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Cooperative sentinel behaviour in the Arabian babbler

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Cooperative sentinel behaviour in Arabian babblers, *Turdoides squamiceps*, appears generally consistent with state-dependent models of individually selfish antipredator behaviour. We examined further detailed aspects of this cooperative behaviour, including the suggestion that by engaging in this behaviour sentinels advertise their status and gain social prestige. Chosen sentinel locations were higher, but no more exposed, than the best alternative locations within 25 m. Sentinels started off closer to the centre of the foraging group than when sentinel bouts were terminated. Change-overs between sentinels were nearly always due to previous sentinels terminating their own bout. On the rare occasions when bouts were interrupted by upcoming sentinels, physical contact or aggression was extremely rare. Dominant males tended to terminate sentinel bouts of other birds, interrupting especially the dominant females. Other than this, there was no effect of an individual's sex or dominance rank on any aspect of sentinel change-overs or location choice when acting as a sentinel. There were also no differences in any sentinel activity between simple family groups, and those more complex nonfamily groups within which individuals compete for reproduction. Rates of alarm calling did not differ between group members, although dominant males did make more territorial calls to neighbouring groups while acting as a sentinel. Therefore, we found relatively little evidence that individuals compete for the chance to act as a sentinel as a means of showing off within groups of Arabian babblers. Instead, our study confirms the primary function of sentinels as a system of cooperative vigilance.

Sentinel behaviour usually involves one member from a cooperative group standing guard in a prominent position, while the rest of the group forages in comparative safety (Gaston 1977; Rasa 1986, 1989; McGowan & Woolfenden 1989; Zahavi 1990; Clutton-Brock et al. 1999; Wright et al., in press). A variety of evolutionary explanations exist for this apparently altruistic behaviour. The high relatedness within cooperative groups suggests kin selection for the purpose of protecting relatives (Hamilton 1964; Maynard Smith 1964; McGowan & Woolfenden 1987). Alternatively, regular rotation of unrelated sentinels might be maintained via reciprocity with score keeping (Trivers 1971), although it seems more likely that cooperative sentinel effort would need to be maintained via mutualistic benefits from investing in future partners and allies, and from maintaining group size (i.e. group augmentation: Woolfenden & Fitzpatrick 1978, 1984; Ligon 1981; Connor 1995; Wright 1998). A recent model has shown that such mutualistic benefits and kin selection may not be necessary, however, because cooperative sentinel behaviour can be evolutionarily stable when based solely upon short-term individually selfish decisions by group members depending upon their internal state (Bednekoff 1997).

For Arabian babblers, *Turdoides squamiceps*, Zahavi (1989, 1990; Zahavi & Zahavi 1997) suggested that sentinel behaviour has evolved as a signal, with individuals benefiting by being seen to act as a sentinel and thereby gaining social prestige. According to this hypothesis, individuals perform sentinel duties and alarm call in order to show off and obtain social returns in terms of access to advantageous collaborations and reproductive opportunities (Zahavi 1995; Wright 1999). This hypothesis assumes that sentinel behaviour is costly in terms of lost opportunities to forage and the predation risk

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inherent in taking up an exposed position. Sentinels therefore have to be effective look-outs and spot predators first, because they are the most exposed members of the group. To defend their high-status positions, dominant group members should thus interfere with the competitive sentinel efforts of subordinates, and use allofeeding and aggression to displace them and take over as sentinels in their place (Zahavi & Zahavi 1997; but see Wright 1999).

