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

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Hiding is a cooperative mother–infant behavioural strategy used by many ungulate species to mitigate infant predation risk. During the late stages of the hiding phase, infants begin a transition out of hiding and show behavioural changes that increase their exposure to predators. Mothers in many hider species are known to show potentially costly changes in habitat use, gregariousness and vigilance behaviour at the onset of the hiding phase. However, the effects of infant transitional behaviour on maternal behavioural patterns are understudied. In this study, we compare the behavioural patterns of Thomson's gazelle, *Eudorcas thomsonii*, females with young and transitioning fawns to determine the effect of fawn behavioural changes on maternal behaviour. We found that, although transitioning fawns were at greater risk than younger fawns while hidden, mothers of transitioning fawns were less vigilant than mothers of younger fawns during hiding periods. Mothers and fawns relied on group membership rather than heightened maternal vigilance to mitigate fawn risk during the transition. Group membership is apparently made possible by the shorter hiding bouts of transitioning fawns relative to younger fawns: more frequent activity bouts probably enable mothers to relocate their fawns more frequently, which helps the mother and fawn to keep up with group movements.

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

Antipredator strategies improve the survival prospects of infants (Barrett, 1978; Fitzgibbon, 1990b; Gaillard, Festa-Bianchet,

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Yoccoz, Loison, & Toïgo, 2000), but sometimes necessitate changes in the mothers' behaviour that can negatively impact mothers' survival or fecundity. For example, mothers in many follower and hider species show changes in habitat preference during parturition and early lactation. Mothers in these species leave their normally preferred habitats in favour of areas with greater visibility (Bangs, Krausman, Kunkel, & Parsons, 2005; Pinard, Dussault, Ouellet, Fortin, & Courtois, 2012; Poole, Serrouya, & Stuart-Smith, 2007; Rearden, Anthony, & Johnson, 2011), lower predator density (Alados & Escos, 1988; Bergerud, Butler, & Miller, 1984; Bergerud, Ferguson, & Butler, 1990; Festa-Bianchet, 1988), or more concealing vegetation (Bongi et al., 2008; Ciuti, Pipia, Grignolio, Ghiandai, & Apollonio, 2009; Fitzgibbon, 1990a; Gosling, 1969; Jarman, 1976; Leuthold, 1977; Roberts & Rubenstein, 2014). Although safer for infants, these habitats often offer poorer foraging conditions for mothers than their normally preferred habitats (Ciuti et al., 2009; Panzacchi et al., 2010; White & Berger, 2001), and they 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 (Bangs et al., 2005; Bergerud et al., 1984; Daleszczyk, 2004; Langbein, Scheibe, & Eichhorn, 1998); in other species, females may show some degree of habitat preference alteration until weaning is completed (Bon, Joachim, & Maublanc, 1995; Grignolio, Rossi, Bertolotto, Bassano, & Apollonio, 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 (Bongi et al., 2008; Byers, 1997; Clutton-Brock & Guinness, 1975; Ozoga, Verme, & Bienz, 1982; Schwede, Hendrichs, & McShea, 1993).

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 (Bergerud & Page, 1987; Byers, 1997; Clutton-Brock & Guinness, 1975; Schwede et al., 1993; Tinbergen, Impekoven, & Franck, 1967). Hider mothers tend to be spatially tethered to their offspring, typically remaining within several hundred metres or less of its hiding location (Bongi et al., 2008; Byers, 1997; Lent, 1974; Schwede, Hendrichs, & Wemmer, 1994). They may therefore find themselves isolated when groups move beyond this radius (Brooks, 1961; O'Brien, 1984; Walther, 1969). 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 predators (Fitzgibbon, 1990a; Foster & Treherne, 1981; Hamilton, 1971).

