

Safe selfish sentinels in a cooperative bird

J. WRIGHT, E. BERG*, S. R. de KORT†, V. KHAZIN‡ and
A. A. MAKLAKOV‡§

School of Biological Sciences, University of Wales, Bangor, Gwynedd LL57 2UW, UK; *Department of Wildlife, Fisheries & Conservation Biology, University of California, Davis CA 95616, USA; †Institute of Evolutionary and Ecological Sciences, Leiden University, NL-2300 RA Leiden, The Netherlands; and ‡Department of Zoology, Tel Aviv University, Ramat Aviv, Tel Aviv 69978, Israel

Summary

1. Sentinel behaviour involves a unique cooperative system of dedicated look-outs which protect members of their social group from attack by predators. Using detailed observations from groups of Arabian babblers, *Turdoides squamiceps*, we tested the original theoretical suggestion that cooperative sentinel systems are simply the result of individually selfish state-dependent patterns of behaviour.

2. Sentinel effort and the number of sentinel bouts per individual per hour were greater for males than females, and both increased with individual dominance status within the group.

3. Sentinel behaviour was unaffected by group social structure, in terms of patterns of relatedness and the number of potential breeders.

4. Total group sentinel effort increased with group size, while the effort per individual decreased irrespective of sex and dominance rank. Simultaneous sentinel behaviour by two or more birds was very rare, but increased with group size.

5. Sentinel effort followed seasonal fluctuations in food availability, but not peaks of raptor migration through the study site.

6. Body mass was greater for males than females and was positively related to dominance rank. Overall, body mass explained much of the variation in individual sentinel effort both within and between birds. However, data on individual foraging performance could not be related to changes in body mass and thus to differences in sentinel effort.

7. Sentinel behaviour in groups of Arabian babblers therefore confirms many of the predictions arising from state-dependent models of cooperative, yet individually selfish, sentinel behaviour.

Key-words: anti-predator behaviour, Arabian babbler, group-living, state-dependent, vigilance.

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Introduction

Sentinel behaviour is an alternative system of anti-predator vigilance, occurring within stable cooperative groups of birds and mammals (Gaston 1977; Rasa 1986, 1989; McGowan & Woolfenden 1989; Zahavi 1990; Bednekoff 1997, 2001). In many species, animals in groups individually trade-off the time and energy

spent being vigilant vs. foraging (Lima 1995). However, in species with sentinels, individuals within the group take it in turns to stop foraging and act exclusively as a sentinel, which involves doing nothing but being vigilant and alarm-calling if a predator is spotted. This allows other members of the group to forage more intensively and in safety. The question is: what maintains this system of cooperative vigilance?

The high relatedness within cooperative groups and the existence of sentinel behaviour even within pairs of Florida scrub jays (*Aphelocoma coerulescens*) led McGowan & Woolfenden (1989) to suggest a kin-selected origin for this behaviour (Hamilton 1964; Maynard Smith 1964). Alternatively, one might imagine that regular rotation of sentinels could be maintained via reciprocity with score-keeping (Trivers

Correspondence: J. Wright, School of Biological Sciences, University of Wales, Bangor, Gwynedd LL57 2UW, UK. Tel: + 44 (0)1248 382313; Fax: + 44 (0)1248 382313; E-mail: j.wright@bangor.ac.uk

§Current address: Mitriani Department of Desert Ecology, Ben Gurion University of the Negev, Midreshet Ben-Gurion, Sede Boqer 84990, Israel.

1971), or if individuals benefit by being seen to sentinel and thereby gaining 'social prestige' within their group (Zahavi 1989, 1990). However, it was Gaston (1977) who suggested first that sentinel effort may depend upon foraging ability and individual energetic state, and that the majority of sentinel duties may be performed by the better foragers in a group. This idea has been formalized recently by Bednekoff (1997, 2001), who modelled a system of stable cooperative sentinel behaviour based upon selfish individual state-dependent decisions. Such a model is an extension of the foraging vs. vigilance trade-off discussed by Lima (1995), but has the potential to explain the evolution of sentinel behaviour without recourse to complex social mechanisms.

The straightforward approach taken by Bednekoff (1997, 2001) succeeds because of certain key assumptions in the model. First, that sentinel behaviour is a low-cost activity performed only when an individual possesses sufficient energy reserves from foraging; secondly, that the benefits of sentinel behaviour arise only via an increase in personal safety, and not from protecting other related or unrelated group members. Therefore, while this model demonstrates that alarm information is necessary for the evolution of stable sentinel behaviour, it does not include any additional adaptive consequences arising from warning group members. Thirdly, safe refuges are assumed not to exist, making the sentinel position the safest place to be if the alternative is to risk foraging without a sentinel. The effectiveness of a single sentinel in protecting the group limits the need for more than one individual to sentinel at a time. Hence, by extending the outcomes of this model, we might predict that larger groups will provide better overall protection for all members whilst allowing each individual to reduce their contribution in sentinel effort.