State-dependent models of cooperative selfish sentinel behaviour (Bednekoff 1997) have recently been supported by observational and experimental evidence from meerkats, *Surricatta surricata* (Clutton-Brock et al. 1999). Wright et al. (in press) suggested similar conclusions for Arabian babblers, showing that sentinel effort within groups was positively related to dominance rank within each sex, and males acted as sentinels more than females of similar rank. Larger groups showed greater overall sentinel effort, but with less effort per individual as only one sentinel was on duty at any one time. All of these effects on sentinel behaviour in Arabian babblers were irrespective of relatedness and group social structure, and could be explained by differences in body mass (i.e. 'state') within and between individual birds (see Wright et al., in press). In addition, experimental food supplementation of individual babblers created similar increases in sentinel effort, again related simply to differences in body mass and not social dominance (Wright et al. 2001). Although generally supportive of the more straightforward antipredator function of sentinel behaviour, these studies do not necessarily discount an additional and more complex social role for it. Along with social prestige, sentinel behaviour might be used in competitive interactions within and between groups. By keeping a look out, dominants might be more likely to spot a neighbouring group, or be more able to monitor the rest of the group (e.g. for the purposes of mate guarding). Sentinels may also gain foraging advantages as sit-and-wait predators (Rasa 1983; Munn 1986; McGowan & Woolfenden 1989).

In this study we examined additional aspects of sentinel behaviour. These involved rates of alarm calling and other vocalizations by sentinels, the nature of changeovers between successive sentinels and the types of sentinel locations used relative to alternative locations and the foraging group. Our aim was to explore thoroughly any signalling and/or social function for this behaviour, including those elements not directly connected to its obvious antipredator function.

METHODS

The Study Population

Arabian babblers live in the Arabian and Sinai deserts in territorial groups of mixed sex ranging in size from two to 22 individuals. In most years groups consist of 3–12 birds, with age-related linear dominance hierarchies within each sex (for further detail, see Zahavi 1988, 1989, 1990). Approximately one-third of groups are 'complex nonfamily groups' which have a varied social structure. These groups are usually newly formed or recently restructured after the death or replacement of a breeding individual or pair and subsequent departure of subordinate group members of one sex (usually the females). Complex groups contain more than one potential breeder of either sex, these being any bird in a group containing at least one unrelated adult of the opposite sex (close inbreeding is avoided in this species, with subordinate males competing and obtaining reproduction only in complex groups, see Lundy et al. 1998; Wright et al. 1999). The remaining two-thirds of groups are 'simple family groups', containing a single breeding pair and their nonbreeding offspring. Simple family groups tend on average to be larger than complex nonfamily groups (Wright et al. 1999), but in the present study there was no significant difference in size between the two types of group (Wright et al., in press).

The study site at Hazeva is a 25-km^2 area of desert, located 30 km south of the Dead Sea in the Arava rift valley in southern Israel. Twenty groups of Arabian babblers have been studied continuously since 1971 at Hazeva by Amotz Zahavi and students from Tel Aviv University. Between 1992 and 1997, up to 40 groups were monitored on a weekly basis and habituated to human observers via occasional hand feeding. All birds were individually colour ringed and their family histories known. Dominance rank within each sex was assigned over many observations, involving the direction of supplants and/or outcomes of aggressive interactions over provisioned food (e.g. pieces of bread). These behavioural observations regarding dominance were confirmed through genetic analysis of group structures and access to reproductive opportunities (see Lundy et al. 1998; Wright et al. 1999).

Hazeva is a very open habitat with sparse vegetation lining the bottom of dry river beds, comprising well-spaced trees (*Acacia* spp.) and a few low bushes and annual plants. However, thicker *Tamarix nilotica* scrub and reed beds (*Phragmytes* spp.) exist in one area receiving regular outflows of water from human settlements and agriculture.

Data Collection

We collected data throughout the year from 1 November 1992 to 30 September 1993, and during part of the nonbreeding season between 30 September and 30 December 1996. Observations were carried out for ca. 3 h in the morning (starting at sunrise as the group left the roost tree) and ca. 2 h in the afternoon (finishing at sunset as the group went to roost). Sentinel behaviour involves a single group member perching in an obvious, prominent and elevated location with its head up, being vigilant. Individual sentinel bouts last for a number of minutes, during which the sentinel provides alarm calls that alert foraging group members to the presence of potential aerial and terrestrial predators (e.g. raptors, foxes).