In addition to these grouping and habitat changes, ungulate mothers may suffer reduced foraging time or efficiency due to heightened vigilance. Ungulates, along with many other animals, use vigilance to detect approaching predators and enable effective escape or defence responses (Creel, Schuette, & Christianson, 2014; Dehn, 1990; Fitzgibbon, 1990b). Vigilance tends to increase when perceived risk is higher (Devereux, Whittingham, Fernández-Juric, Vickery, & Krebs, 2006; Lima & Bednekoff, 1999; Pöysä, 1987) and mothers with dependent young tend to be more vigilant than nonmothers due to the greater vulnerability of their offspring (Alados & Escos, 1988; Clutton-Brock & Guinness, 1975; Fitzgibbon, 1993; Hunter & Skinner, 1998; Roberts, 2014). For many species, vigilance is incompatible with other activities such as foraging and resting (Creel et al., 2014; Hamel & Côté, 2008; Lima, 1998; Lima & Dill, 1990; Toïgo, 1999). Reduced foraging time, in

combination with the high energetic requirements of lactation, may reduce fecundity and prevent mothers from capitalizing on their next reproductive opportunity (Benton, Grant, & Clutton-Brock, 1995; Cook et al., 2004).

The severity of these various maternal costs likely change as infants mature and become less vulnerable to predation, but research on this topic is lacking. As follower infants develop speed and agility, isolation in protective habitats probably becomes less necessary, allowing mothers to return to preferred habitats, rejoin groups, and possibly reduce their investment in vigilance. For hider species, the relationship between maternal costs and offspring age may be less linear. Towards the end of the hiding phase, the infant begins a transition out of the hiding strategy. It emerges from hiding more often, resulting in fewer, shorter hiding periods and more time spent out of hiding (Fitzgibbon, 1990b; Olazábal, Villagrán, González-Pensado, & Ungerfeld, 2013). In addition, the infant initiates the end of hiding periods independently by standing up on its own more frequently, without waiting for its mother to retrieve it (Alados & Escos, 1988; Byers, 1997; Fitzgibbon, 1990b). It appears that this transition typically occurs before the infant has developed sufficient speed and agility to escape predators (Byers, 1997; Fitzgibbon, 1990b); therefore, this period of transition is particularly risky for ungulate infants. Hider infants that survive the transition no longer conceal themselves but instead remain constantly active and in the same social group as their mothers (Lent, 1974). That is, they behave as followers. These transitional changes in offspring behaviour probably alter maternal investment trade-offs and affect the behavioural constraints experienced by mothers. The shorter hiding bouts and more frequent active periods of transitioning infants may allow mothers to relocate their offspring more often and track group movements more effectively, thereby increasing mothers' time spent in social groups and reducing maternal risk. However, increased infant risk during the transition may necessitate greater maternal vigilance.

In this study, we sought to understand how relevant maternal costs change as the hiding phase progresses. We examined maternal and fawn behaviour during the hiding phase in Thomson's gazelle, *Eudorcas thomsonii*, a small-bodied East African antelope species. We first investigated how fawn risk changes throughout the hiding phase by comparing the hiding behaviour of transitioning fawns to younger fawns. Following the findings of previous studies (Fitzgibbon, 1988, 1990b), we expected older, transitioning fawns to emerge from hiding more often than young fawns and to initiate emergence on their own more often, without waiting for their mothers to retrieve them. We hypothesized that these behaviours increase fawn risk by preventing mothers from increasing their vigilance in anticipation of emergence.

We next examined changes in maternal vigilance, maternal grouping behaviour and maternal and fawn habitat use throughout the hiding phase. Since fawn risk is expected to be higher during the transition, we expected mothers of transitioning fawns to be more vigilant than mothers of younger fawns. Adult Thomson's gazelles are normally gregarious and strongly prefer open, short-grass habitats (Brooks, 1961). However, in previous studies, females with young fawns have often been found alone and in tall-grass habitats (Brooks, 1961; Fitzgibbon, 1988; Walther, 1969). We hypothesized that greater fawn mobility resulting from more frequent active periods enables transitional mothers to more closely match nonmaternal grouping and habitat use patterns. Therefore, we predicted that mothers with transitioning fawns would spend more time in short grass, more time in groups, and more time in larger groups than mothers with young fawns. Hiding is likely to be more effective in tall-grass habitats compared to short-grass habitats. We therefore expected all fawns to prefer tall-

grass habitats, but for this preference to be weaker in transitioning fawns, which rely less heavily on the hiding strategy.

