

# Evolutionary stability of vigilance coordination among social foragers

Miguel A. Rodríguez-Gironés<sup>1</sup> and Rodrigo A. Vásquez<sup>2\*</sup>

<sup>1</sup>Department of Plant–Animal Interactions, Centre for Limnology, Netherlands Institute of Ecology, PO Box 1299, NL-3600 BG Maarssen, The Netherlands (mar\_girones@yahoo.com)

<sup>2</sup>Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile

Coordination can greatly improve the efficiency of anti-predatory vigilance scans by increasing predator detection for a constant proportion of time spent vigilant. However, it has been rarely found in nature and most studies have detected or assumed independent scanning by group members. In this study, we analysed the functional consequences of the coordinated alternation of vigilance scanning by group foragers. We introduce coordination by assuming that interscan intervals (ISIs) follow a modified gamma distribution. Depending on the parameters of the distribution, successive scans can be evenly spaced (coordinated scanning) or may present a high overlap (uncoordinated scanning). Comparing evolutionarily stable strategies for animals that do not coordinate their scanning with animals that do coordinate their anti-predator behaviour shows that coordination has a marked effect on survival probability. Moreover, the coordinating strategy is quite robust against mutants that scan independently with exponential distributions of ISIs. However, coordination breaks down when animals can continuously adjust their level of coordination by deciding the proportion of time they spend monitoring the behaviour of other group members. In this case, coordination is only evolutionarily stable if it can be very easily achieved.

**Keywords:** anti-predator behaviour; evolutionarily stable strategies; game theory; group size; vigilance scan

## 1. INTRODUCTION

Anti-predator vigilance in social foragers is a conspicuous and well-studied behaviour in a variety of vertebrates. By increasing survival through predator detection, vigilance has a clear positive effect on an animal's fitness. Theoretical models of social vigilance assume independent scanning by group members (e.g. Pulliam 1973; Pulliam *et al.* 1982), although there is no functional (evolutionary) analysis of this assumption (Bednekoff & Lima 1998). Independent scanning diminishes the probability of predator detection by group members (Ward 1985; Lima 1990), so that if detection information was rapidly shared among group members, predator avoidance would increase significantly if group members coordinate their vigilance (Bednekoff & Lima 1998). Therefore, vigilance coordination, i.e. the alternation of vigilance events into non-overlapping bouts, seems to have an obvious adaptive advantage. However, vigilance coordination has not been detected (e.g. Elcavage & Caraco 1983). Why is this so? There are at least two possibilities. Either coordination is not very efficient or it is too costly to achieve (Ward 1985; Lima 1995). Coordination would be inefficient if there was poor information sharing or if it did not lead to a significant increase in the probability that predators are detected by at least one group member. The former possibility seems unlikely, for two reasons. First, the ubiquitous group-size effect (Lima 1990, 1995; Roberts 1996) is often predicted if detection by an individual improves the probability that other group members survive (see Lima (1990) for other factors that influence the group-size

effect). Second, in several species that form small foraging groups, say of two to eight individuals, information transfer seems to be adequate (e.g. Kenward 1978; Godin *et al.* 1988; Vásquez 1997). Ward (1985) suggests that coordination does not greatly increase the probability that the group detects the predator. In his analysis, Ward (1985) assumes that the goal of group members is to ensure that the proportion of time that no individual of the group is vigilant does not exceed a certain value. He then calculates the proportion of time that each individual must scan for predators in order to achieve this goal, with and without coordination. He found that coordination leads to a tiny decrease in individual scanning time. Ward (1985) therefore concludes that any small cost associated with coordination will offset its benefits. It is important to notice that the probability of not detecting a predator is not directly given by the proportion of time that no individual group member is scanning. Indeed, if one of two foraging groups produces a scan of 1 s every 10 s, and the other a scan of 10 s every 100 s, the proportion of time that no group member scans is the same for both groups, while predation rate is most probably very different. Scannell *et al.* (2001) suggest that the observed distribution of anti-predator scans would be beneficial if predators studied the behaviour of individual prey and timed their attacks accordingly. If, however, prey scanned following a Poisson process as it is normally assumed, there would be no incentive for predators to spend time observing prey, predators would be selected to attack prey as soon as they detected them, and prey would be selected to scan at regular intervals. It seems to us, therefore, that the solution proposed by Scannell *et al.* (2001) is not evolutionarily stable.

\* Author for correspondence (rvasquez@uchile.cl).

The aim of this paper is to quantify how costly coordination must be to make it evolutionarily unstable when we take into account not only the proportion of time spent scanning, but also the temporal distribution of anti-predator scans. To study the problem of coordination of anti-predator scans in groups of foraging animals, we proceed in two directions. We first compare the expected fitness of animals that either participate or do not participate in the coordination of scanning events, and then we develop a model where individuals must determine how much of their time they spend foraging, how much scanning and how much coordinating their behaviour. In this model, we assume that the degree of coordination that ensues is a certain function of the time that individuals spend coordinating their behaviour, and we look for evolutionarily stable values of the proportion of time spent scanning for predators and coordinating anti-predator behaviour. Our approach is focused on social foragers that form loose foraging groups and take advantage of the group-size effect on vigilance behaviour, as occurs in several species of birds (e.g. Bertram 1980; Lima 1995) and mammals (e.g. Monaghan & Metcalfe 1985; Vásquez 1997).

## 2. BASIC MODEL

The idea is to introduce the possibility to coordinate behaviour in as simple a model as possible. For this reason, we start with a game-theory model almost identical to the one by Pulliam *et al.* (1982). The basic model assumes that  $n$  individuals are foraging in a group. Individual  $i$  spends a proportion  $w_i$  of its time scanning for predators: a scan has a fixed duration  $\tau$  and the interval between consecutive scans of an individual is a random variable, which is drawn from some distribution. (Different versions of the model will make different assumptions about the shape of this distribution.) Predators need some time  $T$  to approach the foraging group. Any overlap between this approach time and a vigilance scan implies that the predator is detected. If, however, no individual is scanning for any fraction of the approach time, the predator is not detected. We call  $\rho$  the probability that the predator is not detected. It is a function of how interscan intervals (ISIs) are distributed.

