Sentinel Behavior: A Review and Prospectus

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1. WHAT IS SENTINEL BEHAVIOR?

The sentinels placed by antelopes and by monkeys, … may well be compared with the amount of care and forethought bestowed by many savages in similar circumstances.

Wallace (1875, p. 342).

The word "sentinel" is used in modern culture to designate many things that provides some sort of watchful protection and has its roots in the guards

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deliberately posted around towns and camps to prevent surprise attacks. Within the study of animal behavior, "sentinel" has historically been used to describe any particularly watchful animal. As the quote above illustrates, the term was often used to draw some analogy with human social dynamics. As different humans may draw different analogies from the same observations of animals, these analogies may interfere with the comparison of sentinel behavior across animals.

More recently, coordination of vigilance has been recognized as the defining feature of sentinel behavior (McGowan & Woolfenden, 1989; Bednekoff, 1997). Coordination means that sentinel bouts are spread more evenly through time than we would expect by chance. The emphasis on coordination allows quantitative tests that separate sentinel from nonsentinel behavior. Two other features, occupying high, exposed positions and alarm signals (see Goodwin, 1976; Bednekoff, 1997, 2001), are common in sentinel behavior. As these features can occur outside of sentinel behavior, however, they do not define sentinel behavior. Therefore coordination is the specific and more directly testable aspect of sentinel behavior that provides a strong criterion for distinguishing sentinels and nonsentinels.

Having defined sentinel behavior, the rest of this paper is structured as follows: First I review the literature for cases of sentinel behavior and suggest a straightforward method for testing sentinel behavior. Then I explore the ecological and social factors-associated sentinel behavior. This leads into considerations of the consequences of sentinel behavior for sentinels and others who live with them. Finally, I lay out some unanswered questions and opportunities for future research.

2. REVIEW OF THE LITERATURE

To determine how common sentinel behavior might be, I reviewed published accounts of potential sentinel behavior with the definition based on coordination in mind. Potential accounts were found mainly by following references and hints in the wider literature. Subsequent searches in the Web of Science and GoogleScholar suggested a few recent accounts. In any account, I searched for quantitative or qualitative evidence of coordinated vigilance.

The results of surveying the literature are summarized in Table 1. A consistent finding was that most accounts lacked evidence of coordination. Within mammals I could find no evidence of coordinated vigilance for

Table 1 Review which hypothesized cases of sentinel behavior provide evidence for coordination of vigilance. The third column is marked — where no evidence of coordination was provided

Species	Scientific name	Coordination	Reference
Mammals			
Rock-haunting possum	*Petropseudes dahli*	—	Runcie (2000)
Rock hyrax	*Procavia capensis*	—	Kotler, Brown, and Knight (1999)
Vervet monkey	*Cercopithecus aethiops*	—	Horrocks and Hunte (1986), Baldellou and Henzi (1992)
Chacma baboons	*Papio ursinus*	—	Hall (1960), see also Altmann and Altmann (1970)
Meerkat	*Suricata suricatta*	Tested	Clutton-Brock et al. (1999)
Dwarf mongoose	*Helogale undulata*	Described	Rasa (1986)
Klipspringer	*Oreotragus oreotragus*	—	Dunbar and Dunbar (1974), Tilson (1980)
Birds			
Chukar partridge	*Alectoris chukar*	—	Newbold et al. (2008)
Black cockatoo,	*Calyptorhynchus funereus*	—	Forshaw and Cooper (1981)
Long-billed corella	*Cacatua tenuirostris*	—	Forshaw and Cooper (1981)
Sulfur-crested cockatoo	*Cacatua galerita*	—	Forshaw and Cooper (1981)
Thick-billed parrot	*Rhynchopsitta pachyrhyncha*	—	Snyder, Koenig, Koschmann, Snyder, and Johnson (1994), Snyder, Enkerlin-Hoeflich, and Cruz-Nieto (1999)
Superb fairy-wren	*Malurus cyaneus*	Tested, with mixed results	Yasukawa and Cockburn (2009)
Chestnut-crowned babbler	*Pomatostomus ruficeps*	—	Sorato et al. (2012)

(Continued)

Table 1 Review which hypothesized cases of sentinel behavior provide evidence for coordination of vigilance. The third column is marked — where no evidence of coordination was provided—cont'd

Species	Scientific name	Coordination	Reference
Curl-crested jay	*Cyanocorax cristatellus*	—	Amaral and Macedo (2003)
Mexican jay	*Aphelocoma wollweberi*	—	Brown (1994)
Woodhouse's scrub-jay	*Aphelocoma coerulescens*	Suggested	Hardy (1961), see also Burt (1996)
Florida scrub-jay	*Aphelocoma coerulescens*	Tested	McGowan and Woolfenden (1989), Bednekoff and Woolfenden (2003)
Pinyon jay	*Gymnorhinus cyanocephalus*	—	Balda et al. (1972), see also Gilman (1907)
Common crow	*Corvus brachyrhynchos*	—	Conner, Prather, and Adkisson (1975), see also D'Agostino, Giovinazzo, and Eaton (1981), Knopf and Knopf (1983)
Northwestern crow	*Corvus caurinus*	—	Verbeek and Butler (1981)
White-winged chough	*Corcorax melanorhamphos*	Suggested	Boland (1998)
White-throated laughingthrush	*Garrulax albogularis*	—	Roberts (1991)
Common babbler	*Turdoides caudata*	—	Dharmakumarsinhji (1954)
Striated babbler	*Turdoides earlei*	—	Gaston (1978)
Large gray babbler	*Turdoides malcolmi*	—	Dharmakumarsinhji (1954)
Arabian babbler	*Turdoides squamiceps*	Described	Wright et al. (2001a, 2001b), Wright, Maklakov, and Khazin (2001)
Jungle babbler	*Turdoides striatus*	Described	Gaston (1977)

Black-faced babbler	*Turdoides melanops*	—	Shaw (2001)
Black-lored babbler	*Turdoides sharpei*	Described	Wickler (1985)
Bare-cheeked babbler	*Turdoides gymnogenys*	Described	Shaw (2001)
Southern pied babbler	*Turdoides bicolor*	Described	Ridley et al. (2010)
White-browed sparrow-weaver	*Plocepasser mahali*	—	Ferguson (1987)
Zebra finch	*Taeniopygia guttata*	—	Mainwaring and Griffith (2013)
Red-winged blackbird	*Agelaius phoeniceus*	—, Possibility discussed	Yasukawa, Whittenberger, and Nielsen (1992)
White-banded tanager	*Neothraupis fasciata*	Suggested	Alves (1990), Alves and Cavalcanti (1996)
Black-throated saltator, white-rumped tanager, chalk-browed mockingbird	*Saltator atricollis, Cypsnagra hirundinacea, Mimus saturninus*	Suggested	Ragusa-Netto (2000, 2001, 2002)
Fish			
Foxface rabbitfish	*Siganus vulpinus*	Described	Fox and Donelson (2014)
Blue-spotted spinefoot	*Siganus corallinus*	Described	Fox and Donelson (2014)
Masked spinefoot	*Siganus puellus*	Described	Fox and Donelson (2014)

