Grouping Behavior During the Hiding Phase

When fawns were active, mothers of transitioning fawns ($N = 9$) and mothers of young fawns ($N = 16$) were both highly vigilant on average and did not differ in their vigilance levels (Wilcoxon test: $W = 91.5$, $P = 0.28$). However, contrary to our prediction, mothers of transitioning fawns ($N = 9$) spent significantly less time vigilant than mothers of young fawns ($N = 31$; Wilcoxon test: $W = 240.5$, $P = 0.001$; Figure 1) while their fawns were hidden.

Mothers of young ($N = 31$) and transitioning ($N = 9$) fawns both spent the majority of their time in short grass ($X_{\text{young}} + \text{SE} = 86.1 + 3.8\%$; $X_{\text{transitioning}} + \text{SE} = 85.2 + 8.1\%$). There was no significant difference in the proportion of time spent in short grass between mother types (Wilcoxon test: $W = 134$, $P = 0.86$). Likewise, young ($N = 23$) and transitioning ($N = 9$) fawns also both spent the majority of time in short grass ($X_{\text{young}} + \text{SE} = 71.6 + 8.9\%$; $X_{\text{transitioning}} + \text{SE} = 93.5 + 3.7\%$), and there was no difference between the two fawn groups (Wilcoxon test: $W = 88.5$, $P = 0.48$).

Mothers of young fawns ($N = 31$) spent significantly more time alone than did mothers of old fawns ($N = 9$; Wilcoxon test: $W = 211$, $P = 0.02$) (Figure 2). When they were in groups, mothers of transitioning fawns ($N = 9$) were more likely to be found in large groups (>20 individuals) compared to mothers of young fawns ($N = 31$; Wilcoxon test: $W = 80$, $P = 0.018$). Percent time spent in other group sizes did not differ between mothers of young and transitioning fawns (Figure 3).

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Figure 1. Maternal vigilance levels during fawn hiding and active periods. Error bars represent

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standard error.

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Figure 2. Percent time mothers of young and transitioning fawns are alone. Error bars represent

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standard error.

Figure 3. Percent of time spent in groups that mothers spent in pairs and in small, medium, and large groups. Error bars represent standard error.

Factors Influencing Maternal Vigilance

The best submodels for the overall model included significant effects of fawn age, fawn activity, and the interaction between fawn age and activity. These effects confirm the results described above, demonstrating that mothers with transitioning fawns are less vigilant than mothers with young fawns, but mothers are more vigilant when their fawns are active, regardless of fawn age. When we analyzed the model with the group size variable ($R^2_m = 0.22$, $R^2_c = 0.31$, $\Delta AIC = 1.9$, $df = 7$), group size and the interaction between group size and fawn age were also retained as significant effects (Table 2). When we analyzed the model with the solitary variable ($R^2_m = 0.22$, $R^2_c = 0.32$, $\Delta AIC = 2.0$, $df = 7$), solitary was retained but not significant, but the interaction between solitary and fawn activity was significant (Table 3). Overall, maternal vigilance declines as group size increases and solitary mothers are more vigilant when their fawns are active. However, the interaction between group size and fawn age indicates that mothers of transitioning fawns increase their vigilance as group size increases.

For the young fawn submodel, fawn activity was retained as a significant positive effect regardless of whether the initial model included maternal group size or solitary. When the group size variable was used ($R^2_m = 0.11$, $R^2_c = 0.23$, $\Delta AIC = 1.3$, $df = 5$), group size and the

interaction between fawn activity and group size were both retained but not significant (Table 2). When solitary was used ($R^2_m = 0.11$, $R^2_c = 0.23$, $\Delta AIC = 1.2$, $df = 5$), the interaction between solitary and fawn activity was significant, and solitary was not significant but was retained (Table 3). The results of this model show that mothers of young fawns increase their vigilance when their fawns are active, especially when they are not in a group.

In the best transitioning fawn submodel ($R^2_m = 0.41$, $R^2_c = 0.43$, $\Delta AIC = 0.7$, $df = 4$), maternal habitat type and infant activity were retained as significant effects. Both solitary (Table 3) and group size (Table 2) were dropped from their respective model versions. Mothers of transitioning fawns are more vigilant when their fawns are active and also more vigilant in short grass habitats.

