

# Florida Scrub-Jays Compensate for the Sentinel Behavior of Flockmates

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## Abstract

Sentinel coordination requires that individuals react to the sentinel behavior of others. Previous work showed that Florida scrub-jays are sentinels more often when given supplemental food. Here we measured how birds in pairs reacted when their mates were fed. Scrub-jays were sentinels less when their mates were fed, demonstrating compensation. Indirect evidence suggests that this compensatory decrease in sentinel behavior was smaller than the increase in sentinel behavior by their mates. In addition, males in newly established groups were sentinels less often.

## Introduction

Sentinel behavior is coordinated vigilance, usually from high, exposed positions. Vigilance from high positions has been reported in a variety of bird and mammal taxa. As reviewed previously (Bednekoff 1997), sentinels have been suggested to 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), a hyrax (Kotler et al. 1999) and one marsupial (Runcie 2000). Within each taxonomic group, sentinel behavior occurs in only some species. The taxonomic pattern of occurrence suggests that sentinel behavior has 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). Although coordination has

been suggested in various taxa, it has been quantitatively documented only in meerkats (Clutton-Brock et al. 1999) and Florida scrub-jays (McGowan & Woolfenden 1989; Bednekoff & Woolfenden 2003). Although scrub-jays show coordination, their sentinel bouts 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 (Bednekoff 1997; see also Goodwin 1986; Clutton-Brock et al. 1999).

The current challenge is to show how individual actions lead to coordination. In theory, sentinel behavior can be understood as a form of foraging-predation risk trade-off with individuals acting as sentinels when they are well fed and no other individuals are sentinels (Bednekoff 1997, 2001). The first portion of this theory is supported: meerkats, *Suricata suricatta*, (Clutton-Brock et al. 1999); Arabian babblers, *Turdoides squamiceps* (Wright et al. 2001); and Florida scrub-jays given supplemental food increase their sentinel behavior. A second aspect, however, is necessary for coordination. Others must decrease their sentinel behavior when one individual increases its sentinel behavior. Compensation has been experimentally demonstrated

only in Arabian babblers fed mealworms throughout 5 h of observation during a day (Wright et al. 2001). In that study, alpha and beta male Arabian babblers reduced their sentinel behavior when the other male was fed, but their reduction was less than the increase in sentinel behavior by the fed male. This partial compensation is called undercompensation (Wright et al. 2001).

Our study aimed to document compensation in the sentinel behavior of Florida scrub-jays. We predicted that scrub-jays would compensate by being sentinels less when their mates were fed. While pursuing this aim, we also compared the sentinel behavior of recently and long-established groups.

## Methods

We performed an experiment using the tame, long-studied, color-ringed population of Florida scrub-jays at Archbold Biological Station (Woolfenden & Fitzpatrick 1984, 1990, 1996). Archbold Biological Station is a 2100+ ha preserve located near the south end of the Lake Wales ridge in south-central Florida. Within this preserve, the primary scrub-jay study area is a 400 ha plot of oak scrub. This community exists 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 retained offspring. The demography and cooperative breeding of Florida scrub-jays has been studied at Archbold since 1969 (Woolfenden & Fitzpatrick 1984, 1990, 1996). All of the birds used in the experiments described below were accustomed to human observers and to occasional feedings of bits of peanuts.

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 durations with the bulk of bouts lasting <10 min (Hailman et al. 1994). During winter, adults spend roughly half of the daylight hours as sentinels (DeGange 1976), so a sentinel is present during most times even for small groups.

From 6 to 17 Jan. 2004, we studied scrub-jays of 13 simple pairs, i.e. males and females bonded to each other but without any retained offspring. Of

these 13 pairs, five had not previously bred. Four of the five new pairs had established completely new territories. One formed on an existing territory where the male disappeared and was replaced, then a few months later the female disappeared and was replaced.