Order of mammals follows Wilson, Don E. & Reeder, DeeAnn M. (Eds.), 2005 book *Mammal Species of the World. A Taxonomic and Geographic Reference* (3rd ed.). Johns Hopkins University Press, 2142 pp. Available at http://vertebrates.si.edu/msw/mswcfapp/msw/index.cfm. Accessed 29.10.13. Order of birds follows Gill, F. & Donsker, D. (Eds.), 2013 IOC World Bird List (v. 3.5). Available at http://www.worldbirdnames.org. Accessed 30.10.13.

primates or ungulates, two groups invoked by Wallace and others. Within ungulates, studies of klipspringers provide numbers that I will use below. Evidence of coordination is available for two social mongooses, with coordination quantitatively tested in meerkats and described for dwarf mongooses.

For birds, the record is longer and still distinctly spotty. For example, I was unable to locate any descriptions of coordinated vigilance for parrots. Quantitative tests of sentinel behavior have been conducted for two species. In Florida scrub-jays, sentinels are strongly coordinated. In superb fairy-wrens, sentinels have been suggested at nests. The evidence shows that fairy-wrens watching at the nest have gaps and overlaps similar to what would be expected by chance. Nevertheless, coordinated exchanges occur approximately once more per hour than would be expected by chance. In white-winged choughs, watchers near the nest are described as sentinels and said to have coordinated exchanges. More detailed descriptions are available for several babblers in the genus *Turdoides*, though even here sentinel behavior is sometimes invoked with no explanation. Across a range of other bird species, coordination has been suggested for some other species, including species that also form mixed species flocks in the Brazilian cerrado. The descriptions of these flocks note that usually one sentinel species is present and elsewhere suggest that individuals alternate as sentinels within species. I excluded cases where perched birds were foraging such as white-banded tanagers, which are reported to sometimes forage from a perch for flying insects.

Coordinated vigilance has been described for three species of rabbitfish (Fox & Donelson, 2014). These fish live on coral reefs and forage in crevices and other locations that obscure their vision while foraging. As described in the report (and shown in accompanying videos), one member of a pair forages while the other watches and individuals alternate.

Overall this review shows that most suggested cases of sentinel behavior provide no clear evidence of sentinel coordination. In most cases, we lack the data to evaluate whether the behavior meets the definition of sentinel behavior. Although, I could find of no compelling evidence of coordination of vigilance for parrots, ungulates, or primates, three groups with a rich history of anecdotes invoking sentinels, this is not to say that these groups do not have sentinels. We might productively regard the cases I have listed as "No evidence provided" as observations leading to the hypothesis of sentinel behavior. For example, sentinel behavior has been quantitatively tested in Florida scrub-jays. These tests

came more than half a century after these observations were reported by Howell (1932), "Miss Werner says the birds always have a lookout posted on a high bush, which sentinel remains there while the rest are feeding and gives warning of danger." Descriptions for other species are at least as promising as these observations by Miss Werner, yet have not been followed by quantitative tests.

3. HOW TO TEST FOR COORDINATION?

The preceding review indicates that sentinel behavior has been suggested many times by anecdotes and observations, but only rarely has coordinated vigilance been quantified. To help remedy the situation, I propose a general method of testing for sentinel coordination. Sentinel coordination spreads sentinel bouts across time more evenly than expected by chance. This will reduce the amount of time that no sentinel is present. We can measure coordination as the difference between the observed and the expected time without a sentinel. We expect $\prod_{i=1}^{n} (1 - p_i)$ proportion of the time without any sentinel, where p_i is the proportion of time spent by individual i on sentinel behavior. We compute one expected time for each group. Here are two examples using published data. First, the four individual in a captive group of meerkats spent 0.38%, 0.23%, 0.24%, and 0.43% of the time as sentinels (Moran, 1984). Without coordination, we would expect $(1 - 0.38)(1 - 0.23)(1 - 0.24)(1 - 0.43) = 0.21$ of the time to have no sentinel. The group was observed to have no sentinel 0.03 of the time. Second, we can do the same calculation for a group of klipspringers foraging in the wild (Tilson, 1980). The male was a sentinel 0.199 of the time, the female 0.118, and the juvenile 0.052. From these rates we would expect 0.706 of the time with no sentinel. No sentinel was observed 0.700 of the time.

As coordination is a property of groups, our sample size in tests of coordination will generally be the number of groups. The calculations in the previous paragraph generate one data point for testing the hypothesis that meerkat groups show coordination, and one data point for foraging klipspringers. Once data points from different groups are in hand, coordination can be tested statistically using basic paired tests of expected and observed values. The usual rules for sample size and statistical power apply such that small samples might be sufficient to detect strong coordination, while larger samples would be necessary to detect lesser degrees of coordination.

To compare the degree of coordination across situations and species, we can compare the relative size of the observed and expected. I propose a scale for coordination: $C = (expected - observed)/expected$. For meerkats, $C = (0.21 - 0.03)/0.21 = 6/7 = 0.833$. For klipspringers $C = (0.706 - 0.700)/0.706 = 0.0085$. Thus, this quartet of meerkats reduced gaps between sentinels some 83% below what was expected by chance, while the trio of klipspringers reduced the gaps by less than 1%. Meerkats showed strong coordination, while klipspringers showed weak or no coordination.

4. ECOLOGICAL CONDITIONS FOR SENTINEL BEHAVIOR

In the following sections, I review the ecological and social conditions for sentinel behavior, then move on to whether sentinels are safe and act selfishly. As sentinel behavior involves trade-offs between foraging and predation (see Bednekoff, 1997, 2001), I emphasize how conditions affect feeding and safety. Because sentinel behavior is poorly documented for many species, I rely mainly on the handful of well-documented cases in presenting evidence about the conditions favoring the behavior.

4.1 Habitats

Sentinel behavior has been reported from diverse geographic areas that are broadly similar in that they fall around the tropics and tend to be dry. Some of these areas are deserts. For example, Arabian babblers in the Negev Desert occupy a very open habitat with sparse vegetation and scattered trees and bushes (Wright, Berg, De Kort, Khazin, & Maklakov, 2001a). Chestnut-crowned babblers live in arid Australia (Sorato, Gullett, Griffith, & Russell, 2012). Meerkats and pied babblers in the Kalahari occupy arid savanna with some tall trees. Dwarf mongoose sentinels have been studied most in the Taru Desert, a semidesert savannah in Kenya with scattered trees and termite mounds in a generally grassy area (Rasa, 1987). Florida scrub-jays live in scrub-oak woodland with mostly low trees and a tangled understory of palmettos, lichens, and other vegetation (Woolfenden & Fitzpatrick, 1984). Jungle babblers occur in thorn scrub and dry deciduous woodland. In the classic study of their behavior, they spent most of their time in woodland, which had a closed canopy up to 15 m tall and usually an understory up to 3 m tall (Gaston, 1977).

