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Eavesdropping in an African large mammal community: antipredator responses vary according to signaller reliability

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Alarm calls can provide nontarget receivers with potentially life-saving information on predation risk. However, patterns of eavesdropping among species may be shaped by the reliability of the intercepted information, that is, the degree to which the alarm call represents a pertinent threat to the eavesdropping species ('relevance'). Prey are predicted to respond strongly to alarm calls from species that are attacked by the same predator guild, whereas species consumed by a larger or different subset of the carnivore community may act as a less reliable source of predator information. We used a playback experiment to examine whether the degree of antipredator responses to heterospecific alarm calls varied with the reliability of the calling species in three large African mammals: impala, *Aepyceros melampus*, common wildebeest, *Connochaetes taurinus*, and plains zebra, *Equus quagga*. Alarm calls of all three species were broadcast randomly to herds of their own species or to either of the other two species. In accordance with the reliability hypothesis, we found that all species reacted strongly to zebra alarm calls. Lions are the primary predator of zebra and represent a significant threat to all three prey species. In contrast, impala are consumed by a greater number of predators, and their alarm calls evoked weaker, mixed responses in the other two species.

Alarm calls are prevalent in the antipredator repertories of birds and mammals (Caro, 2005; Klump & Shalter, 1984; Zuberbühler, 2009). These vocalizations can serve to alert conspecifics to impending danger (Klump, Kretzschmar, & Curio, 1986; Turner, 1973; Wheeler, 2008), confuse or deter predators (for review, see Wheeler, 2008), or recruit nearby individuals to engage in joint defence (Cheney & Seyfarth, 1985; Rohwer, Fretwell, & Tuckfield, 1976). The conspicuous nature of alarm calling presents the opportunity for bystanders to hear and interpret the signals, an act known as 'interceptive eavesdropping' (e.g. McGregor, 2005; McGregor & Dabelsteen, 1996; Templeton & Greene, 2007). Eavesdropping on heterospecifics can shape species interactions, such as promoting the formation of mixed-species associations, with concomitant effects on community structure and, thus, has important implications for community ecology (Goodale, Beauchamp, Magrath, Nieh, & Ruxton, 2010; Holt, 2007; Schmidt, Dall, & van Gils, 2010; Seppanen, Forsman, Monkkonen, & Thomson, 2007).

Eavesdropping provides nontarget receivers with information on immediate danger that can reduce the probability of encountering or being captured by predators, a strong selection pressure for recognizing and responding to the calls of sympatric species (Fichtel, 2004; Magrath, Haff, Fallow, & Radford, 2015; Seppanen et al., 2007; Shriner, 1998). Playback experiments have demonstrated appropriate antipredator responses to heterospecific alarm calls within a variety of taxonomic groups (e.g. primates: Fichtel, 2004; Ramakrishnan & Coss, 2000; Zuberbühler, 2000, 2001; sciurids: Blumstein & Armitage, 1997a; Shriner, 1998; birds: Magrath, Pitcher, & Gardner, 2007; Magrath, Pitcher, & Gardner, 2009; Templeton & Greene, 2007), although the extent of eavesdropping behaviours within vocally communicating species has not been well defined (Lea, Barrera, Tom, & Blumstein, 2008; Magrath et al., 2015). Currently, little is known about the factors that determine the extent to which a given species should capitalize upon the alarm calls of another species (Caro, 2005; Magrath et al., 2009, 2015).

Eavesdropping appears to be common in social species that form mixed-species associations (reviewed in Goodale, Beauchamp, & Ruxton, 2017), although it can even occur in nonsocial species as well (Lea et al., 2008). Sociality predisposes individuals to use acoustic signals to warn conspecifics of danger (Blumstein, 1999; Blumstein & Armitage, 1997b), and close heterospecific groupings present an opportunity for members to learn the specific alarm vocalizations of other prey (Bshary & Noe, 1997; Goodale & Kotagama, 2005; Magrath et al., 2009; Sullivan, 1984;

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Zuberbühler, 2000). In addition to augmenting the advantages of group formation via dilution effects and predator deterrence (Curio, 1978; Lima, 1995), mixed-species associations may provide information from heterospecific alarm calls that complements the vocalizations of conspecifics, thereby improving overall knowledge of predation risk (Goodale & Kotagama, 2005; Guatier-Hion, Quris, & Gautier, 1983; Magrath et al., 2015; Nuechterlein, 1981). Associating with a second species that can better detect or communicate danger could provide benefits that exceed the cost of feeding competition, especially if the associating species have divergent diets (Goodale & Kotagama, 2005; Goodale et al., 2010; Seppanen et al., 2007). There is evidence that exploiting heterospecific alarm calls in polyspecific associations can allow utilization of riskier foraging patches (Bshary & Noe, 1997; Guatier-Hion et al., 1983; Ridley, Wiley, & Thompson, 2014) or a reduction in time spent on vigilance (Bell, Radford, Rose, Wade, & Ridley, 2009; Bshary & Noe, 1997; Burger, 1984; Flower, 2011; Ridley & Raihani, 2007).

