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An adaptive dynamic model of a vigilance game among group foragers

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ABSTRACT

In group foraging animals, vigilance tends to decrease as group size increases. A forager in a group receives a vigilance benefit not only when it is being vigilant itself but also when a group mate is being vigilant. The many eyes hypothesis supposes that individuals exhibit lower vigilance in larger groups because of this. However, changes in safety resulting from the vigilance benefit conferred by group mates can change the decision to join or leave a group so as vigilance changes because of changes in group size, group size may also change in response to changes in vigilance. Additionally, individuals may have poor information about the vigilance strategies of their neighbors. We present a game theoretical model of vigilance that incorporates dynamic group sizes and does not require behavioral monitoring of the vigilance strategies of others. For systems at equilibrium, maximum vigilance decreases with increased group size. Furthermore, by varying intraspecific competition we show an inverse relationship between group size and vigilance. Thus, we provide a mechanism in support of the many eyes hypothesis from an evolutionary game theory perspective and conclude that variation in intraspecific competition and its effect on group size may be responsible for the relationship.

1. Introduction

Vigilance is the act of visually scanning the environment for predators and it can improve a forager's chance of survival in the presence of a predator by giving it early warning of an attack (Beauchamp, 2015). While vigilance and foraging can occur simultaneously in some species (Blanchard and Fritz, 2007), there is often a trade-off between scanning for food and scanning the landscape for predators. Therefore, vigilance can be costly in terms of reduced foraging rates (Bernard, 1980) (e.g., birds Lendrum, 1983; Fritz et al., 2002, ungulates Illius and Fitzgibbon, 1994) resulting in a trade off in time allocated to foraging and vigilance. An individual optimizing its foraging time would allocate time foraging and being vigilant so that the perceived benefit from doing one activity more is no greater than the perceived benefit from doing the other more, (i.e., the marginal benefit from foraging would equal the marginal benefit from vigilance) (Brown et al., 1999).

In a group, this optimal allocation of vigilance becomes more complicated because other individuals in the group may be vigilant and alert neighbors by fleeing (Davis, 1975; Proctor and Broom, 2001). In a group setting, individuals often compete for food so the cost of being vigilant also depends on the number of competing neighbors and the intensity of that competition. Additionally, changes in group size alter predation risk to the individual. All of these interacting factors complicate the optimal vigilance problem in group foragers.

Vigilance frequently decreases as group size increases (Sansom et al., 2008; Blank, 2018; van der Marel et al., 2019). The prevailing, not mutually exclusive, hypotheses for why this phenomenon emerges are the encounter dilution hypothesis and the many eyes hypothesis (Roberts, 1996). Under the encounter dilution hypothesis vigilance decreases as a result of a decrease in risk of any one individual being attacked by virtue of there being more individuals that a predator could attack (Hamilton, 1971). Under the many eyes hypothesis, while more individuals are being vigilant, the group as a whole is more likely to be alerted to the presence of a predator. Thus, every individual receives a benefit from an additional vigilant group member, and each individual reacts to the decreased risk by decreasing their vigilance time (Pulliam, 1973; Powell, 1974; Elger, 1989).

Several early models assume that foragers monitor the strategies used by their group mates in real time and make vigilance decisions based on those observations (behavioral monitoring) (Lima, 1995; Lima, 1987; Pulliam, 1973) and/or that the whole

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group flees when a single individual detects a predator (complete collective detection) (Pulliam, 1973; Pulliam et al., 1982; Lima, 1995; McNamara and Houston, 1992). However neither complete collective detection nor behavioral monitoring are well supported in the literature (Lima, 1995; Roberts, 1996). Partial collective detection, meaning neighboring individuals may be alerted to a predator by their neighbor's detection, has been shown to be crucial to the relationship between vigilance and group size but complete collective detection is rarely observed (Lima and Zollner, 1996). Several more recent models have found that the many eyes hypothesis is robust to relaxation of one or both of these assumptions (Beauchamp, 2017; van der Post et al., 2013). These works have focused on identifying the ecological conditions leading to the emergence of the relationship as it is observed. One such model, which considers a forager either foraging in a group of fixed size or choosing between a group of two different sizes, claims to rule out competition as a general explanation for the emergence of the relationship between vigilance and group size (Bednekoff and Lima, 2004). Here we show that when group size can change in response to changes in vigilance, competition can play a crucial role because of the effect of competition on the way individuals may choose to join groups.

While vigilance can change with group size (Lima and Dill, 1990; Pulliam, 1973; Powell, 1974; Elger, 1989), group size can also change in response to changes in vigilance as individuals join and leave groups. Changes in vigilance result in changes in the net benefit of being in a group. As vigilance of group members increases, mortality risk to group members decreases and the time that they spend competing for resources decreases. Thus, the net benefit of joining the group increases as vigilance increases, controlling for group size. These effects therefore must also be impacted by the intensity of competition among group members. When intensity of competition is high the foraging benefit of joining a group is low. Therefore, the vigilance benefit from joining the group must be high to make group formation worth the cost. A framework for considering this feedback between vigilance and group size was made by Beauchamp in 2017 (Beauchamp, 2017). Using a genetic algorithm, he showed that when changes in vigilance impact how individuals join groups, the negative relationship between vigilance and group size frequently emerges in an agent based model. In this model, Beauchamp alludes to the effect of intraspecific competition on the relationship between vigilance and group size through changing the “clumpiness” of available food, but the dynamics of that interaction are hidden by the genetic algorithm.

Here we present a model which incorporates feedback between vigilance and group size and simultaneously avoids arguments of behavioral monitoring for vigilance by considering this game through the lens of evolutionary dynamics of vigilance. We do this with a system of differential equations rather than through an agent based model so we may explore local dynamics and stability both when individuals can join the group freely and when members of the existing group may have some control on its size as these are known to influence the dynamics of group size (Sibly, 1983; Stephens et al., 2005; Jordan et al., 2010). We initially assume that individuals use a constant vigilance strategy and vigilance evolves at a rate much slower than the rate at which group size changes. We then relax this separation of timescales and consider how similar dynamics may emerge through replication at shorter timescales, such as that resulting from social learning (Danchin et al., 2004), again without requiring behavioral monitoring. By constructing an approximation for individual fitness as a function of vigilance and of group size, we use adaptive dynamics in a pairwise invasion approach (Diekmann, 2004; Brännström et al., 2013) to approximate rates of change for both equilibrium vigilance and group size and show the conditions under which the negative relationship between group size and vigilance emerges.