Many of the assumptions and predictions in Bednekoff's (1997, 2001) models are readily testable. For example, the expectation that the relative safety and effectiveness of sentinels depends upon predator visibility is confirmed within and between species by the fact that sentinels are used primarily when groups forage in open desert habitats (e.g. various species of African mongoose, Estes 1991). Furthermore, a recent study on meerkats (*Suricata suricatta*, Clutton-Brock *et al.* 1999) describes a positive effect of group size upon total group sentinel effort, with each individual in larger groups performing less sentinel duty. The same study reports a positive effect of supplemental feeding upon individual sentinel effort, and provides the best evidence to date for Bednekoff's (1997, 2001) models of state-dependent sentinel behaviour. This positive effect of individual state on sentinel effort infers some form of energetic cost, and is therefore also consistent with the alternative hypotheses of kin selection, reciprocity and social prestige. However, compared to the more parsimonious state-dependent hypothesis, these hypotheses also predict additional effects of individual sentinel sex

and dominance rank, and group structure (i.e. in the number of relatives and/or present and future allies in the group).

In the present study, we provide detailed observations concerning sentinel effort within groups of Arabian babblers (*Turdoides squamiceps*, Cretzschmar), a species in which this behaviour has been linked to more complex social interactions (see Zahavi & Zahavi 1997). Data are presented for individual sentinel effort according to sex and dominance rank within groups of different sizes and at different times of year. Observations of individual sentinel effort are combined with detailed data concerning individual body mass and foraging performance, to provide the first critical test of state-dependent sentinel behaviour in a cooperative bird.

Methods

THE STUDY POPULATION

The Arabian babbler is a group territorial, communally breeding thrush-like bird, occurring in the Arabian and Sinai deserts. Groups are of mixed sex and range from two to 22 individuals, but in most years contain three to 12 birds, with age-related linear dominance hierarchies within each sex (for more detail, see: Zahavi 1988, 1989, 1990). Approximately two-thirds of groups are 'simple family groups', containing a single breeding pair and their nonbreeding offspring. The remaining 'complex nonfamily groups' have a more varied social structure, being newly formed or recently restructured groups following the death or replacement of a breeding individual or pair and the subsequent departure of all subordinate group members of one sex (usually the females). Complex groups can therefore be defined by the fact that they contain more than one potential breeder of either sex, where a potential breeder is any bird in a group containing at least one unrelated adult of the opposite sex (babblers almost always avoid close inbreeding, but subordinate males compete for and obtain some reproduction in complex groups; see Lundy, Parker & Zahavi 1998; Wright, Parker & Lundy 1999). Although simple family groups tend, on average, to be larger than complex non-family groups (Wright *et al.* 1999), in the present study there was no significant difference between the two types of group ($t_{19} = 1.19$, $P = 0.250$).

The study site at Hazeva is a 25-km² area of desert, located 30 km south of the Dead Sea in the Arava rift valley in southern Israel. This is a very open habitat with sparse vegetation lining the bottom of dry river beds, and comprising well-spaced trees (*Acacia* spp.) and a few low bushes and annual plants. However, thicker *Tamarix nilotica* scrub and reed beds (*Phragmites* sp.) exist in one area receiving regular outflows of water from human settlements and agriculture. Twenty groups of Arabian babblers have been studied continuously at Hazeva since 1971 by Prof. 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 in the present study were individually colour ringed and their family histories known.

DATA COLLECTION

Data were collected throughout the year from 1 November 1992–30 September 1993, and during part of the nonbreeding season between 30 September and 30 December 1996. Observations were carried out for 3 h in the morning (starting at sunrise as the group left the roost tree) and 2 h in the afternoon (finishing at sunset as the group went to roost). Sentinel behaviour in this species is very obvious and almost always involves a single group member perching in a prominent and elevated location with its head up, looking around and being vigilant. Individual sentinel bouts last for a number of minutes. Alarm calls are given by the sentinel to alert the other foraging group members to the presence of potential aerial and terrestrial predators (e.g. raptors or foxes). Sentinel bouts end when the individual leaves the sentinel position to resume foraging or some other activity, and sometimes this is prompted by another bird replacing the sentinel at the same or an alternative sentinel position.

Observers were able to walk within 20 m of habituated groups and record the identity of any bird acting as a sentinel and the start and end times of each sentinel bout (to the nearest second). While the presence of observers very close to the birds may affect the behaviour of Arabian babblers (e.g. Ostreier 1995), non-disruptive observation techniques can be validated through comparison with data collected at a distance using telescopes (e.g. Wright 1997). In 1996, five groups were also observed for 5 consecutive days, left unobserved for 7 days, and then followed closely for another 5 days. Within this subset of groups, there were no significant differences in any of the recorded sentinel behaviours according to the order of observation days, and before vs. after the break in observations (repeated-measures ANOVA, all P -values > 0.275). Therefore, we feel reasonably confident that our close methods of observation did not influence the results of the present study.