Species with sentinels forage on or near the ground under circumstances where they can detect little while foraging, but they can detect

far more if they move a short distance up from the ground. Detection may be limited by thick vegetation or by intensive foraging including digging. An animal with its head in a hole will not detect approaching predators in the same way as an animal perched above. Although visual detection is likely very important, other forms of detection may be important as well. Thick vegetation blocks many sounds and dry vegetation can be notably noisy.

Sentinel behavior may vary with local variations in habitat. Pied babblers become sentinels sooner when foraging in long grass than when foraging in open areas or thickets, even though foraging returns are similar in all three habitat types (Hollen, Bell, Wade, et al., 2011). Chestnut-crowned babblers were more likely to be sentinels in two areas of sparser vegetation than in areas with abundant trees or shrubs, and encountered predators (Sorato et al., 2012). These observations at first seem to point in different directions, but may be united by the difference in visibility between foraging on the ground and perching above it. In very open habitat a good view can be had even from the ground, and in very dense habitat the view is little improved by being higher in the vegetation.

4.2 Perches

Within their habitats, sentinels choose perches that are likely to have a good view. For dwarf mongooses, sentinels in two groups posted themselves on trees 40.9% and 46.7% of the time; they positioned themselves on termite mounds the rest of the time (Rasa, 1989a). All posts were at least 1 m high, which was tall enough to give a clear view above the surrounding grass. Arabian babblers in an environment with few trees taller than 2 m chose perches that averaged a meter taller than the best alternative within 25 m, but no more exposed than these alternative perches (Wright et al., 2001a). In contrast, jungle babblers in a forest with a closed canopy and an understory of up to 3 m tended to perch in the lower branches of the canopy when engaging in sentinel behavior (Gaston, 1977). Pied babblers occupy a savannah with scattered tall trees. These birds perched on dead trees for 36.2% of sentinel bouts even though dead trees composed less than 10% of tree substrate available (Ridley, Nelson-Flower, & Thompson, 2013). Pied babblers chose perches 3.4 m off the ground on average and perched lower in high wind than in low wind (Hollen, Bell, Wade, et al., 2011). The sentinel perches used by Florida scrub–jays have not been quantified in the literature but are often at the top of short live trees and may be higher where sturdy dead trees are available (pers. obs.).

5. FOOD

5.1 Natural Feeding

Animals are predicted to be sentinels more often when they are better fed. There is some evidence from natural variation in feeding. In Arabian babblers individuals who were heavier were sentinels more often than birds who were smaller. Within individuals, these birds were sentinels more often on days when they were heavier (Wright, Berg, De Kort, Khazin, & Maklakov, 2001b). Meerkats lose weight when babysitting and spend less time as sentinels in the day after they have been babysitters than after days they had spent foraging (Clutton–Brock et al., 1999). Daily weight gain in meerkat helpers more than one year old predicts amount of sentinel behavior in males but not in females. In contrast, daily weight gain predicts contribution to pup feeding for females, but not males. For meerkat helpers younger than one year, daily weight gain was not a good predictor of sentinel behavior, but both males and females who were heavier for their age were sentinels more often, with the effect somewhat stronger for males than for females (Clutton–Brock et al., 2002).

Sentinel behavior varies with local conditions related to feeding. Sentinel behavior by chestnut-crowned babblers was least common at the start of the day and associated with foraging on the ground (Sorato et al., 2012). In jungle babblers, the length of sentinel bouts increased from less than 4 min early in the morning to around 8 min in the afternoon (Gaston, 1977). In pied babblers latency to start sentinel bouts was shorter during a wetter year (2008) than during the following drier year (2009) (Hollen, Bell, Wade, et al., 2011).

5.2 Food Supplements

Short-term food supplements have been given to four species and have led to increases in sentinel behavior. When meerkats were given 25 g of hard-boiled egg, they increased their time spent on sentinel behavior from 19% to 26%—that is by roughly 30%—during the rest of the day compared to five previous days (Clutton–Brock et al., 1999). Arabian babblers given ad libitum mealworms for one day spent an additional 12−14% of their time during that day as sentinels, but the effect of feeding did not carry over to subsequent days (Wright, Maklakov, & Khazin, 2001). Florida scrub-jays fed up to 1.5 peanuts increased their time as sentinels by nearly 9 min during the following 30 min (Bednekoff & Woolfenden, 2003). Individual pied

babblers were fed 10 mealworms or 1 mealworm immediately following a sentinel bout. They became sentinels again far sooner (about 15 min vs 5 min) and stayed as sentinels much longer (about 8 min vs 4 min) when fed 10 mealworms (Bell, Radford, Smith, Thompson, & Ridley, 2010). For meerkats, an individual's latency to the next sentinel bout decreased when sentinel bouts were interrupted after 2 min and decreased further when individuals were interrupted then fed 25 g of hard-boiled egg (median 38.3 to 21.3 to 8.77 min) (Clutton-Brock et al., 1999). Thus, increasing short-term energetic gain consistently increases sentinel behavior in published studies.

Longer-term studies have also been conducted on meerkats. Two published studies report results with broad similarities but different emphases. In the first study (Clutton-Brock et al., 1999), when some helpers in six groups were fed 25 g of hard-boiled egg each day for 30 days, they were sentinels for roughly three times the amount of time as unfed helpers in the same groups (relative frequency 0.15 for supplemented individuals compared to less than 0.05 for controls). The text states, "The extent to which feeding incremented raised guarding time did not differ between male and female helpers." No statistics are presented with this statement, but it suggests that a test was conducted to examine the interaction of feeding with sex of the helper. In a subsequent study (Clutton-Brock et al., 2002), 23 helpers in six groups were fed 25 g of egg per day and compared with 29 unfed helpers in the same groups. Feeding took place for an average of 52 days during periods of babysitting and pup-feeding periods. The study reports an increase in sentinel behavior from roughly 4–6% in females that was not statistically significant and an increase from roughly 7–20% in males that was statistically significant. Despite a difference in emphasis, the average effect of food supplements is similar across the two studies, and a statistical test of the sex by supplement interaction is not reported for either. Supplemental feeding tended to increase the contributions of females to babysitting and pup feeding more than it increased the contributions by males, though again no test for an interaction was reported.