In this experiment, we studied the indirect effect of feeding one bird on the behavior of its mate. To isolate the effect of the experiment from effects of other factors, we observed the same individuals with and without supplemental feeding. One member of the pair was fed during one treatment and not the other, whereas its mate was not fed under either treatment. 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.

For the control treatment, the same individuals were 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 pair, 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 three cases when weather and other disruptions compelled that they be given 2 or 3 d apart. Treatments were counterbalanced for order.

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 and increase sentinel behavior, and indirectly increase foraging and decrease sentinel behavior in the other bird. Because scrub-jays forage on the ground amongst 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). All territorial flights, which involve calling and flying, were noted.

## Results

The mates of the focal scrub-jays ate on average 1.4 peanuts. Focal birds were not fed but occasionally managed to intercept a bit of peanut. When their mates were fed, focal birds were sentinels less

( $t_{12} = -3.8218$ ,  $p = 0.0024$ ), foraged more ( $t_{12} = 5.4538$ ,  $p = 0.0001$ ) and did not greatly change their other behaviors ( $t_{12} = -0.8137$ ,  $p = 0.4316$ , see Fig. 1).

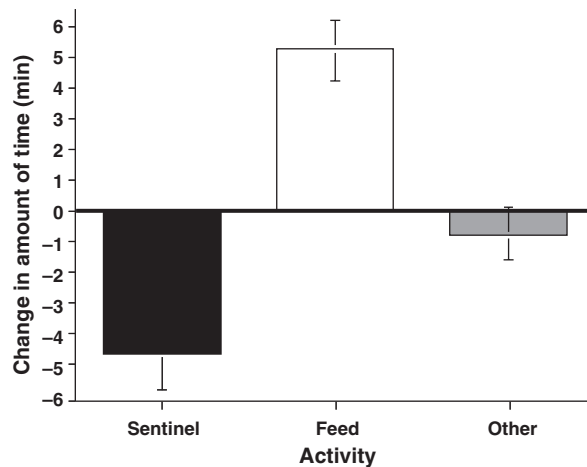
In comparing new and established pairs, the magnitude of the response to treatment was not different. The total amount of sentinel behavior, however, did depend on the interaction of group type with the sex of the bird observed ( $F_{1,9} = 5.4432$ ,  $p = 0.0445$ , Fig. 2). This pattern did not seem to be caused by increased territorial behavior. The number of territorial flights did not depend on the type of

group, the sex of the focal, nor the interaction of these two factors ( $F_{1,9} = 1.9335$ ,  $p = 0.1978$ ). The pattern of the interaction was roughly the same for territorial flights as for sentinel behavior: males in newly established groups were involved in the fewest territorial flights.

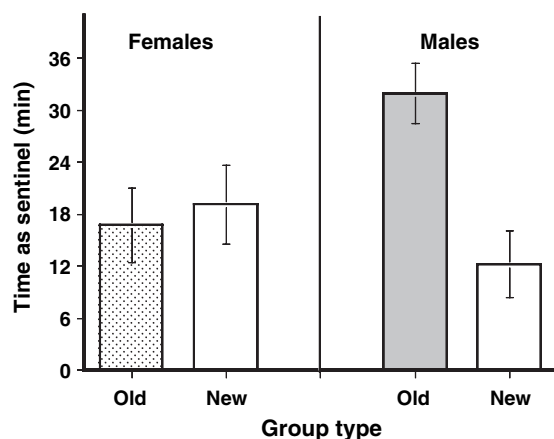
## Discussion

This research clearly demonstrated compensation in the sentinel behavior of Florida scrub-jays. Scrub-jays were sentinels less when their mates were fed. An alternative explanation for sentinel behavior makes the opposite prediction. If sentinel behavior were a competitive display to gain social prestige within groups (see Zahavi 1990), each animal would increase its sentinel behavior in response to increases by others (see also Wright et al. 2001). This hypothesis also was not supported for alpha and beta males in groups of Arabian babblers (Wright et al. 2001). Perhaps mated pairs are not a situation in which social prestige is likely to be important. Because sentinel behavior occurs in mated pairs, however, social prestige cannot be a general explanation for sentinel behavior. The results currently available are most consistent with a sentinel system based on mutual advantage (Bednekoff 1997, 2001).

