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Re-examining safety in numbers: interactions between risk dilution and collective detection depend upon predator targeting behaviour

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Many studies document that individuals visually scan for predators less frequently when in the safety of larger groups. This widely replicated effect has generally been explained in terms of distinct predator detection and risk-dilution effects. We show that a strict distinction between detection and dilution disappears when information about attacks is imperfectly shared (as it is in reality). Furthermore, dilution and detection effects change depending on when during an attack the predator targets a particular prey individual for pursuit. Realistic detection and dilution effects probably interact with each other and also with the targeting behaviour of predators. Instead of considering detection and dilution effects on vigilance, it may be more profitable to consider each prey's probability of being targeted during an attack and its probability of escaping if attacked. This perspective emphasizes that a full understanding of safety in numbers requires an understanding of predator targeting strategies.

Keywords: predator–prey; vigilance; foraging; risk dilution; collective detection; sociality

1. INTRODUCTION

Animals frequently interrupt feeding or some other activity to visually scan their environment. This scanning behaviour, labelled vigilance, changes reliably with changes in predation risk, and is directed in large part towards detecting potential predators (Elgar 1989; Lima & Dill 1990; Roberts 1996). The study of anti-predator vigilance developed after 'safety in numbers' was identified as one of the potentially large advantages for group living (Bednekoff & Lima 1998). Subsequently, the novel theoretical prediction that vigilance should decrease with group size was developed and borne out by many empirical studies. Other studies have shown that animals are more vigilant not only in smaller groups, but also more generally in situations where predation risk is likely to be higher (see Elgar 1989; Lima & Dill 1990; Bednekoff & Ritter 1994). The study of vigilance has enjoyed a productive interaction between theoretical and empirical work, which continues to this day (Lima 1990; McNamara & Houston 1992; Bednekoff & Lima 1998). In the spirit of this interaction, we re-examine existing theory in light of recent empirical findings. To this end, we first review current theory and then the relevant empirical work.

(a) *Existing theory*

The theoretical study of vigilance stems from a single, short paper (Pulliam 1973). This paper developed a mathematical model of how independent scans by group members could decrease the danger to each group member. It assumed that detection by any group member resulted in equal safety for all group members. Implicitly, this amounts to assuming that detection information spreads instantly through a group (see also Bednekoff 1997). This model of the collective detection of attacks did not include the numerical dilution of risk, which has its full impact when the predator can kill only one member of the group during an attack. The term 'dilution effect' apparently derives from Foster & Treherne (1981), based upon wording in Bertram (1978). The idea, however, that a predator might kill only one member of a group of n prey had already been incorporated (among other things) into a model of predator–prey behavioural interactions (Treisman 1975). Although all of these authors prominently cite the selfish-herd model (Hamilton 1971), the dilution effect is not a direct consequence of the selfish herd. Hamilton (1971) most certainly did not assume that risk of predation is divided evenly among all members of a group. His major point was exactly the opposite.

Subsequent models of vigilance incorporated dilution effects but retained the same core of assumptions about detection—foragers scan for predators independently but share information perfectly and instantly when they detect predators (Pulliam *et al.* 1982; Parker & Hammerstein 1985; Lima 1987; Dehn 1990). If any group member detects an attack before the predator gets too close, all group members escape. If no group member detects an attack before the predator is within striking distance, then each of the n group members has $1/n$ chance of being the victim. In this scenario, collective detection and dilution are autonomous issues.

With such perfect collective detection, all group members are at equal risk because, at any instant, they

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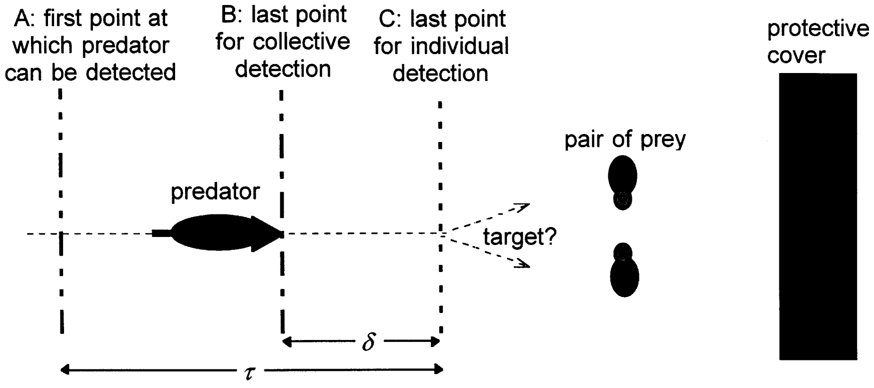

