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# When are two heads better than one? Visual perception and information transfer affect vigilance coordination in foraging groups

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Animals frequently raise their heads to check for danger. In a group, individuals generally raise their heads independently. Earlier models suggest that all group members could gain by coordinating their vigilance, i.e., each member raising its head when others are not. We re-examine these suggestions, considering groups of different sizes, in light of empirical findings that: (1) animals can sometimes detect a predator without raising their heads, and (2) when one member of a group detects a predator, the information does not always spread to other members of the group. Including these effects in models generally decreases the value of coordinated vigilance. Coordinated vigilance is highly favored only when animals have a low probability of detecting predators without lifting their heads but a high probability of being warned when another member of the group detects a predator. For other combinations, coordinated vigilance has little value and may have a negative value. Group size has contrasting effects depending on how social information is obtained. Coordination is favored in smaller groups when one or more detecting individuals provide a constant amount of information to individuals unaware of the predator. On the other hand, coordination is favored in larger groups if each detecting individual provides unaware individuals with an independent source of information (i.e., if the amount of information increases as the number of detecting individuals increases). These results depend on the balance of an escape due to social information and dilution of risk in groups with imperfect information spread. This framework could be tested by examining species with different visual fields and in different environments. *Key words:* anti-predator behavior, collective detection, group size, risk dilution, scanning, vision. *[Behav Ecol 15:898–906 (2004)]*

Animals face a basic tradeoff. Predator detection requires vigilance, but watching for predators often conflicts with the search for food. Social interactions can have a profound effect on this fundamental tradeoff. A solitary forager must use its own vigilance to detect approaching predators, but animals foraging in groups have another source of information. They can, in principle, monitor the behavior of conspecifics to gather clues about approaching predators. Besides obtaining social information to escape predators, an animal in a foraging group may use such information to make decisions about when and whether to scan for predators. Such conditional behavior may lead to certain patterns of scanning within a group (e.g., animals taking turns being vigilant). Although it has seldom been considered in this context, an animal's sensory apparatus will affect the relative ease with which it can obtain information (Fernández-Juricic et al., 2004a), and thus these abilities may strongly influence the value of different patterns of vigilance.

Most models of vigilance behavior assume that scanning is inherently random: members in a foraging group scan independently of one another (Bednekoff and Lima, 1998). If, however, individuals reduce the degree of overlap by taking turns scanning and foraging (coordinated vigilance), they could not only maintain a continuous level of group vigilance but also decrease vigilance time and increase foraging activity accordingly (Bahr and Bekoff, 1999; Bednekoff and Lima, 1998; Ferriere et al., 1999; Rodríguez-Gironés and Vásquez, 2002; Ruxton and Roberts, 1999; Scannell et al., 2001).

Coordination has been found in socially structured groups with sentinels, which take turns watching for potential predators from exposed positions while the rest of the group is feeding (Bednekoff, 1997, 2001). However, there is little empirical support for coordinated vigilance in loose foraging groups (Bertram, 1980; Elcavage and Caraco, 1983; Fernández et al., 2003; Fernández-Juricic et al., 2004b; Lipetz and Bekoff, 1982). This suggests that individuals in such groups do not adjust their vigilance to that of conspecifics (Beauchamp, 2002; Lima, 1995a; Lima and Zollner, 1996). So, why isn't coordination more common, given its advantages in terms of increased survivorship and foraging time?

Some modelers (Pulliam et al., 1982; Ward, 1985) have argued that random scanning is advantageous because group members would need to monitor the vigilance of neighbors in order to fine-tune their own scanning to achieve coordination. However, this rationale assumes that scanning and foraging are mutually exclusive activities (e.g., head-down individuals cannot scan). Although this assumption may be reasonable in some cases (Treves, 2000), recent indirect experimental evidence suggests that it may not always apply (Fernández-Juricic et al., in press; Guillemain et al., 2001, 2002). There is, however, direct evidence in birds that indicates that some species can detect predators when their heads are down (Lima and Bednekoff, 1999). This is because the configuration of avian visual fields (Martin and Katzir, 1999) allows most of the species that forage in groups to use peripheral vision during foraging bouts (Fernández-Juricic et al., 2004a). Consequently, the degree to which social foragers can gather visual information in different body postures (head-up vs. head-down) is expected to influence the

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scanning strategies employed (Bednekoff and Lima, 2002; Fernández-Juricic et al., 2004a).

In an effort to build a broad framework to understand the phenomena of coordination in foraging groups, we present a mathematical model that explores the relationship between coordinated vigilance and sensory abilities (which may be determined by the morphology of a species or even the environmental conditions). We first consider two foragers, and we compute the danger to a focal individual under coordinated and random strategies and assess the value of coordination as the difference in danger between strategies. We then derive a general model to study the effects of group size on the value of coordination. Building on earlier modeling efforts (Lima, 1994; Proctor et al., 2001), we consider two forms of information spread between conspecifics in groups larger in size than two: (1) information available to non-detecting individuals is constant for one or more detecting conspecifics, or (2) available information is a strict monotone increasing function of the number of detecting conspecifics. We then explore how differences in the form of information dissemination affect the value of coordination. By relaxing the conventional assumptions about the sensory constraints on vigilance and information spread in groups, we show the specific conditions favoring coordination and how the traditional approach may have overstated the value of coordinated vigilance.

## PAIR MODEL: DESCRIPTION AND RESULTS

Consider a pair of individuals foraging and scanning for predators over some stretch of time. Assume that each individual in the pair will have its head up a fraction $p$ of this time. For simplicity, we will assume that an individual will detect an approaching predator with absolute certainty if its head is up (e.g., Hart and Lendrem, 1984). If an individual has its head down when the predator approaches, we assume the individual detects the predator with probability $d$. We assume that any individual that detects a predator by itself can escape the attack, which we call personal detection.