In 1996 the body mass of each bird was also collected for as many individual birds as possible at the end of each morning and afternoon observation session (totalling 74.5% of possible occasions). Birds had been trained to stand on electronic top-pan balances (Shekel, model B-2-P, accuracy 0.1 g) using small crumbs of bread as bait. Mass data were recorded only when the value given by the balance remained constant for 2.5 s (i.e. when the bird was standing still), thereby providing only the most accurate body mass estimates. In addition, during the 1996 sentinel observations, a second observer collected data simultaneously on

individual foraging in a total of five groups involving 25 different birds (mean days per group = 7.8, SD = 1.6, range 5–10). Exclusive 5-min focal watches were carried out on each group member in turn during the observation period (mean focals per bird per 2–3-h period = 2.84, SD = 1.53, range 1–10), with the number of pecks and the distance moved recorded for each individual prey capture in turn, along with the relative size (scored 1–3) and type of prey eaten (1 = small fly larvae; 2 = ants; 3 = caterpillar/beetle larvae; 4 = gecko; 5 = other adult invertebrates).

ANALYSIS

For each bird on each day, mean sentinel effort per hour was calculated as the total number of seconds spent as a sentinel in that hour, and the number of separate sentinel bouts involved. The sample comprised 21 groups (11 simple families, 10 complex non-families) 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. Two-tailed P -values are given throughout.

Results

SENTINEL EFFORT WITHIN GROUPS

Sentinel effort per bird per hour was significantly greater in males than females, and increased significantly with dominance rank (Fig. 1a), although only the top three ranks of each sex contained sufficient individuals to be included in the ANOVA model (Table 1a). There was also a significant interaction between sex and dominance rank, as a result of a greater increase in sentinel effort with rank in males compared to females. Within the same analysis, there was no significant difference in individual sentinel

Table 1. The effect on sentinel behaviour of individual sex (d.f. = 1), dominance rank (d.f. = 2), and group structure (d.f. = 1). Results are presented as F ratios and P -values from full ANOVA models for: (a) mean sentinel effort per bird per hour; and (b) mean number of sentinel bouts per bird per hour. See text for details

Factor	(a) Sentinel effort (s/h)		(b) Number of bouts (per hour)	
	F_{90}	P	F_{90}	P
Sex	57.06	< 0.001	44.09	< 0.001
Rank	19.74	< 0.001	16.99	< 0.001
Structure	2.54	0.115	0.00	0.997
Sex × rank	5.88	0.004	2.25	0.112
Sex × structure	1.38	0.243	1.78	0.186
Rank × structure	0.78	0.463	1.16	0.318
Sex × rank × structure	1.20	0.306	0.88	0.417