Observers were able to walk within 20 m of the habituated groups and record: (1) the identity of any bird acting as a sentinel; (2) the start and end times of each sentinel bout (to the second), including the times spent on the different sentinel perches used within a bout; (3) the nature of any change-over in sentinels, including behaviours before and after a sentinel bout; and (4) the type and number of vocalizations by the sentinel and other group members (either sharp warning alarm calls; constant alarm trills once a predator had been spotted; contact calls between group members; or territorial calls on group boundaries).

During 1996, we also recorded more detailed data concerning: (5) the sentinel position height (m) and exposure (0=exposed at the very top of tree or bush; 1=exposed but not quite at top; 2=near top, visible through thin branches; 3=lower down, deeper within branches; 4=bird visible inside tree or bush; and 5=totally obscured inside the tree or bush); (6) the height (m) and exposure (as above) of the 'next best' sentinel location (as judged by the observer in terms of height and providing the widest view) within 25 m of the sentinel; and (7) the mean distance of the foraging group from the sentinel (m). These details were recorded both as the individual sentinel bout started and again when it ended, and always by the same observer (E.B.), thereby obviating the problem of interobserver reliability. These close methods of observation may have influenced the individual behaviours of interest, but there was no evidence for it in this study (see Wright 1997; Wright et al., in press).

Analysis

For each bird on each observation session, these measures of sentinel behaviour were calculated per h and then reduced to means per bird prior to analysis. The sample comprised 21 groups (11 simple families, 10 complex nonfamilies) containing a total of 122 individuals, which were observed performing 7593 individual bouts of sentinel behaviour. All variables conformed to homogeneity of variance and normality requirements for parametric ANOVA and regression analyses. However, the variables concerned with vocalizations and postsentinel behaviour per sentinel bout contained too many zeros, and were therefore subject to nonparametric ANOVA (i.e. Kruskal–Wallis, with all χ^2 values corrected for ties). Two-tailed P values are given throughout.

RESULTS

Sentinel Location

More than 75% of sentinel bouts observed involved birds perched above 1.5 m, and this was often as high as possible in a habitat that contained few trees over 2 m in height. Sentinel locations for all birds were significantly higher than the best alternative sentinel location within 25 m of the sentinel (repeated measures ANOVA: $F_{1,40}$=140.10, P<0.001; Fig. 1a). However, there were no significant differences in mean sentinel location heights used by birds according to sex ($F_{1,40}$=0.00, P=0.960) or dominance rank ($F_{2,40}$=0.33, P=0.719), and no interaction ($F_{2,40}$=0.55, P=0.579). Sentinel height used did not differ between birds in simple family versus complex nonfamily groups (contrast t_{56}=0.74, P=0.460).