2. Model Background

Consider a large uniform population of individuals that either forage on their own or in a group. Suppose every individual in the population has reproductive success proportional to their energy intake and furthermore suppose that there is no senescence or energy storage. Using lifetime energy intake as a proxy for fitness, the fitness of an individual is given by the rate of intake times the expected remaining lifetime. Supposing that an individual faces a risk of death μ, then, following an exponential distribution, its expected remaining lifetime can be approximated as $\frac{1}{\mu}$. If an individual is feeding with energy intake rate α, then that individual's fitness can be given by

$$w = \frac{\alpha}{\mu} \tag{1}$$

This life history approach (Hugie and Dill, 1994), is reasonable when we suppose that every individual converts energy into reproduction at the same constant rate through their entire lifetime (Werner and Gilliam, 1984)

Both α and μ depend on group size and vigilance. For this model, F is the proportion of time spent foraging and V is the proportion of the time spent being vigilant. We express the model in terms of F. Here we assume that time spent engaging in behaviors other than foraging or vigilance is negligible thus $F = 1 - V$. Insights from this model may not extend to the cases where individuals spend appreciable time performing other social behaviors while foraging, such as grooming or mating. Group size is denoted as N throughout. These variables, and all variables used in this model, are organized in Table 1.

First we consider $\alpha(F, N)$. Using the Holling II (Holling, 1959) functional response we formulate $\alpha(F, 1)$ as

$$\alpha(F, 1) = \frac{s_1 F}{s_2 + F} \tag{2}$$

where s_1 is the foraging rate and s_2 is a constant proportional to handling time. When there are more individuals in a group, competition increases and thus foraging rate decreases. Observe that our conception of competition as a decrease in foraging rate differs from other conceptions in previous models (Bednekoff and Lima, 2004; Beauchamp and Ruxton, 2003). Here we consider the foraging rate of an individual to be reduced by the interference of others. To that end, we formulate $\alpha(F, N)$ as

$$\alpha(F, N) = \frac{s_0}{(1 + aF)^{N-1}} \cdot \frac{F}{s_2 + F} \tag{3}$$

where s_0 is the base foraging rate for an individual and a is the intensity of competition. This means that the foraging benefit for an individual increases with foraging time but decreases with competition intensity, a; group size, N; and handling time, s_2.

In supplemental material Section 1 we derive risk of mortality, $\mu(F, N)$, using a probabilistic approach. In this approach, the spread of antipredator information μ can be considered the probability of an individual not fleeing in the event of a predator attacking. For this model we make the assumption that no individual can escape after capture; they can either flee or be killed. We also simplify the model by assuming that all individuals in the group have the same ability to detect the predator when they are being vigilant. The probabilistic approach results in a recursive function which we approximate with a simple rational function to avoid unnecessary complexity. The particulars of the

Table 1
A table of symbols used in the derivation and analysis of the model presented.

Symbol	Meaning	Relationship to other variables
	Model Background	
N	Group size	
w	Fitness	$w = \frac{\alpha}{\mu}$
α	energy intake rate	$\alpha(F,N) = \frac{s_0}{(1+aF)^{N-1}}\frac{F}{s_2+F}$
μ	Risk of death	$\mu(F,N) = (1-(1-F)P_v)\left(1-(1-F)\frac{N}{C+N}P_V\right)^{N-1}\frac{P_0}{\sqrt{N}}$
F	Proportion of time spent foraging	
V	Proportion of time spent being vigilant	$V = 1-F$
s_1	General foraging rate	$\frac{s_0}{(1+aF)^{N-1}}$
s_0	Foraging rate for a single individual	
s_2	Constant proportional to search time	
a	Intensity of competition	
	Derivation of μ	
Φ	Fleeing event	
$\mathscr{V}$	Seeing a predator event	
$C_{x,y}$	Individual “y” perceiving that there is a predator from “x”s flee response	
P_v	Probability of seeing a predator while being vigilant	
P_N	Probability of antipredator information Transmission	
$\neg\,\Phi_N(F)$	Probability of not fleeing in a group of N individuals	$\neg\,\Phi_N(F) = (1-P_v(1-F))((1-P_N)+P_N\neg\,\Phi_{N-1}(F))^{N-1}$
C_I	Inverse of reliability of information	$C_I = \frac{2(1-P_N)}{P_N}$
C_D	proportional to reliability of information	$C_D = 2P_N$
$P_A(N)$	Probability an individual is attacked in a group of size N	$P_A(N) = \frac{P_0}{\sqrt{N}}$
P_0	Probability a solitary individual is attacked	
$\neg\Phi_N^{(m)}$	Probability of a mutant in a population of N-1 residents not fleeing	$\neg\Phi_N^{(m)} = (1-P_v(1-u))((1-P_N)+P_N\neg\Phi_{N-1}(F))^{N-1}$
$\neg\Phi_N^{(r)}$	Probability of a resident in a population of N-1 residents and one mutant not fleeing	$\neg\Phi_N^{(r)} = (1-P_v(1-F))((1-P_N)+P_N\neg\Phi_{N-1}^{(m)})((1-P_N)+P_N\neg\Phi_{N-1}^{(r)})^{N-2}$
μ_m	mutant risk of death	
μ_r	resident risk of death	
	Model	
w_r	Fitness of a resident with one mutant invader	
w_m	Fitness of a mutant invader in a resident group	
$\Delta\tilde{w}$	Fitness differential	$w_r - w_m$
K_0	Constants in fitness differential	
Δw	Adjusted fitness differential for ease of computation	$\frac{\Delta\tilde{w}}{K_0}$
$\xi(F,N)$	Auxiliary function	$\xi(F,N) = (1+aF)\left(1-\frac{(1-F)NP_v}{C+N}\right)$
$\mathscr{I}_1$	First isocline on the Pairwise Invasion Plot	$\mathscr{I}_1 = \{(F,u)\in[0,1]\times[0,1]\mid u=F\}$
$\mathscr{S}$	Fitness differential Surface	$\mathscr{S} = \frac{\Delta w(u,F)}{F-u}$
$\mathscr{I}_2$	Second isocline on the Pairwise Invasion Plot	$\mathscr{I}_2 = \{(F,u)\in[0,1]\times[0,1]\mid\mathscr{S}(u,F)=0\}$
$\mathscr{P}(F)$	Potential change in group fitness from invasion	$\mathscr{P}(F) = \mathscr{S}(F,F)$
ε	Mutation Rate	
N_E^*	External Ideal Group Size	$N_E^*\approxeq\{N\in\mathbb{R}\mid w(F,N)-w(F,1)=0\}$
N_I^*	Internal Ideal Group Size	$N_E^* = \mathrm{argmax}_{N\in\mathbb{Z}}w(F,N)$

derivation can be found in the supplemental material Section 1. We find that

$$(1-(1-F)P_v)\left(1-(1-F)\frac{N}{C+N}P_v\right)^{N-1} \tag{4}$$

is the best simple approximation for the probability that an individual does not escape before it is attacked by a predator, where P_v is the likelihood of seeing a predator during vigilance and C is some constant which is inversely related to the reliability of shared information. To complete the derivation for μ we find in the supplemental material the probability that a particular individual is attacked.