### (a) *Predator detection*

We calculate the probability  $\rho$  for two distributions of ISIs. If scan initiation by each individual follows a Poisson process and predator detection works independently for different animals, then (see, for example, Pulliam *et al.* 1982; McNamara & Houston 1992)

$$\rho = \left( \prod_i (1 - w_i) \right) \times \exp \left\{ - \frac{T}{\tau} \sum_i \frac{w_i}{1 - w_i} \right\}. \quad (2.1)$$

Equation (2.1) underlies most models of the evolution of vigilance behaviour. As Bednekoff & Lima (1998) point out, although the experimental data tend to support the assumption of an (almost) exponential distribution of ISIs with independent behaviour between group members, there is no identified functional reason why this should be so.

To introduce the possibility of coordinated scanning, we proceed as follows. Rather than taking into account how the scanning events of each individual are distributed in time, we look at the group-level distribution of scans. Thus, if there are  $n$  animals foraging in a group, we look at the times  $t_1, t_2, \dots, t_i$  when the first, second, ...,  $i$ th scan events are initiated, regardless of which animal performs each event. We call ISIs the times  $t_2 - t_1, t_3 - t_2, \dots, t_{i+1} - t_i$ . Coordinated scanning is achieved when these ISIs are relatively homogeneous. We use the coefficient of variation (standard deviation/mean),  $\gamma$ , of the distribution of ISIs as an index of coordination. When  $\gamma = 0$  there is no variability in the ISI and coordination is perfect. We will say that there is no coordination if  $\gamma = 1$ . (In principle, the distribution of ISIs may have  $\gamma > 1$ , but we will not consider this possibility here because the exponential distribution considered in previous models has  $\gamma = 1$ .) Notice that we define the ISI as the time between the starts of two consecutive scans by any individual, and not as the time between the end of a scan and the start of the following one by the same individual. Given a group-level distribution of ISIs,  $\rho$  can be calculated in the manner described in Appendix A (equation (A 2)).

In practice, the group-level distribution of ISIs must be the result of individual behaviour. In this article, we do not propose any mechanism through which individual behaviour could lead to a gamma distribution of group-level ISIs. That is, we do not propose any distribution of individual ISIs such that when all members of a group behave according to this distribution the group-level ISIs follow a gamma distribution. We simply explore the consequences that the existence of such a mechanism would have.

### (b) *Probability of survival*

We assume that if the predator arrives undetected it manages to capture a group member with probability 1. If, however, the predator is detected, we assume that the probability that it captures a foraging animal is  $b$ , with  $0 \leq b < 1$ . (We will loosely refer to  $b$  as the scanning efficiency.) For simplicity and to minimize the number of parameters in the model, we assume that when a predator is detected all group members have the same probability of escape, regardless of whether they were scanning or not at the time of the attack. In the case where the predator succeeds to capture a group member, we assume that its prey is selected at random. Hence, the probability that a focal individual survives an attack,  $s$  is

$$s = 1 - \frac{(1 - b) \times \rho + b}{n}, \quad (2.2)$$

where  $\rho$  is given by equation (2.1) or (A 2), as appropriate. An individual must forage for some fixed time  $T_f$  in order to survive. If an animal spends a proportion  $u$  of its time foraging, then the time  $T_g$  that it must remain exposed to predators to achieve a cumulative time of  $T_f$  foraging seconds is

$$T_g = \frac{T_f}{u}. \quad (2.3)$$

Pulliam *et al.* (1982) calculate the relationship between  $s$  and the expected fitness of a strategy as the probability that an individual survives a number of attacks that is the

number expected during a time  $T_g$ . As McNamara & Houston (1992) point out, this method overestimates the probability of predation. If there is a certain probability,  $p_b$  that there are exactly  $l$  attacks during  $T_g$ , then the probability that a focal individual survives the day,  $G$ , is

$$G = \sum_l p_l \times s^l. \quad (2.4)$$

If predator arrival follows a Poisson process with rate  $\theta$ , then

$$p_l = \frac{(\theta \times T_g)^l \times e^{-\theta \times T_g}}{l!}, \quad (2.5)$$

and therefore

$$G = e^{-(l \times s) \times \theta \times T_g}. \quad (2.6)$$

McNamara & Houston (1992) offer a method to calculate the evolutionarily stable strategy (ESS) of related models. Unfortunately, their method assumes that predator detection works independently for different animals, so that  $\rho$  is a product of  $n$  factors, each factor being the probability that one animal in the group detects the predator. Clearly, this assumption does not hold when vigilance is coordinated, so we cannot use the method of McNamara & Houston (1992) for our study. Instead, we notice that, for an individual animal,  $G$  is maximized when the quantity

$$\phi = 1 - \frac{l - s}{u}, \quad (2.7)$$

is maximized, so we take  $\phi$  as the payoff associated with a strategy and look for the values that lead to its maximum value. Thus, although  $G$  is a function of predation pressure  $\theta$  and foraging time  $T_b$ , the optimal behaviour is independent of these parameters and we will therefore ignore them in the rest of this article.

A strategy will be defined as a combination of three values,  $u$ ,  $w$  and  $c$ , where  $u$  is the proportion of time spent foraging,  $w$  the proportion of time spent scanning for predators and  $c$  the proportion of time spent coordinating anti-predator behaviour. As shorthand, we will refer to  $c$  as the 'coordination time'. We assume that these activities are mutually exclusive (but see Lima & Bednekoff 1999) and that they comprise the entire time budget of foraging animals, so that  $u + w + c = 1$ . Figure 1 shows how  $G$  depends on  $c$  and  $w$  when the probability that the predator is not detected is calculated according to equation (A 2). When drawing figure 1, we have assumed that all group members behave equally, so it is of no use when computing the ESS: it is shown merely for illustration purposes.

