



Is sentinel behaviour safe? An experimental investigation

Amanda R. Ridley^{a,b,*}, Martha J. Nelson-Flower^b, Alex M. Thompson^b

^a Department of Biological Sciences, Macquarie University, Sydney, Australia

^b DSTI/NRF Centre of Excellence at the Percy FitzPatrick Institute, University of Cape Town, Cape Town, South Africa

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Sentinel behaviour, where individuals take turns to watch for danger and give alarm calls to approaching predators, has been observed in a number of animal societies. However, the evolutionary causes of this behaviour remain unclear. There are two main, competing hypotheses regarding the evolution of sentinel behaviour. The first hypothesis is that it is a cooperative behaviour, where group members benefit from the detection of danger but share the workload of acting as a sentinel. The second is that it is a safe, selfish behaviour. Under the second hypothesis, once an individual is satiated, being a sentinel is safer because sentinels can detect threats more readily and can therefore escape from predators faster. We examined whether sentinels are safer than foragers in a wild, free-living cooperative bird (the pied babbler, *Turdoides bicolor*) with a well-described sentinel system. We found that sentinel behaviour was costly because (1) sentinels were targeted by predators more often, (2) they were further from cover than foragers, and (3) they took longer to reach the safety of cover following a predator alarm. These results suggest that individuals do not become sentinels because it is safer. This is the first study to demonstrate that sentinels are at greater risk of predator attack than foraging group members and suggests sentinel activity may have evolved as a form of cooperative behaviour.

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The occurrence of a sentinel or guard is well known and widespread in group-living species, and involves individuals taking turns to watch for predators while other group members rest or forage. Sentinel behaviour has been observed in a number of cooperative vertebrates (Rasa 1986, 1987, 1989; McGowan & Woolfenden 1989; Hailman et al. 1994; Clutton-Brock et al. 1999; Manser 1999; Wright et al. 2001a, b; Bednekoff & Woolfenden 2003, 2006; Ridley & Raihani 2007; Hollén et al. 2008; Bell et al. 2009; Ridley et al. 2010; Sharpe et al. 2010) and differs from personal antipredator vigilance in that (1) it is coordinated (usually only one individual is actively scanning for predators at any point in time while the rest of the group forages, McGowan & Woolfenden 1989; Bednekoff 1997) and (2) sentinels usually stand in an elevated position while on look-out, rather than the typical 'head-up' behaviour displayed during personal vigilance (Elgar 1989; Bednekoff & Lima 1998). Studies of sentinel activity have found that this behaviour is beneficial in terms of predator detection: sentinels are more effective at detecting predators than are foraging group members (Rasa 1987; McGowan & Woolfenden 1989; Manser 1999; Ridley et al. 2010), and foragers gain increased biomass intake

when a sentinel is present because they spend less time investing in personal vigilance (Hollén et al. 2008). In addition, research has shown that group members are extremely responsive to the vocal information that sentinels provide, and adjust their behaviour accordingly (Rasa 1986; Manser 1999; Hollén et al. 2008; Bell et al. 2009; Radford et al. 2009).

Despite this evidence of a benefit of sentinel activity for foraging group members, whether sentinel behaviour represents a cooperative or selfish act has been contested. Although this type of behaviour was originally presumed to have evolved as a form of kin selection or reciprocal altruism (Hamilton 1964; Trivers 1971), more recently Bednekoff (1997) suggested that becoming a sentinel was the safest behaviour for a satiated individual, and thus that sentinel activity represented a safe, selfish behaviour. Bednekoff (1997, 2001) also suggested that by being a sentinel, individuals could detect predators sooner than if they were resting elsewhere, and could thus escape to the safety of cover more quickly. Empirical research provided support for Bednekoff's ideas, finding that individuals were more likely to become sentinels after supplemental feeding (Clutton-Brock et al. 1999; Wright et al. 2001b; Bednekoff & Woolfenden 2003), that sentinels tended to be closer to the safety of cover than other group members (Rasa 1989; Clutton-Brock et al. 1999) and that sentinels did not suffer higher predation rates than foragers (Clutton-Brock et al. 1999). Despite considerable empirical evidence for Bednekoff's theory of safe, selfish sentinels, several issues remain unresolved and suggest that sentinel activity may, at

* Correspondence and present address: A. R. Ridley, School of Animal Biology (M092), University of Western Australia, 35 Stirling Highway, Crawley 6009, WA, Australia.

E-mail address: Amanda.ridley@uwa.edu.au (A. R. Ridley).

least in part, represent a cooperative behaviour. For example: why do satiated individuals become sentinels instead of simply resting beneath or near cover, where they would be protected from predator attack? Bednekoff's theory assumes that there are no safe refuges available (Bednekoff 1997), which is not the case for most species living in natural habitats. Therefore, although sentinels may be able to detect predators better than foraging group members (Manser 1999; Ridley et al. 2010), it is likely that resting under the protection of cover (where individuals are already safe from attack) is safer than being exposed. In addition, even though supplemental feeding causes an increase in sentinel activity, it is important to consider that individuals may need to reach a certain energetic state before being able to invest in sentinel behaviour. Supplemental feeding may allow them to reach this state sooner, thus creating an increase in sentinel behaviour without necessarily representing a safe, selfish act.

