

# The contingencies of group size and vigilance

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## ABSTRACT

**Background:** Predation risk declines non-linearly with one's own vigilance and the vigilance of others in the group (the 'many-eyes' effect). Furthermore, as group size increases, the individual's risk of predation may decline through dilution with more potential victims, but may increase if larger groups attract more predators. These are known, respectively, as the dilution effect and the attraction effect.

**Assumptions:** Feeding animals use vigilance to trade-off food and safety. Net feeding rate declines linearly with vigilance.

**Question:** How do the many-eyes, dilution, and attraction effects interact to influence the relationship between group size and vigilance behaviour?

**Mathematical methods:** We use game theory and the fitness-generating function to determine the ESS level of vigilance of an individual within a group.

**Predictions:** Vigilance decreases with group size as a consequence of the many-eyes and dilution effects but increases with group size as a consequence of the attraction effect, when they act independent of each other. Their synergetic effects on vigilance depend upon the relative strengths of each and their interactions. Regardless, the influence of other factors on vigilance – such as encounter rate with predators, predator lethality, marginal value of energy, and value of vigilance – decline with group size.

*Keywords:* attraction effect, contingency, dilution effect, fitness, group-size effect, many-eyes effect, predation risk, vigilance behaviour.

## INTRODUCTION

Animals often take time from feeding to raise their heads and scan their surroundings. This is anti-predator vigilance when it serves to detect approaching predators (Roberts, 1996). In addition to its own vigilance, a foraging animal may gain additional protection from predators through group membership (Hamilton, 1971). With these established views, a major quest of vigilance studies includes documenting and understanding the scanning behaviour of individuals in the context of group size.

Many studies have documented a negative relationship between group size and the rates of scanning by individuals (Lagory, 1986; Elgar, 1989; Lima and Dill, 1990; Quenette, 1990; Roberts, 1996; Hunter

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and Skinner, 1998). Some studies have, however, found either no effect or the opposite effect of group size on vigilance (Lima, 1995; Treves, 2000; Beauchamp, 2003). In Yellowstone National Park, USA, elk (*Cervus elaphus*) and bison (*Bison bison*) failed to show a group size effect (Laundré *et al.*, 2001). For birds and mammals, most correlations have been weak with considerable unexplained variation (Elgar, 1989; Treves, 2000). Lima (1995) found no support for the two essential elements of the group size effect: collective detection and behavioural monitoring. Re-evaluations of the group size effect have, therefore, been suggested (Lima, 1995; Treves, 2000; Beauchamp, 2003).

Here we develop a game theory model of group size and vigilance that includes the documented ways by which group membership can influence predation risk and the value of vigilance. Our goal is to provide a combined modelling framework for generating testable predictions and for evaluating discrepancies in prior theoretical and empirical studies.

Pulliam (1973) modelled the scenario in which the independent scans of group members benefited both the scanning individual and the other group members. As group size increases, progressively more eyes scan the environment for predators (Powell, 1974; Kenward, 1978; Lima, 1995; Bednekoff and Lima, 1998a). While this ‘many-eyes effect’ (which is also referred to as group vigilance, detection effect, or collective detection) has received the most attention, grouping may confer additional benefits such as the ‘dilution effect’. Safety in numbers under the dilution effect occurs when a predator attacks just a single prey per group. Hence, the presence of companions in a group dilutes individual risk (Bertram, 1978; Foster and Treherne, 1981). If vigilance increases with predation risk, then with the dilution effect individual vigilance should decline with group size (Bertram, 1978; Pulliam *et al.*, 1982; Packer and Abrams, 1990; McNamara and Houston, 1992).

In addition to the many-eyes effect and the dilution effect, group size may create an ‘attraction effect’. Aggregations may attract predators (Howe, 1979; Parrish and Edelman-Keshet, 1999; Hebblewhite and Pletscher, 2002). These three effects are not mutually exclusive and all can operate simultaneously to influence predation risk, the optimal level of vigilance, and optimal group size.

Furthermore, under all of these effects the optimal level of vigilance for the individual will depend in part on the vigilance levels of others. Within a group, vigilance becomes a game, and the evolutionarily stable strategy (hereafter ESS) of these vigilance games may predict the individual’s adaptive level of vigilance.