In comparing the short- and long-term effects of food supplementation for meerkats, the difference between treatments is greater in the long-term experiments but the overall level of sentinel behavior is higher for the short-term experiment, with the level of sentinel behavior dramatically lower in unfed animals in the long-term experiments. Although differences due to the length of feeding are possible, the difference may be due to the short-term experiment being done in a national park with high predation pressure

and the long-term study conducted on ranchland where predation risk was lower (see Clutton-Brock et al., 2002).

6. RELATION TO PREDATION RISK

Although sentinels may detect many things, the behavior undoubtedly functions to limit risk from predators. Sentinel behavior seems particularly directed toward threats from the air in that it often varies with risk of attack from birds of prey. More than 70% of predator approaches to pied babbler groups were by raptors (Ridley et al., 2013). For dwarf mongooses, sentinel behavior is best known from a population where the mongooses are frequently attacked by pale chanting goshawks. In this population, predators disturbed groups an average of 1.69 times per hour and attacked 0.13 times per hour, and dwarf mongooses spent 18.6% of their potentially active time hiding from raptors (Rasa, 1989b).

Sentinel behavior may vary with predation risk on several scales. In comparing meerkat populations, at least one sentinel was on watch for a median of 55.6% of foraging time in the national park with many hawks and only 12.0% at the ranchland area with fewer hawks (Clutton-Brock et al., 1999). Across habitats, sentinel behavior by chestnut-crowned babblers was more common in areas where predators were more common, and when foraging on the ground. The probability of having a sentinel is less than 10% for observation sessions with no predator encounter and more than 40% for sessions with a predator encounter (Sorato et al., 2012). Across seasons, sentinel behavior by Florida scrub-jays is most common in fall and winter when large numbers of hawks are present in the area (McGowan & Woolfenden, 1989). In Arabian babblers, however, sentinel behavior was not elevated during the three months of peak raptor migration through the study area (Wright et al., 2001b). On very short timescales, sentinel behavior by pied babblers is increased during the 10 min following detection of a predator or playback of heterospecific alarm calls compared to the 10 min beforehand (Ridley, Raihani, & Bell, 2010).

7. SOCIAL CONDITIONS

7.1 Who Are the Sentinels? Age, Sex, and Dominance

Defining sentinel behavior as coordinated vigilance means that more than one individual is involved. Potentially all members of a group are

sentinels. In practice, some individuals within groups are likely to be sentinels more than others. The most common pattern is that old, high-ranking individuals are sentinels more often than young, low-ranking animals. Rates of sentinel behavior are broadly correlated with age, sex, and status. First, juveniles tend to spend little time as sentinels compared to older individuals (Balda, Bateman, & Foster, 1972; Rasa, 1977; Ferguson, 1987). Second, males tend to be sentinels more than females (Hall, 1960; Horrocks & Hunte, 1986; Ferguson, 1987; Rasa, 1989a). The relationship with dominance seems to vary from species to species. In dwarf mongooses, subordinate males display the highest rates of sentinel behavior (Rasa, 1987). In this study population, the sex ratio was 2.6 males per female, and subordinate males were mainly young, natal individuals that had remained in the group. The one subordinate male that was an immigrant had a lower rate of sentinel behavior than other subordinate males (Rasa, 1989b). In meerkats, dominant males do the most guarding, while dominant females do little (Clutton–Brock et al., 1999). In meerkats, males are sentinels more of the time than are females, with biggest difference occurring when they are yearlings (Clutton–Brock et al., 2002).

Across the bird species studied, the pattern is generally simpler. Dominant pied babblers are sentinels more than subordinates (Hollen, Bell, Wade, et al., 2011). In jungle babblers, adults tended to be sentinels more than younger birds and males more than females. The breeding pair performed approximately 50% of the sentinel behavior in the groups that were observed. Male nonbreeders were sentinels more than female nonbreeders (Gaston, 1977). In Arabian babblers, males and dominant birds are sentinels more often than females and subordinates, and sentinel behavior increases with dominance more in males than in females (Wright et al., 2001b). In Florida scrub–jays, older individuals are sentinels more frequently than are younger birds, and males perform sentinel behavior more than females within each age class. Juveniles are sentinels very little until the autumn of their first year (Hailman, McGowan, & Woolfenden, 1994). As noted elsewhere, time available for sentinel behavior is likely directly related to food finding abilities (see Gaston, 1977). For the social mongooses, other fitness enhancing activities, including babysitting and actually having babies, likely explain why sentinel behavior may decline with age, particularly for adult females.

7.2 Group Size

Vigilance is when animals raise their heads in the midst of feeding or some other activity. One of the most frequently replicated findings in behavioral

ecology is that rates of vigilance decrease as group size increases (Elgar, 1989; Roberts, 1996; Beauchamp, 2008). Individual rates of sentinel behavior may decrease with group size, though the effect is not ubiquitous. In dwarf mongooses, individual rates of sentinel behavior decline with group size. Even so, substantial gaps occur between sentinel bouts when groups have only two members (Rasa, 1989b). For meerkats, per capita rate of sentinel behavior decreases sharply across groups of 3–7 adults, yet is lower for groups of 1 and 2, in which individuals may be prospecting for new opportunities rather than acting like members in established groups (Clutton-Brock et al., 1999). For pied babblers, sentinel behavior decreases with group size (Ridley & Raihani, 2007) yet foraging group size does not have an obvious effect on latency between bouts or bout duration (Hollen, Bell, Wade, et al., 2011).

For Florida scrub-jays, group size had different effects on sentinel behavior during the breeding and nonbreeding seasons. During the breeding season (April–May), breeding pairs with helpers spent slightly longer time as sentinels than did breeding pairs without helpers. During the nonbreeding season, breeding pairs with helpers spent less time overall as sentinels. The data are consistent with helpers lessening care of young during April–May and allowing breeders to do more self-maintenance in other seasons (Hailman et al., 1994).

Other reports have found no decrease in individual rates of sentinel behavior with group size (e.g., Ferguson, 1987). Although the statistical power of these studies is often limited, the effect does appear smaller than expected from studies of vigilance. Sentinel behavior tends to occur in species with small, stable groups and several factors may contribute to the modest effects of group size on sentinel behavior. Low statistical power comes about because many studies include a fairly small number of groups with a modest range of group sizes. The same effect will be more obvious over group sizes 1–40 than over group sizes 2–8. Finally, group size effects may be more apparent where individuals are sometimes in large groups and sometimes alone because individuals can allocate much of their feeding to their time in larger groups (Bednekoff & Lima, 2004). Here we expect animals to change their behavior more if they are sometimes in a group of 2 and sometimes in a group of 8 than if they are always in a group of 2. Group size effects for sentinel behavior may be modest because the species showing sentinel behavior often live in stable groups.