### 3. EFFICIENCY OF COORDINATED SCANNING

Ward (1985) claims that the proportion of time spent scanning for predators required to obtain a certain probability of detecting predators is virtually the same with and without coordination. To check this explicitly, we compare the payoffs at the ESS for two sets of strategies: with and without coordination, and we calculate how much time needs to be spent in coordination for both payoffs to be equal. To do this, we calculate the ESS, as a function of the group size,  $n$ , and scanning efficiency,  $b$ , when  $\rho$  is

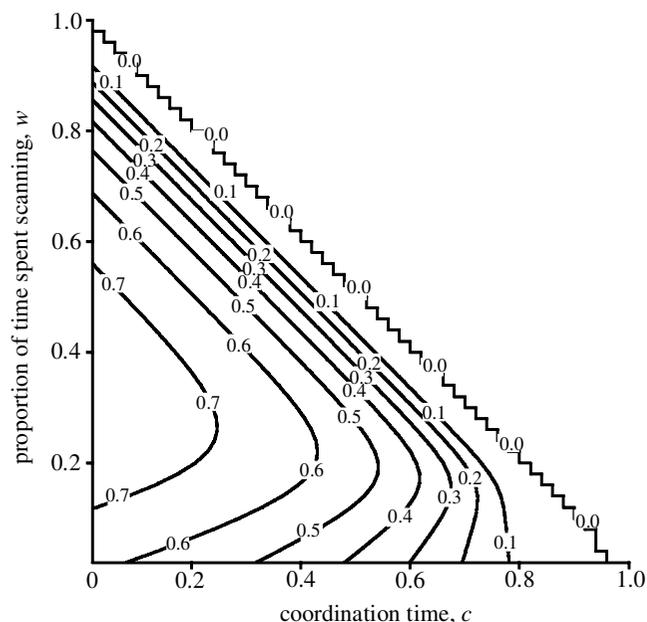


Figure 1. Contour plot of the probability that a focal individual survives the day,  $G$ , versus  $c$  and  $w$ , when the ISI follows a gamma distribution with offset. Parameters are  $T_f - \theta = 1$ ,  $n = 2$  and  $b = 0.3$ . The relationship between  $\gamma$  and  $c$  is  $\gamma = 0.05 + 0.95 - (1 - c)$ . (Calculations become inaccurate for very low  $\gamma$ , hence the lower limit.)

given by equation (A 2) with  $\gamma = 1$  and when individuals do not allocate any time to coordination ( $c = 0$ ). We denote by  $\phi_u$  the associated payoff. We next compute the ESS when the coefficient of variation of the ISI is  $\gamma < 1$  and animals allocate some time to coordination,  $c > 0$ . In these calculations, we assume that  $\gamma$  and  $c$  are fixed. Animals must spend a proportion  $c$  of their time coordinating their scans, and the coefficient of variation of the ISI is  $\gamma$  as a result. The only strategic variable that the animals have is  $w$ . (Notice that, in this scenario, animals must spend the coordination time even if they choose not to scan.) We denote by  $\phi(\gamma, c)$  the associated payoff for this new set of strategies. For  $\gamma < 1$ , because coordinated scanning is more efficient than uncoordinated scanning (Ward 1985; Lima 1990), we have  $\phi(\gamma, 0) > \phi_u$ . As the coordination time increases, however, the payoff decreases. So for every value of  $\gamma < 1$  there is a coordination time  $c(\gamma)$  such that  $\phi(\gamma, c(\gamma)) = \phi_u$ . Figure 2 shows the relationship between  $c(\gamma)$  and  $\gamma$  for different values of the group size  $n$  and of the scanning efficiency  $b$ . This maximum coordination time for which coordination leads to a greater fitness than uncoordinated scans is a decreasing value of  $\gamma$ . This was to be expected: the benefit of coordination increases as  $\gamma$  decreases, and the higher the benefit obtained from coordination, the higher the cost that can be paid for it. Increasing the probability  $b$  that a predator attack is successful even if the predator is detected reduces the maximum cost that can be paid for coordination. It also decreases the proportion of time spent scanning for predators at the ESS (data not shown, but see, for example, Pulliam *et al.* (1982) and McNamara & Houston (1992)). The range of variability of  $c(\gamma)$  with  $b$  is highest for  $n = 2$  and decreases as group size increases. Other than that, group size has remarkably little effect on  $c(\gamma)$ . Contrary to what Ward (1985) suggests, good coord-

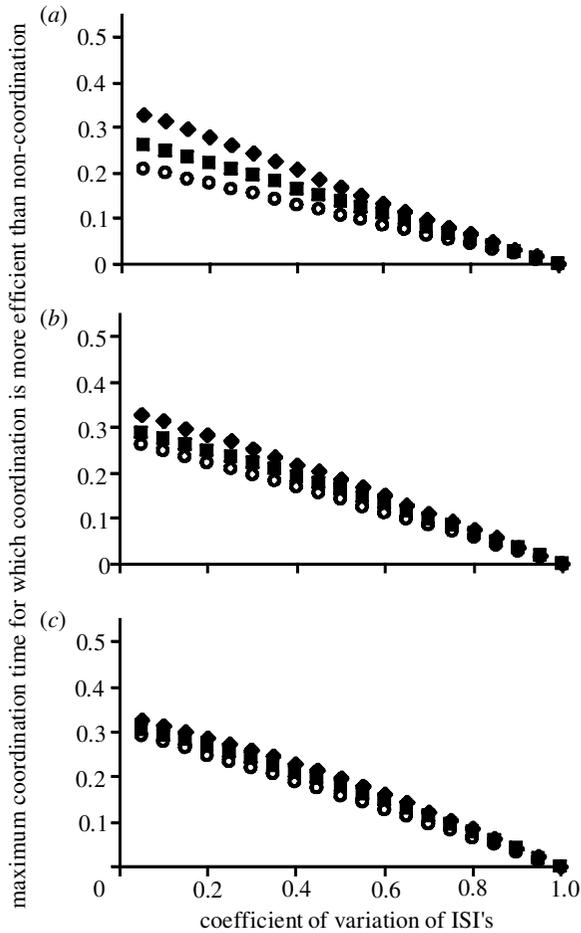


Figure 2. Maximum coordination time  $c(\gamma)$  for which expected survival at the coordinated ESS is higher than survival at the uncoordinated ESS versus the coefficient of variation of the distribution of ISIs,  $\gamma$ . The three panels correspond to different group sizes, (a)  $n = 2$ , (b)  $n = 4$  and (c)  $n = 8$ . For each group size, the data show  $c(\gamma)$  for different values of the probability that a predator attack is successful even if the predator is detected:  $b = 0.1$  (black diamonds);  $b = 0.3$  (black squares); and  $b = 0.5$  (open circles).

dination (low  $\gamma$ ) can be very efficient: group members must spend ca. 30% of their time coordinating their behaviour before coordination is less efficient than uncoordinated scanning.