No models have considered simultaneously all three effects: many-eyes, dilution, and attraction. We extend the vigilance model of Brown (1999) into a game of vigilance with group size as a factor. Group size influences the balance between food and safety of individual members, where group size affects an individual’s predation risk, mean and variability of feeding success, and access to mates. At large sizes, individuals face low risk when they derive benefits from collective detection (the many-eyes effect) and the dilution effect. They face greater risk when, as a group, they are more conspicuous (the attraction effect) and when members interfere with each other’s scanning and movements. The model of this paper determines the ESS level of vigilance for an individual as influenced by its group size and environmental factors associated with predation risk. Here we show that the ESS level of vigilance is a social game, and it is contingent on the strengths of the dilution, attraction, and many-eyes effects.

### THE COMPONENTS OF FITNESS

We envision an organism whose fitness,  $G$  (expressed as a finite growth rate), is the product of surviving predation,  $p$ , and its survivor's fitness,  $F$ , given that it survives to the end of time  $T$ . During this time period, the forager allocates its time among  $n$  different activities. The vector  $t = (t_1, \dots, t_n)$  represents time allocated by the forager to its different activities. While engaged in a foraging activity, the animal gains energy through feeding, loses energy through metabolism, and incurs a risk of predation. We let  $f_i$ ,  $c_i$ , and  $\mu_i$  represent, respectively, the feeding rate (joules per unit time, for instance), metabolic cost (joules per unit time), and predation risk (units of per time) from engaging in the  $i$ th activity.

While engaged in a foraging activity, the animals can use vigilance to trade off feeding rate and predation risk. The vector  $u = (u_1, \dots, u_n)$  represents the fraction of time devoted to vigilance while the forager engages in a particular activity ( $0 \leq u_i \leq 1$  for all  $i = 1, \dots, n$ ). We assume that increasing vigilance,  $u_i$ , reduces predation risk,  $\mu_i$ , while engaged in the  $i$ th activity.

The probability of surviving the foraging period can be expressed as:

$$p = \exp\left(-\sum_{i=1}^n \mu_i t_i\right).$$

By increasing vigilance while feeding, safety increases proportionally with the amount of time allocated to the activity. The effect of changing vigilance on safety yields the following:

$$\frac{\partial p}{\partial u_i} = -p t_i \frac{\partial \mu_i}{\partial u_i}.$$

The forager's survivor's fitness,  $F$ , is determined by its energetic profit,  $e$  (units of joules for instance), over the time period:  $F[e(u, t)]$ . The forager can reduce its risk of predation by increasing its level of vigilance,  $u$ . But vigilance comes at a price. We let the forager's net feeding rate decline linearly with the proportion of time devoted to vigilance:  $f_i = (1 - u_i)f_{\max_i}$ , where  $f_{\max_i}$  gives the forager's feeding rate in the absence of vigilance. Across the  $n$  foraging activities, the animal's net energy gain can be written as  $\sum t_i [(1 - u_i)f_{\max_i} - c_i]$ . Increasing the amount of vigilance while foraging has the following effect on the forager's survivor's fitness:

$$\frac{\partial F}{\partial u_i} = \left(\frac{\partial F}{\partial e}\right) \left(\frac{\partial e}{\partial u_i}\right) = \left(\frac{\partial F}{\partial e}\right) (-f_{\max_i} t_i).$$

With all of these components, we can express the organism's fitness as (Brown, 1999):  $G = pF$ ,

with respect to  $t$  and  $u$  subject to  $\sum_{i=1}^n t_i = T$ .

Brown (1999) uses this model to solve both for the optimal allocation of time and the optimal level of vigilance while engaged in a particular activity. Here we are interested in how group size influences vigilance, and so in the following section we focus on the optimal level of vigilance given that time has been allocated in some manner.

### MODELLING OPTIMAL VIGILANCE WITHIN A GROUP

In this section, we shall determine the forager's optimal level of vigilance while engaged in the  $i$ th foraging activity. For ease of presentation, we shall drop the subscript  $i$  from the parameters and variables associated with the activity, and let it be understood that the level of vigilance is tailored to the particular activity. In Brown's (1999) model of vigilance, predation risk,  $\mu$ , has four components:

$$\mu = \frac{m}{k + bu},$$

where predation risk increases with the encounter rate with predators,  $m$ , and the predator's lethality in the absence of vigilance,  $1/k$ , and decreases with the effectiveness of vigilance,  $b$ . The term that scales predator lethality in theory can take on any positive value, but it makes the most sense if its values are restricted to  $k \geq 1$ , which translates into  $0 \leq 1/k \leq 1$ . A  $k$  of 1 means that an encounter with the predator is always lethal in the absence of vigilance, and as  $k$  gets very large the predator becomes less lethal and harmless even in the absence of vigilance.