Even if an individual fails to detect the predator (i.e., is unaware), it may still escape in two ways. First, the detection by its partner may alert the unaware individual to the predator's presence. Let $I$ be the probability that an unaware focal individual obtains information, and thus escapes, given that its partner has detected the predator. When an unaware individual avoids predation due to its partner's detection, we call this collective detection. The second way in which an unaware individual can avoid being caught occurs when its partner also fails to detect the predator. In this case, there will be two animals susceptible to predation. We assume that the predator will randomly choose one of them. Thus, an unaware focal individual can escape predation if its partner is also unaware through dilution of risk.

The probability that an individual does not escape predation (through personal detection, collective detection, or dilution of risk) is the danger to that individual, $\mathcal{D}_r$, given by:

$$\mathcal{D}_r = (1-p)(1-d) \times \left\{ (d(1-p)+p)(1-I) + (1-d)(1-p)\frac{1}{2} \right\}. \quad (1)$$

Equation 1 is the danger to a focal individual, given that both individuals scan independently of one another, which we label as a RANDOM scanning strategy. Note that in order to be eaten when a predator approaches, a focal individual must fail to personally detect the predator, which occurs with probability $(1-p)(1-d)$. Given that the focal individual fails to perform personal detection, in order to be eaten, it must also fail to benefit from collective detection or dilution of risk. Any focal individual's partner will detect the predator with probability $d(1-p)+p$, which means that a head-down non-detecting focal individual will fail to perform a collective detection with probability $(d(1-p)+p)(1-I)$. Any focal individual's partner will not detect the predator with probability $(1-d)(1-p)$, which means that a head-down non-detecting focal individual will fail to benefit from dilution of risk with probability $(1-d)(1-p)(1/2)$. Thus, the factor in braces in Equation 1 is the probability of failure to escape through the action (or inaction) of the partner, conditioned on the failure to escape through solitary means. The product of this conditional probability with the probability of personal detection failure gives the danger to a focal individual in the pair.

We will also consider a COORDINATED scanning strategy, in which we assume that no more than one individual is scanning at one time. There are two issues to note regarding the COORDINATED case: (1) we do not specify how such coordination occurs, only that it does (see also Rodríguez-Gironés and Vásquez, 2002; Ward, 1985), and (2) if each individual is to scan a fraction $p$ of the time without overlap, then we have a constraint on $p$, namely $p \leq 1/2$. The danger to a focal individual in the COORDINATED case, $\mathcal{D}_c$, is given by:

$$\mathcal{D}_c = (1-p)(1-d) \times \left\{ \frac{d(1-2p)+p}{1-p}(1-I) + \frac{(1-d)(1-2p)}{1-p}\left(\frac{1}{2}\right) \right\}. \quad (2)$$

Equation 2 is derived similarly to Equation 1. However, the factor in braces is altered (the conditional probability of failure to escape through the partner's action given failure to escape through personal means), because members of the pair never scan at the same time.

Finally, we let the value of coordination, $\mathcal{V}$, be the difference between the danger to a focal individual in the RANDOM case and the COORDINATED case. That is,

$$\mathcal{V} = \mathcal{D}_r - \mathcal{D}_c = p^2(1-d)\left( \left\{ d(1-I) + (1-d)\frac{1}{2} \right\} - \{1-I\} \right). \quad (3)$$

To develop an intuition of what the value of coordination means, we compare the RANDOM and COORDINATED time schedules for our pair in Figure 1a. When a focal's head is up, the head posture of its partner is irrelevant to its inevitable personal detection. So, we can ignore the differences between the two schedules when the focal's head is up. When the focal's head is down, we see that these two schedules differ over a single time section, marked with an asterisk. During this time section, the partner's head is down for the RANDOM schedule, whereas it is up for the COORDINATED schedule. The value of coordination is entirely due to the differences between the two schedules within this time section.

$\mathcal{V}$ can be derived directly from Figure 1a. As the focal's head is down over both schedules during the asterisked section, difference between the dangers of the two schedules must result from differences in collective detection and dilution of risk. These effects apply when the focal individual cannot detect the predator directly. Given that the focal is unaware, the danger if its partner's head is down is $d(1-I) + (1-d)(1/2)$. If the partner's head is up, the danger to the unaware focal is simply the probability of failure to get information from its departing partner—namely, $1-I$. Thus, the first term in braces is the danger to an unaware focal during the asterisked time section under a RANDOM schedule, and the second term in braces is the danger to the unaware focal during the asterisked section under a COORDINATED schedule (see Figure 1a). The difference in dangers (in parentheses in Equation 3) gives the value of coordination conditioned on the event that the predator attacks during the asterisked time section and the focal is unaware. Since this time section has length $p^2$ and a head-down individual does not detect with probability $(1 - d)$, the above-mentioned event has the probability $p^2(1 - d)$. The value of coordination comes from the multiplication of this probability by the conditional value.

Equation 3 can be simplified as follows:

$$\mathcal{V} = p^2(1-d)^2\left(I - \frac{1}{2}\right). \qquad (4)$$

We see that neither $p$ (the fraction of time spent head-up) nor $d$ (the probability of predator detection when head-down) affect the sign of $\mathcal{V}$ (only its magnitude). We see that $\mathcal{V} > 0$ if and only if $I > 1/2$. That is, coordination is valuable in pairs when the probability of collective detection is greater than the dilution probability (1/2). This result is echoed in Figure 1a. Specifically, the focal in the COORDINATED schedule has better information during the asterisked time section (because its partner is head-up), whereas the focal in the RANDOM schedule has a better chance of dilution of risk (because its head-down partner is more likely to remain susceptible to predation). If $I > 1/2$, then higher values of $p$ and lower values of $d$ contribute to higher values of $\mathcal{V}$. When $I < 1/2$, these same conditions on $p$ and $d$ contribute to lower values of coordination (e.g., see the $g = 2$ graphs in Figure 2).