Finally, to understand the relative impact of these behavioural changes to mothers' risk perception, we constructed a series of univariate models to examine the effects of fawn age, 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 km^2 conservancy consisting of discrete grassy plains divided by *Acacia drepanalobium* 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 hyaenas, *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; Hvideberg-Hansen, 1970; Walther, 1969). 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 2 months old (Fitzgibbon, 1990b).

Behavioural Observations

Animals at OPC are well habituated to vehicles, allowing slow approaches to within 100 m. At this distance, we were able to observe gazelle through binoculars without disturbing them or eliciting vigilance reactions. To further minimize disturbance of the subject, we waited to begin observations until the vehicle had been stationary for 5 min, 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 (Fitzgibbon, 1990b; Walther, 1973): fawns less than 4 weeks old are considered 'pure' hiders and referred to here as 'young' fawns, while fawns between 5 and 8 weeks old are transitioning fawns. Observations lasted 2 h unless the fawn had not yet emerged from hiding. In this case, we observed the subject for an additional 2 h or until the fawn emerged, whichever occurred first. If the fawn did not emerge after 4 h, 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).

During each observation, we instantaneously sampled the mother's behaviour every 5 min, recording her behaviour as either vigilant, feeding, lying down, self-grooming, or grooming the fawn (Altmann, 1974). Every 15 min we used a laser rangefinder and compass to measure the distance and bearing from our vehicle to the mother and her fawn. With these measurements we used the law of cosines to calculate mother–fawn distances. Every 15 min we also noted the mother's group size (excluding her fawn), and whether she and her fawn were in short (below the mother's hock) or tall grass (above the mother's hock). Following Fitzgibbon

(1990a), subjects were considered to be in a group if they were less than 50 m from their nearest neighbour. We noted when fawn-hiding periods began and ended, as well as whether each hiding period was terminated by the mother retrieving the fawn or by the fawn standing up on its own. Finally, we noted any predator sightings that occurred during the observation. We excluded from all analyses any observations during which predators were sighted.

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

Analyses

We performed all statistical analyses in R 3.1.2 using the base (R Core Team, 2014), lme4 (Bates, Maechler, Bolker, & Walker, 2014), MuMIn (Bartón, 2015), and plotrix (Lemon, 2006) packages. We tested data for normalcy using the Shapiro–Wilk W test. All data were non-normal and therefore subjected to 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 5 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 psuedoreplication, we combined data from repeat observations for each mother–fawn pair.

Changes in mother–fawn behaviour 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 nonparametric 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 behaviour 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 behaviour during the hiding phase

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

We calculated the percentage of 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 the mean percentage of 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 percentage of 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 percentage of time that mothers of young and transitioning fawns spent alone. To understand mothers' grouping patterns when they were not alone, we calculated the percentage of time that mothers were found in pairs and in small (3–4 animals), medium (5–19 animals) and large (≥20 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 percentage of 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 behaviour using a generalized linear mixed modelling 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 5 min behaviour samples coded as either vigilant (1) or nonvigilant (0). We included maternal identity as a random effect in each model to account for the fact that we had 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 (1) in a group. 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 behaviour and maternal grouping patterns between transitioning and nontransitioning 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 behaviour 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 analysed 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 Behaviour during the Hiding Phase

There was a nonsignificant tendency 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 (two-tailed Fisher's exact test: $P = 0.001$; Table 1). In instances where the mother terminated hiding bouts, the fawn's emergence was significantly more likely to be preceded by maternal vigilance behaviour. On average, when they retrieved fawns ($N = 24$), mothers were vigilant in 1.04 out of the two behaviour samples preceding fawn emergence. When fawns emerged on their own ($N = 22$), mothers were only vigilant in 0.47 of the two previous behaviour 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 ($N = 8$; mean $\pm$ SE: young: 102.2 ± 10.5 m; transitioning: 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 ($N = 8$; mean $\pm$ SE: young: 3.5 ± 1.3 m; transitioning: 13.8 ± 5.8 m; Wilcoxon test: $W = 167$, $P = 0.004$).