We used natural observations and playback experiments to determine whether sentinels were safer than other group members in the cooperatively breeding pied babbler, *Turdoides bicolor*, by (1) determining whether sentinels were more likely to be targeted during predator attacks, (2) measuring the difference in distance to cover of sentinels and foragers and (3) determining whether sentinels reached cover quicker than foragers following a predator alarm. Sentinels are a common occurrence in pied babbler groups (present for 30–70% of observation time, Ridley & Raihani 2007) and are more effective at detecting predators than foragers (Ridley et al. 2010). Sentinels provide vocal information to the group in the form of both alarm calls and a continuous 'watchman's song' (as defined by Rasa 1986). The former provide information regarding an immediate predator threat, while the latter provides group members with information regarding the proximity of predators, the height of a sentinel and whether a sentinel is about to terminate its bout (Hollén et al. 2008; Radford et al. 2009, Bell et al. 2010). Foragers respond to information provided by the sentinel by foraging more intensively when a sentinel is present (Hollén et al. 2008), foraging further out in the open when a sentinel is located in a high position (Radford et al. 2009) and adjusting foraging behaviour according to predator presence (Bell et al. 2009). Both sentinels and foragers give alarm calls to approaching predators, but sentinels give these calls considerably more often (86.5% of predator approaches versus 46.9% for foraging group members, Bell et al. 2009). Larger groups have sentinels available for a longer period of time because there are more individuals available to contribute to sentinel activity (Ridley & Raihani 2007), but there is rarely more than one sentinel present at a time (Ridley et al. 2010). We discuss the implications of our results for understanding the cost of sentinel behaviour and whether it represents a cooperative or selfish activity.

METHODS

Study Site

Data were collected from February to December 2010 at the Kuruman River Reserve in the southern Kalahari Desert, South Africa (26°58'S, 21°49'E). The study area is primarily semiarid grassland and acacia savannah. We identified five major habitat types at our study site: grassland (open areas where grass was the primary vegetation type, interspersed with occasional camelthorn, *Acacia erioloba*, trees), dune (areas dominated by dunes and open, sparsely vegetated sandy areas), scrubland (areas where the primary vegetation was the shrub *driedoring*, *Rhigozum trichotomum*, usually standing 0.5–1.2 m high), riverbed (characterized by large camelthorn trees, *Zizyphus* trees and areas of low-lying shrubs, grasses and forbs on primarily clay and silt substrates)

and blackthorn thicket (areas where the primary vegetation was dense thickets of the small blackthorn tree, *Acacia mellifera*, in areas of sandy soils with sparse grass cover).

Study Population

The pied babbler is a medium-sized (70–95 g) passerine inhabiting the semiarid Kalahari desert of southern Africa. Groups typically comprise 2–10 adults (individuals > 12 months old) and one to five juveniles, and actively defend a territory year-round (Golabek et al. 2012). The study population comprises 18 groups of pied babblers (average group size of 3.9 ± 1.3 adults, range 2–7) habituated to close observation by observers (for details of habituation, see Ridley & Raihani 2007), allowing us to walk within 2–3 m of group members and closely document their behaviour without causing them disturbance or alarm. All pied babblers at the study site are individually identifiable by a unique combination of three coloured and one metal ring. Adults are captured for ringing using a walk-in trap baited with a mealworm under ringer licence SAFRING 1263 and ethical permit number R2012/2006/V15/AR (Animal Ethics Committee, University of Cape Town, for further details of trapping and ringing process see Hollén et al. 2011). Groups are monitored continuously year-round, and each group is visited at least twice per week for an average of 3 h per observation session. The main predators of pied babblers are raptors, including pale-chanting goshawk, *Melierax canorus*, gabar goshawk, *Melierax gabar*, and terrestrial predators including slender, *Galerella sanguinea*, and yellow mongoose, *Cynictis penicillata* (Ridley et al. 2010). More than 70% of predator approaches observed at our study site involve raptor species (where an approach is defined as a predator specifically approaching the group, rather than simply passing by in the general area). During the rare occasions that we observed a direct predator strike, we were able to define the target of the strike from predator behaviour: when a predator swooped in and attempted to attack a single individual, this individual was considered to be its target. After initial failure, some predators would repeatedly circle and target this individual by making repeated short strikes and swoops. We were able to determine that a specific individual was targeted for attack when there were no other individuals nearby (<5 m), and the striking predator approached within 1 m of its victim. Owing to the habituated nature of our study species, the sparse vegetation (semiarid area) and the overt nature of predator attacks, it was highly unlikely that attacks on foragers would go unobserved.

We defined a sentinel as an individual perching in an elevated position above the foraging group, giving sentinel calls and actively scanning the surrounding area for predators while not investing in alternative behaviours (such as preening, for details of sentinel calling behaviour in this species, see Bell et al. 2009). An individual was only considered a sentinel if it remained in an elevated position while actively scanning the area for more than 30 s (Ridley et al. 2010).

Data Collection

To determine the safety of sentinels relative to other group members, each time an individual undertook sentinel behaviour we estimated the distance to cover (m) of all group members within 1 min of the sentinel bout commencing. We recorded the source of cover that each individual was on or closest to (dead tree, tree, shrub) as well as the substrate they were currently on (ground, tree, dead tree, shrub). To define individuals as exposed or in cover, we followed the previous definitions used for pied babbler sentinel behaviour by Hollén et al. (2008) and Radford et al. (2009). We defined birds as having reached cover when they were completely

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