Florida Scrub-Jays (*Aphelocoma coerulescens*) are Sentinels More When Well-Fed (Even with no Kin Nearby)

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Abstract

Sentinels occupy high, exposed positions while other group members forage nearby. If sentinel behavior involves a foraging–predation risk trade-off, animals should be sentinels more when fed supplemental food. When individual Florida scrub-jays (*Aphelocoma coerulescens*) were fed fragments of peanuts, during the following 30 min they shifted 30% of their time from foraging to sentinel behavior. In a follow-up experiment, we fed either one or two members in each group. As before, the jays reduced their foraging and spent much more time as sentinels when given supplemental food. In each treatment, pairs were sentinels simultaneously considerably less often than expected by chance. The dramatic shift from foraging to sentinel behavior suggests that for Florida scrub-jays sentinel behavior brings substantial benefits for no greater cost than that of lost opportunities to forage. Because the results held for simple mated pairs of scrub-jays, we argue that kin selection and social prestige are not necessary to explain sentinel behavior.

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Introduction

Sentinels (also known as guards or sentries) are members of animal groups that watch from prominent, exposed positions while the other members of the group are engaged in other activities, usually feeding. Two notable features of sentinel behavior are that it occurs in various taxa of social birds and mammals, and that it shows coordination where it occurs. We discuss each of these features in turn.

Sentinels have been reported in a variety of bird and mammal taxa. As reviewed previously (Bednekoff 1997), sentinels occur in corvids, babblers, parrots, weaver birds, social mongooses, primates, and dwarf antelope. To this list we can add some tropical tanagers (Alves 1990; Alves & Cavalcanti 1996), smooth-billed anis, *Crotophaga ani* (J. Haselmayer, pers. comm.), rock hyraxes, *Procavia capensis*

(Kotler et al. 1999), and rock-haunting possums, *Petropseudes dahli* (Runcie 2000). Within each taxonomic group, sentinel behavior occurs only in some species. The taxonomic pattern of occurrence suggests that sentinel behavior had multiple, independent origins and probably occurs when several widespread ecological factors combine in some particular way (see Bednekoff 1997, 2001).

Coordination of vigilance is the defining feature of sentinel systems (McGowan & Woolfenden 1989). The essential evidence of coordination is that different individuals come and go as sentinels but the number of sentinels varies little. If one sentinel quits its post, it is quickly replaced and if a second sentinel takes a post, the first generally resumes foraging relatively quickly (Gaston 1977; McGowan & Woolfenden 1989; Zahavi 1990). In the only quantitative test of coordination, the timing of beginning or ending sentinel bouts by Florida scrub-jays depended strongly on the actions of other group members (McGowan & Woolfenden 1989). Nonetheless sentinel bouts by scrub-jays show no characteristic duration but instead fit the sort of distribution that would occur if bouts were equally likely to end at any moment (Hailman et al. 1994). In general, sentinel behavior may be highly coordinated without being tightly organized at the group level (see also Goodwin 1986; Clutton-Brock et al. 1999).

Different explanations of sentinel behavior assume different combinations of costs and benefits. Several explanations assume that sentinels are at great risk from predators (see Bednekoff 1997 for discussion). All available evidence, however, suggests that sentinels have such a large advantage in detecting predators that they actually lower their predation risk by taking up exposed positions (McGowan & Woolfenden 1989; Bednekoff 1997; Clutton-Brock et al. 1999; Wright et al. 2001a). If sentinels are actually relatively safe, then sentinel behavior can be understood as a form of foraging–predation risk trade-off (Bednekoff 1997, 2001).

One prediction of modeling sentinel behavior as part of a foraging–predation risk trade-off is that individuals should be sentinels more often when they find food more quickly (Bednekoff 1997). This prediction has been supported for meerkats, *Suricata suricatta*, provided 25 g of boiled egg per day for 30 d (Clutton-Brock et al. 1999) and for Arabian babblers, *Turdoides squamiceps*, given mealworms *ad libitum* (*Tenebrio* spp.) throughout a day (Wright et al. 2001c). We tested for a direct and immediate effect of foraging success on sentinel behavior by experimentally manipulating foraging success in Florida scrub-jays for a few minutes and observing their rate of sentinel behavior during the subsequent 30 min period.

Methods

Study site and species

We performed two experiments using a long-studied, color-ringed population of Florida scrub-jays at Archbold Biological Station (Woolfenden & Fitzpatrick 1984, 1990, 1996). Archbold Biological Station is a 2000-ha preserve located

toward the south end of Lake Wales ridge in south-central Florida. Within this preserve, jays are being studied on a 400-ha plot of oak scrub. This community grows on extremely well-drained siliceous sands and is characterized by a layer of evergreen oaks that rarely exceed 2 m in height and sparse ground cover dominated by palmettos. Oak scrub depends on periodic fires for renewal. Florida scrub-jays are restricted to oak scrub, where they live in groups on large, all-purpose territories. In winter, groups consist of a monogamous pair plus zero to six offspring. The demography and cooperative breeding of Florida scrub-jays has been studied at Archbold since 1969 (Woolfenden & Fitzpatrick 1984, 1990, 1996). All the birds used in the experiments were accustomed to human observers and to being fed bits of peanuts occasionally.