Changes in Vigilance, Habitat Use and Grouping Behaviour 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: $W = 240.5$, $P = 0.001$; Fig. 1) while their fawns were hidden.

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

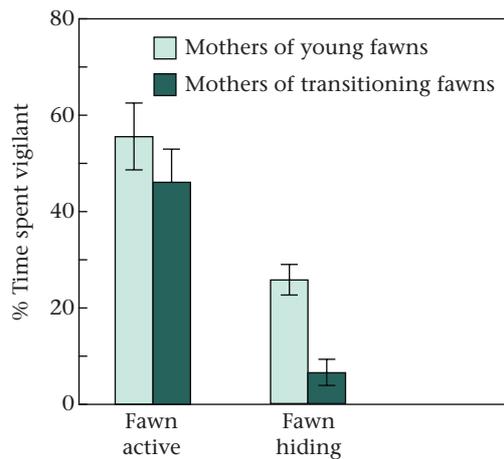| Fawn age	Initiator		Total
	Mother	Fawn	
Young	21	8	29
Old	4	14	18
Total	25	22	47

Figure 1. Mean $\pm$ SE percentage of time that mothers of young and transitioning Thomson's gazelle fawns spent vigilant during fawn hiding and active periods.

Mothers of young ($N = 31$) and transitioning ($N = 9$) fawns both spent the majority of their time in short grass (mean $\pm$ SE: young: $86.1 \pm 3.8\%$; transitioning: $85.2 \pm 8.1\%$). 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 (mean $\pm$ SE: young: $71.6 \pm 8.9\%$; transitioning: $93.5 \pm 3.7\%$), 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: $W = 211$, $P = 0.02$; Fig. 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: $W = 80$, $P = 0.018$). The percentage of time spent in other group sizes did not differ between mothers of young and transitioning fawns (Fig. 3).

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 confirmed the results described above, demonstrating that mothers with transitioning fawns were less vigilant than mothers with young fawns, but mothers were more vigilant when their fawns were active, regardless of fawn age.
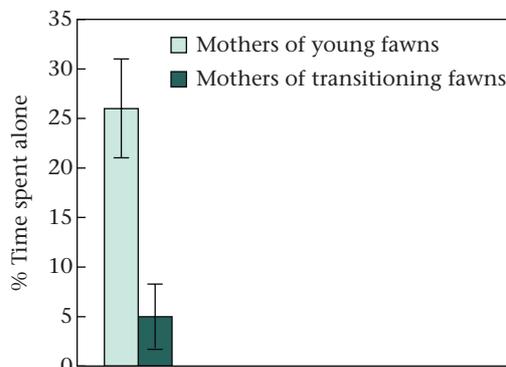

Figure 2. Mean $\pm$ SE percentage of time that mothers of young and transitioning Thomson's gazelle fawns were alone.
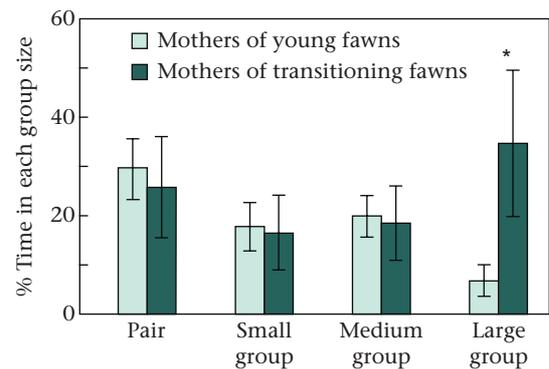

Figure 3. Mean $\pm$ SE percentage of time spent in groups that mothers of young and transitioning Thomson's gazelle fawns spent in pairs and in small (3–4 animals), medium (5–19 animals) and large ($\geq$20 animals) groups.