This completes the formulation of $\mu(F,N)$

$$\mu = (1-(1-F)P_v)\left(1-(1-F)\frac{N}{C+N}P_v\right)^{N-1}\frac{P_0}{\sqrt{N}} \tag{5}$$

We assume that the risk of attack is static as risk of attack does not interact with group size's effect of vigilance (Beauchamp, 2019)

3. The Model

3.1. Fixed Group Size

First, we consider how different strategies of vigilance will invade when individuals, if they forage in a group, are forced to forage in a group which is always of size N. We will later allow group size to change but this assumption allows us to draw conclusions about stable strategies at a particular group size. From Eqs. (1) (3), and (5), in a group of size N, in which every individual is using the same foraging strategy, F, the fitness of any individual is

$$w(F,N) = \frac{(s_0F\sqrt{N})}{\left((1+aF)\left(1-\frac{(1-F)NP_v}{C+N}\right)\right)^{1-N}(1+s_2F)(1-(1-F)P_v)P_0} \tag{6}$$

For the sake of brevity, we define an auxiliary function $\xi(F,N) = (1+aF)\left(1-\frac{(1-F)NP_v}{C+N}\right)$. Thus, we express the fitness function as

$$w(F,N) = \frac{s_0 F\sqrt{N}}{\xi(F,N)^{N-1}(1+s_2F)(1-(1-F)P_v)P_0} \tag{7}$$

We consider a group wherein one mutant individual plays a separate strategy, u. The appearance of such a new strategy we call innovation. Resident (r) and mutant (m) fitnesses in this group are described as

$$\begin{aligned} w_r(u,F,N) &= \frac{(s_0F\sqrt{N})}{\xi(F,N)^{N-2}\xi(u,N)(1+s_2F)(1-(1-F)P_v)P_0} \\ w_m(u,F,N) &= \frac{(s_0u\sqrt{N})}{\xi(F,N)^{N-1}(1+s_2u)(1-(1-u)P_v)P_0} \end{aligned} \tag{8}$$

We consider an arbitrarily large population which has foraging groups of only size N. Individuals may or may not be part of a group but if they are part of a group that group is certainly of size N. The fitnesses of individuals outside of the group do not interact with the fitness of the individuals in the group. Under these conditions we need only compare individuals in the same group. Also note that the trait in question is vigilance in a group, while solitary individuals may behave differently, vigilance behavior while in the group can still be discussed in this way. With these mutant and resident fitnesses we determine a fitness differential between mutant and resident which we call $\Delta\tilde{w}(u,F,N)$. It is formulated as $w_r(u,F,N) - w_m(u,F,N)$; thus, when $\Delta\tilde{w}(u,F,N) > 0$, the resident phenotype is more fit than the mutant phenotype and the mutant cannot invade the resident group. In the opposite case, when mutant fitness is greater than resident fitness, the mutant strategy will invade (Diekmann, 2004). Factoring out the common factors in each term which do not affect the roots of this function as K_0 we find that

$$\begin{aligned} \frac{\Delta\tilde{w}(u,F,N)}{K_0} = &\frac{F}{\xi(u,N)(1-s_2F)(1-(1-F)P_v)} \\ &- \frac{u}{\xi(F,N)(1-s_2u)(1-(1-u)P_v)} \end{aligned} \tag{9}$$

The magnitude of the fitness differential does not matter for our analysis because we are not interested in the rate of fixation so we will discuss $\Delta w(u,F,N)$ which has the same roots as eq. 9. It is still true that when $\Delta w(u,F,N) > 0$ the resident strategy, F, resists invasion from the mutant strategy u.

$$\begin{aligned} \Delta w(u,F,N) = &F\xi(F,N)(1-s_2u)(1-(1-u)P_v) - u\xi(u,N)(1 \\ &- s_2F)(1-(1-F)P_v) \end{aligned} \tag{10}$$

With a fitness differential function we use pairwise invasion analysis by examining where strategies of higher or lower vigilance can invade (Diekmann, 2004). Plotted in Fig. 1 are two pairwise invasion plots (PIPs) where the shaded region represents where the resident strategy resists invasion and the white region represents where the mutant strategy may invade.

Isoclines, which are the boundaries of the shaded areas, are where $\Delta w(u,F,N) = 0$. When isoclines intersect, there is a fixed point because the direction of mutation to which the resident strategy is vulnerable to invasion changes (Diekmann, 2004). The fixed point is stable if strategies of increased foraging may invade to the left of the fixed point and strategies of decreased foraging may invade to the right of the fixed point. Wherever a stable fixed point is present in this model, it represents an Evolutionary Stable Strategy (ESS), which is a strategy which no nearby mutant can invade (Smith, 1982). Geometrically, this can be seen as a vertical linear neighborhood about the singular point on the PIP which lies totally in the region wherein the residents resist invasion (Geritz et al., 1998). A more rigorous proof can be found in the supplemental material as proof 3 More powerfully, these stable fixed points are also Convergent Stable Strategies (CSS), meaning that there exists a neighborhood about this singular point for which an individual closer to the fixed point would be able to invade a group of residents further from the fixed point (Christiansen, 1991). This claim is proven in Proof 4 in the supplemental material.