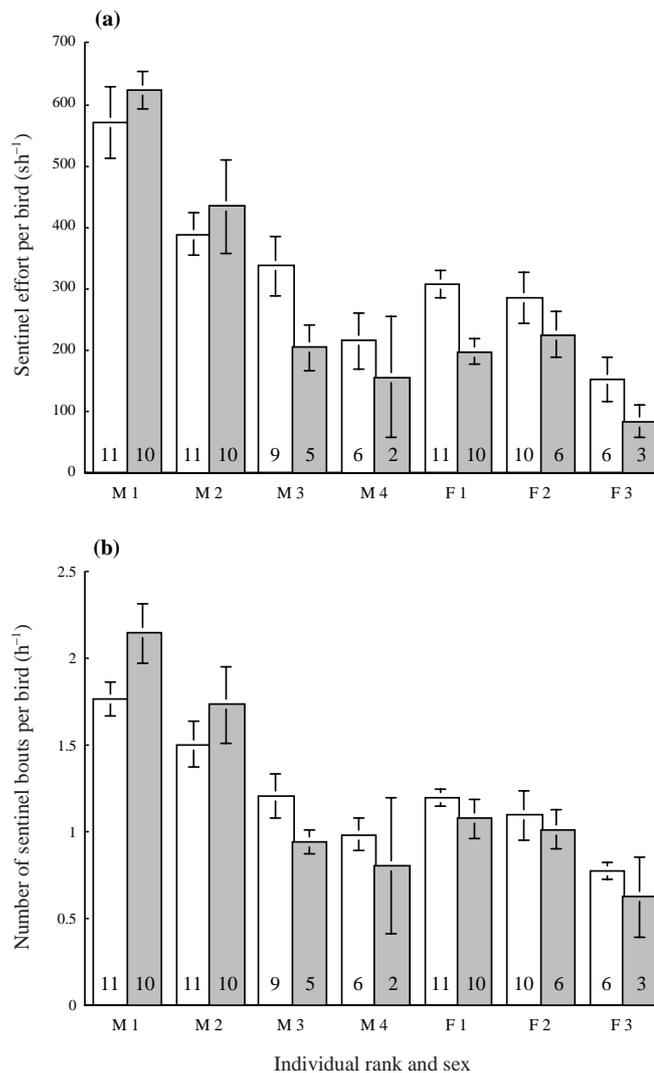


Fig. 1. Sentinel behaviour per bird (mean \pm SE) for the different sex and dominance classes of bird within groups (M1 = alpha male, M2 = beta male, F1 = alpha female, F2 = beta female, etc.). Data are shown for simple family groups and complex non-family groups, for: (a) mean sentinel effort per hour; and (b) mean number of sentinel bouts per hour (see text for details). Sample sizes are shown at base of bars. \square , Simple family groups; \blacksquare , complex non-family groups.

effort in simple family groups compared to complex non-family groups, and no interaction between group type and individual sex and/or dominance rank (Table 1a, Fig. 1a).

The number of sentinel bouts per bird per hour showed a similar pattern to individual sentinel effort, with significant effects of both sex and dominance rank (Table 1b, Fig. 1b). There was, however, no significant interaction between sex and dominance rank. The number of sentinel bouts per bird again showed no significant difference between simple family groups and complex non-family groups, nor any interaction between group type and individual sex and/or dominance rank (Table 1b, Fig. 1b). In addition, there were no significant differences between simple family groups vs. complex non-family groups in any of the other variables associated with sentinel behaviour. Group social structure has therefore not been included in subsequent analyses.

The total number of seconds per hour that a group had at least one sentinel on duty increased significantly with increasing group size (Fig. 2a; $r^2 = 0.22$, $n = 21$, $P = 0.018$), but nevertheless individual sentinel effort per bird per hour decreased significantly with increasing group size (Fig. 2b; $r^2 = 0.51$, $n = 21$, $P < 0.001$). In summary, all group members contributed towards total sentinel effort, especially the most dominant males, with the result that larger groups provided greater overall sentinel protection despite lower sentinel effort per group member.

SENTINEL EFFORT AT DIFFERENT TIMES OF YEAR

Sentinel effort varied significantly across the 11 consecutive months of the year for which data were available ($F_{10,30} = 4.17$, $P = 0.001$). As can be seen from Fig. 3, this was not the result of any significant increase in

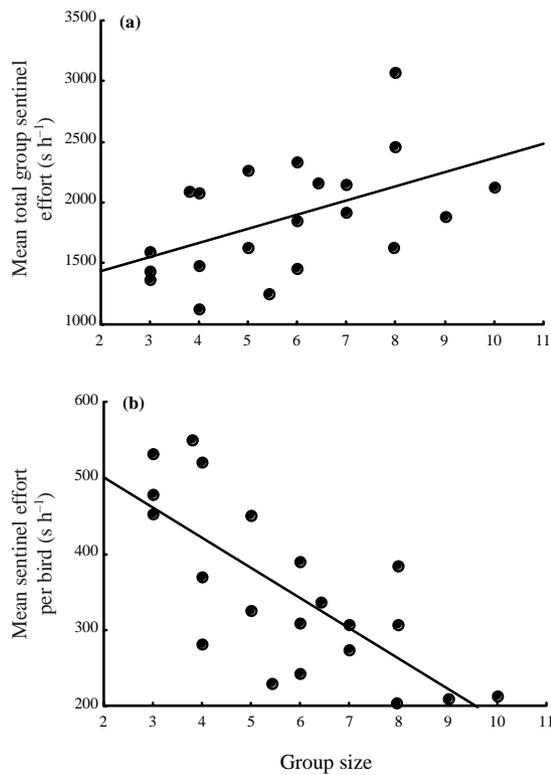


Fig. 2. Effect of group size upon: (a) mean total group sentinel effort; and (b) mean sentinel effort per bird in those groups.

sentinel activity during the 3 months of peak raptor migration through this site (peak autumn and spring migration – March, April and September vs. months of no migration – December, January, June and July: contrast $t_{30} = 0.31$, $P = 0.760$). Instead the effect was due to sentinel effort almost doubling in the mid-winter months compared to the midsummer months (November, December, January and February vs. May, June, July and August: contrast $t_{30} = 4.73$, $P < 0.001$),

and especially in December compared to the average for all other months (contrast $t_{30} = 4.88$, $P < 0.001$).

