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

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

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Predation is a major threat to survival and reproductive success and therefore exerts a powerful selective force on the physical and behavioural phenotypes of prey species (Lima & Dill, 1990). Vigilance is a common behavioural means by which prey animals pre-empt capture by predators and thereby mitigate predation risk: generally, more vigilant individuals are less likely to fall victim to predation than less vigilant individuals (FitzGibbon, 1990c; Godin & Smith, 1988; Quinn & Cresswell, 2004). However, vigilance often comes at a cost. In some cases, it is mutually exclusive to other behaviours such that engaging in vigilance reduces time available for other activities (Lima, 1998), such as foraging (Metcalfe & Furness, 1984) and resting (Switalski, 2003; Toïgo, 1999). In other cases, vigilance can be performed in conjunction with other behaviours, but negatively affects the efficiency of these activities (Abramsky, Rosenzweig, & Subach, 2002; Barnier et al., 2016; Beauchamp & Livoreil, 1997). For example, increased vigilance

during foraging is associated with lower bite rates in bighorn sheep, *Ovis canadensis* (Ruckstuhl, Festa-Bianchet, & Jorgenson, 2003). Thus, prey species commonly face a trade-off between mitigating risk through vigilance and investing in other social or self-maintenance activities (Krause & Godin, 1996). Mismanaging this trade-off can be costly: individuals that are not vigilant enough or not vigilant at the right time risk death from predation, while those that are overly vigilant may suffer loss of body condition, lower fecundity or missed opportunities for social interactions (Cords, 1995; Creel, Christianson, & Winnie, 2011; Maestripieri, 1993).

The risk allocation hypothesis predicts that animals should manage the trade-off between vigilance and other activities by changing their behaviour in response to temporal fluctuations in risk (Lima & Bednekoff, 1999). That is, they should prioritize vigilance when risk of predation is high and invest more in other activities when risk subsides, with the relative levels of vigilance during high- and low-risk states depending on the frequency and duration of each state type. The capacity for an animal to structure its vigilance behaviour as predicted by the risk allocation hypothesis depends on its ability to accurately gauge current risk levels or detect changes in risk (Lima & Bednekoff, 1999; Sih, 1992). There is

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abundant evidence across animal taxa that individuals exhibit 'proactive' responses to predation risk (Creel, Schuette, & Christianson, 2014). That is, they set their vigilance rates to reflect average levels of vulnerability mediated by general cues such as social context and habitat type (Avilés & Bednekoff, 2007; Barnier et al., 2016; Lima, 1995; Roberts, 1996; Underwood, 1982). For example, animals are typically less vigilant when in groups than when alone because group membership reduces individual vulnerability via various mechanisms, including risk dilution and enhanced predator detection (Beauchamp, 2008; Bertram, 1980; Dehn, 1990; FitzGibbon, 1990b, 1990c; Hamilton, 1971; Lehtonen & Jaatinen, 2016). Likewise, animals tend to be more vigilant when utilizing habitats that, on average, confer greater risk of predator encounter and attack (Altendorf, Laundré, López González, & Brown, 2001; Burger, Safina, & Gochfeld, 2000; FitzGibbon, 1988; Frid, 1997; Sansom, Lind, & Cresswell, 2009; Underwood, 1982).

In addition to accounting for general risk factors, prey animals can further fine-tune their antipredator behaviour by responding to indicators of real-time changes in risk level. Individuals across taxa are sensitive to numerous visual, chemical and auditory cues that signal acute high risk due to predator presence (Blumstein, Cooley, Winternitz, & Daniel, 2008; Creel et al., 2014; Kats & Dill, 1998; Périquet et al., 2012; Templeton & Greene, 2007; Wisenden, Vollbrecht, & Brown, 2004). These specific cues override general risk factors: clearly, if a predator is actually present, a prey animal should exhibit an appropriate antipredator response to avoid detection, attack or capture, regardless of its current habitat or social setting. Plains zebras, *Equus quagga*, offer a clear illustration of this concept: in general, zebras use grassland habitat patches during daylight hours but shift to woodland patches at night in order to avoid lions, *Panthera leo*, that emerge from the woodland at night to hunt in grasslands. However, zebras abandon patches of any type in response to actual lion presence on that patch (Fischhoff, Sundaresan, Cordingley, & Rubenstein, 2007).

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

As a result of their maternal care strategy, female Thomson's gazelles, *Eudorcas thomsonii*, with dependent fawns have periodic access to reliable cues indicating predator absence; thus, they offer a rare opportunity to examine whether or not prey animals take advantage of such information and adjust their vigilance behaviour accordingly. In this study, we examine whether female Thomson's gazelles with fawns exhibit temporal vigilance patterns consistent with the predictions of the risk allocation hypothesis. Thomson's gazelles are preyed upon by a wide variety of predator species and rely heavily on vigilance to mitigate this risk (FitzGibbon, 1988, 1989, 1990c). Females with young fawns are generally more vigilant than nonmothers because they must manage their own risk as well as that of their highly vulnerable fawn (FitzGibbon, 1990a, 1993a; Roberts, 2014). Mothers also face heightened energetic demands arising from the simultaneous lactation and gestation that is common in this species (Brooks, 1961; Hvideberg-Hansen, 1970). Therefore, we expect maternal vigilance patterns to be very

sensitive to information regarding probabilistic and actual risk. Female gazelles and their fawns engage in a cooperative strategy of maternal care, known as hiding, that results in discrete periods of high and low fawn risk and generates reliable information regarding predator absence. The hiding strategy is characterized by long periods of separation of the mother and offspring during which the fawn lies hidden in vegetation (Lent, 1974; Walther, 1965). The mother retrieves her fawn from hiding several times per day. During these brief active periods, the mother grooms the fawn and the infant nurses and plays. At the end of the active period, the fawn selects a hiding spot and lies down to begin the next hiding period. Hiding periods typically last at least 2 h, while active periods last approximately half an hour on average (FitzGibbon, 1990a). This alternation of brief active periods and long hiding periods persists for the duration of the hiding phase, which lasts for the first 2 months of life in Thomson's gazelle (FitzGibbon, 1990a; Walther, 1973).

Hiding and active periods constitute states of low and high fawn risk, respectively. Fawns are relatively safe while hidden, when their cryptic coloration, small body size and near immobility protect them from detection by nearby predators. However, risk of detection and attack is higher during active periods, when the fawn is exposed and engages in conspicuous behaviours such as play. Previous studies have found that infant predation risk in hider species increases with time spent out of hiding (Barrett, 1978; FitzGibbon, 1990a). Therefore, according to the risk allocation hypothesis, mothers should be more vigilant during active periods than during hiding periods. This pattern has been previously reported in Thomson's gazelle (Costelloe & Rubenstein, 2015) and other hiding species (Clutton-Brock & Guinness, 1975; White & Berger, 2001). FitzGibbon (1990a) found that heightened maternal vigilance increases the likelihood that an exposed gazelle fawn will survive a cheetah, *Acinonyx jubatus*, attack: more vigilant mothers were able to alert their fawns to the cheetah sooner, enabling the fawn to drop down and hide while the cheetah was still far away.

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

Our second prediction was that females would exhibit very low vigilance rates immediately after the fawn resumed hiding, provided that no predator attack or sighting occurred during the previous active period. We argue that the nonoccurrence of a predator encounter during an active period constitutes a reliable cue indicating predator absence. When predators detect an active Thomson's gazelle fawn they readily attack regardless of maternal presence (FitzGibbon, 1993a; B. R. Costelloe, personal observation) rather than waiting for the fawn to resume hiding and for the