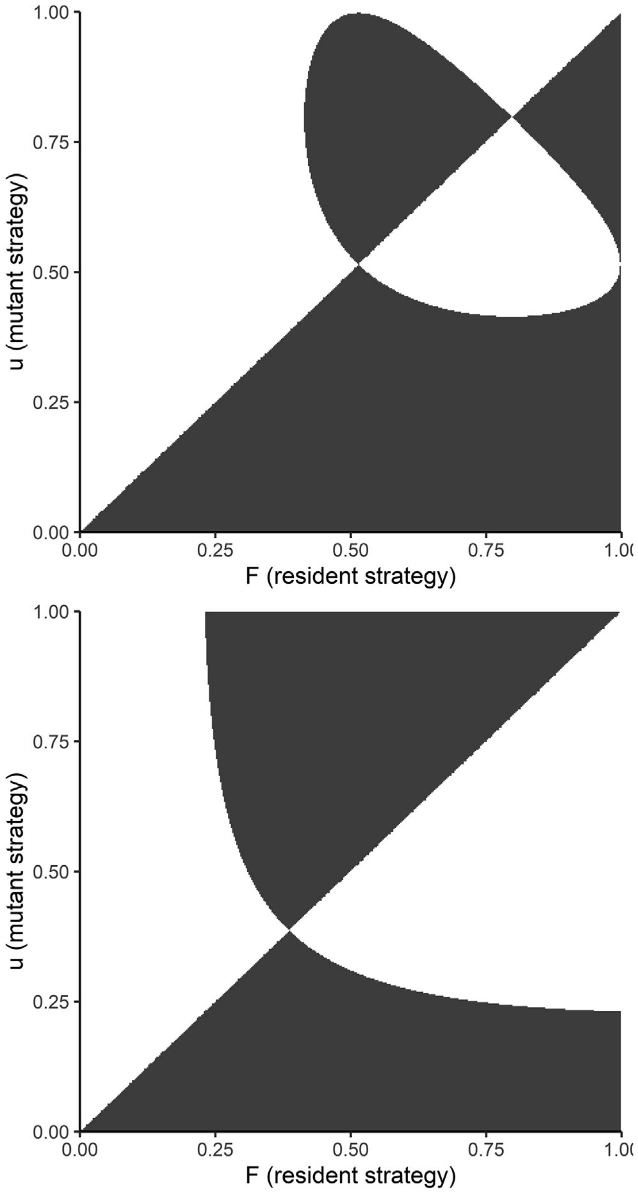

Fig. 1. Pairwise Invasibility Plots in terms of foraging time (Recall $V = 1 - F$). Shaded regions show where the resident strategy (F) resists invasion from the mutant strategy (u). White regions show where the mutant strategy can invade the resident strategy. The boundaries of the region are isoclines where $\Delta w(u,F,N) = 0$. Intersections of isoclines are singular strategies. On the **Top** is the PIP for the parameters $a = 0.16, s_2 = 6, P_v = 0.8, C = 20, N = 45$. On the **Bottom** is the PIP for the parameters $a = 0.16, s_2 = 6, P_v = 0.8, C = 20, N = 38$.

In this model an unstable fixed point is neither an ESS nor a CSS. It is an evolutionary repeller where there exists a neighborhood wherein a mutant farther from the singular strategy can always invade a group of residents closer to the singular point.

We consider a group with no mutant as being on the isocline $u = F$ called $\mathscr{I}_1$. As seen in Proof 2 in the supplemental material, the direction of evolution along $\mathscr{I}_1$ can be captured as

$$\frac{dF}{dt} = \varepsilon\,\mathrm{sgn}(\mathscr{P}(F,N)) \tag{11}$$

where ε is the average magnitude of innovation, $\mathrm{sgn}(x) = -1$ if $x < 0, \mathrm{sgn}(x) = 1$ if $x > 0$ and $\mathrm{sgn}(0) = 0$ and

$$\begin{aligned}\mathscr{P}(F,N) = & -C(-1+P_v+P_v s_2 F^2 + aP_v(2F+(-1+s)F^2) \\ & - a(2F+s_2F^2)) + N(1+P_v(-1+F))^2(1+a(2F+sF^2))\end{aligned} \tag{12}$$

Note that $\mathscr{P}$ can be expressed as a fourth degree polynomial in F. The change in F is not dependent on the magnitude of $\mathscr{P}$ because the magnitude of $\mathscr{P}$ describes the fitness differential and so only determines how quickly a mutation becomes fixed, not the change in F that results from innovation.

At this point, with constant group size, the model shows several interesting trends. Particularly of note is vigilance's change with respect to intensity of competition. Fig. 2 shows two bifurcation diagrams of vigilance with intensity of competition as the bifurcation parameter. We observe a saddle node bifurcation occurs in some regions of our parameter space. This means there is a region of bistability wherein a group, depending on its initial condition may tend towards the zero-vigilance equilibrium or towards the nontrivial equilibrium. The bistability exhibited here does not persist when group size is no longer fixed. Notably, at a constant group size, vigilance decreases with increased competition. This will be important in the discussion of dynamic group size as this result changes in that case.

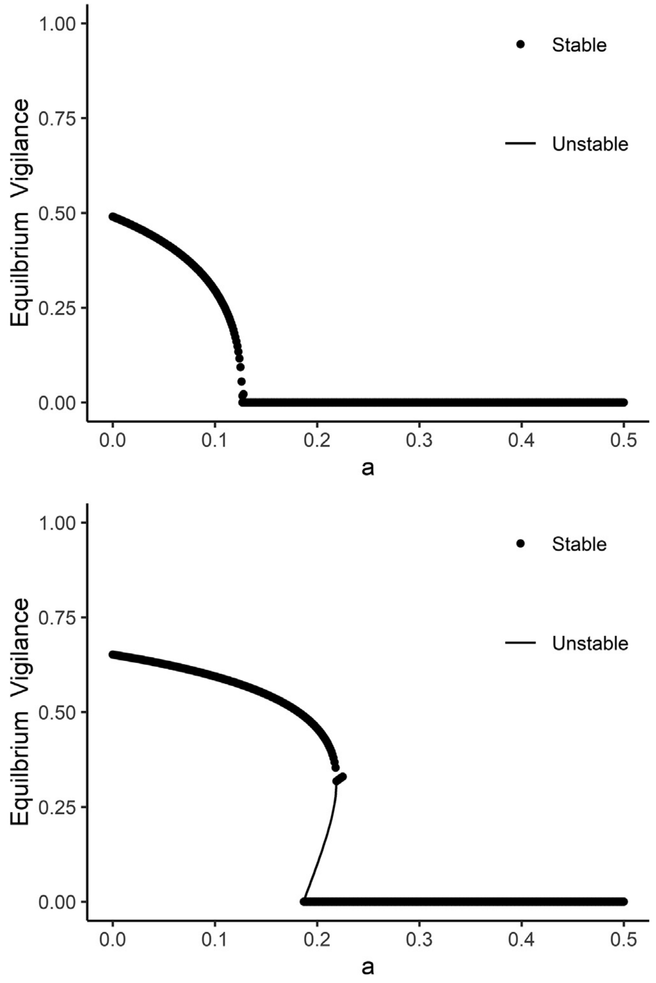

Fig. 2. A bifurcation diagram showing the fixed points of time spent being vigilant (V) with intensity of competition (a) as the bifurcation parameter. **Top** P_v=0.8. **bottom** $P_v = 0.68$ with a prominent saddle node bifurcation. In both cases $s_2 = 6, C = 6$.

