

Coordination of safe, selfish sentinels based on mutual benefits

Peter A. Bednekoff

Biology Department, Eastern Michigan University, Ypsilanti, MI 48197, USA

Received 15 November 1999, accepted 3 April 2000

Bednekoff, P. A. 2001: Coordination of safe, selfish sentinels based on mutual benefits. — *Ann. Zool. Fennici* 38: 5–14.

Sentinels are group members that watch from prominent positions. Sentinel interchanges often appear orderly and the number of sentinels changes little despite the turnover of individuals. I modeled why solitary individuals or group members might take up prominent positions. Such positions can be safe places to rest because they provide a good view of approaching predators, even if undetected predators preferentially attack sentinels. In pairs, coordinated sentinel behavior is favored whenever information spreads from a detecting to a non-detecting individual more than half the time. Under these conditions, safety for a sentinel produces safety for a forager as a by-product. Thus sentinel behavior occurs for selfish safety reasons but coordination of sentinels is based on mutualism. If sentinels can coordinate their individual actions, evidence of the game is hidden from view. The fitness consequences of some games may be best indicated by the strategies organisms take to avoid playing them.

Introduction

Sentinels (also known as guards or sentries) are members of animal groups that watch from prominent, exposed positions while the majority of the group is engaged in some activity, usually feeding. This definition rushes past one issue, choice of position, to get on to another, the fact that other individuals are doing something else at the time. I will first consider why an animal, solitary or not, might take up an exposed position. After doing this I will consider why an animal might do this while others are doing otherwise. Then, at the end of this section, I will

discuss how the taxonomic distribution of sentinels has influenced my approach to modeling sentinel behavior.

First, why might an individual take up a high, exposed position? If we see a solitary bird or monkey in a tree, we generally assume that it is fairly safe. The reasons why it is safe are not suddenly reversed if a group of conspecifics is foraging nearby. A high, exposed position allows one to see and be seen. Seeing approaching predators should lead to safety but being seen by predators could lead to danger.

Evidence indicates that sentinels have an excellent view of impending danger and can

generally avoid it. When predators approached groups containing sentinels during two studies, a sentinel was the first to detect the predator and give an alarm call in over 92% of cases (Rasa 1987, McGowan & Woolfenden 1989). In another study, sentinels gave alarm calls at more than ten times the rate of foragers and generally gave alarm calls to predators that were still far away (Manser 1999). These studies indicate that sentinels probably have an order of magnitude advantage in detecting predators. Evidence suggests that this detection advantage is not reversed by increased odds of being singled out for attack. Suricates were less likely to be killed while sentinels than while foraging (Clutton-Brock *et al.* 1999). Besides the detection advantage, two additional factors may be important. First, sentinels often choose positions that are quite close to some protective retreat (Rasa 1989, Clutton-Brock *et al.* 1999). Second, sentinels are probably less likely than foragers to be targeted by terrestrial predators. Thus we can see that a sentinel can be safer than group members who are foraging or resting on the ground. Though other benefits (such as spotting rivals) could occur secondarily, this article concentrates on the safety advantages of sentinel behavior.

Second, why does sentinel behavior appear to be highly coordinated? The essential evidence of coordination is that different individuals come and go as sentinels but the number of sentinels varies little. If one sentinel abandons 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). Quantitatively, the timing of beginning or ending sentinel bouts by Florida scrub jays depends strongly on the actions by other group members (McGowan & Woolfenden 1989). Nonetheless sentinel bouts, in aggregate, fit the sort of random distribution that would result if bouts were equally likely to end at any moment (Hailman *et al.* 1994). These and other data (e.g. Goodwin 1986, Clutton-Brock *et al.* 1999) suggest that sentinel behavior is highly coordinated despite not being tightly organized at the group level. Previous modeling has shown that tight coordi-

nation can result from simple state-dependent decisions by individuals (Bednekoff 1997). This paper delves more deeply into the conditions necessary for coordination. Our question can be phrased as: Given that individuals reap a safety advantage from taking up high, exposed positions, why should they reap this advantage in turn rather than simultaneously?

