Participation by a male Grant's gazelle in the defence of a fawn

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1 INTRODUCTION

In many ungulate species, females aggressively defend their young against predators (Estes & Estes, 1979; Hamel & Côté, 2009; Jar-nemo, 2004; Reynolds, 1983; Wyman, 1967). This behaviour can improve the offspring's chance of survival, thereby increasing the mother's reproductive success (Grovenburg, Monteith, Klaver, & Jenks, 2012). Paternal defence has been reported in some equids, in which males form temporally stable relationships with females and their mutual dependent offspring (Berger & Rudman, 1985; Klingel, 1969). Similarly, male white-tailed deer (*Odocoileus virginianus*) year-lings have been reported to participate in defence of their infant half-siblings (Grovenburg, Jenks, Jacques, Klaver, & Swanson, 2009). However, most mammals, including most ungulates, exhibit male natal dispersal and isolation of females and infants during parturition and the postpartum period (Roberts & Rubenstein, 2014). Therefore, in most ungulate species, adult males are unlikely to associate with related neonates and therefore are not expected to gain inclusive fit-ness benefits from defensive behaviour (Jacques & Jenks, 2010).

There are a handful of reports of male ungulates acting to defend apparently unrelated infants. The drivers of this behaviour are unclear, and more observations are necessary to identify poten-tial explanations. Here, I report an instance in which an adult male Grant's gazelle (*Gazella granti*) participated in the defence of a fawn against three black-backed jackals (*Canis mesomelas*).

2 MATERIALS AND METHODS

The interaction occurred on 17 August 2012 at Ol Pejeta Conser-vancy in Laikipia, Kenya. I observed and video-recorded the events from a vehicle parked approximately 70 m from the subjects.

3 RESULTS AND DISCUSSION

Shortly before 5:00 p.m., I observed a female Grant's gazelle groom-ing a fawn. The fawn walked unsteadily, and the female frequently

raised her tail away from her body, a typical peripartum behaviour in antelope (Gosling, 1969; Jarman, 1976; Roberts & Rubenstein, 2014). These observations suggested that the fawn had been born earlier that day.

At 5:01 p.m., three jackals attacked the fawn. The mother responded with typical defensive behaviour (Estes, 1967; Walther, 1969; Wyman, 1967). When a jackal approached the fawn, the female would chase it away, allowing another jackal to rush in and seize the infant. The mother would eventually stop chasing one jackal in order to charge the other jackals, forcing them to drop their prey. This general pattern of behaviour persisted for the duration of the attack, which lasted until 5:25 p.m. when the jackals killed the fawn.

An adult male gazelle approached the scene of the attack approximately one minute after the jackals arrived and remained until the jackals killed the fawn. He spent much of this time observ-ing the attack, but also interacted with the fawn and jackals in four distinct ways that hindered the jackals' attempts to kill the fawn (Video S1). First, on at least 18 occasions, the male lowered his horns towards or chased a jackal that came near him, causing the jackal to retreat. Second, on at least six occasions, the male lowered his horns towards or chased a jackal holding the fawn, causing it to drop the fawn and retreat. Third, in one instance, he ran alongside the female as she chased jackals. Finally, in four instances, the male stood over or directly next to the fawn, which prevented the jackals from approaching and seizing it.

In comparison with the female's vigorous and sustained defen-sive efforts, the male's behaviours were markedly less intense. Rather than running in pursuit of the jackals, the male walked or trotted and only gave chase for a short distance. While the female fully lowered her horns when charging, the male lowered his head only slightly. Furthermore, the male's aggression did not seem to be triggered by the jackals' attacks on the fawn: in many instances, the jackal seized and bit the fawn while the male looked on passively.

The male's lower motivation to chase the jackals was advanta-geous for the fawn in one regard: when he was standing near the fawn, and thereby preventing the jackals from seizing it, the jackals could not draw him away into a chase. Although this may have

delayed the fawn's death, the male always eventually wandered away, leaving the fawn exposed to attack.

