The presence of an avian co-forager reduces vigilance in a cooperative mammal

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Many animals must trade-off anti-predator vigilance with other behaviours. Some species facilitate predator detection by joining mixed-species foraging parties and ‘eavesdropping’ on the predator warnings given by other taxa. Such use of heterospecific warnings presumably reduces the likelihood of predation, but it is unclear whether it also provides wider benefits, by allowing individuals to reduce their own vigilance. We examine whether the presence of an avian co-forager, the fork-tailed drongo (Dicrurus adsimilis)—affects rates of vigilance (including sentinel behaviour) in wild dwarf mongooses (Helogale parvula). We simulate the presence of drongos—using playbacks of their non-alarm vocalizations—to test that dwarf mongooses significantly reduce their rate of vigilance when foraging with this species. This is, to our knowledge, the first study to demonstrate experimentally that a mammal reduces vigilance in the presence of an avian co-forager.

Keywords: eavesdropping; heterospecific warnings; vigilance; sentinel behaviour; dwarf mongoose; fork-tailed drongo

1. INTRODUCTION

Many species must trade-off between detecting predators and investing in other behaviours. To facilitate predator detection, animals frequently join mixed-species foraging associations (Noe & Bshary 1997; McGraw & Bshary 2002; Goodale & Kotagama 2005a) and ‘eavesdrop’ on the predator warnings given by other species (see Lea et al. 2008 for review). By responding to heterospecific predator warnings, an individual presumably reduces its likelihood of being predated. However, it remains unclear whether ‘eavesdropping’ provides wider benefits by allowing an individual to reduce its vigilance. Although several researchers have noted a relationship between the presence of heterospecific co-foragers and vigilance (Rasa 1983; Bshary & Noe 1997; Ridley & Raihani 2007), most of these relationships have not been tested experimentally to ascertain causality, and may relate to confounding variables, such as food availability, habitat type, weather, or predator density. Only in two species, the downy woodpecker (Picoides pubescens) and the white-breasted nuthatch (Sitta carolinensis), has it been demonstrated that individuals reduce their vigilance in response to the presence of heterospecific avian co-foragers (Sullivan 1984; Dolby & Grubb 1998).

In this study we examine whether the presence of an avian co-forager—the fork-tailed drongo (Dicrurus adsimilis)—affects the vigilance behaviour of dwarf mongooses (Helogale parvula). Dwarf mongooses are small, cooperatively breeding carnivores that live in stable groups of 3–30 individuals. They forage by day, as a cohesive group, for arthropods scratched from the soil (Rasa 1983). Subject to intense predation, dwarf mongooses post sentinels that watch for predators while the group forages, and prefer to forage with mixed-species bird flocks (Rasa 1983, 1986, 1987; see also the electronic supplementary material). In Kenya, Rasa (1983) found that dwarf mongooses responded to the predator warnings of the birds with which they foraged, and the birds detected predators significantly more often than the mongooses. The mongooses also gave fewer alarm vocalizations than when foraging without birds, suggesting that they relied on avian warnings. Fork-tailed drongos frequently accompany foraging dwarf mongooses (and other mammals and ground-foraging birds), catching flushed insects and occasionally acting as kleptoparasites (Herremans & Herremans-Tonnoy 1997; Ridley & Raihani 2007). They are thought to fulfil the role of ‘sentinel species’ within polyspecific foraging parties, because their sallying foraging technique (and the visual scanning it requires) facilitates predator detection (Goodale & Kotagama 2005b). Drongos also alarm at predators that threaten their heterospecific foraging partners but not themselves (Ridley et al. 2007).

In this study we use observational data to establish whether the presence of fork-tailed drongos affects vigilance in dwarf mongooses. We assess rates of sentinel behaviour in mongoose groups and rates of vigilance scanning in foraging individuals. We then simulate the presence of a drongo experimentally (using playbacks of the bird’s non-alarm vocalizations) to test the causality of any differences in vigilance behaviour.