However, the advantages of intercepting alarm calls are only realized if the two species are vulnerable to the same predators (Kitchen, Bergman, Cheney, Nicholson, & Seyfarth, 2010; Magrath et al., 2009). Otherwise, heterospecific alarm calls are unreliable signals in that there is a low probability that the calls signify danger to the eavesdropper, and there is little selective pressure to respond to them (Goodale et al., 2010; Magrath et al., 2007, 2009; Seppanen et al., 2007). The 'relevance' component of signal reliability, as described by Magrath et al. (2009), varies for each caller–interceptor pair based on vulnerability to overlapping suites of predators. As the number of mutual threats increases, so too does the relevance of the heterospecific's calls (Magrath et al., 2009, 2015; Searcy & Nowicki, 2005). The importance of alarm call reliability in a broad sense on interceptor response has only been examined in a small handful of cases and the significance of relevance as a selective pressure for developing eavesdropping behaviours remains relatively unexplored (Kitchen et al., 2010; Magrath et al., 2009; Rainey, Zuberbühler, & Slater, 2004a, 2004b).

We designed a series of playback experiments to examine the importance of reliability of heterospecific alarm calls, in terms of relevance of predation threat, on the antipredator behaviours of three sympatric herbivores: impala, *Aepyceros melampus*, common wildebeest, *Connochaetes taurinus*, and plains zebra, *Equus quagga*. Each of these species produces an acoustically characteristic alarm call: zebra bray, whinny and snort; wildebeest snort; and impala primarily bark. Thus, there is little chance of mistaking a heterospecific call for that of a conspecific. To our knowledge, auditory eavesdropping behaviours have not previously been investigated in these species despite their use of acoustic alarm calls, sociality and frequent tendency to form mixed-species associations. Other studies have examined changes in vigilance between conspecific and heterospecific groupings of these species, but ours is the first to experimentally disentangle an eavesdropping 'many eyes' (or, in this case, ears) effect from dilution or predator deterrence effects (Pays, Ekori, & Fritz, 2014; Périquet et al., 2012; Schmitt, Stears, Wilmers, & Shrader, 2014). In addition, listening for signals of pertinent threats may provide information at a lower cost and therefore be a more commonly utilized behaviour than visually monitoring other species for threat-reaction cues.

These three species differ substantially in body mass, and consequently, predation risk. Previous research suggests that larger predators exploit a wider range of prey sizes, with a strong correlation between predator mass and maximum prey size (Hopcraft, Olff, & Sinclair, 2010; Radloff & DuToit, 2004). That is to say, all predators have the capacity to take down smaller animals, but only large predators typically handle large prey. Four predator species are present within our study system: lion, *Panthera leo* (161.5 kg), leopard, *Panthera pardus* (55 kg), cheetah, *Acinonyx jubatus* (50 kg), and African wild dog, *Lycaon pictus* (25 kg) (Kingdon, 1977). These carnivores opportunistically consume all focal prey species; however, adult zebra and wildebeest are underselected by smaller predators relative to their abundance, whereas impala are vulnerable to a greater proportion of the predator community (Hayward, 2006; Hayward, Henschel, O'Brien, Hofmeyr, Balme, & Kerley, 2006; Hayward, Hofmeyr, O'Brien, & Kerley, 2006, Hayward, O'Brien, Hofmeyr, & Kerley, 2006; Tambling & Du Toit, 2005). The reliability hypothesis predicts that impala would therefore have the least relevant calls to intercept, as they may be alarming at predators that do not represent a threat to the larger herbivores. The alarm calls of zebra, the largest prey, should be relevant to all prey species, with wildebeest forming an intermediate in terms of relevance between the two (Cheney & Seyfarth, 1990; Hopcraft et al., 2010; Magrath et al., 2009). Juveniles are vulnerable to a greater number of predator species than adults (e.g. Sinclair, 2003), and we therefore additionally predicted that the presence of offspring in herds of wildebeest and zebra might increase the responsiveness of adults to the alarm calls of smaller herbivores.

METHODS

Study Site

We gathered data during June and August 2016 in Pilanesberg National Park (25°08′–25°22′S; 26°57′–27°13′E), North West Province, South Africa. The site covers approximately 580 km^2 of hilly savannah terrain, and contains habitats ranging from mixed *Acacia* and broad-leaf bushveld to open grasslands (Adcock, Hansen, & Linderman, 1998). Daily temperatures during the study period ranged from 12 °C to 25 °C. Since the park's establishment in 1979, diverse populations of large herbivores and predators have been reintroduced. Large carnivores currently inhabiting the park include lion, leopard, cheetah and African wild dog.

Study Animals

We focused our study on the three most prevalent herbivore species: impala, common wildebeest and plains zebra. These species are frequently found in mixed-species associations (Kiffner, Kioko, Leweri, & Krause, 2014; Sinclair, 1985). While all large carnivores present within the reserve consume each of the focal prey species, the smaller carnivores (cheetah, wild dog and leopard), preferentially prey on the impala, the smallest prey species (average body mass: 35.4 kg), whereas wildebeest and zebra (145 kg and 197 kg, respectively) are primarily preyed upon by the apex predator, lions (Hayward, Henschel, et al., 2006; Hayward, Hofmeyr, et al., 2006, Hayward, O'Brien, et al., 2006; Radloff & DuToit, 2004). Lions will attack smaller animals when the opportunity presents itself, and represent a significant threat to all prey species (Scheel & Packer, 1995).

Playback Recordings

We elicited alarm calls from each focal species using a life-size, two-dimensional model of a stalking lion (1.15 x 2.2 m) constructed from a high-quality photograph mounted on durable backing. This model was mounted on a wooden trolley that could be wheeled past a herd of animals with a 30 m rope. The resultant alarm calls were extracted from high-quality video recordings of these 'predator encounters', which were undistorted by wind, nonfocal animal calls or other loud noises. Videos were recorded using a Lumix DMC-FZ70 camera (Panasonic; Osaka, Japan). The vocalizations