Our results demonstrate compensation but do not directly address the relative amount of compensation. Although we did not track the behavior of both birds within pairs, two lines of evidence suggest that the observed compensation was undercompensation, that is, scrub-jays decreased their sentinel behavior by less than the increase in sentinel behavior by their mates. First, although the observed reduction of 4.5 min across 30 min is substantial, it is roughly half the increase observed when feeding one member of a pair (Bednekoff & Woolfenden 2003). Some caution is needed, however, as the current research took place weeks later in the winter than in our previous work (Bednekoff & Woolfenden 2003) and sentinel behavior declines as the breeding season approaches (DeGange 1976). Second, previous work looked for compensation in a well-fed bird. The results were in the direction of compensation but not statistically significant (Bednekoff & Woolfenden 2003). Now that we have demonstrated that scrub-jays do compensate, we interpret this previous result as undercompensation. Probably the birds in the previous study were satiated with peanuts and had little scope to increase their foraging during the next 30 min.



**Fig. 1:** Florida scrub-jays were sentinels less (black bar) and foraged more (white bar) during 30 min of observation following supplemental feeding of their mates. The feeding treatment had little effect on the amount of other behaviors (gray bar)



**Fig. 2:** Female scrub-jays were sentinels for similar amounts of time in established and new pairs (left panel) but males were sentinels much less often in new than in established pairs (right panel). Each bird was observed for 60 min

Overall, sentinel behavior in Florida scrub-jays depends on both an individual's energetic state and the behavior of other members of its group, but undercompensation suggests that individual state weighs more heavily in the decision to be a sentinel. A very hungry individual will feed even if no one is a sentinel and two well-fed individuals may be sentinels simultaneously (Bednekoff & Woolfenden 2003).

We observed newly established pairs based on circumstances that had not been previously observed. On 12 Feb. 2001, a fire spread from the railroad right-of-way and burned 247 h in the central part of the jay study tract at Archbold Biological Station. Scrub-jays largely withdrew from this area, although this involved groups shifting their home ranges rather than groups disbanding. In Jul. to Oct. 2003, four new territories were established in the largely abandoned, regrowing area. In more than 20 previous years of study at Archbold, only 2 of 61 males obtained these *de novo* territories (Woolfenden & Fitzpatrick 1996). Therefore, four *de novo* territories in 1 yr is highly unusual. The fifth new pair we observed was caused by double replacement on a territory not directly impacted by the 2001 fire. This new pair was not obviously different from the other new pairs so our results may apply to new pairs in general, not just to pairs on *de novo* territories.

In newly established pairs, males were sentinels less often than males of established pairs. First-time breeders are less successful in raising young, and nest predation is the leading cause of failure (Woolfenden & Fitzpatrick 1984, 1990, 1996). During the period of this study, which was in winter, males in newly established pairs did not spend extra time on territorial behavior. They genuinely seemed to spend more time foraging. A portion of this foraging time seemed to be spent recaching acorns. During late winter to early spring, males feed their mates during courtship, incubation and brooding (Woolfenden & Fitzpatrick 1996). Acorns are among the foods males feed their mates and are likely to be especially important during late winter to early spring when insects are scarce. During Jan., territorial disputes are relatively infrequent (G.E. Woolfenden, pers. obs.) and foraging for acorns and recaching acorns are relatively frequent (DeGange et al. 1989). Males occupying a new territory probably must spend more time with these tasks compared with males that have been on a territory through the previous summer, when much acorn caching occurs. All of the pairs that established *de novo* territories in 2003 nested in 2004 and three of the five successfully raised young (G.E. Woolfenden, unpubl.

data). The overall reproductive success of new pairs was similar to that of established pairs. Thus, our results suggest that sentinel behavior in Florida scrub-jays may be linked to caching behavior during the previous summer and fall. Within our sample, however, sentinel behavior does not predict reproductive success in the following spring.