2. MATERIAL AND METHODS

We collected the data at Phuza Moya Private Game Reserve, north-eastern South Africa (24°15’S, 30°45’E) between June 2006 and November 2009. The study population consisted of four groups of dwarf mongooses (mean group size = 18.5) that were habituated to the presence of an observer. We accompanied the mongooses on foot (within 2–3 m) during their morning foraging session, recording their behaviour for approximately 3 h. To document sentinel behaviour, we recorded the identity and start and finish times of all sentinels that remained on duty more than 1 min (i.e. climbed more than 10 cm from the ground to watch for predators). We also documented the time of arrival (within 10 m of the group) and departure of fork-tailed drongos, and all predator alarms (cause, level of response and which species raised the alarm). We obtained an average of 81 ± 15 h of data for each of eight group-years (four groups × two separate years), totalling 650 h of observation. To measure rates of vigilance in foraging individuals, we targeted a subset of eight adult mongooses (five females and three males) from two groups. We used continuous focal sampling to record how frequently each individual interrupted foraging to scan its surroundings, using the following categories: parallel scan (mongoose scans above and ahead); sideways scan (mongoose turns head to make a 180° scan) and raised scan (mongoose stands bipedally or raises forepaw to scan the sky). For each individual, we obtained 20 min of foraging data when one or more fork-tailed drongos were present and 20 min when drongos were absent.

We conducted two playback experiments, each on eight adult mongooses, during morning foraging sessions when all birds were absent. In both experiments we collected 10 min of focal data during the playback of drongo non-alarm calls and 10 min during the playback of the control recording. The first experiment controlled for the possible impact of the experimental procedure with a playback of the ‘contact calls’ (uttered almost continuously by foraging mongooses to maintain group cohesion; Rasa 1987) of mongooses from the focal individual’s own group. The second experiment assessed whether the mongooses responded specifically to drongos (rather than the presence of any bird) and the control playback consisted of the territorial calls of the white-bellied sunbird (Cinnyris venustus), a locally abundant species that does not forage with the mongooses. See the electronic supplementary material for further details of the experiments.

We used paired t-tests when the data were normally distributed (based on the Kolmogorov–Smirnov normality test) and Wilcoxon-signed rank tests otherwise. All tests were two-tailed with a significance threshold of 0.05. Means ± s.e.

3. RESULTS
On average, mongoose groups interrupted their foraging to respond to predator alarms 5.3 times per hour. Of the 3475 genuine predator alarms recorded in this study, 30 per cent were initiated by heterospecific alarm vocalizations. Fork-tailed drongos accompanied the mongooses during 38.6 ± 7.1 per cent of the group’s foraging time and initiated 15 per cent of these heterospecific warnings.

The presence of drongos appeared to have a marked effect on the anti-predator behaviour of foraging mongooses. Groups posted sentinels 42.4 ± 3.6 per cent of the time when foraging without a drongo compared with 21.2 ± 1.5 per cent when accompanied by a drongo (paired t-test: \( t_{140} = -5.82, p < 0.001 \)). Because environmental factors may have been responsible for this relationship, we also compared rates of mongoose sentinel behaviour within single morning sessions, for 141 sessions in which drongos were both present and absent for at least 10 min of the session. This analysis yielded identical results, both statistically (paired t-test: \( t_{140} = -9.43, p < 0.001 \)) and with regards to the percentage of time that groups posted sentinels.

The presence of fork-tailed drongos was also associated with a 38.9 ± 7.8 per cent reduction in vigilance at an individual level (paired t-test: \( t_{14} = 4.26, p = 0.004 \)), with a significant decrease in the frequency of all three categories of vigilance scan (figure 1a).