Sentinel behavior is easily distinguished and common throughout the year (McGowan & Woolfenden 1989; Hailman et al. 1994). All group members act as sentinels to some degree, although adult males are most likely to be sentinels (Hailman et al. 1994). Sentinel bouts show a wide, skewed distribution of duration with the bulk of bouts lasting < 10 min (Hailman et al. 1994). During winter, adults spend roughly half their time as sentinels (DeGange 1976), and hence a sentinel is present most of the time even for small groups.

Experiment 1

This experiment tested whether individuals would increase their sentinel behavior when given supplemental food. From 20 to 26 Dec. 1997, we studied a selected individual from each of eight groups. Seven of the birds were males and one was female. To isolate the effect of the experiment from the effects of other factors, we observed the same individuals with and without supplemental feeding. In the feeding treatment, each selected jay was fed fragments of peanuts until it refused to eat more. Scrub-jays ate on average 1.8 peanuts in 9.6 min. Other group members were generally not fed but occasionally managed to intercept a bit of peanut. For the control treatment, each focal individual was approached, shown a peanut, but not fed. So long as the peanut was in view, scrub-jays were attentive to it. At the end of the control treatment, the peanut was hidden from sight and scrub-jays quickly resumed their activities. For each focal individual, the two treatments were given at the same time of day and for the same amount of time. Thus the treatments had equivalent amounts of disruption. The two treatments were given on consecutive days except in one case when weather forced them to be two days apart. The order of treatments was counterbalanced using a structured random assignment of which treatment was given first to each group.

Immediately following each treatment, the behavior of the focal individual was observed for 30 min. The behavior was classified into foraging, sentinel, or other behavior. Supplemental feeding was expected to reduce foraging behavior. If sentinel behavior was costly, we would expect the scrub-jays to increase the time devoted to other behaviors when they reduced their foraging behavior. Because scrub-jays forage on the ground among vegetation, they were frequently out of sight while foraging. Therefore, any time that scrub-jays were active and close to

the ground was classified as foraging. Sentinel behavior was defined as in previous work on Florida scrub-jays – by occupying a high perch while scanning and maintaining a relaxed, tail-down posture (McGowan & Woolfenden 1989; Hailman et al. 1994).

Experiment 2

In this experiment, we again studied the direct effect of feeding and also the coordination between mated pairs and the indirect effect of the feeding of one bird on the behavior of its mate. From 20 to 30 Dec. 1998, we studied mated pairs from 13 small groups (two or three birds each). For one member of the pair, which we label as the focal bird, the procedure was like expt 1: this scrub-jay was fed under one treatment and not the other. Its mate, however, was fed under both treatments. The focal bird was male in six groups and female in seven groups. Each bird was fed up to 1.5 peanuts over a 10-min period and then observed for the subsequent 30 min. Treatments were matched for duration and for time of day, and were counterbalanced for order. Both birds were observed in each treatment. Behavior was classified as in the first experiment.

Using the simultaneous records for two birds from this experiment, we tested coordination of sentinel behavior. Coordination here means that sentinel bouts overlap relatively little, leading to less time with multiple sentinels than would be expected by chance (see McGowan & Woolfenden 1989; Bednekoff 1997). Within pairs we tested for coordination by comparing the amount of time that both were sentinels with that expected by chance. To compute the expected, we multiplied the proportion of time that each bird spent as a sentinel. For example, if one bird had been a sentinel 1/3 of the time and the other 2/3 of the time, we would expect, by chance, that they would be sentinels simultaneously $1/3 \times 2/3 = 2/9$ of the time. Therefore, of 30 min we would expect 6.67 min with two sentinels.

All reported statistics are from paired t-tests. All reported p-values are two-tailed.

Results

In expt 1, supplemental feeding produced the predicted changes in behavior: when fed, scrub-jays reduced their foraging by 9 min ($t_7 = -4.18$, $p = 0.0041$) and increased their sentinel time by almost exactly this amount ($t_7 = 5.00$, $p = 0.0016$, see Fig. 1, left). The amount of time spent on other activities – mainly moving and perching – was not affected by the treatment ($t_7 = 0.12$, $p = 0.90$). None of these effects depended on the order of treatments. Thus, scrub-jays reacted as if sentinel behavior was the most beneficial activity that could be performed in the time not needed for feeding.