3.2. Dynamic Group Size

Group size is dynamic and dependent on vigilance. There are two ways in which group size may be determined. When individuals can leave and join a group whenever they like, we call this external control. When group size is determined by individuals within the group, we call this internal control. We first consider external control.

When individuals can join a group freely, they will do so whenever they can increase their fitness by joining a group relative to being solitary. This means that when fitness of an average individual in a group of size N is greater than the fitness of a single individual, the group will grow until the fitness of the average individual in the group is the same as the fitness of a single individual. This is called the "stable group size" (Giraldeau, 1988). Thus, we can say that group size will change proportionally to the fitness differential $w(F,N) - w(F,1)$

$$w(F,N) - w(F,1) = \frac{s_0 F}{(1+s_2F)(1-(1-F)P_v)}\left(\frac{\sqrt{N}}{\xi(F,N)^{N-1}} - 1\right) \tag{13}$$

By finding a common denominator it becomes clear that group size will grow as

$$\frac{dN}{dt} = \sqrt{N} - \xi(F,N)^{(N-1)} \tag{14}$$

Group size will tend towards the stable fixed point, N_E^*, which we call "External Ideal N." We use this nomenclature to avoid confusion with "equilibrium group size" which, as discussed later, is the group size at equilibrium of the system in either the internal or external control case. There is always at least one fixed point for group size. One fixed point is always $N = 1$, which is typically unstable but may become stable under certain conditions likes very high intraspecific competition. Often another fixed point exists which has the opposite stability of $N = 1$. Finding an analytical solution to N_E^* requires the use of the Lambert W function, so it must be found numerically.

When control of group size is held by members of the group, the group will tend to be the size which maximizes the average fitness of the group members. This is called "optimal group size" (Sibly, 1983) but it gives us a lower bound for group size (which is discussed later and explained in Proof 5 in the supplemental material).

Equilibrium group size in this case, N_I^* "Internal Ideal N", can be solved as

$$N_I^* = \text{argmax}_{n\in\mathbb{Z}} w_r(F,N) \tag{15}$$

More to the point, group size will increase when fitness increases with group size and decrease in the opposite case. This means that for a group with total internal control, group size will grow according to the partial derivative of w with respect to N.

$$\text{sgn}\left(\frac{dN}{dt}\right) = \text{sgn}\left(\frac{\partial}{\partial N}w(F,N)\right) \tag{16}$$

The differentiation is included in the supplemental material as Proof 6. The result can be expressed as

$$\frac{dN}{dt} = 1 + 2N\left(-\log(\xi(F,N)) + \frac{(1-N)}{\xi(F,N)}\frac{\partial}{\partial N}\xi(F,N)\right) \tag{17}$$

By inspection we can see that there is either 1 or 0 solutions to $\frac{dN}{dt} = 0$ which, when it exists, is stable. Again, the location of this equilibrium cannot be solved analytically, so it must be found numerically.

In summary we have two similar systems for vigilance and group size.

Under external control

$$\begin{aligned} \frac{dN}{dt} &= \sqrt{N} - \xi(F,N)^{(N-1)} \\ \frac{dF}{dt} &= \varepsilon(\mathrm{sgn}(\mathscr{P}(F,N))) \end{aligned} \tag{18}$$

and under internal control

$$\begin{aligned} \frac{dN}{dt} &= 1 + 2N\left(-\log(\xi(F,N)) + \frac{(1-N)}{\xi(F,N)}\frac{\partial}{\partial N}\xi(F,N)\right) \\ \frac{dF}{dt} &= \varepsilon(\mathrm{sgn}(\mathscr{P}(F,N))) \end{aligned} \tag{19}$$

4. Results

By varying a on the interval $[0.01, 0.5]$, P_v on the interval $[0.05, 1]$, s_2 on the interval $[1, 10]$, and C on the interval $[2, 20]$ we show the space where the stable attractors occur on the Vigilance×Group Size plane (Fig. 3). Each equilibrium shown corresponds to a point in the reasonable parameter space (see supplemental material 2.1) where the we have the following: neither higher nor lower vigilance strategies can invade, in the external system, individuals do no better by joining or leaving a group, and in the internal system the average fitness of the group is decreased if an individual joins or leaves. With higher equilibrium group size, the upper limit of equilibrium vigilance decreases. This fits the well observed relationship between group size and vigilance. It is of note that the frontier of the equilibria for the external control system is farther from (0,0) than the internal control system. This is supported by the fact that Internal Ideal N is always less than External Ideal N. It is also worth noting here that several solutions appear to escape to infinity. This is impossible in this model and the proof can be found as proof 7 in the supplemental material. These solutions are associated with two-cycles (see supplemental material 2.2). Because, in general, this system has continuity with respect to parameters, solutions which are erroneously determined to escape to infinity can be discarded and solutions found from nearby points in the parameter space will, in general, have similar equilibria.

Fig. 4 depicts all of the fixed points found numerically, colored by the intensity of competition (a) for both the internal and external systems separately. Intensity of competition is the only parameter which shows an easily discernible trend when pictured this way. High competition results in high-vigilance and small-group size strategies while low competition results in low-vigilance and high-group size. This is contrary to the result of varied competition when group size is static (Fig. 2). While trends in other variables are difficult to discern (Fig. S13), it can be shown by varying only one parameter and holding the others constant, that competition is the only parameter whose variation results in a negative relationship between group size and vigilance. Varying any other parameter in this way results in a positive relationship between vigilance and groups size, contrary to the commonly observed relationship in empirical studies. However, for all such variables the relationship is weak in comparison to the effect of variation in competition.

To better understand the relationship among competition, group size, and vigilance, we fix all other parameters and vary competition over the same range with greater resolution. For a particular choice of the other three parameters, equilibria were found by varying a. The results are pictured in Fig. 5 first on the vigilance group size plane then with both group size and vigilance as a function of competition. This reveals several things about the model output. First, it is a reminder that the reason the space on the bottom of the Figs. 3 and 4 are empty is because of poor resolution. In reality stable attractors occupy that space, but because the resolution used in finding the space was too low, the low density of solutions in that space meant that few were found numerically. Secondly, it shows how competition drives the relationship between group size and vigilance.