**4. STABILITY OF COORDINATED SCANNING**

The value of  $c(\gamma)$  gives us an indication of the efficiency of scan coordination, but it tells us little about its evolutionary stability. As a first approximation to study the stability of scan coordination, we consider the following problem. As in the previous section, we assume that animals must spend a proportion  $c$  of their time coordinating their scans and the coefficient of variation of the ISI is  $\gamma$  as a result, where both  $\gamma$  and  $c$  are fixed. We calculate the proportion of time spent scanning for predators at the ESS and the payoff that all group members can expect to obtain at the ESS,  $\phi(\gamma, c)$ . We now introduce a mutant that scans for predators but spends no time coordinating its anti-predator behaviour. This mutant can adjust its behaviour in such a way as to maximize its expected pay-

off,  $\phi_u(\gamma, c)$ , and we ask whether this mutant achieves a higher fitness ( $\phi_u(\gamma, c) > \phi(\gamma, c)$ ) than its flock mates. To calculate the optimal behaviour of the mutant, and its expected fitness, we must calculate the probability that a predator arrives undetected to the foraging group,  $\rho$ . Because the mutant scans independently from its flock members, we can assume that the probability that the predator is not detected is the product of two factors: the probability that the mutant does not detect the predator (calculated according to equation (2.1) for a lone forager) and the probability that its group members do not detect the predator. We calculate this latter probability from equation (A 2) for  $n - 1$  foraging animals. When the cost of coordinating scans,  $c$ , is low, we have  $\phi_u(\gamma, c) < \phi(\gamma, c)$ : coordination is stable against these mutants. But when  $c$  increases,  $\phi(\gamma, c)$  decreases, and for very high coordination times we obtain  $\phi_u(\gamma, c) > \phi(\gamma, c)$ . Figure 3 shows the relationship between gamma and the maximum coordination time for which coordination is stable. Coordination is relatively stable against these mutants if most ISIs have the same duration (low  $\gamma$ ), particularly if scanning is efficient (low  $b$ ). But the coordination time required to make coordination unstable decreases quickly as coordination deteriorates ( $\gamma$  increases). This is particularly true for large groups.

**5. FINDING THE EVOLUTIONARILY STABLE STRATEGY**

In the previous section, we have considered the stability of coordinated anti-predator behaviour when animals must choose either to spend the full coordination time or to completely withdraw from coordination. In practice, it seems possible that animals can choose how much of their time to spend in coordination in a continuous fashion. In a flock where all birds spend a fraction  $c$  of their time coordinating their anti-predator scans, the optimal behaviour of a focal individual may well be to spend a fraction  $c'$  of its time in coordination, where  $c' > 0$  and  $c' \neq c$ .

When individuals can adjust the proportion of  $w$  and  $c$ , the ESS will be a pair  $(c^*, w^*)$ , such that when  $n - 1$  group members play  $(c^*, w^*)$ , the optimal behaviour of the remaining individual is to play  $(c', w') = (c^*, w^*)$ . To calculate  $(c', w')$ , we need to know the relationship between  $c$  and the ensuing temporal distribution of ISI, as given by  $\gamma$ . If all group members spend a proportion  $c$  of time coordinating their behaviour, there will be some relationship  $\gamma = g(c)$  between time spent coordinating and ISI variability. If  $n - 1$  group members play  $c$  and the remaining individual plays  $c' \neq c$ , the ensuing value of  $\gamma$  will be a function  $h(c, c')$  of both  $c$  and  $c'$ . For  $c' = 0$  (i.e.  $n - 1$  individuals coordinate and the remaining individual has an exponential distribution of ISIs, as in the previous section), it can be shown numerically that