The philosophy of this modeling exercise has been guided by considering the taxonomic distribution of sentinel behavior. Sentinels have been reported in a variety of bird and mammal taxa — corvids, babblers, parrots, weaver birds, tanagers, social mongooses, primates, and dwarf antelope — but only in a subset of each taxon (Alves 1990, Alves & Cavalcanti 1996, Bednekoff 1997). Sentinel behavior also occurs in smooth-billed anis (J. Haselmayer, pers. comm.). The taxonomic pattern of occurrence suggests that sentinel behavior has multiple, independent origins. Therefore sentinel behavior is likely to be linked to widespread ecological factors. On the other hand, that it is not found in all members of a taxon would seem to indicate that only particular combinations of these widespread factors are sufficient for sentinel behavior. Below, I construct models of sentinel behavior and coordination based on the general framework used in understanding anti-predator vigilance and other aspects of foraging under predation risk (*see* Houston *et al.* 1993, Bednekoff & Lima 1998). This framework has been highly successful but had not previously been able to bring sentinel behavior into the fold (*see* Lima & Dill 1990).

Models

Game theory analyzes situations where the rewards for each individual's actions depend upon the actions of other individuals (Maynard Smith 1982). I here use simple game theory models of sentinel behavior to complement a previous, more complicated dynamic game model (Bednekoff 1997). The previous model pointed to the crucial importance of sharing of both detection information and predation risk by group members. The current model concentrates on these factors and leaves aside state dynamics and

timing of behaviors. As before, the objective of modeling was to explore how sentinel coordination could result from the selfish actions of individual group members.

Basic formulation

In modeling foraging under predation risk, we have to make assumptions about the fitness value of food. In the previous model, some amount of food was essential but any extra food beyond this requirement was of no value (Bednekoff 1997). Since this could have undervalued foraging, here I deliberately assume a contrasting relationship that might overvalue foraging. My goal is to capture the wide field of the truth through a flanking maneuver. To the extent that the current and previous approaches yield similar conclusions, we can feel confident that those conclusions hold for the variety of relationships likely to be found in nature.

The models below assume that fitness is proportional to the gains from foraging, discounted by the odds of surviving through some period:

$$\text{Fitness} = \exp(-\alpha T \mu) K T \quad (1)$$

Survival is a negative exponential function of α (the attack rate), T (the time available), and μ (the mortality per attack). The fitness gains from foraging are proportional to T if all time is spent foraging. A constant, K , gives the exact exchange rate between foraging time and fitness gains. K happens to cancel out, and will play no major role in our drama.

Model 1: A solitary forager

Consider a single animal that can either forage or be a sentinel. If it spends some proportion of time, p , foraging and the rest, $1 - p$, as a sentinel, its fitness will be:

$$\text{Fitness} = \exp\{-\alpha T [p\mu_f + (1 - p)\mu_s]\} K p T. \quad (2)$$

Here μ_f is the mortality rate while foraging and μ_s is the mortality rate while a sentinel. By taking the derivative for p and setting it equal to

zero, we find the optimal proportion of time spent feeding:

$$p^* = \frac{1}{\alpha T (\mu_f - \mu_s)}. \quad (3)$$

Thus an animal should forage for a proportion of time inversely related to the amount it could reduce its mortality rate by becoming a sentinel. This means that it will be a sentinel more when its mortality is reduced more.

To proceed further, we need two parameters, each of which can potentially vary from zero to one: w , the proportion of attacks that are **not** detected by a foraging animal, and s , the relative likelihood of sentinel **not** detecting an attack as compared with a forager. Since by ‘detect’ we mean detect in time to escape, the per-attack mortality rate is the rate of not detecting attacks — $\mu_f = w$ for foragers and $\mu_s = sw$ for sentinels. For $s < 1$, sentinels detect more attacks and are, therefore, safer. In the equation above, $\mu_f - \mu_s = w - sw$, which can be rewritten as $w(1 - s)$.

Despite this survival advantage, the optimal strategy might be to feed all the time, $p^* = 1$. In looking for cases where animals spend part of their time as sentinels, we note that $p^* < 1$ rearranges to $\alpha T w(1 - s) > 1$. Thus, sentinel behavior is more likely to occur when the number of expected attacks, αT , is high, these attacks go undetected at a high rate, w , or by when sentinels are much more likely to detect attacks than are foragers, i.e. when s is small.

Model 2: A pair of animals

Now consider the behavior of a pair of animals. Each individual acts to maximize its own fitness, but its survival (and therefore its fitness) depends on the actions of another. This dependence on the actions of others brings our analysis into the realm of game theory.