When we analysed the model with the group size variable ($R^2_m = 0.22$, $R^2_c = 0.31$, ΔAIC $= 1.9$, $df = 7$), group size and the interaction between group size and fawn age were also retained as significant effects (Table 2). When we analysed the model with the solitary variable ($R^2_m = 0.22$, $R^2_c = 0.32$, ΔAIC $= 2.0$, $df = 7$), solitary was retained but not significant, but the interaction between solitary and fawn activity was significant (Table 3). Overall, maternal vigilance declined as group size increased, and solitary mothers were more vigilant when their fawns were active. However, the interaction between group size and fawn age indicates that mothers of transitioning fawns increased their vigilance as group size increased.

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 ($R^2_m = 0.11$, $R^2_c = 0.23$, ΔAIC $= 1.3$, $df = 5$), group size and the interaction between fawn activity and group size were both retained but not significant (Table 2). When solitary was used ($R^2_m = 0.11$, $R^2_c = 0.23$, ΔAIC $= 1.2$, $df = 5$), 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 increased their vigilance when their fawns were active, especially when they were not in a group.

In the best transitioning fawn submodel ($R^2_m = 0.41$, $R^2_c = 0.43$, ΔAIC $= 0.7$, $df = 4$), 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 were more vigilant when their fawns were active and also more vigilant in short-grass habitats.

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 behavioural 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 show a weakening of the hiding response with time: Byers (1997) reported 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) suggested 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

Table 2
Estimates of the effects of fawn, habitat and social variables on maternal vigilance from binomial GLMMs

	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

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 shown in bold.

Table 3
Estimates of the effects of fawn, habitat and social variables on maternal vigilance from binomial GLMMs

	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

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 shown in bold.

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 show heightened levels of vigilance, which is thought to increase their chances of detecting lurking predators before exposing their fawns (Byers, 1997; Clutton-Brock & Guinness, 1975; Clutton-Brock, Guinness, & Albon, 1982; Costelloe & Rubenstein, n.d.; Roberts, 2014). When fawns emerge independently, mothers cannot anticipate the end of hiding bouts and are thus less vigilant prior to fawn-initiated emergences than they are prior to 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 were 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 (Burger & Gochfeld, 1994; Clutton-Brock & Guinness, 1975; Li, Jiang, & Beauchamp, 2009; Toïgo, 1999; White & Berger, 2001) as well as in other taxa (e.g. carnivores: Caro, 1987; Hunter, Durant, & Caro, 2007; Pangle & Holekamp, 2010; birds: Griesser, 2002; Yasukawa & Cockburn, 2009; primates: Kutsukake, 2006, 2007; Treves, Drescher, & Snowdon, 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 behaviour. 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 were 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 were 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; Fitzgibbon, 1988; Gwynne & Bell, 1968). 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 (Fisher et al., 2002; Lent, 1974), 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, we found that mothers of transitioning fawns were 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 spent 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 (Alados & Escos, 1988; Elgar, 1989; Lima, 1995; Rieucau & 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 show adult coloration and are thus less easily distinguished from adult group members when active than are younger, dark brown fawns (B. R. Costelloe, 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 coloured conspecifics, but detection may be more difficult as the number of conspecifics increases, requiring an increase in maternal vigilance behaviour.

Despite the tendency of transitional mothers to increase their vigilance with group size, they still showed 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−fawn distance of less than 60 m, if the mother is in a group when the fawn emerges from hiding independently (as is usually the case), then the fawn emerges 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 of transitioning fawns were less likely to detect approaching cheetahs before a control nonmother 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 of transitioning fawns. Whereas mothers of young fawns are spatially tethered to their hidden infants, which remain 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 probably 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 their fawns' hiding spots (Schwede et al., 1993). This behaviour 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 nonmother individuals than do younger fawns (Schwede et al., 1994). In pronghorn, does isolate for parturition but begin forming groups with other does and their fawns starting approximately 3 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.

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

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

Acknowledgments

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