## GENERAL MODEL: DESCRIPTION

Now consider a foraging group of size $g$. As before, each individual has its head up a fixed fraction of the time, $p$, in which it can detect a predator with absolute certainty. When an individual's head is down, its probability of detection is $d$. The complement of a focal individual is the $(g - 1)$ other members of its group. Consider a (head-down) focal that has not detected an approaching predator. We let $\mathcal{I}(n)$ be the probability that the focal obtains information about the predator given that $n$ individuals in the complement have detected the predator. We will again consider both the RANDOM and COORDINATED cases, noting the constraint: $0 \leq p \leq (1/g)$. (In general, we find that the specific value of $p$ within this range does not greatly affect any of our conclusions below; consequently, we will fix $p$ at some value in this range for all of the analyses presented).

As before, the value of coordination is given by the difference in danger to a focal animal in the RANDOM and the COORDINATED cases. We derive the general form for the dangers and the value of coordination in Appendix A. Figure 1b compares the RANDOM and COORDINATED schedules. As in the pair case, we focus on differences in the complement when the focal's head is down (as it always escapes predation when head-up). We see that these two schedules differ over two time sections, labeled as the *MANY-HEADS* section and the *NO-HEADS* section. During the *MANY-HEADS* section, two or more heads are up in the complement for the RANDOM case, but only one head is up in the complement for the COORDINATED case. Note that the *MANY-HEADS* section does not exist when $g = 2$ (i.e., a pair). During the *NO-HEADS* section, no heads are up in the complement for the RANDOM strategy, but one head is up in the complement for the COORDINATED strategy. The *NO-HEADS* section corresponds to the asterisked time section from Figure 1a.

During these time sections, differences in dangers between the two schedules derive from differences in collective detection and dilution of risk. However, the more potential there is for collective detection, the less dilution of risk. Information and dilution are the opposing blades on a double-edged sword; to get information, a focal individual must have detecting flock mates, but in order for risk to be diluted, a focal individual must have unaware flock mates. When the complement has more heads up in the RANDOM schedule compared to the COORDINATED schedule (*MANY-HEADS* section), then coordination provides a greater chance of dilution but a smaller chance of collective detection. When the complement has fewer heads up in the RANDOM schedule compared to the COORDINATED schedule (*NO-HEADS* section), then coordination provides a greater chance of collective detection but a smaller chance of dilution. So, the advantage of coordination must come through better dilution during the *MANY-HEADS* section or better collective detection during the *NO-HEADS* section. We will argue that when coordination is favored, it is generally because of improved collective detection (during the *NO-HEADS* section). However, the value of coordination depends on how information is obtained (i.e., the form of the information function, $\mathcal{I}(n)$). Here we will consider two specific forms of this information function that reveal different assumptions about information transfer and body posture.

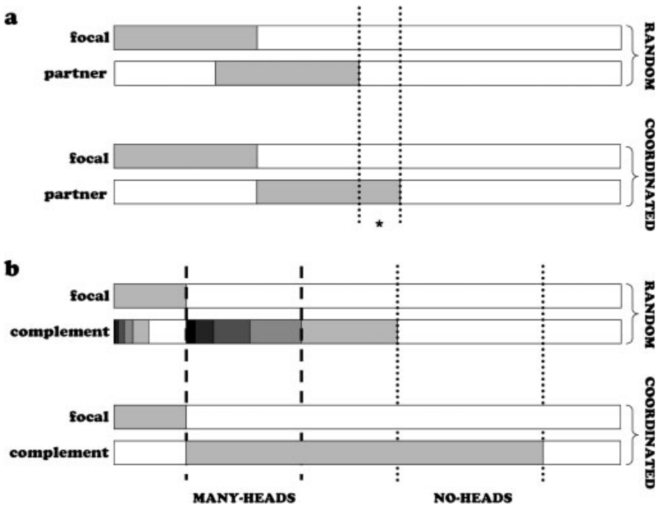

**Figure 1**
Time lines for a RANDOM and COORDINATED schedule. (a) In the case of a pair, both the focal individual's and its partner's body posture patterns are grey when head-up and white when head-down. Note that the COORDINATED schedule has at most a single head up at any one time. In the time interval, an individual will generally go through several head-up and head-down bouts (which, in sum, comprise a fraction $p$ of the interval); however, we have consolidated these bouts for pedagogical purposes. Also, we have lined up the RANDOM and COORDINATED schedules so that the periods of head-up and head-down postures for the focal individual match. During the time period marked with an asterisk, the head posture of the partner differs between the two schedules. (b) In the case of foraging groups of larger sizes, the number of heads that are up in the complement of the focal individual is given by a grey scale (with darker shades representing periods where more heads are up). Note that again the COORDINATED schedule has at most a single head up at any one time. Once again the RANDOM and COORDINATED schedules have been lined up so that the periods of head-up and head-down postures for the focal individual match. During time periods labeled *MANY-HEADS* and *NO-HEADS*, the head configurations in the focal's complement differ between the two schedules.

### (1) Exponentially saturating information function

In this section, we assume the focal individual will obtain information about the predator from each of the $n$ detecting