At this point we add two parameters to the framework from above: i — the proportion of times that an individual that has not detected a predator learns of its approach somehow through the actions of a detecting individual; and d — how risk is diluted between a sentinel

and a forager when neither the sentinel nor forager have detected the predator. Each of these parameters can potentially vary from zero to one.

Now we have four mortality terms, depending on whether each of the two animals is a sentinel or a forager. For each term, the first subscript gives the action of the focal animal and the second subscript the actions of its companion. For example, $\mu_{f,s}$ is the mortality rate of a forager when its companion is a sentinel.

$$\mu_{f,s} = w(1-sw)(1-i) + (1-d)sw^2 \quad (4)$$

$$\mu_{f,f} = w(1-w)(1-i) + 0.5w^2 \quad (5)$$

$$\mu_{s,f} = sw(1-w)(1-i) + dsw^2 \quad (6)$$

$$\mu_{s,s} = sw(1-sw)(1-i) + 0.5(sw)^2 \quad (7)$$

In each of these four equations, the left term shows when the focal animal has not detected an attack but its companion has. Mortality occurs when the information does not spread, $(1-i)$. Although detection information is probably spread by alarm calls in most cases, information transfer does not require deliberate announcement by individuals that detect approaching predators. For instance, vervet monkeys take the sudden departure of a sentinel as cause for alarm (Horrocks & Hunte 1986).

In each of these four equations, the right term occurs when neither animal has detected an attack. When the two animals are doing the same thing, they are equally likely to be attacked by the predator. When one animal is a sentinel and the other a forager, the sentinel is attacked some proportion of the time, d , and the forager the rest, $1-d$. (For more on information and attack sharing, see Bednekoff & Lima 1998b).

We are now ready to consider sentinel games. We start with a case where the companion essentially refuses to play. If the companion is never a sentinel, the fitness of the focal animal is:

$$\text{Fitness} = \exp\{-\alpha T[p\mu_{f,f} + (1-p)\mu_{s,f}]\} KpT, \quad (8)$$

and the optimal proportion of time to forage is:

$$p^* = \frac{1}{\alpha T(\mu_{f,f} - \mu_{s,f})}. \quad (9)$$

This is not much of a game. The companion is essentially a fixture of the environment. Therefore, we are not surprised that the results for this game look almost exactly like those for an animal alone. The only difference is that:

$$\mu_{f,f} - \mu_{s,f} = w(1-w)(1-i)(1-s) + (0.5 - sd)w^2. \quad (10)$$

This will be positive for most values (e.g. whenever $sd < 0.5$), but is generally smaller than the equivalent function for a single animal ($\mu_f - \mu_s = w(1-s)$). Thus, a solitary animal will generally feed less and be a sentinel more than a member of a pair (Fig. 1). Also note that d , the risk dilution parameter, has little effect unless s is simultaneously large (Fig. 1). In other words, the relative odds of being targeted by a predator have little effect on the decision to become a sentinel unless the view from a high position is little better than the view from the ground.

Now we consider the value of alternation within a set allocation of time to foraging and sentinel behavior. Alternation is favored if it is less dangerous to forage when another is a sentinel and be a sentinel when another is foraging than to match the actions of the other. Since the total time allocation is the same, most terms from the full fitness equation cancel out such that the condition for alternation is $\mu_{f,f} + \mu_{s,s} > \mu_{s,f} + \mu_{f,s}$. In full form, this initially looks formidable:

$$w(1-w)(1-i) + 0.5w^2 + sw(1-sw)(1-i) + 0.5(sw)^2 > sw(1-w)(1-i) + dsw^2 + w(1-sw)(1-i) + (1-d)sw^2. \quad (11)$$

After rearranging and canceling, however, this yields the simple condition: $i > 0.5$. Sentinel coordination should occur whenever information has more than half a chance of getting from an animal that has detected a predator to one that has not. Furthermore, information spread, i , has a minor impact on the value of taking up sentinel positions (Fig. 2). In this figure, the region where such positions are worth taking is neatly divided into regions where they are worth taking in turns versus worth taking simultaneously.