The effect of vigilance,  $u$ , on fitness is:

$$\frac{\partial G}{\partial u} = p \frac{\partial F}{\partial u} + F \frac{\partial p}{\partial u}.$$

By setting the above equation equal to zero,  $\partial G/\partial u = 0$ , we can solve for the optimal level of vigilance for a solitary forager (see Brown, 1999, for a more detailed development):

$$u^* = \sqrt{\frac{mF}{bf_{\max}\partial F/\partial e} - \frac{k}{b}}. \quad (1)$$

The optimal level of vigilance,  $u^*$ , increases with the encounter rate with predators,  $m$ , the forager's survivor's fitness,  $F$ , and the predator's lethality,  $1/k$ . Vigilance decreases with potential feeding rate,  $f_{\max}$ , and the marginal value of energy,  $\partial F/\partial e$ . Vigilance increases and then decreases with the effectiveness of vigilance,  $b$ . In the event that this expression yields a value of  $u > 1$ , then the animal chooses complete vigilance,  $u = 1$ , while engaged in the activities. Similarly, if this expression yields a value of  $u < 0$ , then the animal should exhibit an absence of any vigilance,  $u = 0$ .

Brown's (1999) model predicts the vigilance behaviour of a solitary forager. We now incorporate the three group size effects into the model of predation risk:

$$\mu = \frac{\frac{mN^\alpha}{N}}{k + (N-1)\beta\bar{u} + bu} \quad (2)$$

In equation (2), we incorporate the dilution effect by dividing the encounter rate with predators by group size,  $N$ . Multiplying the encounter rate with predators by  $N^\alpha$  captures the attraction effect. The scaling exponent,  $\alpha$ , determines the interaction between the dilution effect and the attraction effect. For instance, when  $\alpha = 0$ , there is a dilution effect but no attraction effect. When  $\alpha = 1$ , the attraction effect exactly cancels the dilution effect. This means there is no net effect of group size on the individual's encounter rate with

predators. The situation  $\alpha > 1$  causes the attraction effect to dominate the dilution effect. The individual's encounter rate with predators increases with  $N$ . When the condition is  $\alpha < 1$ , the dilution effect is stronger than the attraction effect and encounter rate with predators declines with  $N$ .

The terms  $\beta$  and  $\bar{u}$  in the denominator of predation risk incorporate the many-eyes effect, where  $\beta$  scales the value of others' vigilance in reducing an individual's risk of predation, and  $\bar{u}$  is the average vigilance of the other  $N - 1$  individuals in the group. When  $\beta = 0$ , the vigilance of others provides no safety for the individual (no many-eyes effect). Under the  $\beta < b$  scenario, the vigilance of others is valuable but less so than one's own vigilance. When  $\beta > b$ , the vigilance of others is more valuable than one's own vigilance. The term  $\bar{u}$  is the mean vigilance of everybody else in the group except for the focal individual whose vigilance is  $u$ . Measures of vigilance may have units of scans per unit time or percent of time spent scanning. For our purposes here, we see vigilance as taking on any value between 0 and 1.

Using equation (2) as the expression for predation risk, we can solve for the optimal level of vigilance for the individual within a group of size  $N$  in which the others have an average vigilance of  $\bar{u}$ :

$$u^* = \sqrt{\frac{FmN^\alpha}{bf_{\max}N(\partial F/\partial e)}} - \frac{k + (N - 1)\beta\bar{u}}{b} \tag{3}$$

Appropriately, equation (3) collapses to equation (1) of Brown's (1999) model when  $N = 1$ . (If  $u^* \leq 0$  for  $\bar{u} = 0$ , then the optimal level of vigilance for all individuals in the group is 0: there will be no anti-predatory vigilance.)

An individual's vigilance level,  $u^*$ , depends on the size of the group,  $N$ , and on the average vigilance level of others,  $\bar{u}$ . In other words, equation (3) represents a game of vigilance in which the optimal level of vigilance of the individual depends upon the vigilance levels of others. At the ESS, an individual does best by using the same level of vigilance as everyone else. In other words, at the ESS level of vigilance, an individual will experience lower fitness if it unilaterally changes its strategy from the group's average level of vigilance. The ESS value of vigilance,  $u^*$ , can be found by setting the strategy of the individual equal to the mean strategy of the group, i.e.  $u^* = \bar{u}$ , and solving for  $u^*$ :

$$u^* = \frac{\sqrt{\frac{bFmN^\alpha}{f_{\max}N(\partial F/\partial e)}} - k}{b + (N - 1)\beta} \tag{4}$$

This ESS value of vigilance (equation 4) contains the dilution effect through the term  $N$  in the denominator of the square-root term. The attraction effect emerges as the  $N^\alpha$  term. And, the many-eyes effect emerges through the  $(N - 1)\beta$  term in the denominator.