7.3 Adjustments to Sentinel Behavior of Others

For sentinel bouts to be coordinated, animals must adjust the beginning or ends of bouts based on what others are doing. Meerkats were much more likely to go directly from foraging to sentinel behavior if another sentinel is not already present. Also, focal meerkats increased the length of their sentinel bouts when the sentinel bouts of other group members were interrupted after 2 min (by gently shaking the branch on which the sentinels were perched). When Arabian babblers were fed and became sentinels, others reduced their sentinel behavior. The compensation was partial such that the total sentinel effort of the group was greater with supplemental feeding (Wright, Maklakov, & Khazin, 2001). In Florida scrub-jays the unfed partner of a fed jay reduced its sentinel behavior by about 4.5 min of a 30 min observation session (Bednekoff & Woolfenden, 2006). When both birds were fed, however, both engaged in sentinel behavior for extended periods. Birds fed in both trials showed only a nonsignificant trend to compensate by approximately 1 min when their partners were also fed (Bednekoff & Woolfenden, 2003).

8. ARE SENTINELS SAFE?

The key feature of models of sentinel behavior (Bednekoff, 1997, 2001) is that sentinels are safe because their increased ability to detect approaching predators more than compensates for any increased danger when predators do approach closely. In these models, safety comes about through limiting close encounters with predators. To test these ideas, it is useful to remember that a predator must approach, pursue, and capture a prey individual before killing it. Antipredator behavior can reduce any or all of these phases (Lima & Dill, 1990).

In comparing the safety of sentinels and foragers, the ideal would be to compare sentinels to the foragers they could have been. An approximation is to compare sentinels not just to foragers at the same time but to foragers without a sentinel. This comparison supposes that times without a sentinel are equivalent to times with a sentinel. To the extent that sentinels are more likely in times of greater danger, this comparison likely overestimates the danger to sentinels and underestimates it to foragers—and thereby is conservative in estimating sentinel safety.

The scenario for sentinel safety focuses on birds of prey that rely on surprise for their attacks. If warned of a possible attack, animals can take cover in

burrows or thick vegetation. From atop the vegetation, sentinels can detect a falcon, hawk, and eagle when it is still far away. Results from the field show that sentinels have a large advantage in detecting potential attacks. In meerkats, sentinels gave alarm calls at more than 10 times the rate of foragers and generally gave alarm calls to predators that were still far away (Manser, 1999). When predators approached groups of dwarf mongooses, a sentinel was first to give an alarm call in 92.3% of cases (Rasa, 1989b). Similarly, when predators approached groups of Florida scrub-jays, a sentinel was first to given an alarm call in 62 of 67 predator approaches, or 92.5% of cases (McGowan & Woolfenden, 1989). Since the group sizes averaged 2.96 for scrub-jays and 5.25 for dwarf mongooses, these data show that one sentinel is detecting predators about 12 times as often as the several foragers combined.

For pied babblers, sentinels detected 98.4% of potential attacks whereas groups without sentinels detected 89.9% of attacks (Ridley et al., 2010). Group size was approximately 4 in this study. I use these numbers to estimate the relative detection rates for foragers and sentinels. Using the symbols from Bednekoff (2001), each forager fails to detect attack at some rate w and each sentinel at some rate sw (where $s < 1$, and gives the relative failure rate of sentinels in detecting attacks). If individuals scan independently, a group of n foragers will fail to detect attack with probability w^n and a group with one sentinel and $n - 1$ foragers with probability sw^n. Thus, $sw = 0.016$ and $w^n = 0.111$. Using $n = 4$, we can work out that $s = 0.028$. This number indicates that a pied babbler sentinel detects 97% of the attacks that a forager would not and shows that sentinels have a great advantage in detecting attacks.

The potential costs of a high-exposed position come about through greater targeting for attack by predators and greater probability of capture during an attack. Data on attacks are difficult to gather. As a first approximation, scientists have examined distance to safety. Three studies have found that sentinels take up comparatively safe positions. Dwarf mongoose sentinels were generally closer to escape burrows than were foragers and "The trees selected as guard posts all afforded the guard some form of protection or a rapid means of retreat to a safe shelter." (Rasa, 1989a, p. 134). Meerkat sentinels were considerably closer on average to safety (around 1.5 m compared to more than 3 m) than were the foragers in their groups and were usually among the first members of the group to enter an escape burrow (Clutton-Brock et al., 1999). Arabian babbler sentinels were

described as closer to cover than were foragers (Wright et al., 2001b). In contrast, pied babbler sentinels were on average further from cover (2.4 m) than were foragers (1.6 m). This overall difference depended on the type of perch occupied by sentinels: when on shrubs or live trees sentinels were a similar distance from cover as foragers, but when sentinels were on dead trees, they were considerably further from cover (3.9 m vs 1.1 m) than were foragers (Ridley et al., 2013).

Studies on two species have gathered data on actual attacks that allow us to estimate predation risk for sentinels and foragers. In meerkats, the overall danger for sentinels was less than for foragers. This result is straightforward given that sentinels were first to detect attacks and also generally closer to safety (Clutton-Brock et al., 1999). For pied babblers, the advantage in detection needs to be weighed against danger if a predator is not detected in a timely manner. In 14 of 16 strikes by raptors, sentinels were the last to reach cover. Sentinels were targeted by predators in 13 of these 16 attacks. In one case the sentinel was killed, and in another case it was captured but then escaped (Ridley et al., 2013).

Using again the symbols from Bednekoff (2001), sentinels have an absolute safety advantage if $sd < 1/n$, where s is the relative reduction in undetected attacks and d is the probability of the predator targeting the sentinel, should a predator approach undetected. The right hand side of the equation, $1/n$, gives the average probability of any one forager being targeted in an attack on group of n foragers. From the calculations above, $s = 0.023$. Sentinels were targeted in 13 of 16 attacks, so we can use $13/16 = 0.81$ for d. Multiplying s times d is about 0.028—or an order of magnitude smaller than $1/n$ where group size averaged about 4. As suggested theoretically (Bednekoff, 1997, 2001), the relative odds of being targeted in undetected attacks do little to reverse the safety gains by reducing the number of undetected attacks. Given the advantage in detection shown for pied babblers, sentinels would gain a safety advantage even if targeted in every attack that they did not detect.

Thus, sentinels seem to be safer than foragers for both meerkats and pied babblers. In contrast to the assumptions of the models, meerkat sentinels seem to enjoy both an advantage in detection and escape. The data for pied babblers better fit the assumptions of the sentinel safety models. The large advantage in detection makes up for the substantial disadvantage in being targeted in attacks. Even if sentinels were always targeted in attacks, this n-fold increase (from $1/n$ to 1) in targeting during attacks

would be more than offset by the roughly 40-fold reduction in undetected attacks.