In the second experiment, supplemental feeding produced strong direct effects on the bird that was fed, but no strong indirect effects on its partner. Birds fed in one treatment reduced their feeding ($t_{12} = -6.16$, $p < 0.0001$) and spent much more time as sentinels ($t_{12} = 6.19$, $p < 0.0001$) when fed (Fig. 1, middle).
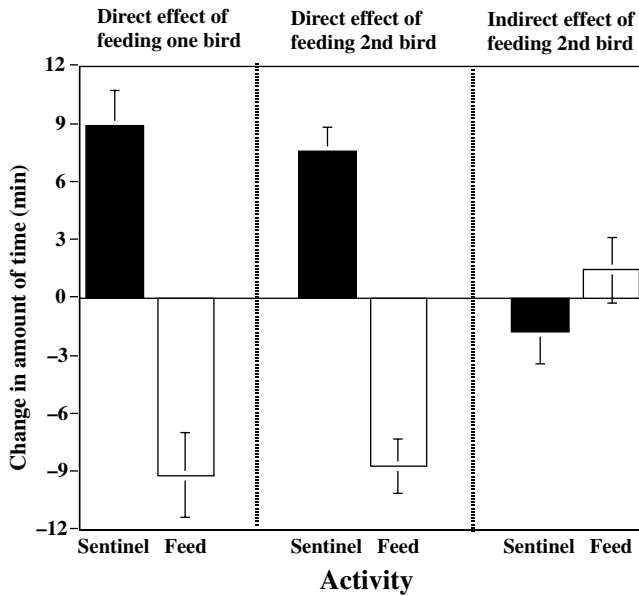
Fig. 1: Supplemental feeding led to large direct, but small indirect, changes in the sentinel behavior (black bars) and feeding behavior (white bars) of Florida scrub-jays during 30 min of observation following supplemental feeding. The left panel comes from expt 1, when one individual was fed. The central and right panels come from expt 2. The indirect effect is the change in behavior of one bird when another bird is fed

Birds fed under both conditions were sentinels slightly less often ($t_{12} = -1.09$, $p = 0.29$) and fed slightly more ($t_{12} = 0.88$, $p = 0.40$, Fig. 1, right) when another bird in the group had been fed (and so was a sentinel more often). The amount of time spent on other behaviors did not shift much either as a direct or indirect
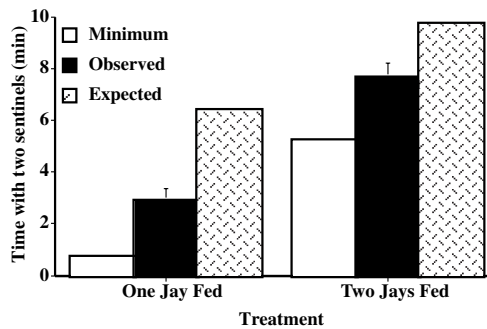

Fig. 2: In both conditions of expt 2, two birds were sentinels at the same time less than expected by chance. Expected values come from multiplying together the proportions of time that each individual was a sentinel. Minimum overlap is greater than zero when the total amount of time that the two birds spend as sentinels exceeds the observation period (30 min). For example, if one bird is a sentinel for 20 min and the other for 15 min, they must be sentinels simultaneously for at least 5 min

result of supplemental feeding ($t_{12} = 1.56$, p = 0.15 and $t_{12} = 0.30$, p = 0.77, respectively). None of these effects depended on the sex of the bird or the order of treatments.

Pairs of scrub-jays showed coordinated sentinel behavior under both conditions of the second experiment. Pairs overlapped as sentinels far less than expected by chance when one bird ($t_{12} = 7.14$, p < 0.001, Fig. 2) or both birds ($t_{12} = 3.62$, p = 0.0035) were fed (Fig. 2). Some overlap was inevitable if a pair spent more than a total of 30 min as sentinels, and this frequently occurred when both birds were fed (Fig. 2). When two sentinels were present, they generally sat on separate perches and did not interact aggressively.

Discussion

When fed, Florida scrub-jays greatly reduced their foraging and increased their sentinel behavior. This dramatic shift in behavior suggests that the cost of sentinel behavior for Florida scrub-jays is a foraging opportunity cost. This cost is true by definition – all activities except foraging come at the cost of not foraging more – but is not particular to sentinel behavior and therefore is unlikely to explain why sentinels occur in some species and not others.

This study demonstrated a direct link between feeding and sentinel behavior (see also Clutton-Brock et al. 1999; Wright et al. 2001c). In various species, males are sentinels more frequently than females and adults are sentinels more frequently than juveniles (Rasa 1989; Zahavi 1990; Hailman et al. 1994; Wright et al. 2001b,c). These findings could result from a general correlation between sentinel behavior and foraging proficiency, with dominance, age, sex, and other factors affecting foraging. Detailed studies are needed if we want to determine if such factors directly affect sentinel behavior rather than acting indirectly through effects on foraging (see Gaston 1977; Wright et al. 2001b,c). A direct effect is suggested in Arabian babblers: body weight explains much of the individual variation in sentinel behavior but males are sentinels more than females even when the effects of body weight are removed (see Wright et al. 2001b,c).