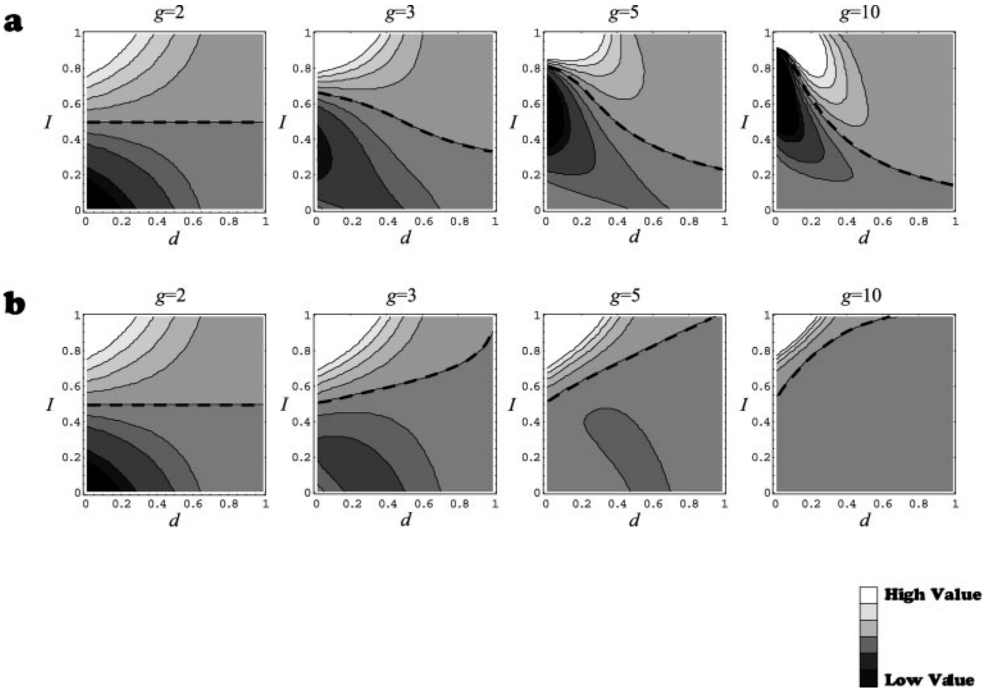

**Figure 2**
The value of information ($\mathcal{V}$) is plotted as a function of the parameters $d$ (personal head-down detection probability), $I$ (collective detection parameter), and $g$ (group size) for information functions (a) $\mathcal{I}(n) = 1 - (1 - I)^n$ and (b) $\mathcal{I}(n) = 0$ for $n = 0$, and $\mathcal{I}(n) = I$ otherwise. Lighter shades of grey correspond to higher values (and the same shade of grey is comparable in all graphs). The dashed line gives the $\mathcal{V} = 0$ level curve. For $I$ values above this curve, $\mathcal{V} > 0$, and for $I$ values below this curve, $\mathcal{V} < 0$. For all graphs, we let the fraction of time spent scanning $p = 0.04$.

members of its group independently with probability $I$. This leads to an exponentially saturating form for the information function:

$$\mathcal{I}(n) = 1 - (1 - I)^n \tag{5}$$

Using the function given by Equation 5, we have the following expression for the value of coordination (see Appendix A):

$$\begin{aligned}\mathcal{V} = {} & \frac{1 - pg}{g}\left\{\sum_{j=0}^{g}\binom{g}{j} d^j[(1-d)(1-(1-I)^j)]^{g-j}\right\} \\ & + p\left\{\sum_{j=0}^{g-1}\binom{g-1}{j} d^j[(1-d)(1-(1-I)^{j+1})]^{g-1-j}\right\} \\ & - \frac{1}{g}\left\{\sum_{i=0}^{g}\sum_{j=0}^{g-i}\binom{g}{i, j, g-i-j}\right. \\ & \qquad \left. \times\, p^i[(1-p)d]^j[(1-p)(1-d)(1-(1-I)^{i+j})]^{g-i-j}\right\}\end{aligned} \tag{6}$$

**(2) Step information function**

The exponentially saturating information function always approaches unity. Thus, given enough detecting individuals in the rest of the group, the focal individual will obtain information about the predator with (near) certainty. In this section, we assume that there is a limit to collective information gathering in the head-down posture. For simplicity, we will assume that a head-down focal individual will receive information with a constant probability (which is strictly less than 1) if one or more group members detect the predator. This leads to the following step form for the information function:

$$\mathcal{I}(n) = \begin{cases} 0 & \text{if } n = 0 \\ I & \text{if } n > 0 \end{cases} \tag{7}$$

While the constant nature of Equation 7 is probably unrealistic in general cases (i.e., $\mathcal{I}$ should increase monotonically with $n$), it does capture the idea of a limit to information gathering in the head-down posture.

Using Equation 7, we have the following expression for the value of coordination (after some rearrangement and simplification of Equation A4 from Appendix A):

$$\begin{aligned}\mathcal{V} = {} & \frac{1}{g}\{[(1-p)^g - (1-pg)][(1-d)I]^g + [d + (1-d)I]^g \\ & + pg(1-d)(1-I)[d + (1-d)I]^{g-1} \\ & - [p + (1-p)d + (1-p)(1-d)I]^g\}\end{aligned} \tag{8}$$

## GENERAL MODEL: RESULTS

Under either the exponentially saturating function or the step function, coordination tends to be favored when $d$ is low and $I$ is high (Figure 2). That is, the COORDINATED schedule is superior when there is little chance of personal detection of predators in the head-down posture, but a good chance of collective detection. Why is this so? If we focus on the *NO-HEADS* section from Figure 1b, we see that during this period there is one head up in the complement in the COORDINATED schedule while there is no head up in the complement in the RANDOM schedule. If head-down individuals do not easily detect predators ($d$ is low), then a head-down focal individual relies on head-up individuals for information. If social information is good ($I$ is high), then the focal individual in the COORDINATED schedule has a major information advantage over the focal individual in the RANDOM schedule during the *NO-HEADS* section. At the extreme (when head-down individuals do not detect predators), the COORDINATED focal individual performs collective detection with probability $I$ (under either information function), and the RANDOM focal individual performs collective detection with probability 0 during the *NO-HEADS* section.

Thus, when $d$ is low and $I$ is high, coordination yields information gains during the *NO-HEADS* section. Furthermore, these gains outweigh the losses due to the poorer dilution found in the COORDINATED schedule. However, information does work against coordination during the *MANY-HEADS* section, where the COORDINATED focal individual has a single head up in its complement, while the RANDOM focal individual has two or more heads up (see Figure 1b). The same factors working for coordination during the *NO-HEADS* section (low $d$, high $I$) should now work against coordination during the *MANY-HEADS* section. So why is it that the *NO-HEADS* section is more important than the *MANY-HEADS* section with regard to information flow? There are actually two reasons. First, the *NO-HEADS* section is always longer than the *MANY-HEADS* section (this is proved in Appendix B).