The quality of these data is a testament to years of dedicated fieldwork. Even after such careful observations, however, several questions remain. First, it is unclear whether sentinel behavior confers consistent benefits to different types of predators. Rasa (1989b) found that sentinels always detected terrestrial predators before they attacked, but that dwarf mongooses were sometimes killed in the subsequent interactions with terrestrial predators. When sentinels were present in groups of Florida scrub-jays, they only initiated 7 of 15 instances of mobbing a terrestrial predator (McGowan & Woolfenden, 1989). This did not differ from what was expected by chance. It may be that sentinels are not nearly so effective at detecting threats on the ground as they are threats from the air. On the other hand, occupying a position off the ground might decrease the risk of being targeted by terrestrial predators.

Second, we do not know whether the presence of sentinels deters predators from approaching groups (see Bednekoff, 1997). Predators may abandon approaches early if an attack is almost certain to fail. Although a direct effect of sentinels is not noted, smaller groups of dwarf mongooses are attacked three times as often as larger groups, even though smaller and larger groups were disturbed by raptors at roughly equal rates (Rasa, 1987). These data suggest that raptors "call off" attacks. It would also be interesting to know how predators detect and approach groups with sentinels, and if the timing of approaches depends on sentinel behavior. During observations of dwarf mongooses, 5 of 8 adults who were killed were taken during periods when sentinels were running to rejoin the group (Rasa, 1989b). It is not clear if attacks were more likely during these times or just exceptionally successful. Because the best time to have sentinels is when attacks are likely, and the best time to attack is when sentinels are unlikely to be present, groups with sentinels and their predators may keep each other guessing. A potential aspect of this is that sentinel bouts by Florida scrub-jays do not have a characteristic length but instead follow an exponential distribution (Hailman et al., 1994).

The final mystery comes about during the final phase of fleeing to safety. Pied babbler sentinels not only start out on average farther from safety than foragers, but they also move to safety at a slower average rate than do foragers (Ridley et al., 2013). Using the data in Ridley et al. (2013), sentinels move to cover at an average rate of 0.83 m/s when a forager gives an alarm call and 0.56 m/s following experimental playback of an alarm call. These

speeds are well below human walking speed. Given that sentinels could accelerate with gravity, these data suggest that pied babbler sentinels are doing something other than moving to safety as quickly as they could. Two possibilities are that sentinels continue to gather information on the potential threat as long as they safely can, and that sentinels draw attacks away from other group members. The possibility that sentinels are doing more than saving themselves is the subject of the next section.

9. ARE SENTINELS SELFISH?

The original model of sentinel safety (Bednekoff, 1997) denotes sentinels as "selfish." The logic of this label is that one sentinel in a population of nonsentinels would have a fitness advantage. In this model, however, the basis for coordination is mutual benefits. Given that coordination is the defining feature of sentinel systems, sentinel behavior is predicted when sentinels are not simply selfish but when they protect themselves best by being sentinels when other individuals are not sentinels already.

At present, models of sentinel behavior do not include any value for saving others and show that sentinel behavior could potentially be advantageous without such effects. Models without kin-selected benefits, for example, do not show sentinel behavior must occur in the absence of kin-selected benefits. Nonetheless, simple explanations are favored in science until the data compel more complex explanations. Although earlier observations did not find a consistent effect of relatedness on sentinel behavior by meerkats (Clutton-Brock et al., 1999), more recent observations are most consistent with some sentinel behavior being a form of care for others. Sentinel behavior by meerkats is much more common in the part of the year when pups are moving with the group. Furthermore, individuals are sentinels more often when they have pups near them than when the sentinels are further away (Santema & Clutton-Brock, 2013). Similarly, sentinel behavior is much more common for chestnut-crowned babblers when a group contains juveniles or fledglings (Sorato et al., 2012).

These observations suggest kin selection to the extent that sentinels and young are related. Protecting unrelated young could also provide delayed benefits for the sentinels through the many ways the fitness of an individual may intertwine with that of others nearby, some of whom might be kin. Models of group augmentation capture some of these intertwined effects, and group size can matter in the species with sentinel behavior: Larger

groups of dwarf mongooses are attacked less often than smaller groups (Rasa, 1987), and individuals in small groups do not seem to be able to successfully raise enough offspring to become a larger group (Rasa, 1989b). That said, sentinels may act more to prevent the loss of valuable social partners than to increase group size per se. To allow for a full range of social effects, I discuss mutual dependence in fitness without further discussion of group augmentation.

Mutual dependence in avoiding predation could take many forms. The presence of another individual during a future attack can lower the risk to a focal individual simply because the predator has to choose which to attack when both individuals are vulnerable. Further benefits come about from behaviors that increase the probability the other individual will warn the focal individual, and also if larger groups are better able to disrupt or deter some predators. A focal individual might risk itself during a current attack in order to have available these benefits during future attacks. Across the group, each individual could risk itself occasionally to maintain a social safety net.

Individuals might also show mutual dependence in future reproductive success. Many species with sentinel behavior also breed cooperatively. Sentinels might do well to protect individuals who are likely to be helpers when the sentinels are breeders. Besides breeding in their natal groups, the saved individuals might aid the focal individuals in dispersing to and breeding in another group, establishing a new group elsewhere, or (as seen in Florida scrub-jays) expanding the natal territory and then "budding" off a new breeding territory in part of the expanded territory (Woolfenden & Fitzpatrick, 1984).

Overall, mutual dependence is also likely to be important in the lives of the animals demonstrated to have sentinel behavior. For these reasons, I do not believe it is useful to speak of sentinels as "selfish." It is still relevant to consider how safe sentinels are compared to alternative positions and behaviors.

10. COORDINATION AND ASSOCIATED VOCALIZATIONS

Sentinel behavior is often associated with a suite of vocalizations. Although sentinels generally give alarm calls when they spot danger, and may sometimes give territorial calls, these calls do not obviously aid coordination of sentinels. Instead attention has focused other calls often given by sentinels.

These calls given by sentinels resemble calls given elsewhere. Dwarf mongoose sentinels regularly give what is described as a general contact call with increased volume (Rasa, 1986). Florida scrub-jays sometimes give a short, low frequency contact calls known as a conversational guttural (Bednekoff, Bowman, & Woolfenden, 2008). Pied babbler sentinels give a call very similar to the "chuck" call by foragers (Bell et al., 2010). For Arabian babblers, only 11.9% of sentinel bouts included nonalarm vocalizations (and 13.3% included an alarm call). Contact calls were given at indistinguishable low rates by all age and sex classes (Wright et al., 2001a). Meerkat sentinels vocalize about 80% of the time they are on guard. Over 95% of the vocalizations given by sentinels consisted of single to multiple notes of short duration (Manser, 1999). On a slightly different note, jungle babblers sometimes give a low intensity cackle call in the minute before leaving their perch (Gaston, 1977). This same type of call is given to observers and other kinds of potential but not imminent danger.