Figure 1. The attack scenario. A predator is approaching from the left. It can first be detected at point A. If a prey individual detects the predator before point C, that individual can escape to protective cover. If a prey individual detects the predator before point B, not only does it escape, but also the other prey has time to react and escape. The predator takes τ seconds to move from A to C and δ to move from B to C. At some point, the predator targets one of the prey for attack. The figure shows targeting at point C, as assumed by model 3.

either all know about the approaching predator or none knows. However, it is reasonable that the individual who first detects the predator should be less at risk than those who learn about it secondarily. Two further models considered this possibility and its implications for vigilance in groups (Packer & Abrams 1990; McNamara & Houston 1992). In order to do so, however, these models side-stepped the details of detection and assumed that predators are sometimes successful even when detected by some group members (see also Pulliam *et al.* 1982), but that when this occurs, predators are less likely to kill detectors than non-detectors. Although the underlying idea that detectors have some advantage is biologically realistic, the exact forms of these theoretical modifications are difficult to relate to any recognizable behaviours. Below we develop models that provide a behavioural basis for evaluating the potential advantage to group members that detect predators directly. In doing so we specify the consequences of a detector advantage for our understanding of detection and dilution effects.

(b) *Empirical update*

A recent series of experiments has shown that collective detection is far less efficient than envisaged, at least for species that do not routinely give alarm calls (Lima 1994*a*, 1995*a*,*b*; Lima & Zollner 1996; see also FitzGibbon 1989). In these experiments, one to three members of a flock of emberizid sparrows were given privileged information about an approaching threat. Although these 'informed' flock members reacted rapidly and realistically, the rest of the flock rarely flushed unless several informed birds reacted within a very short time period (Lima 1995*a*,*b*). Other flock members clearly noticed these threat-driven departures because they often glanced up immediately after departures, but they quickly resumed feeding on most occasions. From this work it seems that threat-induced departures in such species are little different than other departures from a flock. Therefore, flock members can 'collectively' respond to attacks either through glancing up after a departure and detecting a predator themselves or by unquestioningly joining the flush of several flock members. Collective detection of a sort occurs in that flock members probably react much sooner than they would have otherwise, but this collective detection is clearly inefficient in that 'reactors' at best flee to safety well after detectors (Lima 1994*a*,*b*).

At first glance, this inefficient form of collective detection would not seem to alter the 'distinctiveness' of dilution and detection. As we will show, however, the exact nature of dilution depends on how and when the predator targets prey and which prey are available at that moment. Which prey are available, in turn, depends upon the development of collective detection through time.

2. MODELS

We describe three simple models of vigilance in groups. For illustrative purposes we analyse the smallest of groups—pairs of animals—but the same principles apply to larger groups. The first model assumes perfect collective detection. The other two models incorporate imperfect collective detection but assume different targeting behaviours by predators. All three models assume the same scanning process and attack scenario (figure 1). During attacks, predators must rush across some open space and begin this rush without regard to the scanning behaviour of the potential prey. To be successful, such a predator must overtake the prey before the prey can reach protective cover. The predator takes τ seconds to rush from the location at which it could first be detected to the first point from which it can win this race to cover (point C, figure 1). After this point, even if prey notice impending death they can do nothing to avoid it. This time τ will depend on the relative speeds of predator and prey, the distance that prey are from cover, and how closely the predator can approach the feeding site before becoming detectable (Lima 1987).