Second, we note that our information functions are concave increasing functions. The increase in information as we move from 0 to 1 detecting individuals in the complement is greater than the increase in information as we move from 1 to 2 individuals, and so on. That is, two heads are better than one, yet the increase from no heads to one head is greater than the increase from one to two. This is most obvious when looking at the information functions themselves (see Figure 3). In the figure, we label $\Delta_{y,z}$ as the increase in information when moving from $y$ detecting individuals to $z$ detecting individuals (where $y < z$). In the *NO-HEADS* section, we are comparing information from one head-up (and thus detecting) individual from the COORDINATED complement to information from zero head-up individuals from the RANDOM complement. This increment is $\Delta_{0,1} = I$ in both information functions (see Figure 3) and thus is large when $I$ is large. In the *MANY-HEADS* section, we are comparing information from one head-up individual from the COORDINATED complement to information from two (or more) head-up individuals from the RANDOM complement. These increments are the values $\Delta_{1,z}$, where $z \in \{2,3,4, \ldots g-1\}$. In the case of the exponentially saturating information function, these $\Delta$ values are small when $I$ is large. These $\Delta$ values are always zero for the step information function (see Figure 3). Thus, when $d$ is small and $I$ is large, the gain in social information for the COORDINATED schedule during the *NO-HEADS* section ($\approx\Delta_{0,1}$) can be greater than the loss of information for the COORDINATED schedule during the *MANY-HEADS* section ($\approx\Delta_{1,2}, \Delta_{1,3}, \Delta_{1,4}, \ldots$).

To understand the roles of these time sections further, it helps to rewrite the value of coordination as follows:

$$\mathcal{V} = \alpha + \beta, \tag{9}$$

where $\alpha$ gives the contribution to $\mathcal{V}$ from the *MANY-HEADS* section and $\beta$ gives the contribution from the *NO-HEADS* section. For instance, in the case of the value from Equation 8, we have:

$$\begin{aligned}\alpha &= [(1-p)^g - (1-pg)]\\ &\quad\times\left[\frac{1-(d+(1-d)I)^g + ((1-d)I)^g}{g} - \frac{1-(d+(1-d)I)^{g-1}}{g-1}\right],\\ \beta &= \frac{1-(p+(1-p)d+(1-p)(1-d)I)^g}{g}\\ &\quad - \frac{(1-p)^g[1-(d+(1-d)I)^g]}{g}\\ &\quad - \frac{[(1-p)-(1-p)^g][1-(d+(1-d)I)^{g-1}]}{g-1}.\end{aligned}$$

In Figure 4, we graph $\alpha$, $\beta$, and $\mathcal{V}$ for the case of $g = 10$ for both of our information functions. From the figure we see that the value of coordination is the highest through contributions made by the $\beta$ term (i.e., improved information with $d$ low and $I$ high during the *NO-HEADS* section). The lowest value for coordination comes from the $\alpha$ term (i.e., this is where there is value in a random strategy). We also note that the $\alpha$ term tends to hit its higher values where the $\beta$ term hits its lower values and vice versa—attesting to the tradeoff between information and dilution.

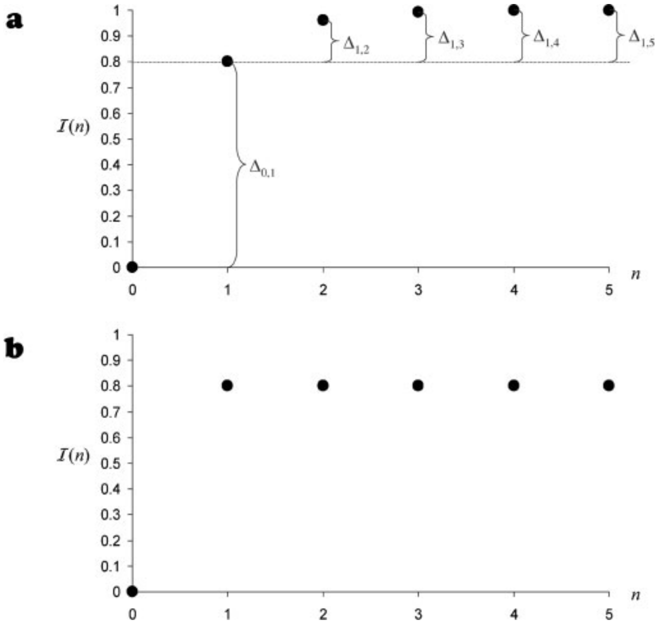

**Figure 3**
(a) The exponentially saturating information function, $\mathcal{I}(n) = 1 - (1-I)^n$, where $n$ is the number of detecting individuals in a focal's complement. Relevant increments in information are given by the values $\Delta_{y,z}$, which is the difference in the probability of collective detection by a focal when moving from $y$ detecting individuals in its complement to $z$ detecting individuals in its complement (where $y < z$). (b) The step information function, $\mathcal{I}(n) = 0$ for $n = 0$, and $\mathcal{I}(n) = I$ otherwise. For both information functions pictured, we let group size $g = 6$ and the collective detection parameter $I = 0.8$ (a relatively large value).

What works against coordination? We see from Figure 2 that low values of $I$ tend to work against coordination. For any set of parameters, there will be some threshold value of $I$ that must be surpassed to favor coordination. This again suggests that collective information is critical in making coordination valuable. The effects of group size and head-down detection on the value of coordination appear to be dependent on the form of the information function. In the case of the exponentially saturating information function, the region where $\mathcal{V} > 0$ increases initially with $g$. However, in the case of the step information function, the region where $\mathcal{V} > 0$ decreases with $g$. Lastly, while small values of $d$ tend to favor coordination, large values of $d$ also favor coordination for the exponentially saturating information function, but not for the step information function.