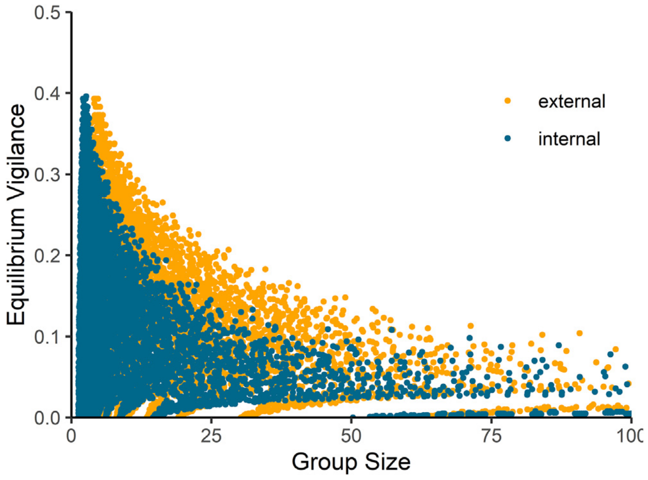

Fig. 3. Shows a low resolution image of the space wherein there is a stable attractor for this system. Each dot represents the equilibrium in the group size-vigilance system for a particular point in the parameter space. Orange dots are equilibria in the external system, blue dots are equilibria in the internal system.

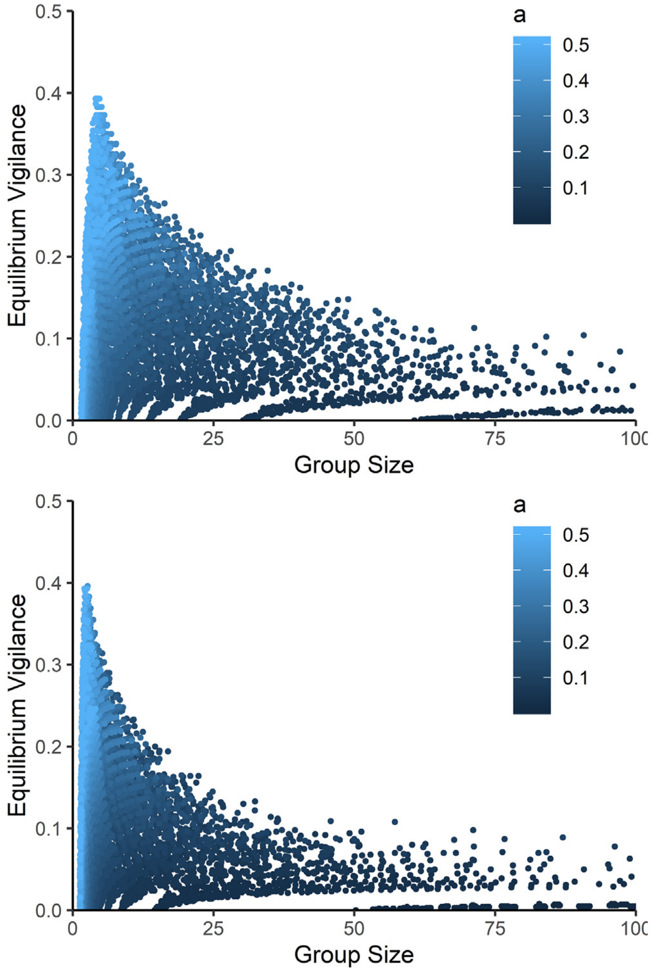

Fig. 4. Equilibrium position resulting from varying all four parameters for both the **Top** external control system and **Bottom** the internal control system Displayed by color is intensity of competition (a).

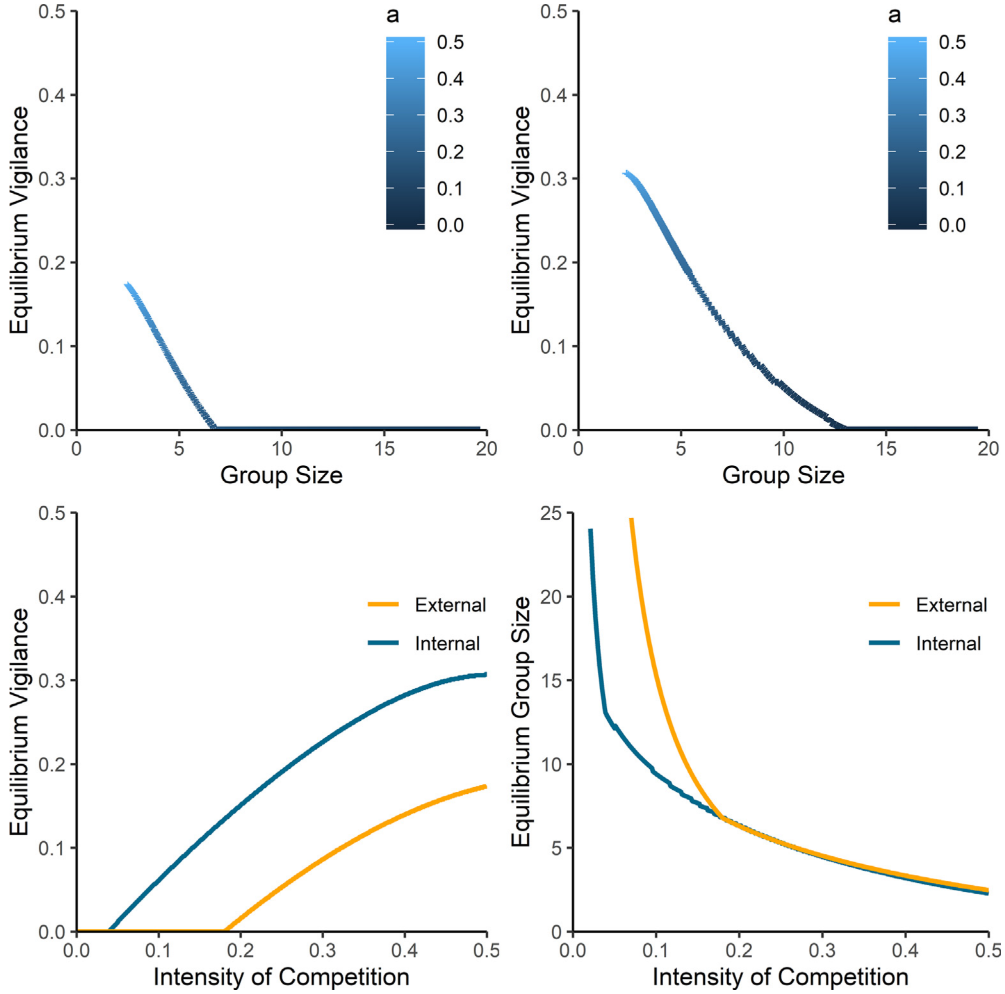

Fig. 5. Equilibrium position resulting from varying only intensity of competition (a) **top left** shown for external control system as a manifold of fixed points parameterized by a and **top right** for the internal control system again as a manifold of equilibria parameterized by a. **bottom left** Both internal (blue) and external(orange) equilibrium vigilance plotted against competition (a) and **bottom right** equilibrium group size also plotted against competition. In each case $s_2 = 4, P_v = 0.75, C = 6$.