$$\gamma_0 = a + \frac{1 - a}{1 + 0.6 \times (1/g(c)^2 - 1)}, \tag{5.1}$$

provides an excellent approximation to  $h(c, 0)$  if

$$a = 0.15 + \frac{0.85}{1 + 0.6 \times (n - 1)}. \tag{5.2}$$

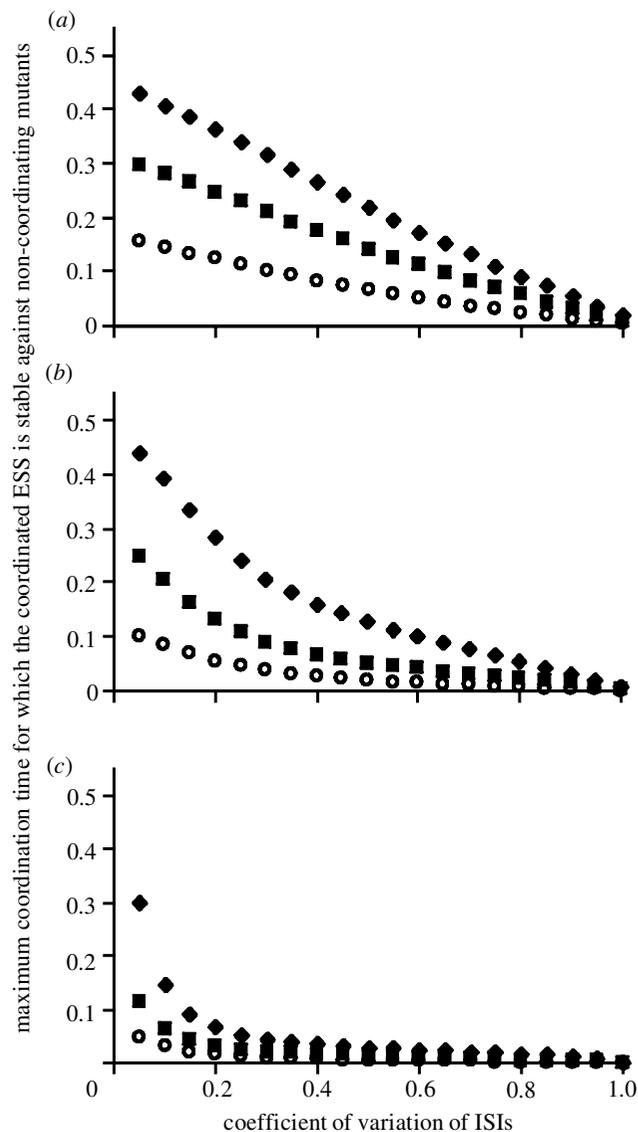


Figure 3. Maximum coordination time for which expected survival at the coordinated ESS is higher than survival for a mutant that does not spend the coordination time plotted versus the coefficient of variation of the distribution of ISIs,  $\gamma$ . The three panels correspond to different group sizes, (a)  $n=2$ , (b)  $n=4$  and (c)  $n=8$ . For each group size, the data show  $c(\gamma)$  for different values of the probability that a predator attack is successful even if the predator is detected;  $b=0.1$  (black diamonds);  $b=0.3$  (black squares); and  $b=0.5$  (open circles).

We also know that  $h(c, c') = g(c)$ . The precise shapes of  $g(c)$  and  $h(c, c')$  will depend on the mechanism that individuals follow to achieve coordination. We look for the ESS when

$$g(c) = 0.05 + 0.95 \times \exp(-m \times c), \quad (5.3)$$

where  $m$  is the steepness of  $g(c)$  (equivalent to its slope when  $g(c)$  is a linear function), and

$$h(c, c') = \max \left\{ 0.05, \gamma_0 \times \exp \left[ \log \left[ \frac{g(c)}{\gamma_0} \right] \times \frac{c'}{c} \right] \right\}. \quad (5.4)$$

We set the minimum possible value of  $g$  and  $h$  equal to 0.05 to avoid overflows in the numerical calculations. The function  $g$  shows diminishing returns, in the sense that a

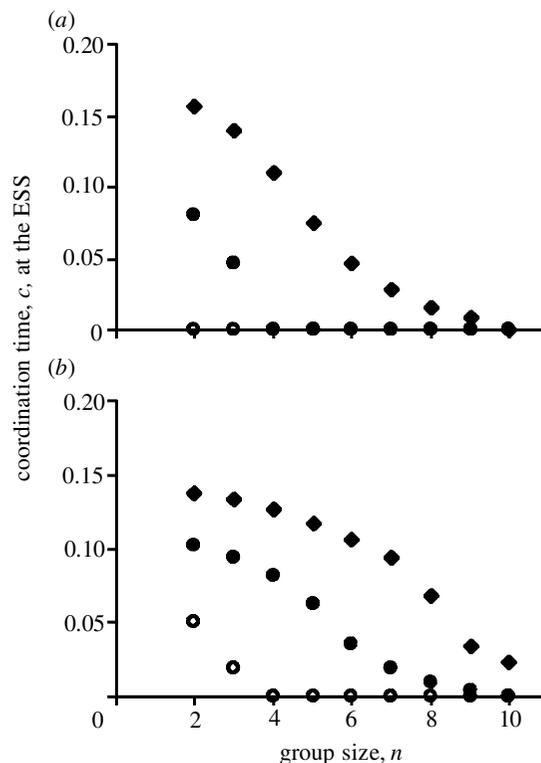


Figure 4. Proportion of time spent coordinating the scans,  $c$ , at the ESS when  $g(c) = 0.05 + 0.95 \times \exp(-m \times c)$  and (a)  $m=8$  or (b)  $m=16$ . The figure shows  $c$  versus  $n$ , for:  $b=0.1$  (black diamonds);  $b=0.3$  (black circles); and  $b=0.5$  (open circles).

fixed increment in coordination time has a larger impact when the coordination time,  $c$ , is low than when it is large. The same is true of the relationship between  $h$  and  $c'$ . For large values of  $m$  in equation (5.3), a relatively low coordination time leads to highly coordinated scanning behaviour, while for low  $m$  a large fraction of available time must be invested into coordination in order to obtain regular ISIs. At the ESS, coordination ( $c^* > 0$ ) is present for  $m > 4$ . Coordination is favoured by high coordination efficiency (large  $m$ ), high scanning efficiency (low  $b$ ) and small group size (low  $n$ ). Figure 4 shows coordination time at the ESS for  $b=0.1, 0.3$  and  $0.5$  and  $m=8$  and  $16$ .

Using linear relationships instead of equations (5.3) and (5.4) leads to similar trends. When both  $g$  and  $h$  are linear functions, coordination at the ESS tends to be absent or reach its maximum value ( $\gamma=0.05$ ). When  $g$  is given by equation (5.3), a linear relationship between  $h$  and  $c'$  disrupts coordination (in the sense that coordination breaks down for lower group sizes than when equation (5.4) is used).

## 6. ATTAINABILITY OF THE EVOLUTIONARILY STABLE STRATEGY

In the absence of a mechanistic model that tells us how group-level coordination is obtained from individual behaviour, it is difficult to ascertain whether the coordinating ESS can be reached by starting with a population of non-coordinating individuals. It is possible, however, to study the conditions under which a coordinating mutant can invade a population of non-coordinators. Consider a

population where scanning behaviour is not coordinated ( $\gamma = 1$ ). At the non-coordinating ESS, each individual obtains a payoff  $\phi_w$ . We introduce into this population a 'coordinator'. Because the behaviour of group mates is unpredictable, we will consider a mutant that spaces evenly in time its own scans. (More precisely, the ISIs of the mutant have a modified gamma distribution with coefficient of variation  $\gamma < 1$ .) Because the mutant behaves independently from other group members, the probability that the predator reaches the flock undetected is the product of the probabilities that it is not detected by the mutant and by its group mates. Assuming that the mutant must spend a proportion  $c$  of its time in timing its behaviour, it can adjust the amount of time it dedicates to scanning,  $w$ , in order to maximize its payoff. The maximum expected payoff of the mutant is a decreasing function of  $c$ . For  $c = 0$ , the payoff of the mutant is larger or equal than the wild-type payoff in a group without mutants. As coordination time increases, there is a point where both payoffs are equal, and for larger values of  $c$  the payoff of the mutant is lower than the wild-type payoff. Figure 5 shows the coordination time,  $c$ , for which the mutant and wild-type payoffs are equal versus the coefficient of variation of the mutant's distribution of ISIs,  $\gamma$ . Coordinating mutants can invade when the coordination time associated with timing their scans lies below the curves of the figure.