Now, let us consider two animals that perfectly coordinate their sentinel behavior. If the focal animal forages p proportion of the time and its companion \hat{p} , we first consider situa-

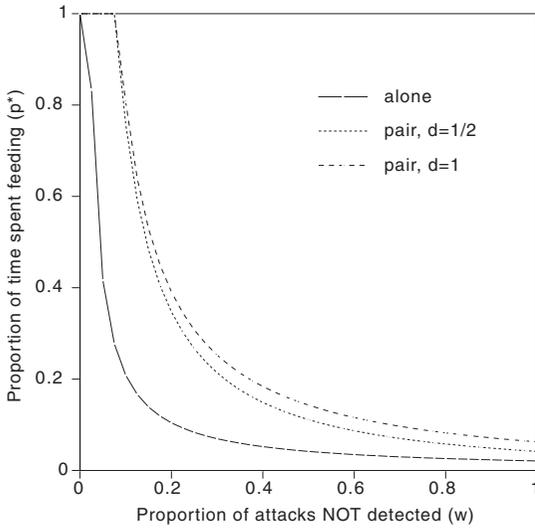


Fig. 1. Effect of failure to detect attacks on the optimal proportion of time spent feeding. The three curves show that animals in pairs feed more than if alone, with the probability of sentinels being targeted, d , having little effect. Here $\alpha T = 64$, $s = 0.25$ and $i = 0.75$.

tions where $p + \hat{p} \geq 1$ — that is where at least one sentinel is available at all times. Here the fitness of the focal animal is:

$$\text{Fitness} = \exp\{-\alpha T[(p + \hat{p} - 1)\mu_{r,f} + (1 - \hat{p})\mu_{r,s} + (1 - p)\mu_{s,r}]\} KpT. \quad (12)$$

Here both animals forage simultaneously some but the focal animal forages through the time its companion is a sentinel and the companion forages throughout the time the focal animal is a sentinel. Solving for p^* yields exactly the same value as Eq. 9. Since \hat{p} does not appear in this equation, it appears that the amount of time a companion spends as a sentinel is irrelevant to the optimal action (but *see* below).

For $p + \hat{p} \leq 1$, the equation changes somewhat to:

$$\text{Fitness} = \exp\{-\alpha T[p\mu_{f,s} + \hat{p}\mu_{s,f} + (1 - (p + \hat{p}))\mu_{s,s}]\} KpT. \quad (13)$$

Here the focal animal forages only when its companion is a sentinel and its companion forages only when it is a sentinel, but both animals are also sentinels simultaneously for some time. The optimal amount of time spent foraging is:

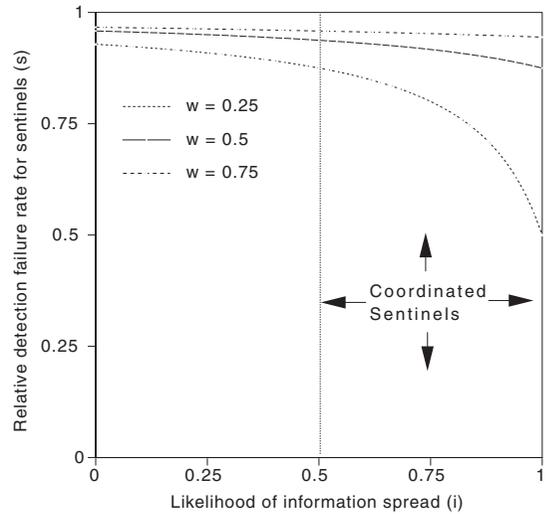


Fig. 2. High exposed positions are worth occupying when the relative rate of detection failure for sentinels, s , is lower than some critical value. This graph shows how this critical value depends on the likelihood of information spread, i , and the rate at which foragers fail to detect attacks, w . The vertical line gives the critical condition for sentinel coordination, $i > 0.5$. Here $d = 0.5$, and $\alpha T = 64$.

$$p^* = \frac{1}{\alpha T(\mu_{f,s} - \mu_{s,s})}. \quad (14)$$

Once again, p^* does not explicitly depend on \hat{p} . However, the mortality difference in the denominator will be smaller here than in Eq. 9, because both mortality terms are smaller by similar proportions. Thus, this equation will yield larger values of p^* than Eq. 9. Implicitly, this gives a region of response hidden in the switch of equations at $p + \hat{p} = 1$: The equation appropriate if $p + \hat{p} < 1$ produces a p^* such that $p^* + \hat{p} > 1$ and the equation appropriate if $p + \hat{p} > 1$ produces a p^* such that $p^* + \hat{p} < 1$. Thus, the optimal response actually produces a region when $p + \hat{p} = 1$ (Fig. 3). An implication of this analysis is that groups might converge on having a sentinel at all times despite differences in group size and composition.