### HOW DOES GROUP VIGILANCE COMPARE WITH VIGILANCE BY A SOLITARY FORAGER?

In Brown's (1999) vigilance model, the optimal level of vigilance of a solitary forager increases with the encounter rate with predators, the forager's survivor's fitness, and the predator's lethality. Vigilance decreases with the marginal value of energy. It increases

**Table 1.** Predictions for the effects on vigilance level from increasing: (1) encounter rate with predator, (2) forager’s survivor’s fitness, (3) predator lethality, (4) marginal value of energy, and (5) effectiveness of vigilance

Variables	Vigilance rate
Encounter rate with predator	↑
Forager’s survivor’s fitness	↑
Predator lethality	↑
Marginal value of energy	↓
Effectiveness of vigilance	at low $b$ ↑, at high $b$ ↓

and then decreases with the effectiveness of vigilance (equation 1). The ESS of the vigilance-game within a group shows the same patterns (see Table 1, Fig. 1a–e).

However, increasing group size causes the relationship between vigilance and these parameters to become shallower. As group size increases, the effect on vigilance of predator encounter rate, survivor’s fitness, predator lethality, marginal value of energy, feeding rate, and the effectiveness of vigilance becomes weaker (Fig. 1a–e).

As group size increases, the hump-shaped relationship between vigilance and the value of vigilance becomes much shallower and more likely positive. When vigilance is useless ( $b = 0$ ) there is no point to vigilance, and when vigilance is extremely valuable (very large  $b$ ) then little vigilance is required. However, within a group, the ESS value of vigilance increases more slowly with  $b$  at low values of  $b$  and declines much more slowly at larger values of  $b$ .

The ability of any given individual to free-load off of the vigilance of others means that an individual’s ESS level of vigilance is more muted in response to changing environmental factors and more strongly influenced by group size itself.

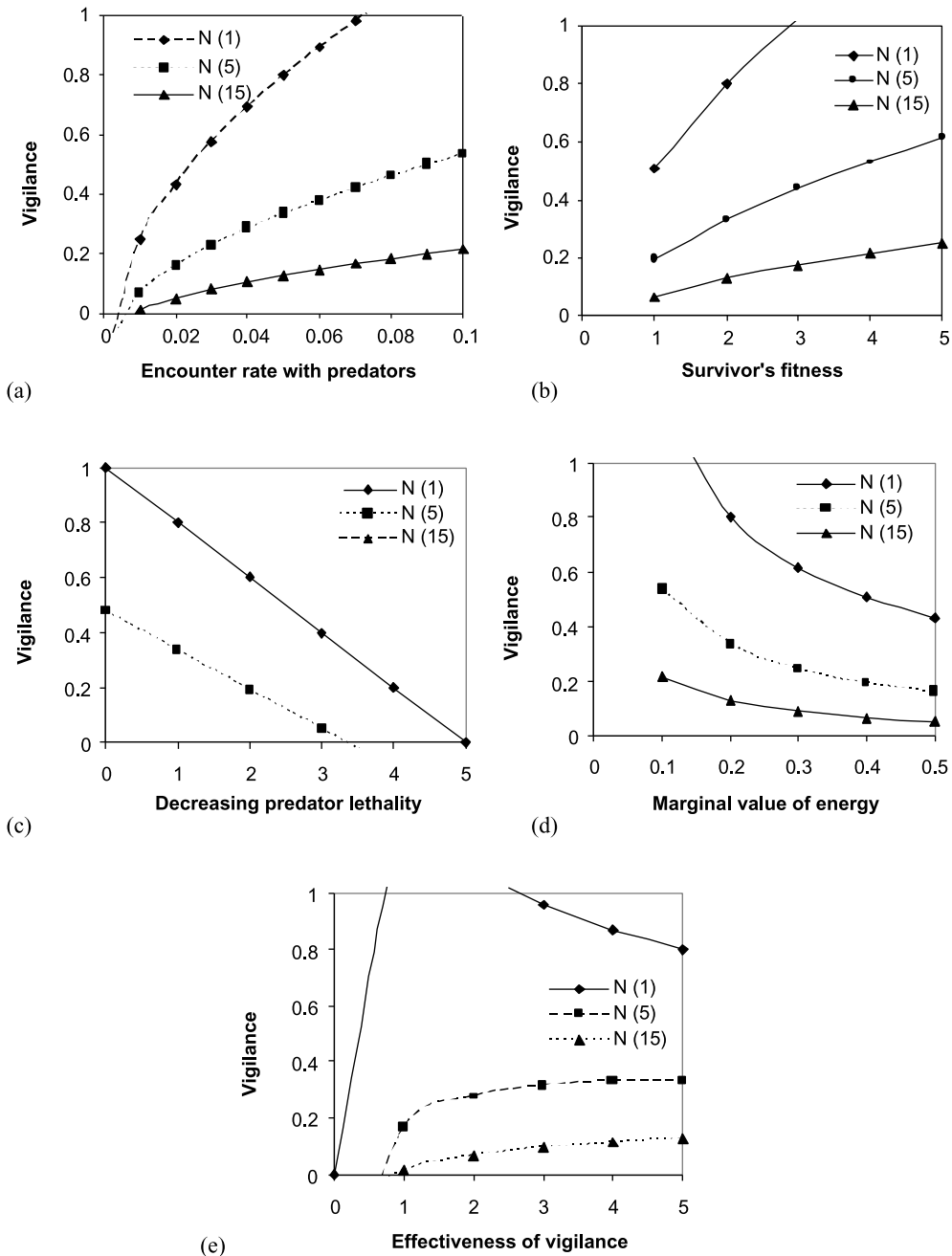
### GROUP SIZE EFFECT AND ESS LEVELS OF VIGILANCE