## DISCUSSION

Decisions depend on information. Therefore, foraging decisions in most animal groups are based on the quality and quantity of information (Ydenberg, 1998). Previous analyses have assumed that animals need to raise their heads to gather information about predators (Pulliam et al., 1982; Ward, 1985). However, animal visual fields allow some species

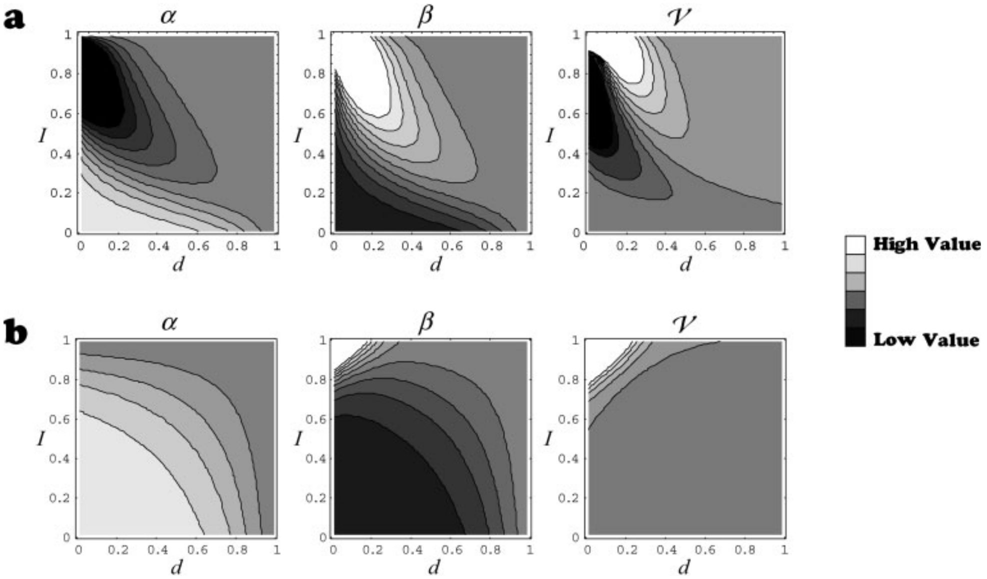

**Figure 4**
The value of coordination ($\mathcal{V}$) is broken into two components, α and β, giving the value of coordination during the *MANY-HEADS* and *NO-HEADS* time sections from Figure 2, respectively. We plot α and β for information functions (a) $\mathcal{I}(n) = 1 - (1 - I)^n$, and (b) $\mathcal{I}(n) = 0$ for $n = 0$, and $\mathcal{I}(n) = I$ otherwise. We let group size $g = 10$, and the fraction of time spent scanning $p = 0.04$ for all graphs. (Note that the greyscale for α and β covers a larger range than the greyscale for $\mathcal{V}$).

to monitor for food while head-up (Hodos and Erichsen, 1990) or for predators while head-down (Arentz and Leger, 1997; Lima and Bednekoff, 1999). Our model incorporates personal and collective detection in both head-up and head-down postures. As our results show, the variability in visual information gathering affects the survival value of different scanning strategies.

Our model specifies the value of coordinated vigilance according to the degree to which information is gathered in different body postures. Overall, coordination is expected in systems where the ability of individuals to detect predators in head-down postures is low but the transfer of information between group members is high. This may be the case for species with low visual acuity (degree of visual resolution) but with visual fields wide enough to detect the behavior of conspecifics while head-down (Martin and Katzir, 1999). Another example might be groups foraging where habitat obstructions (e.g., grass, rocks) decrease the chances of directly detecting predators but where neighbors are located close to each other so that information could spread rapidly. Although we have focused some of the implications of our results on birds, our results are likely to apply generally for species with laterally placed eyes and peripheral vision.

Moreover, the model unites models of vigilance and sentinel behavior in a common framework that may help explain coordination in other systems that combine visual and auditory information. For instance, consider a system in which predator detection is primarily through visual means, and individuals have a low probability of personally detecting a predator when head-down, (i.e., $d$ could be low). Coordination would be favored if unaware individuals have access to high quality information (i.e., $I$ would be high) through the alarm calls given by detecting individuals. Such a scenario may be likely in species exhibiting sentinel behavior. In fact, our model makes the same predictions if the head-up/head-down dichotomy is replaced with a sentinel/forager dichotomy. The model predicts that coordination of sentinels will be valuable if sentinels have a large advantage in detecting threats and information spreads readily from sentinels to foragers. This type of coordination has been corroborated by empirical evidence (Bednekoff and Woolfenden, 2003).

A persistent question in the literature is why coordinated vigilance is not widespread in loose foraging aggregations given its putative benefits? Previous studies have suggested that coordination is always beneficial but not attainable either because of costs (Lendrem et al., 1986; Ward, 1985) or lack of evolutionary stability (Rodríguez-Gironés and Vásquez, 2002). We do not discount these possibilities but note that they may not be necessary to explain the lack of vigilance coordination. In our model, the value of coordination can be negative. Thus, coordination may not be favored even if it has little or no explicit cost. The original analysis of coordinated vigilance (Ward, 1985) combined conditions that are optimal for coordination: no personal detection when head-down ($d = 0$) and extreme collective detection when head-down ($I = 1$). For other realistic combinations, a random strategy may become more profitable than coordinated vigilance. For example, small granivorous birds can detect predators when head-down (Lima and Bednekoff, 1999) and have limited spread of information through collective detection (Lima and Zollner, 1996). Thus, they have moderate levels of both $d$ and $I$. Empirical evidence suggests that these species follow a random scanning strategy (Bekoff, 1995; Elcavage and Caraco, 1983). Likewise, studies with species with low head-down personal and collective detection due to the location of their eyes and the configuration of their visual fields, such as ostriches, show that individuals scan randomly (Bertram, 1980; Fernández et al., 2003). Overall, an inability to gather information from conspecifics while head-down ($I$ is low) will be an important factor working against coordination.

We consider only two possible information functions that make different, plausible assumptions about the flow of information in groups. Because non-detectors flee some time after detectors, they are probably in greater danger (Lima, 1994). Also, foraging birds often raise their heads briefly following even a single departure of their flock mates (Lima, 1995b). They would spot a real attacker at some point, but perhaps too late to escape. The step function shows that the second-hand information of collective detection will not be as clear and timely as that from direct detection. In birds without alarm calls, an entire flock of birds is more likely to flush in response to two near-simultaneous departures than to one departure and more likely in response to three departures than to two (Lima, 1995b). The exponential saturating function demonstrates this finding. Thus, the two information functions that we used incorporate two key aspects of imperfect collective detection. Many other information functions are possible, but plausible functions mostly combine elements of our two functions and therefore are intermediate between them. Results that are general to our two functions may hold for intermediate functions (see Bednekoff [2001] for a similar argument). Therefore, it is likely that imperfect information spread generally decreases the value of coordinated vigilance.