Combining the results of figures 4 and 5, we can conclude that, if the relationship between time spent timing one's behaviour and the ensuing distribution of ISIs is given by the function  $g(c)$  of equation (A 2), non-coordinating would be a stable ESS for all situations considered in figure 4. It seems, however, unlikely that spacing out one's scans, independently of other group members, should be so costly.

## 7. DISCUSSION

Previous game-theory models of anti-predator vigilance assumed independent scanning for mathematical convenience (Bednekoff & Lima 1998). Our model shows that coordinating anti-predator scans among group members can be more efficient than independent scanning even if individuals must spend a large share of their time coordinating their behaviour (figure 2), contrary to the results of Ward (1985). Efficiency, however, does not guarantee stability. Although figure 3 indicates that coordinating anti-predator scans might be rather robust, this result does not hold under closer scrutiny. The problem is that, when drawing figure 3, we have assumed that animals can choose between coordinating their behaviour or not doing so in an all-or-nothing fashion. When this restriction is imposed, coordination ensues unless the time that animals must allocate to coordination is relatively high (figure 3). A different picture appears when animals can make small adjustments to their coordination effort. Here, it often pays to spend a little less than one's flock mates in coordinating anti-predator scans. The result is that, at the ESS, there may be little or no coordination. The absence of coordination at the ESS is particularly noticeable for large groups and when detecting the predator helps little to escape the attack (a large probability  $b$  that the detected predator captures a foraging animal). Coordination increases the efficiency of scanning but it is costly to achieve

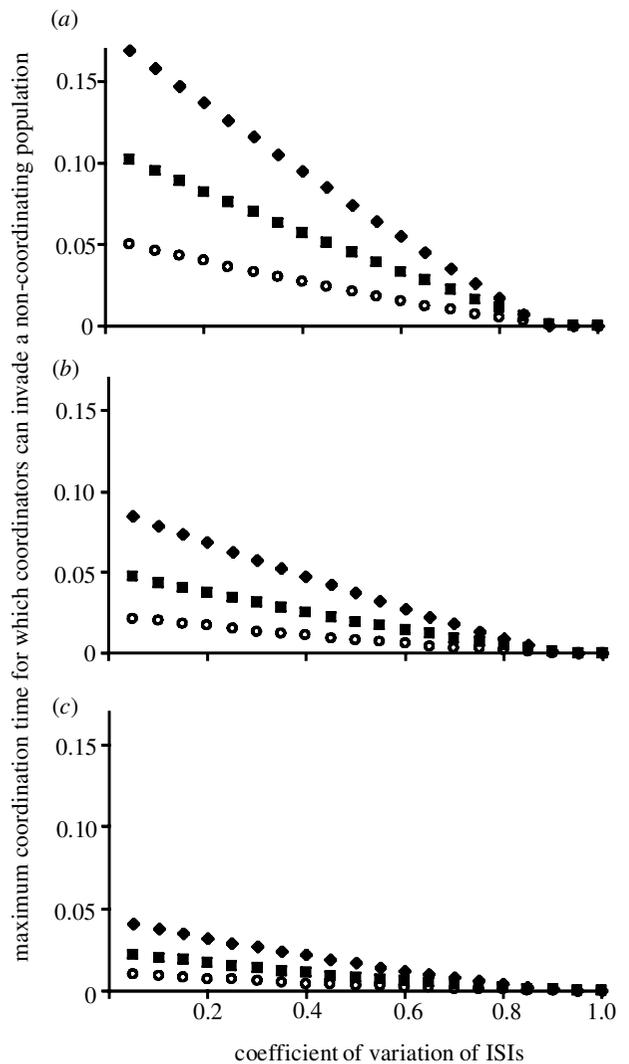


Figure 5. Maximum coordination time that a mutant can spend to space its ISIs with coefficient of variation  $\gamma$  if it is to achieve a higher payoff than its non-coordinating group mates. The three panels correspond to different group sizes, (a)  $n = 2$ , (b)  $n = 4$  and (c)  $n = 8$ . For each group size, the data show  $c(\gamma)$  for different values of the probability that a predator attack is successful even if the predator is detected:  $b = 0.1$  (black diamonds);  $b = 0.3$  (black squares); and  $b = 0.5$  (open circles).

and is prone to cheating, because individuals that do not coordinate their scanning still benefit from the coordination of other group members. It is therefore not surprising that coordination becomes less and less likely as group size increases, as it has been shown in theoretical models of cooperation (Boyd & Richerson 1988).

Still, according to the model we should observe coordinated scanning for small groups and, when scanning is efficient (low  $b$ ), even for relatively large groups (figure 4). The absence of coordination among group foragers may have different explanations. First, if self-timing were costly, the coordinating ESS might not be attainable (figure 5) and non-coordinating would be the only ESS. It seems, however, unlikely that spacing one's scans evenly in time should be so wasteful. A more likely explanation may be that the unpredictability of scans is required to avoid stalking predators (see Bednekoff & Lima (1998)

and references therein). Notice, however, that even when fooling stalking predators is a must, coordination may still be useful to decrease the proportion of time when several group members are simultaneously scanning. Furthermore, a gamma distribution of ISI conserves some randomness so long as the coefficient of variation of the ISI is greater than zero (see Scannell *et al.* (2001) for discussion).