	Overall model			Young fawn model			Transitioning fawn model		
	Estimate±SE	z	P	Estimate±SE	z	P	Estimate±SE	z	P
Fawn age	-2.31±0.54	4.26	< 0.001	NA	NA	NA	NA	NA	NA
Fawn activity	1.43±0.24	5.89	< 0.001	1.88±0.34	5.47	<0.001	2.69±0.49	5.44	<0.001
Maternal group size	-0.04±0.02	-2.12	0.034	-0.03±0.02	-1.46	0.146	–	–	–
Fawn habitat	–	–	–	–	–	–	–	–	–
Maternal habitat	–	–	–	–	–	–	1.84±0.80	2.31	0.021
Maternal group size * fawn age	0.05±0.02	2.34	0.019	NA	NA	NA	–	–	–
Maternal group size * fawn activity	–	–	–	-0.09±0.05	-1.82	0.069	–	–	–
Fawn age * fawn activity	1.37±0.54	2.53	0.011	NA	NA	NA	NA	NA	NA

Table 2. Estimates of the effects of fawn, habitat, and social variables on maternal vigilance from binomial GLMMs. All models included mother identity as a random variable. The overall model included fawn age as a fixed effect. Blank cells indicate that the term was dropped in the best final model; NA indicates that the term was not included in the initial full model. Models in this table were run using the maternal group size variable. Significant p-values are bolded.

	Overall model			Young fawn model			Transitioning fawn model		
	Estimate±SE	z	P	Estimate±SE	z	P	Estimate±SE	z	P
Fawn age	-1.95±0.51	-3.83	< 0.001	NA	NA	NA	NA	NA	NA
Fawn activity	1.19±0.27	4.38	< 0.001	1.18±0.28	4.21	<0.001	2.69±0.49	5.44	<0.001
Solitary	0.14±0.32	0.45	0.65	0.11±0.33	0.32	0.75	–	–	–
Fawn habitat	–	–	–	–	–	–	–	–	–
Maternal habitat	–	–	–	–	–	–	1.84±0.80	2.31	0.021
Solitary * fawn age	–	–	–	NA	NA	NA	–	–	–
Solitary * fawn activity	1.36±0.58	2.35	0.019	1.59±0.64	2.49	0.013	–	–	–
Fawn age * fawn activity	1.59±0.55	2.89	0.004	NA	NA	NA	NA	NA	NA

Table 3. Estimates of the effects of fawn, habitat, and social variables on maternal vigilance from binomial GLMMs. All models included mother identity as a random variable. The overall model included fawn age as a fixed effect. Blank cells indicate that the term was dropped in the best final model; NA indicates that the term was not included in the initial full model. Models in this table were run using the solitary variable. Significant p-values are bolded.

DISCUSSION

Transitioning fawns in our system are at greater risk of predation than their younger counterparts due to their tendency to stand up more frequently and terminate a higher proportion of hiding bouts on their own. Fitzgibbon (1990b) described the same behavioral patterns in 3 to 8 week old gazelle fawns in the Serengeti and demonstrated that more frequent emergence from hiding resulted in a steady increase in the amount of time older fawns spent out of hiding and therefore exposed to predators. Pronghorn (*Antilocapra americana*) fawns also exhibit a weakening of the hiding response with time: Byers (1997) reports that fawns older than 5 days of age are more likely to jump up and run away when humans approach their hiding spots, whereas younger fawns remain immobile. Barrett (1978) suggests that a peak in pronghorn mortality between 11 and 20 days of age was the result of fawns spending more time out of hiding. Our results suggest that by emerging on their own, fawns increase their risk of predation by forfeiting adaptive maternal vigilance. When returning to retrieve their offspring, ungulate mothers in many hiding species exhibit heightened levels of vigilance, which is thought to increase their chances of detecting lurking predators before exposing their fawns (Clutton-Brock & Guinness 1975; Clutton-Brock et al. 1982; Byers 1997; Roberts 2014; Costelloe & Rubenstein, in prep). When fawns emerge independently, mothers cannot anticipate the end of hiding bouts and are thus less vigilant prior to fawn-initiated emergences than mother-initiated emergences. Thus, whereas hiding periods are relatively safe intervals for young fawns, they are risky for older fawns due to their unpredictable and unprotected emergences.