Group size influences ESS levels of vigilance as a consequence of the many-eyes, dilution, and attraction effects. We can evaluate the group size effect by evaluating how  $N$  influences the ESS level of vigilance (derivative of equation 4 with respect to  $N$ ):

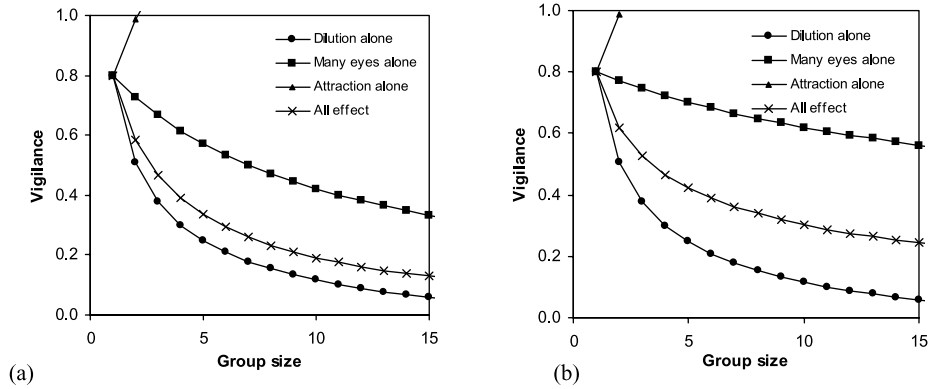
$$\frac{\partial u^*}{\partial N} = \frac{\frac{1}{2}[b + (N - 1)\beta] \left( \sqrt{\frac{f_{\max} N (\partial F / \partial e)}{b F m N^a}} \right) - \left( \sqrt{\frac{b m F N^a}{f_{\max} N (\partial F / \partial e)}} - k \right) \beta}{(b + (N - 1)\beta)^2} \tag{5}$$

The ESS level of vigilance increases with the attraction effect, but decreases with the many-eyes effect and the dilution effect (Fig. 2a). Vigilance may decline with group size owing to the combined effect of all three effects (Fig. 2a), but this depends on the strength of the attraction effect (Fig. 3).

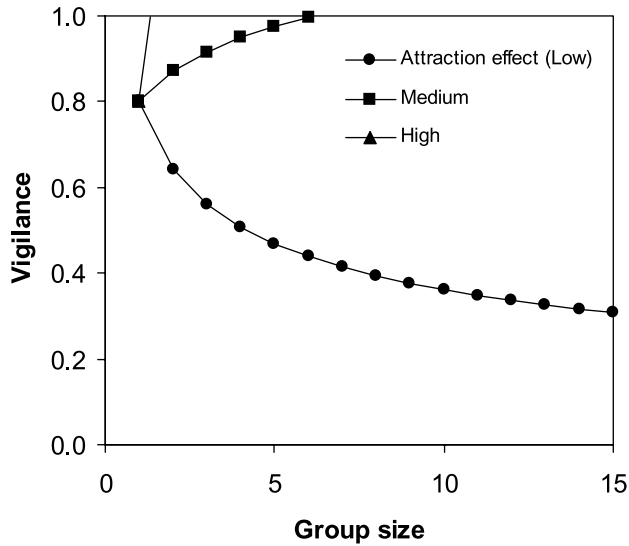
With a sufficiently high attraction effect, individual vigilance does not decline with group size but rather increases with it. With a moderate attraction effect, vigilance first increases and then decreases with group size. With a low attraction effect, it declines continuously with group size (Fig. 3). In general, the attraction effect makes the group size–vigilance curve shallower or hump-shaped (Fig. 4).