SENTINEL GAPS AND OVERLAPS

For six of the groups in 1996, a record was kept of the number of seconds prior to a sentinel bout, during which time there was no sentinel. Gaps with no sentinel tended to be significantly shorter the larger the group ($r^2 = 0.71$, $n = 6$, $P = 0.021$). However, the length of non-sentinel gaps prior to the resumption of sentinel cover tended to be significantly longer for males than females ($F_{1,23} = 8.24$, $P = 0.009$), and significantly longer for the more dominant group members ($F_{2,23} = 3.74$, $P = 0.039$), with no sex \times dominance interaction ($F_{2,23} = 0.92$, $P = 0.411$). This suggests that as well as performing more sentinel duties (see Fig. 1), high-ranking males were also more likely to be the first to sentinel after a long gap without a sentinel.

In 89.4% of the sentinel bouts observed, there was only one bird at a time acting as sentinel. Two birds acted simultaneously as sentinel during only 9% of bouts, three birds during 1.5% and four birds during 0.1%. The mean duration of overlap between two or more sentinels within a group did not differ significantly with sex ($F_{1,23} = 0.28$, $P = 0.602$) or dominance rank ($F_{2,23} = 1.29$, $P = 0.294$), and there was no sex by dominance interaction ($F_{2,23} = 1.01$, $P = 0.381$). The greater total amount of sentinel activity in larger groups meant that mean duration of overlap by simultaneous sentinels was related positively to group size ($r^2 = 0.64$, $n = 6$, $P = 0.035$). There was also a tendency for the amount of sentinel overlap per group member to increase with group size, but due to the small number of groups for which these data were available the regression was non-significant ($r^2 = 0.55$, $n = 6$, $P = 0.056$). Therefore, overlap between simultaneous sentinels was relatively rare and appears part of the

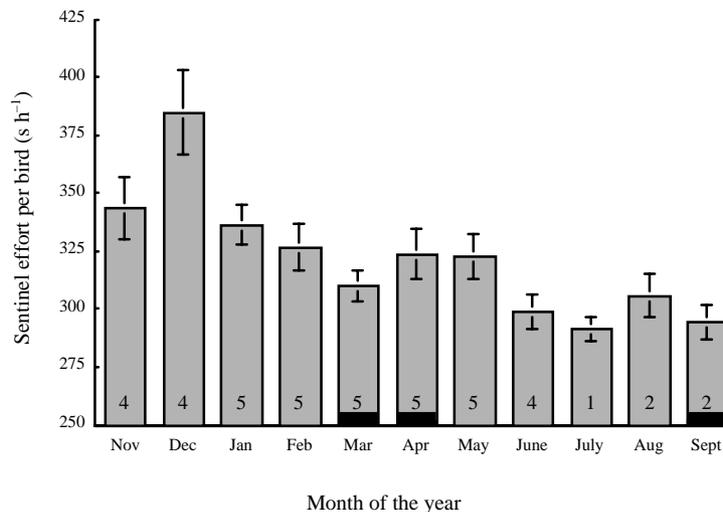


Fig. 3. Sentinel effort per bird (mean \pm SE) for the 11 months of the year for which data were available. The 3 months of peak raptor migration are indicated by thick lines at the base of the bars. Number of different groups observed per month is indicated at base of each bar.