Finally, if sentinel behavior were not coordinated, the sentinel and foraging periods of individuals would overlap at random. This would lead to the following equations:

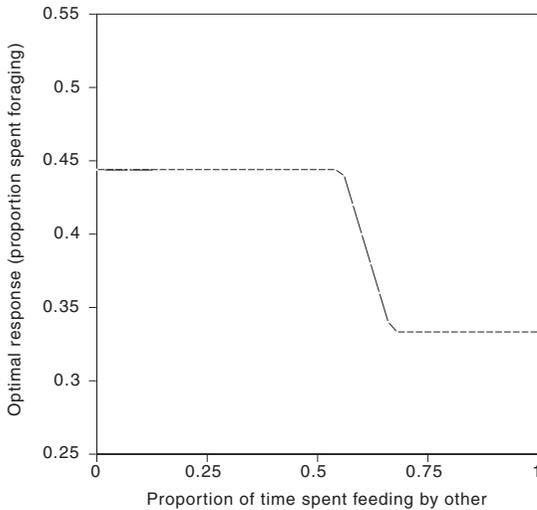


Fig. 3. Optimal response of a focal animal to the proportion of time that the other member of a pair is feeding. Along the downward slope, one member of the pair is always a sentinel while the other feeds. Here $d = 0.5$, $s = 0.25$, $w = 0.5$, $i = 0.75$ and $\alpha T = 16$.

$$\text{Fitness} = \exp\{-\alpha T [p \hat{p} \mu_{f,f} + p(1 - \hat{p}) \mu_{f,s} + (1 - p) \hat{p} \mu_{s,f} + (1 - p)(1 - \hat{p}) \mu_{s,s}]\} K p T \quad (15)$$

$$p^* = \frac{1}{\alpha T (\hat{p} \mu_{f,f} + (1 - \hat{p}) \mu_{f,s} - \hat{p} \mu_{s,f} - \hat{p} \mu_{s,s})}. \quad (16)$$

Here, the optimal amount of sentinel behavior does depend on the actions of the other animal. We are left with a bit of a paradox. Interdependence of mortality rates sets up the basic game, but the response, coordination, can essentially eliminate the surface evidence of the game. At least in this case, the fitness importance of the game is inversely related to the likelihood of showing behavior that would suggest a game is occurring. This may prove to be true for many cases of cooperation under predation risk or other situations dominated by the possibility of mutual benefits.

Discussion

These models show that improved predator detection combined with the spread of detection information can provide a simple, sufficient basis for coordinated sentinel behavior. The occurrence of sentinels depends on various fac-

tors affecting danger to the sentinel but sentinel coordination depends simply on the spread of detection information. These conclusions complement and extend those reached previously using a considerably different model (Bednekoff 1997). That such different models produce similar outcomes greatly increases our confidence in the generality of the conclusions.

The current models provide much more detailed insight into the relationship between coordination and information spread. In the models developed above, coordination is favored whenever $i > 0.5$. With a group of two, this is when the gain due to information makes up for the loss of risk dilution (*see* Bednekoff & Lima 1998b). Although previous work indicated that information spread was important (Bednekoff 1997), the new models show precisely how information spread makes safety for foragers a by-product of the safety of sentinels. With $i > 0.5$, the safety of a sentinel produces enough safety for a forager to make coordination favorable. If such positions were safe but detection information did not spread reliably (i.e. $i < 0.5$), we would most likely observe the entire group shuttling in unison between foraging and high positions.

In the model above, a single sentinel in a population of non-sentinels gains a selfish survival benefit. Furthermore, in a population where sentinels were not coordinated, any individual that placed its sentinel bouts around those of others would gain an additional benefit. Whenever information spreads from detectors to non-detectors with sufficient frequency, the rewards of sentinel behavior are greatest when group members avoid being sentinels at the same time. Through the spread of detection information, these individuals would incidentally also improve the survival of other group members. As selfish behavior happens to produce benefits for others, sentinel coordination is based on by-product mutualism (Dugatkin 1996).