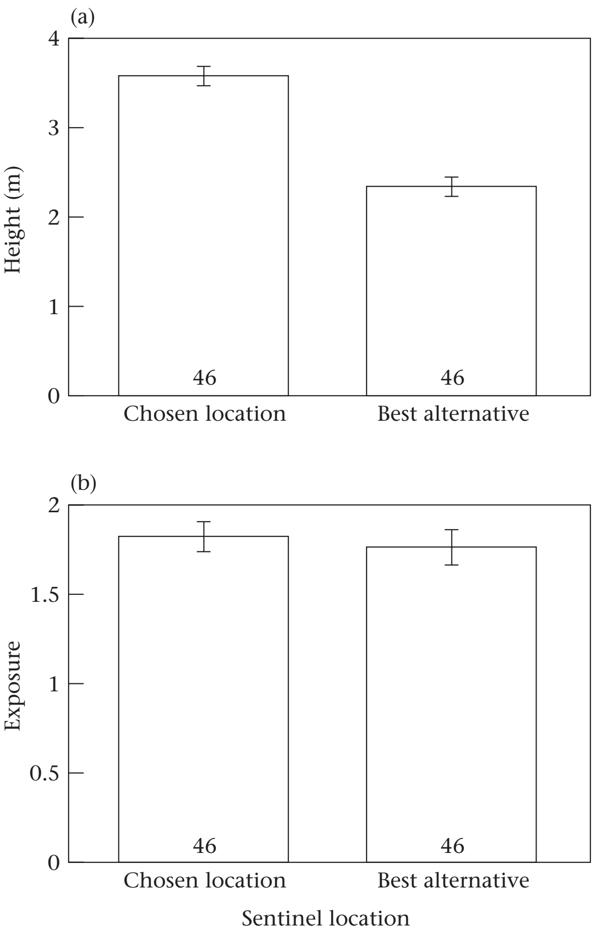

Figure 1. Comparison between the chosen sentinel location and the best alternative location within 25 m for: (a) sentinel location height, and (b) sentinel location exposure. Values are means±SE, and sample sizes (number of birds) are shown at the bottom of the bars (see text for details).

Sentinels did not appear to seek out the most exposed locations, with only 37% of locations being on the very exposed top of trees, 32% being just below the top of the tree, and as many as 31% being further inside the cover of the tree. Sentinel locations were not significantly more exposed than the best alternative sentinel location within 25 m of the sentinel (repeated measures ANOVA: $F_{1,40}$=0.63, P=0.432; Fig. 1b). There were also no significant differences in sentinel location exposure between birds according to sex ($F_{1,40}$=0.89, P=0.352) or dominance rank ($F_{2,40}$=0.17, P=0.848), and no interaction ($F_{2,40}$=1.14, P=0.331). There was no significant difference in the level of exposure of sentinel locations used by birds in simple family versus complex nonfamily groups (t_{56}=0.70, P=0.488). Therefore, all birds in all groups appeared to act as sentinels using similar types of location, which was as high up as possible but not particularly exposed.

Sentinels usually placed themselves as close as possible to the middle of the foraging group and tended to stop

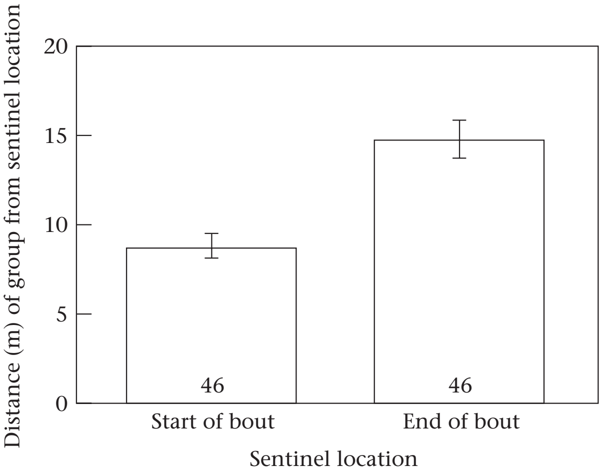

Figure 2. Comparison of the distance between the foraging group and the sentinel location at the start and end of the sentinel bout. Values are means±SE, and sample sizes (number of birds) are shown at the bottom of the bars (see text for details).

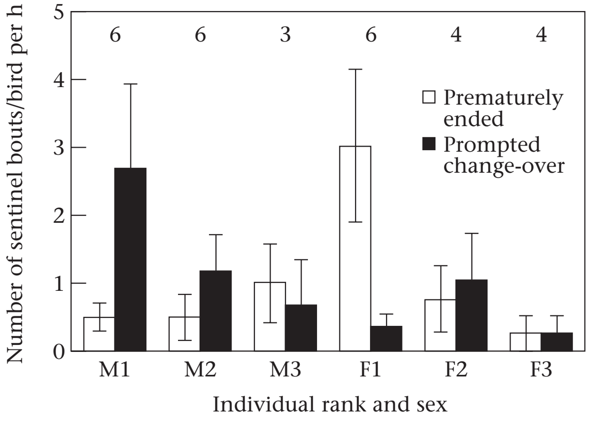

Figure 3. Mean number of sentinel bouts per bird±SE when the bout was either 'prematurely ended' by another bird beginning to act as sentinel or was preceded by a 'prompted change-over' when the bird itself ended another's sentinel bout. Data are divided according to the different sex and dominance classes of bird within groups (M1=alpha male, M2=beta male, F1=alpha female, F2=beta female, etc.). The number of groups involved is shown above the bars.