Mothers of both fawn age groups are more vigilant during fawn active periods than during hiding periods. This suggests that, although they are older, transitioning fawns are still highly vulnerable to predators when exposed, and that maternal vigilance is key to mitigating this risk. Fitzgibbon (1990b) demonstrated that maternal vigilance during active periods strongly affects fawn survival of cheetah attacks by enabling the mother to alert her fawn to the cheetah while it is still far away. Similarly, during one of our observations a jackal approached a group with a transitional mother and her active fawn. The mother detected the jackal and fled with her fawn before the jackal got close enough to begin a successful pursuit. Heightened vigilance is a common trait of parents accompanied by dependent young in ungulates (Clutton-Brock &

Guinness 1975; Burger & Gochfeld 1994; Toïgo 1999; White & Berger 2001; Li et al. 2009) as well as other taxa (e.g. carnivores: Caro 1987; Hunter et al. 2007; Pangle & Holekamp 2010; birds: Griesser 2002; Yasukawa & Cockburn 2009; primates: Kutsukake 2006, 2007; Treves et al. 2003).

Although transitioning fawns are at greater risk during hiding periods due to their unpredictability, mothers do not appear to compensate for this risk via vigilance behavior. Hypothetically, heightened vigilance would not only allow transitioning mothers to monitor the area for predators, but also check that their fawns have not unexpectedly emerged from their hiding spots. However, contrary to our prediction, transitional mothers are significantly less vigilant than mothers of younger fawns during hiding periods.

This decline in vigilance may be expected if transitional mothers or their fawns use safer habitats than younger mother-fawn pairs. However, although changes in habitat use by ungulate mothers are common during early lactation, we found little variation in habitat selection among our subjects and no differences in habitat use between mothers of young and transitioning fawns or between young and transitioning fawns themselves. Thomson's gazelles are strictly open habitat species (Brooks 1961); therefore, grass height is the main source of habitat heterogeneity. Grass height is biologically relevant as well: tall grass may provide additional cover for hiding fawns, but it increases risk to adult gazelle by concealing stalking predators and reduces foraging efficiency (Brooks 1961; Gwynne & Bell 1968; Fitzgibbon 1988). Females in this study spent the majority of their time in short grass, with only a few females spending any time in tall grass during our observations. Likewise, fawns were usually hidden in short grass and only rarely in tall grass. Although some females in our study population seek out tall grass areas for parturition (Roberts & Rubenstein 2014), use of tall grass habitat clearly does not persist for the duration of the hiding phase. The hiding strategy is usually associated with bush or forest habitats (Lent 1974; Fisher et al. 2002), but their small body size may allow Thomson's gazelle fawns to hide effectively even in short grass (Walther 1969), enabling this species to use the hiding strategy in females' normally-preferred open habitat.

Interestingly, our results show that mothers of transitioning fawns are more vigilant in short grass than in tall grass. The risk level of short grass to mothers is unlikely to change throughout

the hiding phase, suggesting that this increase in vigilance is in response to an increase in fawn risk. Compared to younger fawns, transitioning fawns may be more vulnerable to detection in short grass if their larger size prevents them from taking advantage of the limited visual cover available in these habitats.

Reduced vigilance in transitional mothers may also be expected if these mothers are mitigating risk by joining social groups. As predicted, mothers of transitioning fawns spend less time alone and more time in large groups compared to mothers of young fawns. Our overall model indicates that maternal vigilance declines with increasing group size, a phenomenon common in many taxa (Bertram 1980; Lipetz & Bekoff 1982; Alados & Escos 1988; Elgar 1989; Yáber & Herrera 1994; Lima 1995; Roberts 1995; Shorrocks & Cokayne 2005; Rieucan & Martin 2008). However, this model (but not the submodel specific to transitioning mother-fawn pairs) also indicates that mothers of transitioning fawns increase their vigilance in larger groups. Transitioning fawns exhibit adult coloration and are thus less easily distinguished from adult group members when active than are younger, dark brown fawns (personal observation). We therefore reason that they should at least partially benefit from the risk dilution effect afforded by larger groups. Thus, rather than indicating a higher level of fawn risk, we hypothesize that the increase in vigilance in larger groups may reflect the need of transitional mothers to regularly monitor their fawn's activity status since fawns in this age class emerge from hiding unpredictably. It may be easy for the mother to rapidly detect her fawn among a small group of similarly-colored conspecifics, but detection may be more difficult as the number of conspecifics increases, requiring an increase in maternal vigilance behavior.