Two hypotheses have been suggested for how calls from sentinels might aid coordination of sentinel bouts in groups. First, the Watchman's song hypothesis suggests that sentinels call steadily to signal their continued presence. Wickler (1985) gives the analogy of medieval watchmen calling out the hour through the night. Second, sentinels might call to signal when their bouts were ending, like a shift whistle at a factory (Gaston, 1977). These hypotheses make divergent predictions about the timing of calls by sentinels. Unfortunately the data do not clearly fit either pattern. For example, Florida scrub-jays give conversational gutterals more frequently in the second half of bouts, but not clearly at the end of each bouts (Bednekoff et al., 2008). In pied babblers, calling in the last minute of a sentinel bout is higher than calling in the first minute (Bell et al., 2010). Pied babblers give a slightly different call, known as a fast chuck, at the end of 44% of sentinel bouts (Hollen, Bell, Russell, et al., 2011). In contrast, calling by meerkats drops off toward the end of bouts, and sometimes ceases entirely before the sentinel leaves its perch (Manser, 1999).

Calls given by sentinels vary with external circumstances. Dwarf mongooses gave a Watchman's song in 57% of sentinel bouts. They were more likely to call in this way in a habitat with dense vegetation and when foragers were far away (Kern & Radford, 2013). In windier conditions, pied babblers are somewhat more likely to give fast chuck calls at the end of sentinel bouts (Hollen, Bell, Russell, et al., 2011). Pied babbler sentinels have good access to indirect information about threats, including heterospecific alarms, heterospecific flight behavior, vegetation movement,

and dust clouds, that is not readily received or evaluated by foragers (Bell, Radford, Rose, Wade, & Ridley, 2009).

Calling by sentinels also reflects the internal state of signalers. In pied babblers, both sentinels and foragers call at lower rates when given more food. Naturally occurring sentinel bouts show a negative correlation between their length and the rate of calling by sentinels at the start of bouts (Bell et al., 2010).

The value of signaling depends on how the signals change the behavior of receivers. Other group members respond to calls by sentinels. Meerkats are less vigilant, more likely to feed, and less likely to become a sentinel when they hear a sentinel calling (Manser, 1999). Pied babbler foragers reduce their vigilance and also spread out into new foraging areas when they hear calls from a sentinel (Hollen, Bell, & Radford, 2008). Foraging intake was three times as high when sentinel calls were played back compared with times when background noise was played back (Hollen et al., 2008). Furthermore, biomass intake was around four times as high when sentinels emitted calm calls compared to times they gave surveillance calls (Bell et al., 2009). In comparing across the two studies, intake rates when hearing disturbed surveillance calls were similar to when hearing background noise. Pied babbler foragers are far more likely to fly to cover if alarm calls follow disturbed surveillance calls than if alarm calls follow calm ones (Bell et al., 2009). Pied babbler foragers also react to sentinel calls played back from higher perches by being less vigilant, spreading out more, and greatly increasing their biomass intake compared to when the same calls are played from lower perches (Radford, Hollen, & Bell, 2009). Finally, pied babbler foragers are less likely to become sentinels when they hear calls indi‐cating satiated sentinels, and sentinels end sentinel bouts quickly if they hear calls indicating satiated foragers (Bell et al., 2010).

Against the background of strong reactions by pied babblers to sentinel calls, it is surprising that fast chuck calls at the end of bouts do not obviously enhance sentinel coordination. Fast chucks are somewhat more common in higher winds, and given most often by subordinate females, least often by dominant females, and at intermediate rates by males, whether they are dominant or subordinate. Latency to the next sentinel bout is no shorter, and perhaps less consistent, following bouts naturally ending in fast chuck calls compared to bouts without fast chuck calls. In a playback experiment, fast chuck calls did not consistently lead to shorter latencies than playbacks of wingbeats, like a sentinel flying down (Hollen, Bell, Russell, et al., 2011). The results indicate that four groups showed much shorter latencies in

response to fast chuck calls, and four groups showed short response latencies to both playback treatments (Hollen, Bell, Russell, et al., 2011). It may be that fast chuck calls occur when the sentinel "fears" a long gap, and this may reflect the information state of the current sentinel instead of the energetic state of current foragers.

While the information from fast chucks is unresolved, overall it is clear that calls by sentinels can carry information about both the state of the environment and the state of the sentinel. In meerkats calling by sentinels decreased overlap of sentinels and gaps between sentinels (Manser, 1999). Thus calling by sentinels can improve coordination of sentinel bouts. The effects of sentinel calling are likely to function through benefits to receivers (Kern & Radford, 2013). Current foragers benefit by being able to concentrate on foraging while they know a sentinel is watching for potential danger. The current sentinel is both giving other members of its stable group a chance to forage in safety and recruiting other group members to be sentinels sooner and more often in the future (see Bell et al., 2010). Although calling likely takes a bit of energy, any energetic cost is dwarfed by the great increase in foraging intake seen in pied babblers. Calling by sentinels has the short-term effect of enhancing overall foraging intake. Enhancing intake in turn could increase overall time with sentinels.

Finally, information from sentinels may be just a fraction of the information exchanged between sentinels and other members of the group. Within small, stable groups, contact calls provide information about where others are and how they are doing. Sentinels probably hear soft vocalizations from other group members that are not obvious to human observers and almost certainly have a better overview of the activities of other group members than do researchers nearby on the ground. Wind might affect both how easily foragers hear the sentinel, and how well sentinels can hear calls and inadvertent sounds from foragers. Thus when pied babbler sentinels choose lower perches in windy conditions, they might be increasing their chances of both getting their message through and of receiving information back from other group members (Hollen, Bell, Wade, et al., 2011).

An ideal sentinel system would have one sentinel on guard at all times, with no gaps and minimal overlap. Sentinel systems rarely approach this ideal. Sometimes sentinels are rare. For chestnut-crowned babblers, sentinels were recorded sometime in 66 of 256 tracking sessions with tracking sessions lasting up to 3 h. The probability of having a sentinel was about 0.42 for the portion of a tracking session after a predator encounter and 0.09 for the

portion before a predator encounter (Sorato et al., 2012). Even when sentinels are regularly present, the amount of time with sentinels varies with circumstances. In meerkats, sentinels were present a median of 55.6% of group foraging time in the national park and 12.0% for groups at the ranchland site (Clutton-Brock et al., 1999). In dwarf mongooses, sentinels were present throughout foraging time for a group of 9, 81.6% of foraging time for two groups of 5, and 69.6% of foraging time for a group of 2 (Rasa, 1989b). At a different study site, dwarf mongoose groups posted sentinels 42.4% of time when not foraging with drongos, and 21.2% when foraging with drongos (Sharpe, Joustra, & Cherry, 2010). Pied babblers had sentinels present 59% of observed time, with a range of 7–100% per hour-long observation session (Bell et al., 2009). Arabian babblers had at least one sentinel on watch around 55% of the time, though group averages ranged between about 30% and 85% (Wright et al., 2001b). For jungle babblers, a sentinel was recorded as present 82% of the time for observations in December and January (Gaston, 1977). For Florida scrub-jays, at least one sentinel was present for 58% of daylight hours throughout the year, but for about 80% of the time during November–February, the winter nonbreeding season (McGowan & Woolfenden, 1989).