using a particular sentinel location when the foraging group had moved on. Hence, there was a significantly greater distance between the sentinel and the centre of the foraging group at the end of a sentinel bout than at the start (repeated measures ANOVA: $F_{1,40}=51.90$, $P<0.001$; Fig. 2). The distance between the sentinel and the centre of the foraging group did not differ for males and females ($F_{1,40}=2.83$, $P=0.100$), although there was a tendency for more dominant individuals to act as sentinels at greater distances from the group ($F_{2,40}=3.48$, $P=0.040$). There was also no interaction between sex and dominance rank ($F_{2,40}=0.08$, $P=0.921$). The distance of sentinel locations from the foraging group did not differ between simple family versus complex nonfamily groups ($t_{56}=1.75$, $P=0.085$). Sentinels therefore appeared to position themselves so that they could most easily see any approaching predator, as well as being as close to the foraging group as possible.

The Nature of Sentinel Change-Overs

On 94% of occasions, the change-over between individual sentinels involved the first bird coming down before the second bird took over. This probably reflects the mobility of the foraging groups, requiring new sentinels to use alternative locations nearer the new centre of the group. Therefore, in only a small minority of cases did a new sentinel take the initiative and prompt the timing of the change-over, and birds very rarely had their sentinel bouts terminated prematurely by another bird. We calculated the difference between the number of change-overs prompted by each individual versus the number of its own sentinel bouts that were ended in this way. As Fig. 3 shows, the only obvious trend was for dominant alpha males to prompt the end of far more sentinel bouts than were terminated for them by another bird, with the reverse being true for dominant alpha females. This was reflected in a significant effect of sex ($F_{1,23}=4.39$, $P=0.047$), no overall effect of dominance rank ($F_{2,23}=0.36$, $P=0.703$), but a significant interaction between dominance rank and sex ($F_{2,23}=4.77$, $P=0.019$). If competitive sentinel behaviour had been occurring, we might have expected a close association in change-overs between closely competing individuals, such as the alpha and beta males. There was also no significant difference in these measures between simple family versus complex nonfamily groups ($t_{38}=0.06$, $P=0.952$).

The pattern of prompted change-overs shown in Fig. 3 did not reflect differences in individual sentinel effort within groups (i.e. males doing more than females and an increase in effort with dominance rank, see Introduction, Wright et al., in press). Therefore, the data in Fig. 3 cannot be explained as a simple negotiation concerning the exact timing of change-overs in a small but consistent proportion of sentinel bouts. However, within this 6% of change-overs between successive sentinel bouts that were apparently interrupted, just over half involved the new sentinel taking up a completely new location, thereby causing the first sentinel to end its bout without any physical prompting. Overall, less than 3% of prompted sentinel bout change-overs involved actual physical (or potential physical) contact between successive sentinels. Even fewer of these involved any classifiable social interaction (e.g. allopreening 1.9%, or allofeeding 0.3%), including aggression. As a result, no statistical analyses could be carried out on patterns of physical contact between sentinels, but our data strongly suggest that this is a relatively minor aspect of sentinel behaviour.

Behaviour After Sentinel Bouts

Upon completion of a sentinel bout, birds performed a variety of behaviours, which were observed in 66.1% of cases. On 28.5% of occasions they went straight to feed, either on the ground or in trees. Nonfeeding activities were carried out on 37.6% of occasions, such as