Although our model does not propose any individual-based mechanism that leads to group-level coordination, Ferriere *et al.* (1996, 1999) suggest an interesting possibility (but see Ruxton & Roberts 1999). They envisage a pair of animals foraging together. One of them scans for predators with chaotic dynamics. The other, called the coordinator, can therefore make relatively accurate short-term predictions concerning the duration of the ISI, and adjusts its own behaviour accordingly in order to coordinate their anti-predator behaviour. Although this possibility deserves further study, we must point out a number of shortcomings. First, the coordinator must have, at all times, precise information on the duration of the last ISI performed by its companion. This information is presumably rather costly to obtain, contrary to what Ferriere *et al.* (1996, 1999) suggest. Second, this model tells us little about the conditions under which the coordinator strategy can invade (two or more coordinators do not work well together). Finally, it seems difficult to implement the coordinator strategy. Time estimation is a noisy process (see Gibbon *et al.* (1984) for details). Humans in controlled laboratory conditions make estimation errors in the order of 18–20% (e.g. Rodríguez-Gironés & Kacelnik 2001). The error is greater (20–25%) for animals solving time-estimation tasks, and for animals that must forage at the same time as they estimate the ISI of their flock mates, it is unlikely to be any smaller. Errors of the order of 20% or more in the estimation of the ISI may seriously damage the applicability of the coordinator strategy proposed by Ferriere *et al.* (1996).

Another mechanistic model that is definitely worth looking into is the one by Barh & Bekoff (1999). In this model, individuals determine their behaviour (foraging or scanning for predators) on the basis of the behaviour of their nearest neighbours. This model finds ‘coordination’ among group members and claims that such coordination has actually been observed in the field (data from Bekoff (1995)), but for these authors ‘less coordination... means that there were fewer instances when all the birds... were scanning or not scanning at the same time’ (Bekoff 1995). That is, according to this definition there is coordination when all birds do the same thing at the same time. Although this is indeed a form of coordination, it has little to do with what most articles on predator scanning understand by coordination (what Bertram (1980) calls sequential organization) and we prefer to refer to it as synchronization. Indeed, coordination as understood by Bekoff (1995) is extremely wasteful from a functional perspective. Although the precise behavioural rule used by Barh & Bekoff (1999) in their model does not lead to coordination as we understand it, and even if this rule is most probably not evolutionarily stable, their modelling approach can be extended in order to look for evolutionarily stable behavioural rules. Besides, because some degree of synchronization has also been observed by

Lazarus (1979) and Bertram (1980), we must either identify a factor favouring synchronization or, possibly, change gear and concentrate on more mechanistic models of anti-predator scanning.

Although rare in loose foraging groups, coordination seems to occur in other contexts. For example, sentinel behaviour in socially structured groups, where individuals spend prolonged periods scanning continuously from elevated positions where they are highly visible by other group members, tends to occur in an alternating fashion (e.g. McGowan & Woolfenden (1989) for birds and Rasa (1986) and Clutton-Brock *et al.* (1999) for mammals). Bednekoff (1997) developed a theoretical model of sentinel behaviour and showed that, when sentinels are safe and they efficiently communicate detection information, sentinel behaviour becomes highly coordinated in an organized rota, and group members alternate into non-overlapping vigilance bouts (see also Bednekoff 2001). Therefore, it seems that coordination can occur when coordination is inexpensive or extremely efficient, and social cohesion and ecological conditions allow efficient sharing of detection information.

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## APPENDIX A: CALCULATING THE PROBABILITY OF DETECTING PREDATORS

We assume that the ISIs are random samples the probability density function of which corresponds to a gamma distribution with offset. Specifically, we assume that the probability that an ISI lasts  $x$  is  $f(x - \tau/n | \alpha, \beta)$  if  $x > \tau/n$ , and zero otherwise, where  $f(x | \alpha, \beta)$  is the gamma distribution with parameters  $\alpha$  and  $\beta$ ,

$$f(x | \alpha, \beta) = \frac{\beta^\alpha}{\Gamma(\alpha)} \times x^{\alpha-1} \times e^{-\beta \times x} \quad (x > 0). \quad (\text{A } 1)$$

Notice that the introduction of the offset  $\tau/n$  ensures that, at any point in time, there are at most  $n$  individuals scanning.

To calculate the probability that a predator is not detected, we proceed as follows. Let  $t$  be the time when the predator starts its attack. If scans are initiated at times  $t_1, t_2, \dots$ , let  $t_i \leq t < t_{i+1}$ . Hence, the predator initiates its attack between the initiation of the  $i$ th and  $(i + 1)$ th scans. For the predator to be undetected, two conditions must be satisfied: (i) it must start its attack after the  $i$ th scan is over ( $t > t_i + \tau$ ), and (ii) it must finish its attack before the  $(i + 1)$ th scan starts ( $t + T < t_{i+1}$ ). If predator attacks follow a Poisson process, they are independent of the initiation of scan events. Hence, the probability that conditions (i) and (ii) are verified simultaneously is equal to the proportion of time during which they can be satisfied,  $(t_{i+1} - t_i - T - \tau) / (t_{i+1} - t_i)$ . Because  $t_{i+1} - t_i$  is the ISI, when we multiply by the probability that the ISI lasts some time  $x = t_{i+1} - t_i$  and integrate over all possible durations of the ISI for which (i) and (ii) can be simultaneously verified, we obtain

$$\rho = \int_{T+\tau \times (1-1/n)}^{\infty} \frac{x}{E(x)} \times f\left(x - \frac{\tau}{n} \middle| \alpha, \beta\right) \times \frac{x - T - \tau \times (1 - 1/n)}{x} \times dx. \quad (\text{A } 2)$$

For  $n = 1$ , this equation is a particular case of equation 6 in Lendrem (1986). Lendrem gives a more detailed explanation of how equation (A 2) is derived (see also Hart & Lendrem 1984). Notice, however, that he calculates the probability that the predator is detected (i.e.  $1 - \rho$ ) and that his definition of the ISI is slightly different from the one used here.

