



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



Blair R. Costelloe^{*}, Daniel I. Rubenstein

Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, U.S.A.

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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.

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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,

^{*} Correspondence: B. R. Costelloe, née Roberts, EEB Department, 106A Guyot Hall, Princeton, NJ 08544, U.S.A.

E-mail address: bcostelloe@princeton.edu (B. R. Costelloe).

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-Juricic, 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-

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