This work emphasizes that we should not take behavioral alternation as a sign of reciprocal altruism. Although our hypothetical examples of by-product mutualism often involve simultaneous actions and our hypothetical exam-

ples of reciprocal altruism often involve alternating actions, behavioral alternation is not a distinguishing feature of reciprocal altruism. By-product mutualism and reciprocal altruism are defined by pay-off structures and can only be differentiated by measuring the actual pay-offs (see Clements & Stephens 1995, Dugatkin 1996). Many instances of alternation in evolutionary ecology may in fact be based on mutualism. For example, complicated alternating choruses or group displays could arise because each animal best advertises itself when others are not (see Greenfield 1994).

The models developed in this paper differ in one important way from previous efforts (Bednekoff 1997). The current models predict a graded response to factors influencing danger whereas the previous model basically predicted an all-or-nothing result. This difference in output is due to using different assumptions about the fitness value of food. The current approach matches with observations that individual rates of sentinel behavior decline with group size (Hailman *et al.* 1994, Clutton-Brock *et al.* 1999) while the previous did not (see also Lima & Bednekoff 1999b). Because it allows graded responses by individuals, the current approach suggests that individuals may often adjust their own rates of sentinel behavior such that the group generally has one sentinel at all times.

Testing the selfish sentinel framework

Various lines of evidence could show that sentinel behavior leads to selfish benefits. Comparing the mortality rates of sentinels and other group members is logically straightforward, but logistically challenging. To my delight, this has actually been accomplished (Clutton-Brock *et al.* 1999). Fortunately for researchers without a small army of observers, some alternative tests of this framework are possible.

One simple phenomenon, in fact, could potentially separate the selfish sentinel explanation from its competitors: Animals are sentinels even when not members of groups (see Clutton-Brock *et al.* 1999). Explanations of sentinel behavior involving dynamics within groups do

not apply when groups are not present. Thus, the occurrence of solitary sentinels points directly to selfish benefits and relegates kin selection, reciprocal altruism, mutual dependence, and other explanations to complementary roles (see Zahavi 1990, Bednekoff 1997, Clutton-Brock *et al.* 1999).

In contrast, testing for a rota of guard duties does little to refute any of the candidate explanations (see Rasa 1989, Clutton-Brock *et al.* 1999). Failure to find any pattern in the sequence of sentinel interchanges would be some evidence against a role for reciprocal altruism, but the test faces two major problems. First, no particular pattern is predicted so failure to find a rota could be due to testing for the wrong pattern. Second, no patterns are forbidden by the other candidate explanations. For example, state-dependent selfish decisions (see Bednekoff 1997) might well produce a rota if foraging was fairly predictable.

Similarly, the models above cannot be refuted by observing that sentinel behavior is rich in details that are beyond the scope of the models. For example, sentinels often give special calls either throughout sentinel bouts or shortly before ending sentinel bouts. These calls lead to more efficient coordination of sentinel bouts (Manser 1999). To my mind, these are fascinating as ways to ensure the mutual benefits of coordination, but do not illuminate the primary basis for sentinel behavior.

Considering sentinel behavior within a foraging-predation trade-off suggests that animals that find food more quickly will have more time to spend as sentinels. In nature, sentinel behavior is often most frequent by those individuals whose age, sex, and status would allow them to find food most quickly (reviewed in Bednekoff 1997). If food finding is directly linked to sentinel behavior, supplementary feeding should lead to more sentinel behavior (Bednekoff 1997). In two studies, this prediction has been borne out (Clutton-Brock *et al.* 1999; P. A. Bednekoff & G. E. Woolfenden, unpubl. data). These tests show that animals act as if sentinel behavior has benefits but do not, on their own, show that these benefits are selfish rather than mediated by, for example, kin selection.

When does sentinel behavior occur, and not occur?

Even within species sentinel behavior is more pronounced in some times and places. In general, sentinel behavior is most likely in moderately open habitats (*see* Bednekoff 1997). It seems that sentinels occur only when high, exposed perches offer a substantially better view of the surrounding world. In very open habitat, a good view is available without leaving the ground. In very dense habitats, no position affords much of a view. Also, since cover is always at hand in dense habitats, potential prey do not need to detect predators at as great a distance in order to escape.