Previous work suggests that coordination is more beneficial in small groups (Rasa, 1986; Rodríguez-Gironés and Vásquez, 2002; Ward, 1985). Using our step information function, we obtain a similar result. However, with the exponentially saturating function, we realized a novel result; the region favoring coordination actually grows with group size. Given the sensitivity of the model to the shape of the information function, we suggest that further empirical work is needed to discern the form of these functions in natural conditions. Unlike the effect of imperfect information, the effect of group size on the value of coordination is equivocal.

Our model assumes that head-up individuals always detect predators and that detecting individuals always escape predation. While such assumptions may seem extreme, the general conclusions of the model are robust to changes in these assumptions. For instance, we extended our model to allow individuals that detected a predator to remain vulnerable to predation. While the magnitude of the value of coordination generally decreases within this new framework, the conditions that favor coordination do not qualitatively change. We also explored a model extension in which head-up individuals do not always detect predators. Although this alteration complicates the model, the basic conclusions about the conditions favoring vigilance coordination remain unchanged.

In our model we also assume that all individuals within the group have equal access to personal and collective information. However, empirical evidence suggests that foragers get more information from closer neighbors (Fernández-Juricic and Kacelnik, 2004; Hilton et al., 1999) and most foraging groups have an inherent geometry that engenders information-gathering asymmetries between different individuals (Stankowich, 2003). For instance, a foraging group has individuals in the center and individuals on the periphery. It seems likely that individuals in the center may have an easier time getting collective information (from surrounding conspecifics), whereas peripheral individuals may have an easier time obtaining direct information about approaching predators. Group geometry would also influence the distribution of risk among the various members. Thus, different members of the same group will often gain different amounts from coordination. Because this decreases the chances that all group members will benefit from coordination, it is possible that such information-gathering asymmetries within groups will limit the conditions for the coordination of vigilance. However, to formally investigate these issues, it would be worthwhile to construct a model that explicitly incorporates heterogeneity in the procurement and flow of information.

### Implications for future studies

An important implication for empirical studies is that coordination in non-permanent foraging groups should be studied in species with different visual systems or, more specifically, in species that differ in the way that body posture affects personal and collective detection. This study supports the view that a better understanding of the visual systems of different species would certainly allow us to reduce the mismatch between theoretical models of vigilance and empirical studies (Bednekoff and Lima, 2002; Fernández-Juricic et al., 2004a).

## APPENDIX A

### Derivation of the value of coordination

Let the event that the focal individual's head is down when the predator approaches be given by $\mathbf{D}$. Let $\mathbf{S}_i$ be the event that $i$ individuals in the complement have their heads up (and thus, $g-1-i$ individuals have their heads down). Let $\mathbf{P}_j$ be the event that $j$ individuals with their heads down in the complement detect the predator at the moment it approaches. Note that given $\mathbf{S}_i$, we have the following constraints on $\mathbf{P}_j$: $j \leq g-1-i$. The danger, $\mathcal{D}$, to our focal individual is the probability of being caught (call this event $\mathbf{E}$) by the predator. Incorporating all the events above, we have:

$$\mathcal{D} = \sum_{i=0}^{g-1} \sum_{j=0}^{g-1-i} \Pr\{\mathbf{E} \mid \mathbf{P}_j \cap \mathbf{S}_i \cap \mathbf{D}\} \Pr\{\mathbf{P}_j \mid \mathbf{S}_i \cap \mathbf{D}\} \times \Pr\{\mathbf{S}_i \mid \mathbf{D}\} \Pr\{\mathbf{D}\}. \tag{A1}$$

For both the RANDOM and COORDINATED cases we have the following:

$$\begin{aligned}
\Pr\{\mathbf{D}\} &= 1-p \\
\Pr\{\mathbf{P}_j \mid \mathbf{S}_i \cap \mathbf{D}\} &= \binom{g-1-i}{j} d^j (1-d)^{g-1-i-j} \\
\Pr\{\mathbf{E} \mid \mathbf{P}_j \cap \mathbf{S}_i \cap \mathbf{D}\} &= (1-d)(1-\mathcal{I}(i+j)) \\
&\quad \times \left\{ \sum_{x=0}^{g-1-i-j} \left(\frac{1}{x+1}\right) \binom{g-1-i-j}{x} \right. \\
&\qquad \left. \times (1-\mathcal{I}(i+j))^x \mathcal{I}(i+j)^{g-1-i-j-x} \right\} \\
&= \frac{(1-d)\{1-\mathcal{I}(i+j)^{g-i-j}\}}{g-i-j}
\end{aligned}$$

To compute $\Pr\{\mathbf{E} \mid \mathbf{P}_j \cap \mathbf{S}_i \cap \mathbf{D}\}$, we note that first of all, in order to be caught the focal individual cannot detect the predator (i.e., no personal detection). This is the first factor on the right-hand side. Also, the focal individual cannot gather information from other individuals that have detected the predator (i.e., no collective detection). This is the second factor. The last (braced) factor is simply the probability of being chosen by the predator after all individuals performing personal or collective detection have left the group. If $x$ head-down individuals in the complement are neither aware nor informed about the predator, the probability that our unaware focal individual is caught is $(1/(x+1))$. This quantity is multiplied by the probability that there are $x$ head-down individuals both non-detecting and uninformed and then summed over all possible values of $x$. Above we see that $\Pr\{\mathbf{E} \mid \mathbf{P}_j \cap \mathbf{S}_i \cap \mathbf{D}\}$ simplifies into a tidy expression.