Following other models of vigilance (Pulliam 1973; Pulliam *et al.* 1982; Lima 1987), we assume that scans are initiated at a constant rate per unit of time spent feeding (see also Bednekoff & Lima 1998). In each model, the focal animal initiates scans at a rate λ per second and the other animal in the pair at a rate $\hat{\lambda}$. Each animal initiates scans independently of the other (Bednekoff & Lima 1998).

We first introduce a baseline model with perfect collective detection. Here, if either animal detects an attack before the predator is τ seconds into its rush, both get away. The probability that an animal fails to look up before the predator has reached the critical point (i.e. point C), is a negative exponential function of that animal's scanning rate and the time that the predator takes to reach this point, i.e. $e^{-\lambda\tau}$ (Pulliam 1973). Because the animals scan independently of one another, the probability that both will fail to look up in time is simply the probability that one will fail multiplied by the probability that the other will fail. When an attack occurs, the danger to an individual if we assume perfect collective detection (D_p) is the probability that both fail to detect the attack divided by two, as the predator will kill only one of the pair:

$$D_\text{p} = (\mathrm{e}^{-\lambda\tau}\mathrm{e}^{-\hat{\lambda}\tau})/2. \tag{1}$$

Here the terms in the numerator describe detection and the 2 in the denominator describes dilution.

Next we modify collective detection so that it takes some time to occur (see Lima 1994*a*). We still assume that a focal animal must detect an attack before τ seconds have elapsed, and that it can either detect the attack directly through its own scanning or react to detection by another group member. Because reacting to others takes some time, δ, the focal animal reacts in time to escape only if its companion detected the attack before the predator was $\tau - \delta$ seconds into its attack (i.e. before the predator reached point B in figure 1). If a group member detects the predator after $\tau - \delta$ but before τ has passed (i.e. between points B and C), that individual has time to escape but its companion does not have time to react effectively. Assuming that the predator commits itself to pursuing one member of a pair of animals before it is $\tau - \delta$ seconds into its attack, the danger for the focal animal under early targeting (D_e) is

$$D_\text{e} = (\mathrm{e}^{-\lambda\tau}\mathrm{e}^{-\hat{\lambda}(\tau-\delta)})/2. \tag{2}$$

The focal animal is in danger when three things occur: (i) it does not look up by τ; (ii) the other animal does not look up by $\tau - \delta$; and (iii) the predator happens to target it rather than the other animal (with probability 1/2).

Equation (2) is the same as equation (1) except for the inclusion of the delay, δ. As δ increases in equation (2), collective detection becomes less effective, but this does not alter the probability that one animal is targeted instead of the other (so long as targeting occurs by $\tau - \delta$ seconds into the attack). As with equation (1), the numerator describes detection and the denominator represents dilution. Thus, if the predator chooses a target near the beginning of its attack rush, the targeting behaviour that produces dilution actually precedes detection, but dilution and detection are still separable entities.

In our final model, the predator does not target a particular individual until τ, the last point for effective detection. Here the logic of the situation changes considerably because the departure of any group member before τ can alter the dilution of risk for those remaining. We illustrate this by assuming that the predator chooses at random from among prey that have not reacted by the time it is τ seconds into its attack. For a pair of animals, the danger to the focal animal is

$$D_\tau = \mathrm{e}^{-\lambda\tau}\left[(\mathrm{e}^{-\hat{\lambda}(\tau-\delta)} - \mathrm{e}^{\hat{\lambda}\tau}) + \frac{\mathrm{e}^{-\hat{\lambda}\tau}}{2}\right] = \mathrm{e}^{-\lambda\tau}\left(\mathrm{e}^{\hat{\lambda}(\tau-\delta)} - \frac{\mathrm{e}^{-\hat{\lambda}\tau}}{2}\right). \tag{3}$$

This equation reads: danger equals the probability of not looking up by τ multiplied by [(the probability that the other animal will look up between $\tau - \delta$) plus one-half of the probability that the other animal does not look up in time to escape]. In equation (3), the '2' signifying dilution appears only in one term rather than across the board, because the probability of the focal animal being targeted depends on whether and when the other animal detects the predator. Thus, both detection and dilution change with vigilance rates in late-targeting scenarios. As the delay term, δ, increases, not only does collective detection become less effective, but dilution also decreases because the focal animal becomes increasingly likely to be the sole target of the predator. At the extreme, when $\delta \geqslant \tau$, collective detection does not have time to occur and any effective detection by one group member shifts the undiluted risk of attack to its group mate. At the other extreme ($\delta = 0$), equations (2) and (3) collapse to equation (1).