Sentinel behavior also is linked to intense predation pressure. Suricates living in similar habitats were sentinels much more often in an area with many predators than in an area with few (Clutton-Brock *et al.* 1999). In general sentinel behavior seems to be often linked to the intensity of raptor predation, but the balance of terrestrial and aerial predators is perhaps also important.

Moderately open habitats and intense predation pressure can favor taking up high, exposed positions. Fairly efficient spread of detection information, however, is the key basis for a coordinated sentinel system. Recent work has shown that members of bird flocks often cannot distinguish escape flights from normal departures and so gain little information when other individuals detect approaching threats (Lima 1995a, 1995b, Roberts 1997). Such haphazard spread of detection information matches with sentinel alternation **disfavored** when $i < 0.5$ in our models of pairs of animals. Instead of a subset of a group being sentinels at any one time, we would expect the whole group to forage or roost simultaneously. Such behavior is so normal that we generally fail to notice it.

Origins and tests of sentinel behavior

I offer a few anecdotes as evidence that sentinel behavior is not fundamentally different from other behaviors. The tail-down posture and regular scanning that characterize scrub jay sentinel

behavior in the field (McGowan & Woolfenden 1989) occurred in the laboratory when scrub jays did not seem very interested in their “work” of caching or recovering food (*see* Bednekoff *et al.* 1997). Thus sentinel behavior is basically this watchful resting. On Santa Cruz Island, where raptors pose almost no threat, scrub jays sometimes rest in high positions, but are far less watchful than the sentinels of Florida scrub jays (P. A. Bednekoff, personal observations). Finally, mockingbirds sitting on shrubs look very much like scrub jay sentinels from a distance (P. A. Bednekoff, personal misobservations). What is clearly different between these is the presence of conspecifics nearby.

With these things in mind, I suggest we should study sentinel behavior where it is not fully developed. Knowing that sentinels may be present only in some habitats or under certain forms or intensities of predation threat allows us to look more widely for sentinels. Sentinel behavior might occur, for example, in response to the passage of large numbers of migratory raptors. We may even be able to build experimental feeding areas in which animals demonstrate sentinel behavior. The response to these areas might be very different when comparing species that regularly give alarm calls to those that do not. Also, phenomena akin to sentinel behavior may be common in mated pairs. Alternate watching during gathering of nest materials has been reported for both scrub jays and blue jays (Hardy 1961) and adults may watch over their mates and nests to prevent predation (Morton & Shalter 1977, Yasukawa *et al.* 1992). Although not all these phenomena will be strongly linked to sentinel behavior, I suggest that noting the similarities will greatly increase our understanding of the possible origins of sentinel behavior.

Taking vigilance to the highest level

This article has assumed that sentinel behavior is best understood using the general principles of foraging under predation risk and anti-predator vigilance (Lima & Dill 1990, Houston *et al.* 1993, Bednekoff & Lima 1998a, 1998b). This perspective has proven fruitful but an obvious contrast remains — sentinels place their watches around

those of others whereas foragers show no coordination of their vigilance glances (Bednekoff & Lima 1998a, 1998b), even though coordinated vigilance would apparently yield benefits (Ward 1985). We can harmonize this contrast by examining two principles: The spread of detection information from detector to non-detector and the amount that behavior increases the chances of predator detection. We have already discussed information spread but not information gathering. Recent work indicates that non-vigilant animals can often detect attacks, though not as well as vigilant animals (Lima & Bednekoff 1999a). Vigilance and sentinel behavior represent parts of a continuum on which gathering of food is sacrificed to increase gathering of information about predation risk. By recognizing this continuum we can see that sentinel behavior is literally taking vigilance to the highest level.

Acknowledgments

Many of the specific skills used to write this paper were developed during my collaboration with Steve Lima. I thank the other symposium participants for many stimulating discussions in Jyväskylä and two anonymous reviewers for helpful comments on the manuscript. Permission to visit the Santa Cruz Island Reserve was granted by the University of California Natural Reserve System. I was funded by the Graduate Studies and Research Support Fund and World College at Eastern Michigan University, and by National Science Foundation grant IBN-9723437.