Because in the COORDINATED case one individual, at most, can have its head up at any one time, we have the following restrictions: $\Pr\{\mathbf{P}_j \mid \mathbf{S}_i \cap \mathbf{D}\}$ and $\Pr\{\mathbf{E} \mid \mathbf{P}_j \cap \mathbf{S}_i \cap \mathbf{D}\}$ are defined only where $i = 0{,}1$ (we will define $\Pr\{\mathbf{P}_j \mid \mathbf{S}_i \cap \mathbf{D}\} = 0$ and $\Pr\{\mathbf{E} \mid \mathbf{P}_j \cap \mathbf{S}_i \cap \mathbf{D}\} = 0$ if $i \geq 2$).

All that remains is the expression $\Pr\{\mathbf{S}_i \mid \mathbf{D}\}$. This expression is different between the RANDOM and COORDINATED cases. In the RANDOM case, we have the following:

$$\Pr\{\mathbf{S}_i \mid \mathbf{D}\} = \binom{g-1}{i} p^i (1-p)^{g-1-i}.$$

In the COORDINATED case, if the focal individual's head is down, then either 0 or 1 individual in the rest of the group has its head up scanning. Since

$$\Pr\{\mathbf{S}_i \mid \mathbf{D}\} = \frac{\Pr\{\mathbf{S}_i \cap \mathbf{D}\}}{\Pr\{\mathbf{D}\}},$$

and the only non-zero cases are $\Pr\{\mathbf{S}_0 \cap \mathbf{D}\}/\Pr\{\mathbf{D}\}$, and $\Pr\{\mathbf{S}_1 \cap \mathbf{D}\}/\Pr\{\mathbf{D}\}$, we have:

$$\Pr\{\mathbf{S}_i \mid \mathbf{D}\} = \begin{cases} \frac{1-pg}{1-p} & \text{with } i = 0 \\ \frac{p(g-1)}{1-p} & \text{with } i = 1 \\ 0 & \text{with } i \geq 2 \end{cases}$$

Using Equation A1 and all the above probabilities, we can compute the danger to a focal individual under the RANDOM and COORDINATED schedules. After some rearrangement and simplification, the RANDOM schedule gives:

$$\mathcal{D}_r = \frac{1}{g}\left[1 - \sum_{i=0}^{g}\sum_{j=0}^{g-i}\binom{g}{i, j, g-i-j} \times p^i[d(1-p)]^j[(1-d)(1-p)\mathcal{I}(i+j)]^{g-i-j}\right]. \quad \text{(A2)}$$

Equation A2 is quite satisfying. In brackets we see the probability that at least one individual is left susceptible to predation (the multinomial expression gives the probability that all individuals in the group escape predation). The factor 1/g is there because the danger is shared uniformly across the entire group (i.e., there are no asymmetries between individuals). For the COORDINATED strategy we have:

$$\mathcal{D}_c = \frac{1}{g}\left[1 - (1-pg)\left\{\sum_{j=0}^{g}\binom{g}{j} d^j[(1-d)\mathcal{I}(j)]^{g-j}\right\} - pg\left\{\sum_{j=0}^{g-1}\binom{g-1}{j} d^j[(1-d)\mathcal{I}(j+1)]^{g-1-j}\right\}\right]. \quad \text{(A3)}$$

Similar to Equation A2, the bracketed factor in Equation A3 is the probability that at least one individual is left susceptible to predation (the first term in braces gives the probability that all individuals in the group escape predation when all heads are down and the second term in braces gives the probability that all individuals in the group escape predation when exactly one head is up). Finally, the value of coordination is simply the difference between the dangers:

$$\mathcal{V} = \frac{1-pg}{g}\left\{\sum_{j=0}^{g}\binom{g}{j} d^j[(1-d)\mathcal{I}(j)]^{g-j}\right\} + p\left\{\sum_{j=0}^{g-1}\binom{g-1}{j} d^j[(1-d)\mathcal{I}(j+1)]^{g-1-j}\right\} - \frac{1}{g}\left\{\sum_{i=0}^{g}\sum_{j=0}^{g-i}\binom{g}{i, j, g-i-j} \times p^i[(1-p)d]^j[(1-p)(1-d)\mathcal{I}(i+j)]^{g-i-j}\right\} \quad \text{(A4)}$$

## APPENDIX B

### Proof of time difference

Figure 1b shows the *MANY-HEADS* and *NO-HEADS* time sections. The length of the *MANY-HEADS* section is $(1-p) - (1-2p+gp)(1-p)^{g-1}$, and the length of the *NO-HEADS* section is $(1-p)^g - (1-pg)$. Here we use an induction proof to demonstrate the following relation:

$$(1-p) - (1-2p+gp)(1-p)^{g-1} < (1-p)^g - (1-pg), \quad \text{(B1)}$$

given $g \in \{2,3,4, \ldots\}$ and $0 < p < 1/g$. Since

$$(1-p) - (1-2p+2p)(1-p)^{2-1} = 0 < p^2 = (1-p)^2 - (1-2p),$$

Equation B1 holds in the case of pairs (i.e., $g = 2$). Now assume

$$(1-p) - [1-2p+(g-1)p](1-p)^{g-2} < (1-p)^{g-1} - [1-p(g-1)].$$

Multiplying both sides by the quantity $(1-p)$, we have:

$$(1-p)(1-p) - [1-2p+(g-1)p](1-p)^{g-1} < (1-p)^g - [1-p(g-1)](1-p)$$

$$(1-p) - (1-2p+gp)(1-p)^{g-1} < (1-p)^g - (1-pg) - p + p[1-p(g-1)] + p(1-p) - p(1-p)^{g-1}$$

$$(1-p) - (1-2p+gp)(1-p)^{g-1} < (1-p)^g - (1-pg) + pC$$

If we can show that the term $C = -p + [1-p(g-1)] - (1-p)^{g-1}$ is negative, then we have

$$(1-p) - (1-2p+gp)(1-p)^{g-1} < (1-p)^g - (1-pg),$$

which will complete our proof by induction. We note

$$C = -p - \{(1-p)^{g-1} - [1-p(g-1)]\}.$$

However, because $(1-p)^x - (1-px) \geq 0$ for all $x \in \{1,2,3,4, \ldots\}$, we have $C < 0$. Therefore, Equation B1 holds for all $g \in \{2,3,4, \ldots\}$.

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