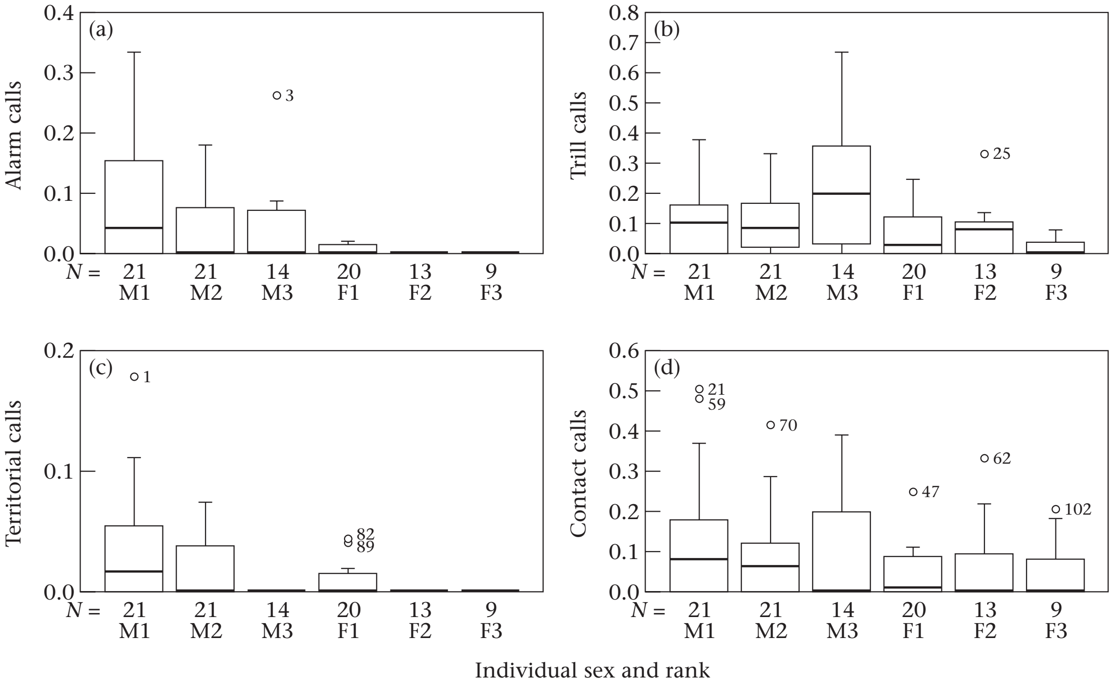

Figure 4. Median values for the number of vocalizations per sentinel bout (box indicates interquartile range and bars indicate 95% confidence intervals, with outliers shown) for (a) alarm calls; (b) alarm trills; (c) territorial calls; and (d) within-group contact calls (see text for details). Data are divided according to the different sex and dominance classes of bird within groups (M1=alpha male, M2=beta male, F1=alpha female, F2=beta female, etc.). The number of birds is shown below the bars.

allopreening (16.4%), preening (1.6%) or resting (0.3%). Sentinels could also lead the group in movement (8.8%), or be forced to follow the group as it moved (5.8%), usually to another foraging location. The remaining nonfeeding postsentinel behaviours included avoidence of predators by hiding in bushes or trees (4.2%), territorial encounters with another group (0.3%) and predator mobbing (0.2%). However, there was no significant effect of individual sex or dominance rank on any of these postsentinel behaviours (Kruskal–Wallis: all *P* values >0.07), and no significant differences between simple family versus complex nonfamily groups (Mann–Whitney *U* test: all *P* values >0.22).