To calculate  $\rho$ , it remains to be seen how  $\alpha$  and  $\beta$  are related to individual behaviour. For a gamma distribution,  $\gamma = \alpha^{-0.5}$ . Therefore,  $\alpha = \gamma^{-2}$ . In this model,  $\gamma$  will depend on the amount of time spent coordinating, but not on the amount of time spent scanning. Notice that  $\gamma$  is not exactly the coefficient of variation of the ISI, but rather of their random part. We calculate  $\beta$  from the relationship between the average duration of the ISI ( $\alpha/\beta + \tau/n$ ) and the proportion of time spent scanning by group members. Namely,

$$\sum_i w_i = \frac{\tau}{E(x)} = \frac{\tau}{\frac{\alpha}{\beta} + \frac{\tau}{n}}. \quad (\text{A } 3)$$

It is easy to check that for  $\alpha = 1$  and when  $\beta$  is given by equation (A 3), equation (A 2) is identical to equation (2.1) for a lone forager ( $n = 1$ ) but not for greater group sizes. Thus, the uncoordinated ( $\alpha = 1$ ) gamma distribution with offset is only identical to Pulliam *et al.*'s (1982) model for  $n = 1$ .

## REFERENCES

- Barh, D. B. & Bekoff, M. 1999 Predicting flock vigilance from simple passerine interactions: modelling with cellular automata. *Anim. Behav.* **58**, 831–839.
- Bednekoff, P. A. 1997 Mutualism among safe, selfish sentinels: a dynamic game. *Am. Nat.* **150**, 373–392.
- Bednekoff, P. A. 2001 Coordination of safe, selfish sentinels based on mutual benefits. *Ann. Zool. Fenn.* **38**, 5–14.
- Bednekoff, P. A. & Lima, S. L. 1998 Randomness, chaos and confusion in the study of antipredator vigilance. *Trends Ecol. Evol.* **13**, 284–287.
- Bekoff, M. 1995 Vigilance, flock size, and flock geometry: information gathering by western evening grosbeaks (Aves, Fringillidae). *Ethology* **99**, 150–161.
- Bertram, B. C. R. 1980 Vigilance and group size in ostriches. *Anim. Behav.* **28**, 278–286.
- Boyd, R. & Richerson, P. J. 1988 The evolution of reciprocity in sizeable groups. *J. Theor. Biol.* **132**, 337–356.
- 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.
- Elcavage, P. & Caraco, T. 1983 Vigilance behaviour in house sparrow flocks. *Anim. Behav.* **31**, 303–304.
- Ferriere, R., Cazelles, B., Cézilly, F. & Desportes, J. P. 1996 Predictability and chaos in bird vigilant behaviour. *Anim. Behav.* **52**, 457–472.
- Ferriere, R., Cazelles, B., Cézilly, F. & Desportes, J. P. 1999 Predictability chaos and coordination in bird vigilant behaviour. *Anim. Behav.* **57**, 497–500.
- Gibbon, J., Church, R. M. & Meck, W. H. 1984 Scalar timing in memory. In *Timing and time perception* (ed. J. Gibbon & L. Allan), pp. 52–77. New York Academy of Sciences.
- Godin, J.-G., Classon, L. J. & Abrahams, M. V. 1988 Group vigilance and shoal size in a small characin fish. *Behaviour* **104**, 29–40.
- Hart, A. & Lendrem, D. W. 1984 Vigilance and scanning patterns in birds. *Anim. Behav.* **32**, 1216–1224.
- Kenward, R. E. 1978 Hawks and doves: attack success and selection in goshawk flights at wood pigeons. *J. Anim. Ecol.* **47**, 449–460.
- Lazarus, J. 1979 The early warning function of flocking in birds: an experimental study with captive quelea. *Anim. Behav.* **27**, 855–865.
- Lendrem, D. 1986 *Modelling in behavioural ecology: an introductory text*. London: Croom Helm.
- Lima, S. L. 1990 The influence of models in the interpretation of vigilance. In *Interpretation and explanation in the study of animal behavior. 2. Explanation, evolution and adaptation* (ed. M. Bekoff & D. Jamieson), pp. 246–267. Boulder, CO: Westview Press.
- Lima, S. L. 1995 Back to the basics of anti-predatory vigilance: the group-size effect. *Anim. Behav.* **49**, 11–20.
- Lima, S. L. & Bednekoff, P. A. 1999 Back to basics on anti-predatory vigilance: can non-vigilant animals detect attack? *Anim. Behav.* **58**, 537–543.
- McGowan, K. J. & Woolfenden, G. E. 1989 A sentinel system in the Florida scrub jay. *Anim. Behav.* **37**, 1000–1006.
- McNamara, J. M. & Houston, A. I. 1992 Evolutionarily stable levels of vigilance as a function of group size. *Anim. Behav.* **43**, 641–658.
- Monaghan, P. & Metcalfe, N. B. 1985 Group foraging in wild brown hares: effects of resource distribution and social status. *Anim. Behav.* **33**, 993–999.
- Pulliam, H. R. 1973 On the advantages of flocking. *J. Theor. Biol.* **38**, 419–422.
- Pulliam, H. R., Pyke, G. H. & Caraco, T. 1982 The scanning behaviour of juncos: a game-theoretical approach. *J. Theor. Biol.* **95**, 89–103.
- Rasa, O. A. E. 1986 Coordinated vigilance in dwarf mongoose family groups: the watchman's song hypothesis and the costs of guarding. *Ethology* **71**, 340–344.
- Roberts, G. 1996 Why individual vigilance declines as group size increases. *Anim. Behav.* **51**, 1077–1086.
- Rodríguez-Gironés, M. A. & Kacelnik, A. 2001 Relative importance of perceptual and mnemonic variance in human temporal bisection. *Q. J. Exp. Psychol. A* **54A**, 527–546.
- Ruxton, G. D. & Roberts, G. 1999 Are vigilance sequences a consequence of intrinsic chaos or external changes? *Anim. Behav.* **57**, 493–495.
- Scannell, J., Roberts, G. & Lazarus, J. 2001 Prey scan at random to evade observant predators. *Proc. R. Soc. Lond. B* **268**, 541–547. (DOI 10.1098/rspb.2000.1388.)
- Vázquez, R. A. 1997 Vigilance and social foraging in *Octodon degus* (Rodentia: Octodontidae) in central Chile. *Rev. Chil. Hist. Nat.* **70**, 557–563.
- Ward, P. 1985 Why birds do not coordinate their vigilance? *J. Theor. Biol.* **114**, 383–385.

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