Although sentinels are more frequent in more dangerous situations, it is surprising that sentinels are often absent. As a striking example, annual mortality of meerkat adults was 0.68 in the national park (compared to 0.34 at the ranchland site), yet groups at the national park had no sentinel a median of 44.4% of the time (Clutton-Brock et al., 1999). Even though sentinel calls allow for faster feeding by meerkat and pied babbler foragers, these species do not achieve uniformly high sentinel protection. On the rather sketchy evidence described above, I hypothesize that Watchman's song calls from sentinels occur most where foraging returns are low. The suggestion is that meerkats, dwarf mongooses, and pied babblers need the effects of Watchman's song calls to achieve overall rates of having a sentinel similar to what jungle babblers, Arabian babblers, and Florida scrub-jays achieve without these calls. By giving calls that allow foragers to greatly increase their rate of intake (Hollen et al., 2008; Bell et al., 2009), pied babbler sentinels may substantially decrease the gap until another animal is ready to become a sentinel. That gaps remain for all species suggests either that the benefits of achieving even more continuous sentinel protection are limited or that social dynamics or direct costs prevent even more and better-coordinated sentinel behavior.

11. PROSPECTS

As shown it Table 1, sentinel coordination has rarely been quantified. Surely coordination is not limited to meerkats and Florida scrub-jays, though it remains to be quantitatively documented even for other well-studied species. Besides documenting which species in Table 1 show coordinated vigilance, quantitative measures could allow us to compare coordination across species. The index of coordination that I have proposed could also be used to gauge how coordination varies within a species, e.g., across habitats or in response to call from sentinels.

Researchers may wish to test for coordination in other situations, regardless of the positions from which animals watch. Evidence suggests that vigilance in foraging flocks is not coordinated, and even somewhat anticoordinated (see Pays et al., 2007). One possible case of coordination without high positions is from mated pairs of ptarmigans. A complicated analysis found that females were more likely to feed when males were more vigilant (Artiss, Hochachka, & Martin, 1999). It would be worth testing for coordinated vigilance in mated pairs of ptarmigan and other animals.

Most research on sentinel behavior has considered the function of sentinel behavior. Clearly sentinel behavior is important for detecting potential danger. Although I have argued that sentinels generally decrease danger to themselves, sentinel behavior can further protect others, monitor rivals, and detect mating opportunities. These functions are not mutually exclusive. Within sentinel bouts, dominant male Arabian babblers give territorial calls at a higher rate than that of other group members. (Wright et al., 2001a). Sentinels in neighboring groups might simultaneously be maintaining a territorial boundary and gaining information that a predator is not approaching from the direction of their rival. In meerkats, males are sentinels more in the period just before dispersing than earlier in the same group, or later after having dispersed to another group (Clutton-Brock et al., 2002). These results suggest that males could be gathering information on meerkats in different groups while sentinels, in addition to prospecting by forays on the ground.

With regard to Tinbergen's other three questions, very little research has been done on the mechanisms of sentinel behavior and most of the work on ontogeny has observed natural changes as young grow up in natural groups (e.g., Hailman et al., 1994; Clutton-Brock et al., 2002). An exception is the observation that hand-raised dwarf mongooses did not become sentinels

even when raised in pairs. When raised in captivity with experienced individuals, the young dwarf mongooses seem to first sit together with an experienced sentinel (Rasa, 1977, 1989a). These observations are worth replicating and extending to other species. Given that meerkats are popular in captivity, research could start by surveying the sentinel behavior of meerkats born in various captive settings.

The evolutionary origin of sentinel behavior is not clear. The distribution of sentinel behavior is likely wider than revealed in the current literature. Although ecological conditions seem to play a role, the reports suggest taxonomic bias. Certain groups such as the *Turdoides* babblers seem to have sentinel behavior readily in a variety of habitats whereas other birds in the same habitat do not display sentinel behavior. Although there could be something about how *Turdoides* foraging or family life that predisposes them to sentinel behavior, at present that factor is not known. Nonetheless, the best odds to find sentinel behavior are probably in the close relatives of species already known to display sentinel behavior.

By general principles, we know that apparently complex systems are often cobbled together from existing pieces, with those pieces previously serving other functions. Therefore we note other instances where one individual watches over others, and other instances where individuals perform coordinated actions. One member of a mated pair may watch while the other feeds. This watchfulness might be guarding against rivals or predators. If the mates took turns in guarding each other, they would be performing sentinel behavior. Parents often watch over their dependent offspring. Here the roles are obviously not symmetrical. Other aspects of pairing together and raising offspring are more symmetrical and many interchanges between mated pairs suggest coordination. For example, white-whiskered puffbirds take turns watching while their mate excavates a nesting burrow (Rasmussen, Collar, del Hoyo, & Elliott, 2002). Males and females may duet in singing, and this involves coordination. Except for a few lines in Wickler (1985), no connections between duet and sentinel behavior have been noted. Males and females often relieve each other at the nest. The calls given at the end of sentinel bouts by jungle babblers resemble calls given by other species for brood relief (Wickler, 1985). Although one could imagine coordinated sentinel behavior facilitated by calls used for animals to trade off care of offspring, this link seems most likely for babblers. In Florida scrub–jays, the female breeder does the vast majority of brooding and helpers none (Woolfenden & Fitzpatrick, 1984). In meerkats and dwarf mongooses, babysitting and watching over pups tend to occur in long bouts

(Clutton-Brock et al., 1999, 2002). Although species with sentinel behavior often breed cooperatively, any causal link between these two important topics remains to be determined.

Taken together, results of this review indicate that much remains to be learned about sentinel behavior. Specifically, large gaps in knowledge exist in our understanding of the distribution, causes, fitness consequences, mechanisms, and evolutionary origins of sentinel behavior. Without more widespread testing for coordinated vigilance, it will be hard to know how widespread sentinel behavior is, and how ecological and social conditions interact in causing sentinel behavior. Long-term studies of a few species have demonstrated that sentinel behavior has antipredator functions and may have other functions. Additional insights into function would come from species that show sentinel behavior only in some seasons, habitats, or social conditions. Species with partial or facultative sentinel behavior could also provide insights into the evolutionary origins of sentinel behavior. Finally, little work has been conducted into proximate questions of sentinel behavior. Opportunities to close this gap include testing animal raised in captivity for other purposes.

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