The primary consequence of imperfect collective detection is that different group members will react to an attack at different times. By comparing equation (3) with equation (2), we see that detection and dilution effects combine in different ways depending on how and when the predator targets prey. These two equations serve to illustrate this principle, but they also embody two particular points from a wider continuum of possibilities: predators could target between $\tau - \delta$ and τ, or even after τ. In general, dilution effects become less distinct from detection effects as predators can put off committing to one target until later in an attack. In the extreme, if a predator pursued only the last member of a group to detect its approach, detection and dilution effects would be inseparably intertwined. Group members would gain a dilution benefit when the predator pursued someone else, but the odds of this would depend entirely on detecting the predator before others did (i.e. the odds of being targeted would be $\hat{\lambda}/(\hat{\lambda} + \lambda)$ for the focal animal and $\lambda(/\hat{\lambda} + \lambda)$ for the other member of the pair).

Besides blurring the distinction between dilution and detection, imperfect collective detection has other consequences for the idea of safety in numbers. First, imperfect collective detection leads to more danger than does perfect collective detection. In our models, we can see this by dividing the danger expected under the second and third models by that expected under the first model (equation (1)). For any set of parameters, if predators target early (equation (2)) the relative danger (D_e/D_p) is $\mathrm{e}^{\hat{\lambda}\delta}$. If predators target at the critical point τ (equation (3)), the relative danger (D_τ/D_p) is ($2\mathrm{e}^{\hat{\lambda}\delta} - 1$). These expressions equal 1 for $\delta = 0$, and always increase with increasing δ. Thus, as collective detection becomes more faulty (δ increases), the benefits of feeding with another individual decrease.

This above result indicates that the benefits of sociality are influenced less by the vigilance of group members as collective detection declines in effectiveness. With perfect collective detection, danger declines distinctly as the vigilance of the other animal increases (figure 2). With imperfect collective detection and early targeting, danger to the focal animal declines steadily but less quickly with the vigilance of the other forager (figure 2). With imperfect collective detection and targeting at τ, the danger can sometimes increase with the vigilance of the other forager. We can see this by examining the partial derivative of equation (3) relating danger for the focal animal to the vigilance rate of the other forager:

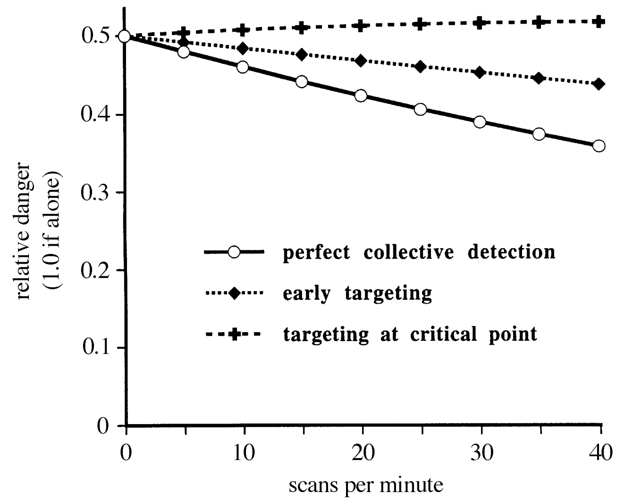

Figure 2. How danger to the focal animal is affected by the scanning rate of the other member of the pair under the three models. This graph is scaled to the danger of foraging with the same rate of scanning, λ, while alone ($e^{-\lambda\tau}$). The delay term (δ) is 0.3 s and the time available for detection (τ) is 0.5 s.

$$\begin{aligned}\frac{\partial D_\tau}{\partial \hat{\lambda}} &= e^{-\lambda\tau}\left(-(\tau-\delta)e^{-\hat{\lambda}(\tau-\delta)} + \tau\frac{e^{-\hat{\lambda}\tau}}{2}\right) \\ &= e^{-(\lambda+\hat{\lambda})\tau}\left(\frac{\tau}{2} - (\tau-\delta)e^{\hat{\lambda}\delta}\right).\end{aligned} \tag{4}$$