Alarm Calls and Vocalizations

Only 13.3% of sentinel bouts included an alarm (warning) call, and 11.9% included other nonalarm vocalizations, but these were almost always by the sentinel. Less than 1.8% of sentinel bouts included a vocalization by a foraging individual, and all of these were alarm calls. The chance that a sentinel bout included an alarm call appeared significantly dependent upon the sex and dominance rank of the sentinel (Kruskal–Wallis: χ^2_5=11.66, *N*=98, *P*=0.038). As Fig. 4a shows, this was because dominant males were more likely to give alarm calls. However, when we controlled for differences in the duration of sentinel behaviour by different classes of group member (see Introduction, Wright et al., in press), this effect of sex and dominance rank on the number of vocalizations per time spent as a sentinel became nonsignificant (Kruskal–Wallis: χ^2_5=8.39, *N*=98, *P*=0.136). The proportion of bouts that involved alarm trills (i.e. predator mobbing vocalizations) differed according to sex and dominance rank (Kruskal–Wallis: χ^2_5=13.00, *N*=98, *P*=0.023), although this was due to a few extreme values for gamma males (Fig. 4b). Again, this effect became nonsignificant when we controlled for differences in the duration of sentinel behaviour by different types of group member (Kruskal–Wallis: χ^2_5=9.45, *N*=98, *P*=0.092). The rates of alarm calls did not differ between simple family versus complex nonfamily groups (Mann–Whitney *U* tests: all *P* values >0.341).

For vocalizations that were not alarm calls, there was a significant difference in the probability that a sentinel bout included a territorial call depending upon the sex and dominance rank of the sentinel (Kruskal–Wallis: χ^2_5=14.60, *N*=98, *P*=0.012), dominant males being more likely to give these territorial calls (Fig. 4c). This result held even when we controlled for differences in the duration of sentinel behaviour (Kruskal–Wallis: χ^2_5=12.94, *N*=98, *P*=0.024). There was no significant difference in the proportion of bouts that involved within-group contact calls by birds of different sex and dominance rank (Kruskal–Wallis: χ^2_5=5.49, *N*=98, *P*=0.359; Fig. 4d), and this effect was also nonsignificant when we controlled for differences in the duration of sentinel behaviour (Kruskal–Wallis: χ^2_5=1.910, *N*=98, *P*=0.861). Again, there was no significant difference in the frequency of these nonalarm calls within simple family versus complex nonfamily groups (Mann–Whitney *U* test: all *P* values >0.437).

DISCUSSION

Almost all details of sentinel behaviour presented here for Arabian babblers were consistent with a simple system of cooperative antipredator vigilance, with all group members behaving in a similar manner while acting as sentinel irrespective of group type. This is in agreement with the finding that nearly all differences in sentinel effort within and between individuals can be explained by variation in body mass (Wright et al., in press). Our study therefore lends further support to Bednekoff's (1997) simple state-dependent model as the most parsimonious explanation for the evolution of cooperative sentinel behaviour.

Sentinel locations appeared to be chosen for the purpose of spotting predators, rather than for deliberately exposing the sentinel to predation risk. In his study of jungle babblers, *Turdoides striatus*, Gaston (1977) reported sentinel locations at heights similar to those observed here (i.e. 1.5 m), even though his groups were within open woodlands with a canopy at 6 m. For both habitats, this may be the height required to see a certain distance and to protect foraging birds on the ground (e.g. from low-flying sparrowhawks, *Accipiter nisus*). It may also represent an acceptable energetic cost in terms of the distance birds had to travel to and from foraging on the ground. Either way, Arabian babbler sentinels at this height did not appear to be unnecessarily exposed, and as a result sentinels were positioned much closer to cover than the majority of foragers. These observations agree with work on sentinel behaviour in cooperative mammals (Rasa 1989; Clutton-Brock et al. 1999), and are in line with theoretical assumptions that sentinel behaviour may be a relatively safe activity (Bednekoff 1997).

Sentinels did use perches that allowed them to see, or be seen by, the foraging group. This might have been the result of sentinels simply taking up a position close to the centre of the group in an open habitat. However, such locations may also have ensured the effectiveness of group protection offered, by allowing both the sentinel and the group to know where each other was. Arabian babbler sentinels did occasionally produce a quiet subsong, which may have had the same role as the meerkat and dwarf mongoose, *Helogale undulata rufula*, watchman's song (Rasa 1986) in communicating to the foraging group that there is someone on guard. However, subsong was produced much less often and was much less distinct than in other species, possibly because babblers do not forage all the time with their heads down holes, and so can instead visually monitor sentinel presence.