The causality of this relationship was confirmed by the results of the playback experiments. In the first experiment, foragingmongooses scanned their environment 3.92 ± 0.36 times min\(^{-1}\) during the control session (when mongoose ‘contact’ calls were played), but only 1.95 ± 0.21 times min\(^{-1}\) when the presence of a drongo was simulated by the playback of its non-alarm calls (paired t-test: \( t_{7} = 5.47, p < 0.001 \); figure 1b). In the second experiment, the mongooses scanned for danger 4.02 ± 0.38 times min\(^{-1}\) during the playback of the calls of a non-co-foraging bird species (the white-bellied sunbird), but only 1.65 ± 0.17 times min\(^{-1}\) during the playback of drongo calls (paired t-test: \( t_{7} = 7.48, p < 0.001 \); figure 1c).

4. DISCUSSION
Dwarf mongooses responded to the presence of fork-tailed drongos by significantly reducing their anti-predator vigilance. Individuals halved the period they spent on sentinel duty, allowing them to re-allocate this time to other behaviours. Because dwarf mongoose sentinels are known to suffer an elevated risk of predation (Rasa 1987), individuals probably gained direct survival benefits also. Mongooses also reduced the frequency with which they interrupted foraging to scan for danger. This is likely to significantly improve foraging efficiency in a species that preys on highly mobile invertebrates. The causality of the relationship between vigilance and the presence of a co-foraging bird species was confirmed by the playback experiments (figure 1), which simulated the presence of a drongo using vocal cues.

Dwarf mongooses presumably reduced their vigilance when accompanied by drongos because they capitalized on the birds’ predator warnings (although the mongooses’ use of heterospecific alarms (Rasa 1983) is yet to be confirmed experimentally). The mongooses are unlikely to have benefited from a dilution effect.
Diana monkeys (Sullivan 1984), and both mixed-species flocks. Downy woodpeckers and white-breasted nuthatches are less vigilant when foraging in
2007), and both downy woodpeckers and white-(but not large) pied babbler groups (Ridley & Raihani

demonstrated experimentally that fork-tailed drongos alarm at terrestrial predators when accompanying ground-foraging pied babblers (Turdoides bicolour) but not when alone, and we observed drongos assisting the mongooses to mob puff adders (Bitis arietans) and an African civet (Civettictis civetta), neither of which poses a threat to drongos.

Dwarf mongooses are known to coordinate sentinel behaviour among group members (Rasa 1986), but our findings suggest that they can also facultatively adjust their behaviour to take into account contributions to vigilance by another, unrelated, species. Our experiments do not exclude the possibility that the mongooses were responding to the presence of a vocalizing co-foraging bird species, rather than to a drongo specifically. However, they were clearly able to discriminate between bird species on the basis of vocal cues, and they did not lower their vigilance in the simulated presence of a non-co-foraging species (figure 1c).

This is, to our knowledge, the first study to demonstrate experimentally that a mammal responds to the presence of an avian co-forager by reducing its vigilance. Observations of mixed-species foraging parties in Kenya found a negative correlation between number of sentinel posted by dwarf mongooses and number of birds present (Rasa 1983). Similarly, red colobus (Colobus badius) look down less frequently when foraging with Diana monkeys (Cercopithecus diana; Bshary & Noe 1997). However, these relationships were not tested experimentally and short-term environmental factors could explain the findings. For example, a lack of predator activity, a locally abundant food source or the lessening of predation risk owing to weather, cover or habitat type could lead to both a relaxation of vigilance and a tendency for heterospecific individuals to gather. Among birds, fork-tailed drongos are known to be associated with reduced sentinel behaviour in small (but not large) pied babbler groups (Ridley & Raihani 2007), and both downy woodpeckers and white-breasted nuthatches are less vigilant when foraging in mixed-species flocks. Downy woodpeckers reduced their vigilance when played the contact calls of hetero-specific flock members (Sullivan 1984), and both species increased vigilance after the removal of two flocking species (Dolby & Grubb 1998).

In conclusion, this study shows that the benefits of using heterospecific predator warnings can extend beyond a presumed reduction in mortality rates by allowing individuals to divert time and resources from vigilance to alternative uses. These findings strengthen our understanding of the importance of this form of interspecies communication, not only its capacity to shape the behaviour of individual species or foraging assemblages, but also its potential role in coevolution.

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