Within a pair, here, danger to one member of the pair increases initially with the vigilance of the other animal (i.e. as $\hat{\lambda}$ increases from 0) if $\delta > \tau/2$; that is, if the time needed to react to detection by another is more than half the time it takes the predator to reach the critical point in its approach. In this range, late detection by the other animal subtracts from the benefit of risk dilution more than early detection adds to the benefit of collective detection.

This mathematical result suggests the fascinating possibility that an animal could be safer if paired with a less vigilant animal than when paired with a more vigilant one. Before pursing this possibility, we must check whether such an outcome is biologically plausible. Emberizid sparrows, at least, may frequently skulk along the borderline of this region (i.e. $\delta \approx \tau/2$); the delay in reacting to a threat-induced departure by another bird is about 0.3 s (Lima 1994*a*) and τ is likely to be less than 1 s, and could plausibly be much shorter when under attack by *Accipiter* hawks (Lima 1994*b*). Thus, such sparrows might be somewhat more in danger if their flock-mates are more rather than less vigilant. This endangerment, however, seems to be very small for realistic vigilance rates (figure 2). Furthermore, feeding in a pair is always much safer than feeding alone, regardless of the vigilance level of that group-mate (see also Motro & Cohen 1989). Whether or not danger increases or decreases slightly with the vigilance of the other member of the pair, the danger of feeding socially is roughly half of the danger of feeding alone (figure 2).

(a) *Comparison to previous models*

Two previous papers have assumed that animals that detect a predator directly are less in danger than those that react secondarily to detection by others (Packer & Abrams 1990; McNamara & Houston 1992). From our models, we see that this advantage applies to detections that occur between $\tau - \delta$ and τ, and depends upon assumptions about when predators target prey. Working within our framework, when predators target at τ, the probability of capture for a non-detector paired with a detector equals the proportion of total detections that occur after $\tau - \delta$, which is

$$\frac{e^{-\hat{\lambda}(\tau-\delta)} - e^{-\hat{\lambda}\tau}}{1 - e^{-\hat{\lambda}\tau}}.$$

This quantity can take on values from zero to one depending on the length of the delay, δ. When predators target before $\tau - \delta$, the danger to non-detectors is the above quantity divided by n, and thus is at most $1/n$. From this we can see in hindsight that McNamara & Houston (1992) implicitly assumed early targeting when they assumed that the danger for a non-detector in a group containing detectors is always less than $1/n$. Packer & Abrams (1990) consider this case (their model 1) and also consider the case when the danger might exceed $1/n$ (their model 2). If we take the phrase 'at the time of the attack' from Packer & Abrams (1990) to mean at the critical point, τ, our second model closely parallels their model 1 and our third model parallels their model 2. Thus our models are consistent with previous modelling efforts and provide a unified basis for evaluating divergent assumptions about the advantage to detectors.

3. DISCUSSION

Safety in numbers for animals has frequently been discussed in terms of discrete detection and dilution effects (e.g. Turner & Pitcher 1986; Lima 1987; Dehn 1990; McNamara & Houston 1992). Dilution and detection effects, however, are likely to be intertwined because collective detection is imperfect. In reality, animals that detect predators directly will probably have a considerable advantage over those that react indirectly to detection by others. Furthermore, the prey targeting behaviour of predators will influence the nature of this advantage and the manner in which detection and dilution effects interact. Although treating detection and dilution as separate entities may often prove useful (or at least convenient), prey can be more broadly viewed as acting to avoid becoming a target for attack and, if targeted, of avoiding capture. From this perspective, we immediately see the importance of understanding how and when predators target prey for attack. Although we have based our models on knowledge of small birds attacked by hawks, the lessons drawn about the spread of detection information among prey and targeting by predators apply very widely. In other situations where detection information spreads even less quickly and efficiently, e.g. via chemical cues, interactions of detection with targeting behaviour may be even more important and apparent.