Because initially we consider group size to change much faster than vigilance, we find solutions to the systems with the iterative process described in the supplemental material Section 2.1. However, under these conditions, in parameter spaces where there are two cycles (Fig. S7), a curve like those shown in Fig. 5 seems to be discontinuous with respect to a. Relaxing the separation of timescales to solve the system gives us insight about periodic solutions (see supplemental material 3). We continue to use the same variation in competition as an example. Solving the system without the separation of timescales violates the assumption that group size changes much faster than vigilance, but we can use this method to better understand solution behavior. When solved in this way our expression for the change in F changes. We now consider

$$\frac{dF}{dt} = \varepsilon \mathscr{P}(F) \tag{20}$$

where ε now means the rate of innovation, and the speed at which an innovation is fixed has an effect on the solution. We see numerically that there are periodic solutions in many cases (Fig. 6), especially when a is very high or when P_v is very high. These periodic solutions however have amplitude dependent on ε. We can demonstrate in general, but not yet prove, that as ε decreases, amplitude of the limit cycle decreases to zero.

5. Discussion

The goal of producing this model was to offer an explanation for the emergence of the well-observed relationship between group size and vigilance. We sought to do this while allowing for group size to vary in response to changes in vigilance and loosening the requirements for behavioral monitoring and collective detection. By allowing group size to change in response to changes in vigilance, we find that varying intensity of competition results in a negative relationship between vigilance and group size.

Intensity of intraspecific competition has a potent effect on equilibrium group size and the effect that this change in group size has on vigilance is key to the results of this model. We have shown that the relationship between group size and vigilance across populations on long timescales can be explained by the following mechanism: when competition is high, for instance when space for foraging is limited, group size, whether it is controlled by current group members or potential joiners, decreases. That decrease in group size produces a favorable environment for increased vigilance strategies to invade. Small changes in group size, in reaction to innovation and fixation of new vigilance strategies, continues until the group reaches the convergent stable strategy. In the opposite case, when competition is very low, group sizes may become high and as a result decreased vigilance strategies can invade.

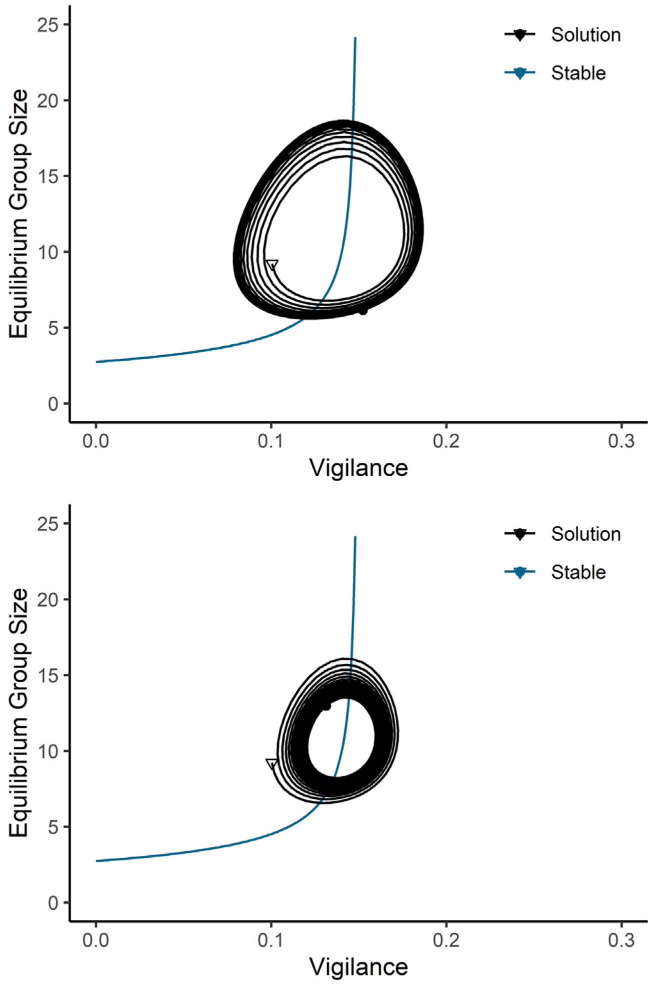

Fig. 6. A solution solved typically with high and low ε. The initial condition is indicated by the open triangle. In the top figure $\varepsilon = 0.001$ and the solution spirals out to a stable limit cycle. In the bottom figure $\varepsilon = 0.0008$ and the solution spirals into a stable limit cycle. For both figures $a = 0.2, s_2 = 4, P_v = 0.95, C = 6$.

Group size and vigilance adjust incrementally until, again, the group reaches a convergent stable strategy.

When risk of death is low, the cost of not being vigilant decreases, so lower vigilance strategies will tend to invade and become fixed until the benefit from foraging is equal to the cost of not being vigilant. This leads to the case where zero vigilance strategies are evolutionarily stable. Group size can grow large enough and risk becomes so diluted that there is no amount of vigilance worth the time spent not foraging. This indicates that as group size grows very large the benefit of own detection decreases to zero. This is a behavior that we observe in the recursive formulation for μ (supplemental material 1) and in our approximation for μ used throughout this model. At large N, an individual seeing a predator itself provides almost no more protection than relying of the cues of its neighbors. This case may highlight a shortcoming in the model which supposes that all vigilance time comes at the cost of foraging. This is not necessarily the case. For instance, it has been shown that some birds have a visual field wide enough for simultaneous foraging and vigilance (Fernández-Juricic et al., 2008). In other cases, an individual may need to pause its foraging to process or to move between patches (Fortin et al., 2004) and could then scan for predators without a cost to foraging.

In our model, equilibrium vigilance increases with increased intensity of competition (Fig. 5) when group size is dynamic. In contrast, when group size is fixed, equilibrium vigilance decreases with increased intensity of competition. This is because high competition reduces the benefit from feeding per unit time so individuals are less likely to risk not being vigilant for as much time in the high competition case. The results of this model show that vigilance increases when competition increases, which, when all other parameters are kept constant results in the emergence of the negative relationship between vigilance and groups size as is predicted by the many eyes hypothesis. This is consistent with the findings of Beauchamp (Beauchamp, 2017) if we suppose that intraspecific competition is higher when available food is more clumped together.