References

- 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. Neotropical* 7: 43–51.
- Bednekoff, P. A. 1997: Mutualism among safe, selfish sentinels: a dynamic game. — *Am. Nat.* 150: 373–392.
- Bednekoff, P. A., Balda, R. P., Kamil, A. C. & Hile, A. G. 1997: Long term spatial memory in four seed caching corvid species. — *Anim. Behav.* 53: 335–341.
- Bednekoff, P. A. & Lima, S. L. 1998a: Randomness, chaos and confusion in the study of anti-predator vigilance. — *Trends Ecol. Evol.* 13: 284–287.
- Bednekoff, P. A. & Lima, S. L. 1998b: Re-examining safety in numbers: interactions between risk dilution and collective detection depend upon predator targeting behavior. — *Proc. R. Soc. Lond. B* 265: 2021–2026.
- Clements, K. C. & Stephens, D. W. 1995: Testing models of non-kin cooperation: mutualism and the Prisoner's Dilemma. — *Anim. Behav.* 50: 527–535.
- 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.
- Dugatkin, L. A. 1997: *Cooperation among animals*. — Oxford University Press, Oxford, U.K.
- 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 ed.) — British Museum (Natural History), London.
- Greenfield, M. D. 1994: Cooperation and conflict in the evolution of signal interactions. — *Ann. Rev. Ecol. Syst.* 25: 97–126.
- 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.
- Hardy, J. W. 1961: Studies in behavior and phylogeny of certain new world jays (Garrulinae). — *University of Kansas Science Bulletin* 42: 13–149.
- Horrocks, J. A. & Hunte, W. 1986: Sentinel behaviour in vervet monkeys: who sees whom first. — *Anim. Behav.* 34: 1566–1567.
- Houston, A. I., McNamara, J. M. & Hutchinson, J. M. C. 1993: General results concerning the trade-off between gaining energy and avoiding predation. — *Phil. Trans. R. Soc. Lond. B* 341: 375–397.
- Lima, S. L. 1995a: Back to the basics of anti-predatory vigilance: the group size effect. — *Anim. Behav.* 49: 11–20.
- Lima, S. L. 1995b. Collective detection of predatory attack by social foragers: fraught with ambiguity? *Animal Behaviour* 50: 1097–1108.
- Lima, S. L. & Bednekoff, P. A. 1999a: Back to the basics of antipredatory vigilance: can nonvigilant animals detect attack? — *Anim. Behav.* 58: 537–543.
- Lima, S. L. & Bednekoff, P. A. 1999b: Temporal variation in danger drives anti-predator behavior: the predation risk allocation hypothesis. — *Am. Nat.* 153: 649–659.
- Lima, S. L. & Dill, L. M. 1990: Behavioral decisions made under the risk of predation: a review and prospectus. — *Can. J. Zool.* 68: 619–640.
- Manser, M. B. 1999: Response of foraging group members to sentinel calls in suricates, *Suricata suricatta*. — *Proc. R. Soc. Lond. B* 266: 1013–1019.
- Maynard Smith, J. 1982: *Evolution and the theory of games*. — Cambridge University Press, Cambridge.
- McGowan, K. J. & Woolfenden, G. E. 1989. A sentinel system in the Florida scrub jay. — *Anim. Behav.* 34: 1000–1006.

- Morton, E. S. & Shalter, M. D. 1977: Vocal response to predators in pair-bonded Carolina Wrens. — *Condor* 79: 222–227.
- Rasa, O. A. E. 1987: Vigilance behaviour in dwarf mongooses: selfish or altruistic? — *S. Afr. J. Sci.* 83: 587–590.
- Rasa, O. A. E. 1989: Behavioural parameters of vigilance in the dwarf mongoose: social acquisition of a sex-biased role. — *Behaviour* 110: 125–145.
- Roberts, G. 1997: How many birds does it take to put a flock to flight? — *Anim. Behav.* 54: 1517–1522.
- Ward, P. 1985: Why birds do not coordinate their vigilance. — *J. Theor. Biol.* 114: 383–385
- Yasukawa, K., Whittenberger, L. K. & Nielsen, T. A. 1992: Anti-predator vigilance in the red-winged blackbird, *Agelaius phoeniceus*: do males act as sentinels? — *Anim. Behav.* 43: 961–969.
- Zahavi, A. 1990: Arabian babblers: the quest for social status in a cooperative breeder. — In: Stacey, P. B. & Koenig, W. D. (eds.), *Cooperative breeding in birds: long-term studies of ecology and behavior*: 103–130. Cambridge University Press, Cambridge.