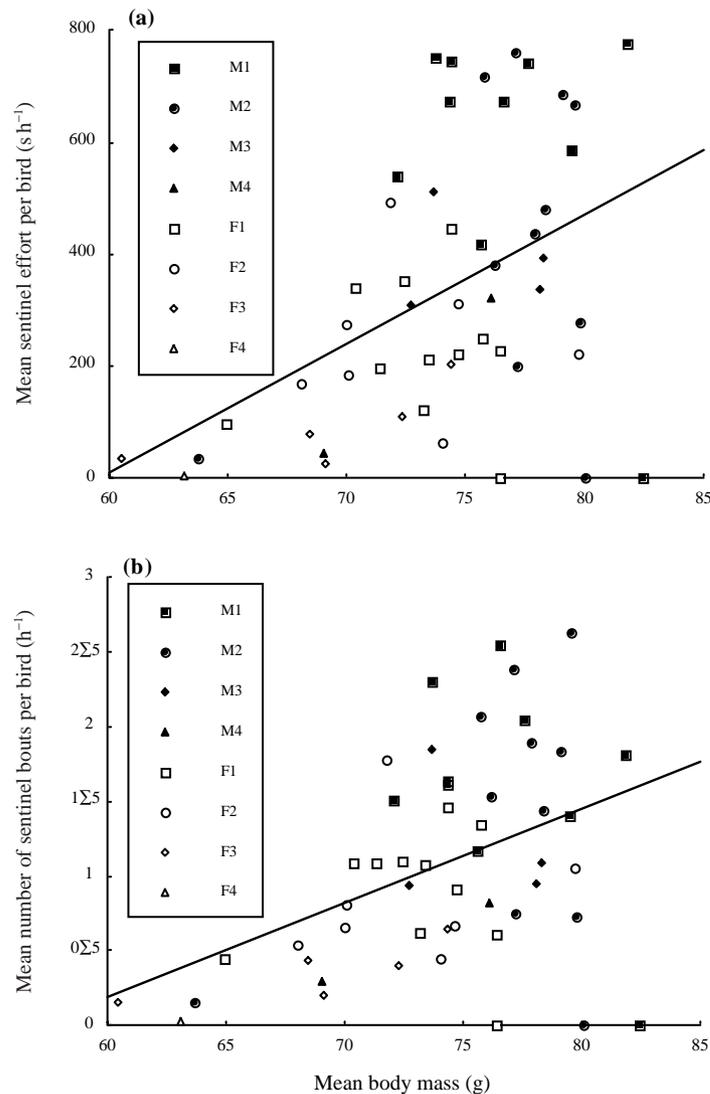


Fig. 4. Mean sentinel effort per bird against mean body mass per bird for: (a) seconds sentinel effort per hour; and (b) number of sentinel bouts per hour. Data are split by the different sex and dominance classes of bird within groups (M1 = alpha male, M2 = beta male, F1 = alpha female, F2 = beta female, etc.).

normal phenomenon of increased sentinel effort within groups (see Fig. 2).

SENTINEL EFFORT, BODY MASS AND FORAGING SUCCESS

Mean individual body mass followed a very similar pattern to sentinel behaviour, in that males were significantly heavier than females ($F_{1,43} = 15.38$, $P < 0.001$) and mass increased with dominance rank ($F_{3,43} = 3.18$, $P = 0.033$), but with no sex \times rank interaction ($F_{3,43} = 0.62$, $P = 0.604$). It is therefore not surprising that mean body mass had a significant and positive effect upon mean sentinel effort per bird (Fig. 4a; $r^2 = 0.19$, $n = 50$, $P < 0.001$) as well as upon the number of different sentinel bouts performed per hour (Fig. 4b; $r^2 = 0.16$, $n = 50$, $P = 0.002$). However, when body mass is included with sex and dominance rank in an ANCOVA on sentinel effort, the effect of sex is reduced but remains significant ($F_{1,42} = 6.58$,

$P = 0.014$), while the effects of dominance rank ($F_{3,42} = 2.11$, $P = 0.113$) and body mass ($F_{1,42} = 0.53$, $P = 0.472$) both become non-significant because they explain the same portion of variation in sentinel effort (i.e. the model is calculated using Type III sum of squares), with no sex by dominance rank interaction ($F_{3,42} = 0.86$, $P = 0.468$). The same result holds for an ANCOVA on number of sentinel bouts, with a marginally significant effect of sex ($F_{1,42} = 4.24$, $P = 0.046$), and the effects of dominance ($F_{3,42} = 1.78$, $P = 0.165$) and body mass ($F_{1,42} = 0.41$, $P = 0.524$) again both becoming non-significant due to explaining the same part of the variation in the number of sentinel bouts, and no sex \times dominance rank interaction ($F_{3,42} = 0.13$, $P = 0.941$). This suggests that dominance rank and mean individual body mass are statistically indistinguishable in their effects upon sentinel behaviour, but that males still tend to act as sentinels somewhat more often than we might expect from their greater body mass alone (see Fig. 4).

Mean foraging behaviour was assessed as search effort and foraging success (number of pecks per prey or per minute, and prey captured per minute), the mean distance travelled between successive prey captures, and the relative size and type of prey consumed. However, none of the measures differed significantly according to individual sex (all ANOVA P -values > 0.626) or dominance rank (all P -values > 0.471), with no sex \times dominance interactions (all P -values > 0.418). There was also no significant effect in any regression analyses of the foraging measures upon mean sentinel behaviour per individual, either on their own (all P -values > 0.163) or in a stepwise multiple regression once the effect of body mass had been removed (all P -values > 0.289). In addition, none of these foraging measures had any significant effect upon mean body mass per individual (all P -values > 0.169).

WITHIN INDIVIDUAL SENTINEL EFFORT, BODY MASS AND FORAGING SUCCESS

Looking at the data for each bird separately, individual regressions were carried out concerning the effects of relative body mass and foraging upon changes in sentinel effort. The mean slopes from these regressions per bird echo the between bird effects in Fig. 4, and show that individuals were relatively heavier during those observation sessions in which they carried out relatively large amounts of sentinel behaviour per hour (mean slope = 38.79, SD = 121.08 s/h sentinel effort per gram body mass; one-sample t -test of slopes against zero: $t_{46} = 2.20$, $P = 0.033$). Relative individual mass also had a significant positive effect on the number of sentinel bouts performed per hour by individuals (mean slope = 0.07, SD = 0.25 bouts/h sentinel effort per gram body mass; one-sample t -test of slopes against zero: $t_{46} = 2.02$, $P = 0.048$). However, the mean slopes of similar regressions between each of the foraging measures and sentinel activity were non-significant (all P -values > 0.076).