In this model, the fact that group size can change as a result of changes in vigilance is crucial for the proposed adaptive mechanism for the emergent relationship. The Bednekoff and Lima model in 2004 (Bednekoff and Lima, 2004) seems to contradict the results of this model. Although they find that foraging effort increases with competition for fixed group size and decreases with increased competition when groups can change, they argue that competition is not a general explanation for the group size effect on vigilance. Crucial differences in the models presented mean that the models do not contradict one another. In the model by Bednekoff and Lima, competition is a emergent property of the group, not a property of the environment in which the group feeds as we have considered it here. Additionally in the model presented here, group size changes continuously whereas Bednekoff and Lima were considering an individual which may choose between a group and feeding individually. These differences make the model results difficult to compare and not necessarily contradictory.

McNamara and Houston's 1992 model (McNamara and Houston, 1992) has, for a long time, been the standard model of vigilance and group size. The model presented here produces results which are largely consistent with this model. When we examine the shape of the manifolds of equilibria in the group size-vigilance space (Figs. 3–5) we observe the same general shape found by McNamara and Houston. One of the key differences in our approach is that at large group sizes, the advantage of own detection reduces to near zero while there is always a benefit to own detection in McNamara and Houston's model. This means that we predict equilibrium vigilance strategies near or at zero while McNamara and Houston do not. The largest difference in the models is that here group size may change. In McNamara and Houston's model, competition is not thought to be relevant to the relationship in question, just as when group size is not allowed to change in the present model, competition does not explain the relationship between vigilance and group size. In this model however, because group size may change, competition becomes an important part of the emergence of the relationship between vigilance and group size.

We cannot, from our model, claim that no other factors are relevant to the relationship between vigilance and group size. We see that some parameters included in the model shape the relationship weakly and still other parameters are factored out during the pairwise invasion analysis. Predation risk is a parameter which has been crucial to past discussions of group size and vigilance that is conspicuously absent from the results of this model. Simplifying assumptions used to make this game suitable for pairwise invasion analysis have resulted in the elimination of risk of attack as a parameter in the final model. We may interpret this to mean that regardless of the risk of attack, equilibrium vigilance and equilibrium group size will stay the same. This result means that this model could not reasonably be used to predict equilibrium vigilance or equilibrium group size directly. However, this model aims to study the relationship between vigilance and group size. Predation rate, while having a large impact on vigilance itself, may have little impact on that relationship (Beauchamp, 2019) so we find these assumptions appropriate.

We avoid in this model any decision making based on an understanding of resident strategy. Individuals are not choosing to be more or less vigilant because they perceive the average vigilance of the group. Thus, we avoid the requirement for behavioral monitoring. Additionally, it is not assumed that every individual definitely perceives another individual's flee response, so we loosen the requirement for total collective detection. While there is still the possibility for partial collective detection (supplemental material 1), which is reasonable (Lima and Zollner, 1996), relaxing the requirement for both of these assumptions, which are poorly supported (Lima, 1995; Roberts, 1996), strengthens our model.

The pairwise invasion analysis on which the model relies requires the separation of timescales where nearly faithful replication of vigilance strategies results in rare innovation followed by much faster fixation. Thus, the model can only explain variation in the group size-vigilance relationship on long time scales if we only consider natural selection as the means of fixation. However, by amending the notions of innovation and fixation, the dynamic model presented here could apply to within-population, short-term variation in vigilance and group size. Consider the case where, instead of vigilance being fixed and maintained through the entire life of the individual, vigilance strategy is inherited behaviorally through social learning. Group foragers necessarily encounter inadvertent public information (Danchin et al., 2004) such as cues given by the location and performance of others, which is known to be transmissible through mimicry (Giraldeau, 1997). This suggests that group foragers mimicking their neighbors could be a method of behavioral replication for vigilance strategies (Jablonka et al., 1998; Danchin et al., 2004; Mesoudi et al., 2004).

By considering mimicry to be the means of replication, the difference in timescales shrinks as individuals will change vigilance strategy during their lifetime. Vigilance behavior is known to spread through mimicry in bighorn rams (*Ovis canadensis*) (McDougall and Ruckstuhl, 2018; McDougall and Ruckstuhl, 2018) and more generally the use of such public information is thought to be selected for across many taxa (Dall et al., 2005). Importantly the stable attractors in the system do not change. Thus, the same mechanism as before can partially explain the negative relationship between vigilance and group size that is observed on short times scales as well. If the group is in an environment which allows it to grow large, lower vigilance strategies will become more common as they are mimicked in the group whereas if the group is in an environment which limits its size, higher vigilance strategies would invade because low vigilance individuals would be performing worse and thus less likely to be mimicked. This last piece of the mechanism may require that the group faces predators frequently relative to innovation. This perhaps introduces demographic effects which may limit the scope of the social mechanism alone, but the combination of the social and inherited mechanisms can explain the relationship between group size and vigilance both on very long timescales and on shorter ones. Further support for these conclusions would require further inquiry into the extensions of adaptive dynamics into replication through public information.

Although the results of the model when competition is varied are consistent with observed trends across many taxa (Elger, 1989; Lendrum, 1983; Fritz et al., 2002; Illius and Fitzgibbon, 1994), there is little experimental evidence to support the claim that variation of competition is the driving factor behind the relationship. Support for this hypothesis would involve a reliable quantification of competition intensity across many taxa on long timescales. Experimental support, which is more feasible on a short timescale, as discussed above, would require a controlled adjustment of competition intensity. For instance, changing the density of food available and observing if differences in competition significantly affect group size and vigilance in the way this model predicts could be one way of testing this model.

Through investigation of equilibrium solutions both with rare low magnitude innovation, as with genetic inheritance, and with common innovation, as with behavioral inheritance through inadvertent social information, this model captures the well-observed phenomenon of the inverse relationship between vigilance and group size. We find that when group size is allowed to change in response to vigilance, variation in intraspecific competition intensity results in a negative relationship between vigilance and group size. Thus, we have provided an adaptive mechanism that provides theoretical support for the many eyes hypothesis.

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CRediT authorship contribution statement

John S. McAlister: Conceptualization, Methodology, Software, Formal analysis, Writing - original draft, Visualization. **Ian M. Hamilton:** Conceptualization, Resources, Writing - review & editing, Supervision, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary Material

Supplementary material associated with this article can be found, in the online version, athttps://doi.org/10.1016/j.jtbi.2022.111030.

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