Our manipulation dramatically altered scrub-jay behavior in the short term. How great an overall impact might we expect from allowing scrub-jays to gain rich food in a short period? Adult Florida scrub-jays normally consume about 28 kJ/h while foraging in winter (Fleischer 2000) and forage for 4.7 h/d in December (DeGange 1976). Because a peanut has an energetic value of about 29 kJ (Fleischer 2000), eating 1.5 peanuts satisfied about one-third of a scrub-jay's daily needs and released a bit more than 1.5 h for other activities. From the results above we see that this time was largely spent being a sentinel. The lack of order effects indicates that feeding had little effect on behavior on subsequent days. Thus our manipulation seems to have had a substantial impact on the time budget only for the hours immediately following feeding.

Scrub-jays acted as if sentinel behavior had only foraging opportunity costs and had larger benefits than other possible activities. From other studies, we find that safety is the primary benefit of sentinel behavior. In scrub-jays, sentinels are

out of reach of terrestrial predators and their view of the horizon allows them to spot most aerial predators so well that, 'when sitting on exposed perch above scrub, birds are nearly invulnerable (Woolfenden & Fitzpatrick 1996, p. 13)'. An exposed perch is probably safer than dense brush or a burrow because predators cannot sneak up near a sentinel. When aerial predators appear, sentinels are far more likely to spot them than the non-sentinels (McGowan & Woolfenden 1989).

This study supported the prediction that sentinel behavior increases the safety of the sentinel. Response to supplemental feeding alone is not sufficient to reject three other processes – kin selection, pursuit of social prestige, and reciprocal altruism – that have been advanced as potential explanations of sentinel behavior (see Clutton-Brock et al. 1999; Wright et al. 2001a,b,c). As we examine sentinel behavior in simpler groups, however, the roles for these candidate explanations are reduced. In the extreme, sentinel behavior by solitary animals (see Clutton-Brock et al. 1999) can only be explained by a selfish benefit to the sentinel (Bednekoff 2001). For this study, we need an explanation for sentinel behavior by mated, but unrelated, scrub-jays with no offspring nearby. Kin selection does not apply because the animals are not related. We can also rule out pursuit of social prestige among the members of the same sex within groups because each pair contained one member of each sex. The results cannot rule out sentinel behavior as a signal to members of other groups, but the studies took place during the seasonal low in territorial interactions among groups (DeGange 1976) and we observed very few interactions between groups. Finally, the results give no hints of reciprocity. It is not clear if reciprocity makes unique predictions about sentinel behavior. The results of this and other studies generally indicate that sentinel behavior is well explained by sentinel safety, with no indication of roles for kin selection, social prestige, or reciprocity (Clutton-Brock et al. 1999; Wright et al. 2001a,b,c). In this particular study, an additional benefit to sentinels could come through protecting their mates. This would be a form of mutualism based on mutual gains from breeding together in the future. Although this form of mutualism could be a common phenomenon in nature, it seems to have no label more specific than by-product mutualism (see Dugatkin 1997).

Scrub-jays showed coordination even when both were well fed. Thus this study, while using a novel method of analysis, replicates previous results (McGowan & Woolfenden 1989). Even if something that can be labeled as coordination emerges, it seems to be the product of fairly simple individual actions. Sometimes scrub-jay sentinels and foragers call softly to each other (see McGowan & Woolfenden 1989; see also Manser 1999; Wright et al. 2001a,b,c), but such calling occured in a minority of interchanges. Sometimes a jay would emerge from foraging and perch. If the sentinel did not quickly move to forage, this jay would resume foraging. At other times, the sentinel would leave its post abruptly and later be replaced. Sentinel interchanges seem to occur largely as opportunistic reactions to current state and the actions of other jays in the group.

Overall, sentinel behavior is predicted if individuals receive a safety benefit from resting in such prominent positions rather than elsewhere, and information spread leads to a mutual advantage for coordination (Bednekoff 1997, 2001).

The taxonomic distribution of sentinels suggests that this behavior occurs most frequently for animals that live in relatively small, stable groups in scrub habitats and face intense predation pressure (usually from raptors – see Clutton-Brock et al. 1999). The benefits of any form of coordinated vigilance are expected to be greater in smaller groups and under greater attack risks (Ward 1985) and the benefits of scanning from a high position instead of the ground are likely to be greatest in moderately open habitats, such as scrub woodland (Bednekoff 1997, 2001). Further experimental work is needed to explore the causal relationships between the occurrence of sentinel behavior and these factors.

Acknowledgements

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