None of the regression slopes of body mass or foraging on sentinel effort differed according to sex (P -values > 0.716) or dominance rank (P -values > 0.778), with no sex \times dominance interaction (P -values > 0.664). In addition, none of the measures of relative foraging success had any effect upon changes in body mass within each bird (all P -values > 0.246).

Discussion

Variation in sentinel behaviour both between and within individual Arabian babblers was best explained by differences in body mass. This positive effect of body mass accounted for a number of trends in sentinel effort which would otherwise have been attributed to differences in individual sex and dominance rank. More importantly, individual birds spent more time on sentinel effort during those observation sessions when they were known to be relatively heavy compared to

their mass on other days. If we assume that these differences in body mass translate into differences in individual energy (fat) reserves, then these data provide strong support for state-dependent sentinel behaviour in Arabian babblers. Food supplementation experiments on this species also support this conclusion, with concurrent increases in both the body mass and individual sentinel effort of supplemented individuals (Wright, Khazin & Maklakov 2001a).

As expected from state-dependent explanations, the peak of sentinel activity occurred during the rains in the winter months, especially December, when there was more food available and less foraging time was lost due to midday heat. The increase in sentinel effort during the winter months was mirrored by a parallel peak in individual body mass in these same birds during this period (Anava 1998). Low sentinel effort during the plentiful spring breeding season may therefore seem surprising, but individuals provisioning young in the nest are often widely dispersed, decreasing the usefulness of normal sentinel activity (Wright 1997, 1998b). McGowan & Woolfenden (1989) attribute winter peaks in sentinel effort in groups of Florida scrub jays to greater raptor activity during the winter months. However, in the present study there was no increase in sentinel effort in response to the spring and fall raptor migrations, probably because the babblers were aware that few migrating raptors hunt actively (i.e. alarm calls decrease over time to migrant species, but are maintained to resident hunting species; P. Edelaar & J. Wright unpubl. data). Meerkats demonstrate greater sentinel effort at sites with greater predation pressure (Clutton-Brock *et al.* 1999), and Arabian babblers are probably also capable of adjusting sentinel effort in this way, if necessary. Experiments are now required to examine the possibility that perceived predation pressure affects group sentinel effort.

Data presented here on individual foraging behaviour do not appear sensitive enough to reveal a link between short-term rates of food intake, subsequent changes in energy reserves (i.e. relative body mass) and therefore minute-to-minute behavioural decisions regarding sentinel effort. Our focal observation periods may have been too short in duration relative to variation in individual foraging success. However, food supplementation experiments on Arabian babblers resulted in elevated levels of sentinel effort in only supplemented individuals (Wright *et al.* 2001a), due probably to increased energetic state overriding any natural short-term variation in energy budgets. More detailed study is now required to link natural rates of food intake with sentinel effort, and to identify the time scale over which these state-dependent decisions operate.

The effects of group size on both individual and collective levels of sentinel effort were as predicted from an extension of state-dependent sentinel theory. The larger the group, the greater the number of individuals possessing sufficient energy reserves to act as sentinel at any one time, if necessary. Hence, there is

greater total sentinel coverage in larger groups, due to shorter periods without a sentinel. One bird at a time acted as sentinel on almost 90% of occasions (compared with 82% in jungle babblers, *Turdoides striatus*, Gaston 1977), although two or more sentinels became more likely when groups were very large. As only one sentinel was required at a time, sentinel effort per individual decreased in larger groups. We can also assume that minimum energetic state at the commencement of sentinel behaviour was higher on average in larger groups. Similar group size effects were described by Clutton-Brock *et al.* (1999) in meerkats, supporting our expanded explanation for sentinel behaviour based on individual state.

The general patterns observed in the sizes of gaps between sentinel bouts and the amount of overlap between sentinels also followed those expected from a cooperative antipredation perspective (see McGowan & Woolfenden 1989). When more than two birds did act as sentinel, it was nearly always in response to sighting a nearby predator or a neighbouring group of babblers (see Wright, Berg, de Kort, Khazin & Maklakov 2001b). It was also clear that sentinels were used when foraging groups were in more open habitats with clear lines of sight. A similar effect has been reported for sentinel behaviour in groups of vervet monkeys (*Cercopithecus aethiops*, Horrocks & Hunte 1986), and parallels the pattern observed across species (see Introduction). Presumably, sentinels need to be able to detect predators at a distance, and it is this that makes their position relatively safer than if they were foraging or in a refuge (Bednekoff 1997, 2001). Although safe refuges from predators clearly do exist for babblers, in the form of thorn bushes and trees, it may be that they do not represent an effective option for foraging groups which need to keep moving. Indeed, sentinels were invariably observed going on watch for a number of minutes prior to group movement out of one of these refuges, for example following midday roosts. Therefore, the apparently unrealistic assumption in sentinel models that there are no safe refuges (Bednekoff 1997, 2001) might in fact be appropriate for mobile foraging groups targeted by ambush predators, such as the Arabian babbler.