Contrary to earlier reports (Zahavi 1990; Zahavi & Zahavi 1997), sentinel change-overs did not normally include aggression or interference by dominants towards subordinates. The vast majority of bouts ended without prompting, suggesting that the sentinels themselves decided to stop and go and do something else, probably based upon their low energetic state and so need to forage (Bednekoff 1997; Wright et al., in press) or because of the benefits from some other nonforaging activity (see above). This pattern in sentinel change-overs is similar to that described for jungle babblers by Gaston (1977). However, there was little consistent evidence that babblers vocalized prior to coming down from a sentinel bout, as described for Florida scrub jays, *Aphelocoma coerulescens* (Barbour 1977, cited in McGowan & Woolfenden 1989). Again, it is possible that the relatively open nature of babbler habitat instead allowed the visual monitoring of sentinel presence, and the termination of sentinel bouts needed to be signalled vocally in only a minority of cases. Indeed, the more open habitat occupied by Arabian babblers might explain why they use so few vocalizations, compared with the closely related jungle babbler (Gaston 1977). In the present study, dominant males also appeared to bias their sentinel take-overs towards their breeding partner, the dominant female. However, this was the only regular pattern in sentinel change-overs, and there was little evidence for competitive acting as a sentinel for social prestige (sensu Zahavi & Zahavi 1997). Dominance-based interactions may regularly occur within the context of sentinel change-overs, but we would suggest that this happens no more frequently than in other behavioural contexts.

As in the Florida scrub jay (McGowan & Woolfenden 1989), there was no evidence that babblers used sentinel positions as part of a 'sit-and-wait' foraging strategy (but for interspecific competitive foraging interactions involving sentinels, see Rasa 1983; Munn 1986). Indeed, surprisingly few sentinels went straight to feed at the end of their bout. This suggests a more complex time and energy budget than that assumed in the Bednekoff (1997) model of cooperative sentinel behaviour. In reality, sentinel behaviour will involve trade-offs with a number of alternative activities relating to individual energetic state and competitive interests within and between groups (see Wright et al., in press).

Alarm calls were nearly always given by the sentinel and very rarely by foragers, similar to observations in Florida scrub jays (McGowan & Woolfenden 1989) and meerkats (see Clutton-Brock et al. 1999, and references therein). This may indicate that sentinels are safer from predator attack than foragers (see Clutton-Brock et al. 1999), although this comparison does not take into account the expected decrease in forager vigilance when sentinels were present. Overall, observations of predation in the babbler system are consistent with Bednekoff's (1997) assumption that sentinel behaviour is a relatively safe activity compared to foraging without a sentinel (see Wright et al., in press). The frequency of alarm calls per time spent acting as a sentinel was relatively high at 13.3%, but was similar for the different sexes and dominance ranks. This indicates that there were no obvious differences in sentinel vigilance between different group members (see also Wright et al., in press), provided also that we assume predator abundance did not differ when different types of group member were acting as sentinels. Observations of predators during alarm call events have shown that babblers make relatively few errors, with almost no occasions of obvious cheating with sentinels giving false alarm calls (P. Edelaar & J. Wright, unpublished data). However, our study shows that dominant males used sentinel activity to maintain vocal contact with neighbouring groups, again suggesting an additional social role for sentinel behaviour, if only a minor one for dominant males.

In conclusion, sentinel behaviour in Arabian babblers provides little evidence that it has a signalling function relating to social prestige theory. Sentinels watched from locations that provided good views of incoming predators, but where cover limited their exposure and risk of predation. Sentinel bouts were started from close to the centre of the group and within sight of foraging individuals, but probably only for effective cooperative sentinel cover. Change-overs between sentinels rarely revealed any social context, and very few involved physical contact. All sentinels provided alarm calls at a similar rate, although alpha males did additionally use sentinel bouts for calling to neighbouring groups. Our observations are consistent with an antipredator function to this behaviour as described in recent theoretical and empirical studies concerning state-dependent sentinel behaviour in birds and mammals (Bednekoff 1997; Clutton-Brock et al. 1999; Wright et al., in press).

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