**Fig. 1.** The effects of (a) the encounter rate with predators, (b) the survivor's fitness, (c) predator lethality, (d) the marginal value of energy, and (e) the effectiveness of vigilance, on the optimal level of vigilance across group sizes. The lines shift to lower levels of vigilance as group size increases, and the relationship between vigilance and the model parameter weakens with increasing group size. For illustration:  $m = 0.05$ ,  $\partial F / \partial e = 0.2$ ,  $k = 1$ ,  $f = 0.1$ ,  $b = 5$ ,  $F = 2$ ,  $\beta = 0.5$ , and  $\alpha = 0.5$ .



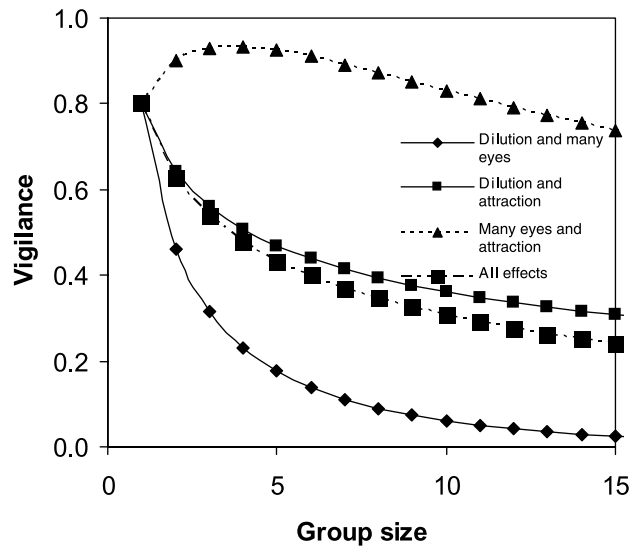
**Fig. 2.** (a) Only under the attraction effect does the ESS vigilance,  $u^*$ , increase with group size. With the dilution and many-eyes effects, acting alone, vigilance declines with group size. Given the parameters of this example, vigilance declines with group size when all effects are combined. (b) The group optimum ( $\bar{u}^*$ ), or social vigilance, increases with group size under all effects combined and the many-eyes effect. With the attraction and dilution effects, acting separately, the group optimum is essentially the same as the ESS vigilance. The following values of  $\alpha$  and  $\beta$  were used: dilution effect ( $\alpha = \beta = 0$ ), many-eyes effect ( $\alpha = 1, \beta = 0.5$ ), attraction effect ( $\alpha = 1.5, \beta = 0$ ), and all effects combined ( $\alpha = \beta = 0.5$ ). Other parameters as in Fig. 1.



**Fig. 3.** The effect of increasing the attraction effect on the relationship between vigilance and group size. Each successive line represents a higher attraction effect. At a very high attraction effect, the ESS level of vigilance jumps to 1 with just a small increase in group size. For the three lines: High  $\alpha = 2$ , Medium  $\alpha = 1.2$ , and Low  $\alpha = 0.5$ . Other parameters as in Fig. 1.

Vigilance is higher when the animal values self-scanning ( $\beta < b$ ) more than the vigilance of its associates ( $\beta > b$ ). When the value of  $\beta$  is larger than  $b$ , the resulting decline in ESS vigilance with group size is very steep. Individuals prefer the vigilance of others in the group





**Fig. 4.** The effect of combinations of effects on the relationship between the ESS level of vigilance and group size. The attraction effect (the value of  $\alpha$ ) determines the shape of the group size–vigilance curve. When the attraction effect is low, there is an inverse relationship between group size and vigilance. For illustration purposes, the following values of  $\alpha$  and  $\beta$  were used for different combinations: dilution–many-eyes ( $\alpha = 0, \beta = 0.5$ ), dilution–attraction ( $\alpha = \beta = 0$ ), attraction–many-eyes ( $\alpha = 1.5, \beta = 0.5$ ), and for all effects combined ( $\alpha = \beta = 0.5$ ). Other parameters as in Fig. 1.

with the increase of group size (Fig. 5). This leads to a very sharp decline in the ESS level of vigilance with  $\beta$ .