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## Literature Cited

- Alves, M. A. S. 1990: Social system and helping behavior in the White-banded Tanager (*Neothraupis fasciata*). *Condor* **92**, 470–474.
- Alves, M. A. S. & Cavalcanti, R. B. 1996: Sentinel behavior, seasonality, and the structure of bird flocks in a Brazilian savanna. *Ornitol. Neotrop.* **7**, 43–51.
- Bednekoff, P. A. 1997: Mutualism among safe, selfish sentinels: a dynamic game. *Am. Nat.* **150**, 373–392.
- Bednekoff, P. A. 2001: Coordination of safe, selfish sentinels based on mutual benefits. *Ann. Zool. Fenn.* **38**, 5–14.
- Bednekoff, P. A. & Woolfenden, G. E. 2003: Florida scrub-jays (*Aphelocoma coerulescens*) are sentinels more when well-fed (even with no kin nearby). *Ethology* **109**, 895–904.
- Clutton-Brock, T. H., O'Riain, M. J., Brotherton, P. N. M., Gaynor, D., Kansky, R., Griffin, A. S. & Manser, M. 1999: Selfish sentinels in cooperative mammals. *Science* **284**, 1640–1644.
- DeGange, A. R. 1976: The daily and annual time budget of the Florida scrub jay. MSc thesis, Univ. of South Florida, Tampa, FL.
- DeGange, A. R., Fitzpatrick, J. W., Layne, J. N. & Woolfenden, G. E. 1989: Acorn harvesting and caching by Florida Scrub Jays. *Ecology* **70**, 348–356.
- Gaston, A. J. 1977: Social behaviour within groups of jungle babblers, *Turdoides striatus*. *Anim. Behav.* **25**, 828–848.
- Goodwin, D. 1986: Crows of the World, 2nd edn. British Museum (Natural History), London.
- Hailman, J. P., McGowan, K. J. & Woolfenden, G. E. 1994: Role of helpers in the sentinel behaviour of the Florida scrub jay (*Aphelocoma c. coerulescens*). *Ethology* **97**, 119–140.

- Kotler, B. P., Brown, J. S. & Knight, M. H. 1999: Habitat and patch use by hyraxes: there's no place like home? *Ecol. Lett.* **2**, 82–88.
- McGowan, K. J. & Woolfenden, G. E. 1989: A sentinel system in the Florida scrub jay. *Anim. Behav.* **34**, 1000–1006.
- Runcie, M. J. 2000: Parental care and obligate monogamy in the rock-haunting possum, *Petropseudes dahli*, from tropical Australia. *Anim. Behav.* **59**, 1001–1008.
- Woolfenden, G. E. & Fitzpatrick, J. W. 1984: The Florida Scrub Jay: Demography of a Cooperative-Breeding Bird. Princeton Univ. Press, Princeton, NJ.
- Woolfenden, G. E. & Fitzpatrick, J. W. 1990: Florida Scrub Jays: a synopsis after 18 years of study. In: Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior (Stacey, P. B. & Koenig, W. D., eds). Cambridge Univ. Press, Cambridge, pp. 240–266.
- Woolfenden, G. E. & Fitzpatrick, J. W. 1996: Florida Scrub-Jay (*Aphelocoma coerulescens*). In: The Birds of North America (Poole, A. & Gill, F., eds). Academy of Natural Sciences, Philadelphia & American Ornithologists' Union, Washington, D.C. No. 228.
- Wright, J., Maklakov, A. A. & Khazin, V. 2001: State-dependent sentinels: an experimental study in the Arabian babbler. *Proc. R. Soc. Lond. B Biol. Sci.* **268**, 821–826.
- Zahavi, A. 1990: Arabian babblers: the quest for social status in a cooperative breeder. In: Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior (Stacey, P. B. & Koenig, W. D., eds). Cambridge Univ. Press, Cambridge, pp. 103–130.