As Clutton-Brock *et al.* (1999) suggest for meerkats, sentinels in the Arabian babbler were always much closer to the safety of cover than were foraging group members (Wright *et al.* 2001b). During our many hours of observation, numerous predators were sighted and alarm calls nearly always given by the bird acting as sentinel (Wright *et al.* 2001b), but we observed only four attempted (and unsuccessful) attacks on sentinels (by falcons, *Falco peregrinus* sp., swooping with the advantage of the sun directly behind them). In comparison, we saw two ambush predator attacks (by sparrowhawks, *Accipiter nisus*) on unprotected foraging babblers, rather than sentinels. These attacks came much closer to being successful, and occurred during the relatively shorter period of observation of

groups in cover and without sentinels, suggesting a much greater danger for unprotected foragers compared to sentinels. These observations do not provide appropriate comparison of predation rates on sentinels vs. foragers under differing degrees of sentinel protection and vegetation cover, but they are broadly consistent with Bednekoff (1997, 2001).

The pattern of sentinel effort within groups of Arabian babblers was not as described previously for this species (e.g. Zahavi & Zahavi 1997). The linear increase in sentinel effort with dominance rank reported here does not appear to have been linked to differences in social standing, but rather to body mass and therefore to differences in individual energy budget (see also Wright *et al.* 2001a). The consistent patterns in sentinel effort across different group members and our direct observations suggests that dominant birds did not interrupt subordinate group members from acting as sentinel (see Wright *et al.* 2001a, 2001b). Sex differences in sentinel activity may have been the result of males competing for social prestige. However, we have no evidence to suggest more intense male sentinel activity or active interference between males in complex non-family groups, compared to simple family groups (Wright *et al.* 2001b). Rather, the documented sex differences probably reflect additional effort by dominant males in monitoring and calling to neighbouring groups whilst acting as sentinel (Wright *et al.* 2001b).

Individual sentinel effort within groups broadly matched that described by Gaston (1977) for jungle babblers. However, a very different pattern has been described for mongooses and meerkats (where the dominant female performs by far the least, Rasa 1989; Clutton-Brock *et al.* 1999). Different divisions of sentinel effort in different species may reflect contrasting benefits experienced by each type of group member, as well as alternative time and energy budgets for different group members. For example, dominant females may not have time to act as sentinels during reproduction, and dominant males may benefit by being additionally vigilant while competing with other males within and between groups (Wright *et al.* 2001b).

Given the high relatedness within Arabian babbler groups (Lundy *et al.* 1998; Wright *et al.* 1999), it is likely that sentinel behaviour in this species carries kin-selected fitness consequences (Hamilton 1964; Maynard Smith 1964). However, variation in individual sentinel effort within and between groups failed to follow any known patterns of relatedness (Lundy *et al.* 1998; Wright *et al.* 1999). As with the evolution of alarm calling, sentinel behaviour may carry direct fitness benefits (by-product mutualism) arising from the prevention of predators reducing the size of one's social group (for recent review, see Dugatkin 1997). The cooperative Arabian babbler may well benefit 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 1998a). State-dependent sentinel behaviour, as described here, is therefore consistent with investment in the protection of one's group members. However, Bednekoff's (1997, 2001) models are based upon short-term individual interests in personal safety, and they provide a more parsimonious explanation for the evolution of this cooperative behaviour. Therefore, although hypotheses concerning the adaptive protection of other group members cannot be ruled out, there is nothing in our data to suggest that they are of particular importance in the evolution of sentinel behaviour in Arabian babblers.

Conclusions

Cooperative sentinel behaviour in Arabian babblers appears entirely consistent with recent models of selfish state-dependent sentinel behaviour (Bednekoff 1997, 2001). Our main finding is that differences in sentinel effort within and between individuals closely match differences in body mass. Hence, variation in energy (fat) reserves has the potential to explain many of the observed patterns in sentinel behaviour, including variation with differences in group size, time of year and individual dominance rank and sex. More complex social mechanisms, such as kin selection, reciprocity, group augmentation and social prestige, do not appear necessary to explain any of the patterns in cooperative sentinel behaviour in Arabian babblers. Instead, almost all aspects of our data can be satisfactorily explained by the more straightforward hypothesis that each group member follows a simple and selfish short-term strategy based upon their internal state and the sentinel behaviour of others.

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