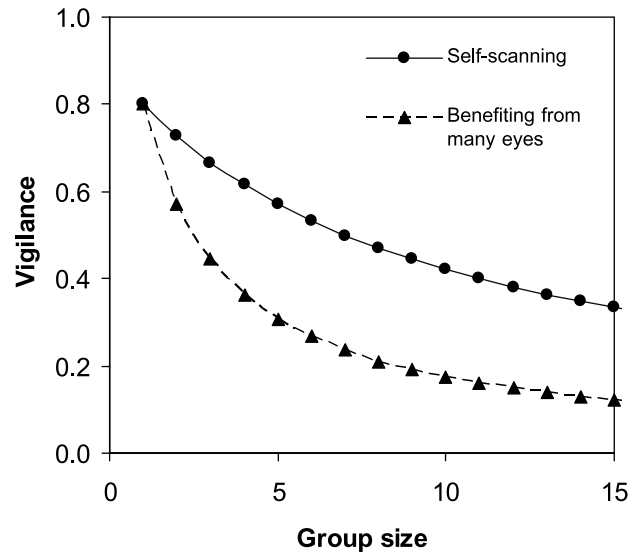
### SOCIAL VIGILANCE AND THE GROUP OPTIMUM

Vigilance and group size can become a kind of producer–scrounger game where there are benefits to free-loading off of the vigilance of others. A given individual may prefer others to be very vigilant while contributing little vigilance itself. As a consequence, the ESS level of vigilance may be less than the level that would maximize collective benefits. We might expect the group optimum of vigilance to be greater than the ESS, particularly when  $\beta$  (value of others’ vigilance) is comparable to  $b$  (value of one’s own vigilance). Such a group optimum may apply to species exhibiting social vigilance where reciprocal altruism, social coercion, or kin selection favours the group optimum.

To calculate the group optimum, we replace  $u$  with  $\bar{u}$  in equation (2) for predation risk, i.e.

$$\mu = \frac{\frac{mN^a}{N}}{k + (N - 1)\beta\bar{u} + b\bar{u}}$$

When we use this altered expression for predation risk, we can determine the group optimum by using the necessary condition of  $\partial G/\partial \bar{u} = 0$ , and solving it for  $\bar{u}$ :



**Fig. 5.** The decline in the ESS level of vigilance with group size becomes stronger as the value of others' vigilance increases. For illustration purposes, the following values of  $\alpha$  and  $\beta$  were used: self-scanning ( $\alpha = 1$ ,  $\beta = 0.5$ ) and benefiting from many-eyes ( $\alpha = 1$ ,  $\beta = 2$ ). Other parameters as in Fig. 1.

$$\bar{u}^* = \frac{\sqrt{\frac{FmN^a[b + (N-1)\beta]}{f_{\max}N(\partial F/\partial e)} - k}}{b + (N-1)\beta} \quad (6)$$

As group size increases, the group optimum ( $\bar{u}^*$ ) increases under the attraction effect, but decreases with the dilution and many-eyes effects (Fig. 2b). These effects are similar to those of the ESS. However, the group optimum always involves an equal or greater amount of vigilance than the ESS; expression (6) has an extra positive term in its numerator relative to expression (4) for the ESS. The group optimum is strictly greater than the ESS only when there is the many-eyes effect (with or without the other effects), and the divergence between the group optimum and the ESS increases with group size and with the strength of the many-eyes effect ( $\beta$ ) (Fig. 2a, b).

## DISCUSSION

The ESS level of vigilance decreases with group size as a consequence of the many-eyes and dilution effects but increases with group size with the attraction effect, when they act independent of each other. The relation between vigilance and group size is contingent on the relative strengths of each and the interactions of components of the group size effect – the many-eyes, dilution, and attraction effects. In nature, all components of the group size effect likely intertwine with each other. Our findings re-enforce how vigilance within a group context is a game. The optimal vigilance of a forager depends on that of its group mates. As a game of private costs and public benefits, the relationship between individual vigilance and group size is not straightforward. The contingent relation between vigilance and group

size effects becomes predictable when the many-eyes, dilution, and attraction effects are considered jointly within the same model of vigilance. With the many-eyes effect, the game of vigilance becomes a free-loader problem in which the ESS level of vigilance is less than that which would maximize each individual's fitness if individuals were to work cooperatively towards a group optimum.

The model can consider the group optimum that might emerge when vigilance is a social game where social contracts, kin relationships, or tit-for-tat behaviours permit a cooperative solution. As group size increases, the proportional difference between the cooperative solution and the ESS level of vigilance diverges. Under the many-eyes effect, the ESS level of vigilance declines more swiftly with group size than the cooperative solution.