Despite the tendency of transitional mothers to increase their vigilance with group size, they still exhibit markedly less vigilance than mothers of younger fawns during fawn hiding periods regardless of group size. We attribute this unexpected result to the gregarious grouping tendencies of transitional mothers and posit that Thomson's gazelle mothers and fawns rely on group membership, rather than heightened maternal vigilance, to mitigate increased fawn risk during the transition out of hiding. The short distances between transitional mothers and their hiding offspring further suggest that transitional fawns are protected by social effects: given a mean mother-infant distance of less than 60 m, if the mother is in a group (as is usually the

case), when the fawn emerges from hiding independently it does so in the immediate vicinity of a group and may therefore benefit from group dilution and vigilance effects. Furthermore, Fitzgibbon (1988) found that, compared to mothers of young fawns, mothers with transitioning fawns were less likely to detect approaching cheetahs before a control non-mother female in the same social group. This supports our conclusion that mothers of transitioning fawns rely more heavily on the collective vigilance of the group for offspring protection than do mothers of younger fawns.

The more gregarious tendencies of transitional mothers are likely made possible by the shorter hiding bouts and more frequent active periods exhibited by transitioning fawns. Whereas mothers of young fawns are spatially tethered to a hidden infant that is stationary for hours and whose distance from conspecifics may increase over time, transitional mothers are able to track group movements by changing their fawns' locations much more frequently. By joining groups, mothers and fawns both benefit from enhanced predation detection and risk dilution. Mothers also likely gain energetic benefits, as their reduced vigilance requirements free up time for foraging and resting. Spending more time in groups may also facilitate fawn socialization. Transitioning fawns are further from their mothers during active periods than are younger fawns, suggesting that transitioning fawns are spending their active periods apart from their mothers but within her social group, possibly socializing with other group members.

The tendency for mothers to rejoin groups during their offsprings' transition out of hiding is evident in other hider species as well. After parturition, white-tailed deer (*Odocoileus virginianus*) does are aggressive and defend small territories around fawn hiding spots (Schwede et al. 1993). This behavior wanes as hiding decreases, and mothers associate with conspecifics more frequently as the fawn ages. Distances between mothers and their active fawns also increase with fawn age, and older fawns spend more time associating with non-mother individuals than younger fawns (Schwede et al. 1994). In pronghorn (*Antilocapra americana*), does isolate for parturition but begin forming groups with other does and their fawns starting approximately three weeks after birth, when the fawn begins its transition out of hiding (Autenrieth & Fichter 1975; Byers 1997). Interactions between fawns and group members during this time are critical to fawn socialization.

485 Although the transition from hiding to following is a risky time for fawns, mothers do not
486 appear to bear the cost of this risk. Rather than mitigating fawn risk through vigilance, they rely
487 on group effects to protect the fawn. These effects may include social concealment, risk dilution
488 and collective vigilance. Mothers in fact lower their own risk during the transition by spending
489 more time in the safety of groups.

490 Ungulates are a diverse and widespread taxon, numbering over 450 species (Groves &
491 Grubb 2011) and inhabiting most of the world's terrestrial ecosystems. In these systems they
492 play a variety of ecological roles, including serving as common prey items for many predator
493 species. Risk and mortality rates during infancy strongly affect recruitment and therefore
494 population growth and viability in ungulate populations. By studying the costs and constraints to
495 mothers and their infants and how these change over time, we can come to better understand
496 the pressures facing hiding ungulates during this influential life stage and use this knowledge to
497 inform management and conservation practices.

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