There are several possible adaptive explanations for the male's defensive behaviour. Defence could be a mating strategy, an antipredator tactic, a means of learning about predators (the "Naïve Prey Hypothesis"; Berger, 1979), a form of paternal effort or an attempt at mate guarding. The "mating strategy" hypothesis suggests that the male's defensive efforts may lead to mating opportunities with the fawn's mother (Smuts & Gubernick, 1992) or with the fawn itself if it is female and survives to adulthood (Berger, 2005). It is possible that female gazelle mate preferentially with males that have defended their previous fawns, although if this is true, one might expect male defensive behaviour to be more commonly reported because mating access would constitute a significant fitness benefit. If the purpose of defence is to promote the survival of fawns that represent future mating opportunities, then males should only protect female fawns (Berger, 2005). I was unable to determine the sex of the fawn during my observation.

The "antipredator" hypothesis predicts that aggressive behaviour by prey towards predators will discourage the predators from hunting that prey in the future, thereby reducing the risk of predation to the aggressor or its kin (Berger, 1979, 2005). This explanation seems unlikely because jackals routinely attack gazelle fawns despite consistent maternal defence behaviour. Similarly, coyotes (*Canis latrans*) attacked by female pronghorn (*Antilocapra americana*) are no less likely to attack fawns in the future (Lipetz & Bekoff, 1980). On the other hand, although jackals are capable of killing adult antelope, attacks on adults are uncommon because their size, speed and strength make them difficult prey (Klare, Kamler, Stenkewitz, & MacDonald, 2010; Wyman, 1967). It is possible that this avoidance is reinforced by opportunistic aggressive behaviour from adult gazelle.

The "Naïve Prey Hypothesis" suggests that predator harassment may arise when low-risk encounters offer prey an opportunity to learn about predators (Berger, 1979; Jacques & Jenks, 2010). However, because black-backed jackals rarely hunt adult gazelle, inspection probably confers little benefit to the male.

If the male gazelle was in fact the father of the fawn, the defence could be a form of paternal effort, aimed at increasing the male's reproductive success. Although it is possible that the male sired the fawn, the fluid social system of Grant's gazelles (Estes, 1967) and frequency with which males gain and lose territories (Ezenwa & Snider, 2016) suggest that the fawn and male are unlikely to be closely related.

Finally, some cases of apparent male defence may actually be instances of the male attempting to prevent the female from leaving his territory (Lipetz & Bekoff, 1980). The male Grant's gazelle did not chase the female, and she was not attempting to leave the area; therefore, I reject this explanation for my observation.

As an alternative to these adaptive explanations, I suggest that the male gazelle's behaviour was not targeted towards the defence of the fawn, but rather resulted from a series of proximate stimuli that elicited investigative and defensive reactions. First, the male may have been attracted to the scene of the attack by the high level

of activity, the fawn (Roberts & Rubenstein, 2014) or the female, whose raised tail may have suggested sexual receptivity (Estes, 1967). Once during the observation, the male approached the female with his head and tail raised in a courtship posture (Estes, 1967) (Video S1), which supports the latter interpretation. His tendency to approach and sniff the prone fawn also suggests an investigative motive. Once the male was drawn to the scene of the attack, his brief chases and threats towards the jackals may simply have been defensive reactions to their aggressive behaviour, aimed at protecting himself rather than the fawn. Male ungulates commonly behave aggressively towards predators when they are threatened (Gese, 1999; Hamel & Côté, 2009). The male's departure soon after the death of the fawn could be interpreted as evidence that his actions were intended to protect the fawn. However, once the jackals killed the fawn and began feeding, their aggressive behaviour and the movements of the fawn ceased. If these stimuli attracted the male and elicited his aggressive behaviour, it follows that he would leave once they were no longer present.

The male's behaviour likely incurred little fitness cost because he faced very low risk of injury or death from the jackals, the interaction was brief, and his actions, unlike the mother's, were not characterized by heightened or sustained physical exertion. The fitness benefits of his behaviour were potentially quite high, if the fawn was related to him, if he gained mating opportunities or if he reduced his own risk of predation by the jackals in the future. However, the male's rather spiritless efforts, especially when contrasted to the mother's focused and vigorous defence, suggest that his behaviour, unlike hers, was not shaped by strong evolutionary selection. Therefore, I argue that this observation does not represent evolved infant defence behaviour, but rather a sequence of responses to attractive and threatening stimuli.

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