Predation is a prime driver of social evolution (Wilson, 1975). Factors such as competition and scrounging may be important, and these additional aspects of social foraging may also influence vigilance in a group context (Beauchamp, 2003). If predation risk is relatively high, then predation risk may trump starvation costs and other social costs and benefits in the evolution of sociality (Abrams, 1993). Our understanding of predation as leading to sociality derives mainly from studies of aggregation in prey and individual vigilance. As an explanation of the evolution of aggregation, 'selfish herd' models suggest how individuals decrease their danger by putting other individuals between themselves and other predators (Hamilton, 1971). The idea of the selfish herd, however, could not justify why individuals at the edge of a group would not depart, thereby disintegrating groups. Pulliam (1973) proposed that animals benefit by grouping, assuming that detection of predators by any group member results in equal safety for all members (many-eyes effect). The direct relationship between vigilance and aggregation was attractive because animals in groups may rely on associates for an early warning of danger.

The many-eyes effect, largely based on Pulliam's (1973) work, generated alternative ideas for explaining how vigilance may decline with group size. Through a dilution of risk, individuals within a group may experience lower predation risk than solitary individuals. This reduction of risk with group size could then generate a decline in individual vigilance with group size. At least part of the group size effect may be due to a reduced risk of capture in larger groups – the dilution effect (e.g. Bertram, 1978; Lazarus, 1979). Evidence for the dilution effect came early on from the insect world (Foster and Treherne, 1981). Meanwhile, assumptions of the many-eyes models concerning (1) collective detection of predators by group members and (2) behaviour monitoring of group mates can be difficult to evaluate under controlled conditions (Lima, 1995; Roberts, 1996). These models assume an equal risk of predation for all group members. But this may not be realistic. Individuals who first detect the predators should be less at risk than those who learn about it secondarily (McNamara and Houston, 1992; Bednekoff and Lima, 1998b). Field studies on predators show that large predators target less vigilant prey (Schaller, 1972; Fitzgibbon, 1989).

Because the many-eyes and dilution effects may not work independently, biologists have integrated the dilution effect in their models (e.g. Pulliam *et al.*, 1982; Parker and Hammerstein, 1985; Dehn, 1990; Beauchamp, 2003). A model incorporating both effects explains more of the variance in the relationship between group size and vigilance of foraging elk *Cervus elaphus* than does a solely many-eyes effect (Dehn, 1990). Both the many-eyes and dilution effects are important, with the many-eyes effect especially important at small group sizes and the dilution effect at larger group sizes (Dehn, 1990). Studies suggest the dilution and many-eyes effects likely act together because collective detection by group members may be imperfect (Bednekoff and Lima, 1998b).

We suggest that vigilance models should combine not only the many-eyes and dilution effects, but also the attraction effect. Our model shows that the synergetic effect of group size on vigilance behaviour is contingent upon the strength of interacting effects, particularly the attraction effect. Incorporating the attraction effect makes our model more complete. This is important, as empirical results regarding changes in vigilance with group size have been varied and equivocal. Our model predicts when the relationship between vigilance and group size should be positive, negative, and/or hump-shaped.

In support of an attraction effect, Hebblewhite and Pletscher (2002) found that wolves (*Canis lupus*) encountered larger elk (*Cervus elaphus*) groups and killed more elk from larger groups than expected based on numbers of encounters in Banff National Park, Alberta. Lions (*Panthera leo*) succeeded in capturing prey from the largest and smallest groups of zebra (*Equus burchelli*), wildebeest (*Connochaetes taurinus*), and gazelles (*Gazella* spp.) (Schaller, 1972; Van Orsdol, 1984). African wild dogs (*Lycaon pictus*) more likely attacked gazelles from groups of >200 than from groups of 1 (Fanshawe and Fitzgibbon, 1993). Half a century ago, Crisler (1956) reported that wolf attack success increased with the group size of migratory caribou (*Rangifer tarandus*).

The predator's attraction to large aggregations of prey is not only a property of predator-prey systems (Parrish and Edelman-Keshet, 1999), but also of plant-animal interactions. For instance, clumps of fruiting trees attract frugivores, which, in turn, attract their predators (Howe, 1979). Larger groups may be more likely to be detected and attacked by a predator (Turner and Pitcher, 1986; Cresswell, 1994), albeit this increase is unlikely to keep pace with an increase in group size (Roberts, 1996). Both the attraction and dilution effects may act together. The combined effects have been referred to as an 'encounter-dilution effect' (Mooring and Hart, 1992). These studies suggest that the attraction effect is an important variable influencing the relationship between vigilance and the group size effect. Here we have shown that the attraction effect may diminish, cancel, or even override the dilution effect. When it overrides the dilution effect, vigilance may increase with group size.

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