Predators that kill one member of a group must choose a target for their attack at some point. For *Accipiter* hawks, our impression is that they target a group member early in their (brief) attack. Nonetheless, these hawks have sometimes been reported to switch targets during more extended attack flights (Rudebeck 1950, 1951; Kenward 1978). At any rate, prey seem to know whether or not they are potentially a target. When hawks attack large, scattered flocks, birds not on the hawk's line of flight often freeze or fly perpendicular to the line of flight rather than fleeing directly to the nearest cover (S. L. Lima and P. A. Bednekoff, unpublished results). Such behaviour could serve to prevent the hawk from switching targets.

The animal that is the target, on the other hand, might act to induce the predator to switch targets. It might do this by crossing paths with others while fleeing. This may disrupt the predator's ability to target any individual (i.e. the 'confusion effect' (see Pitcher 1986)), but, given that the predator might switch targets, other individuals might avoid crossing paths with the target. The common case of highly synchronized movements in an escaping group (Bertram 1978; Pitcher 1986) may in part result from non-targets not allowing the targeted individual to cross paths with them.

In our models, predators do not directly target less vigilant prey but may do so by default given that relatively vigilant prey have already detected the attack and thus removed themselves from consideration by the time of targeting (see equation (3)). Although our models may accurately describe *Accipiter* hawk attacks on small birds, other predators do sometimes directly target less vigilant prey (Schaller 1972; FitzGibbon 1989; Krause & Godin 1996). The possibility that predators can directly target relatively vulnerable group members could lead to intricate games between prey anti-predator and predator targeting strategies (see Packer & Abrams 1990). Incidentally, if collective detection was perfect, predators could not profit by targeting less vigilant animals.

The interaction between targeting by predators and the spread of detection information among prey provides a realistic basis for the advantage to detectors included in other models (Packer & Abrams 1990; McNamara & Houston 1992). We see our present modelling efforts as complementary to these previous ones. The previous models provided a broad framework for analysing the qualitative behavioural effects of some advantage to detectors. Our models provide the explicit behavioural details necessary to understand how and why detectors have an advantage in avoiding predators and to estimate the likely magnitude of such an advantage. The basic consequences of a detector advantage should remain as discussed previously (Packer & Abrams 1990; McNamara & Houston 1992).

By including details about predator and prey behaviour, we are also able to offer a quantitative comment on previous game-theoretical analyses of scanning behaviour. After fitting data to a particular model of vigilance behaviour, Pulliam *et al.* (1982) suggested that observed vigilance rates in birds might be maintained by a tit-for-tat-like strategy where flock members monitor each other's vigilance rates and alter their own rates accordingly. This suggestion now seems highly unlikely. We currently have overwhelming evidence that birds and mammals alter their vigilance rates in response to the presence of other individuals and absolutely no evidence that they alter their vigilance rates in response to the vigilance rates of those other individuals (Bertram 1980; Lima 1995*a*). Our calculations suggest that animals might have little to gain by reacting to the vigilance rates of group-mates (see also Ferriere *et al.* 1996; Ruxton & Roberts 1998). In many situations, danger may vary greatly with group size and relatively little with the vigilance level of flock-mates. Given that monitoring the vigilance of others must involve some cost, it is not surprising that these animals are not pursuing whatever small benefit may be available (Ward 1985).

The simple models presented in this paper are not meant to reflect the full range of decisions made by either predators or prey. Targeting by predators probably depends on prey positioning within the group (see Krause 1994), and may involve a more gradual narrowing of focus rather than a single instant of decision. In addition, the existence and strength of collective detection may result from sequences of state- and situation-dependent decisions by the individual members of the groups (Lima 1994*b*, 1995*b*), and larger groups allow far more possible paths for indirect reaction to predator detection. The existence of this rich array of details, however, reinforces the lessons of the simple models developed in this paper, because these details take time and make target selection and collective detection overlap temporally. Whenever target selection by the predator overlaps with the time course of individual decisions leading to collective detection, detection and dilution effects will interact in some way. This set of interacting decisions deserves further study from the perspectives of both predators and prey.

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