An Adaptive Dynamic Model for a Vigilance Game among Group Foragers

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April 13, 2023

Vigilance

- **Vigilance** is the act of scanning the environment for predators.
- Vigilance is costly to foraging[1]
- It is well observed that vigilance decreases in animal groups as group size increases[2]
- **Many Eyes Hypothesis**[3] suggests that this relationship is due to the fact that the vigilance burden can be distributed across the entire group.

[1] Illius, A.W., Fitzgibbon, C., 1994. Costs of vigilance in foraging ungulates.

[2] Sansom, A., Cresswell, W., Minderman, J., Lind, J., 2008. Vigilance benefits and competition costs in groups: do individual redshanks gain an overall foraging benefit?

[3] Roberts, G., 1996. Why individual vigilance declines as group size increases

Current Models

Previously models of this relationship have relied on

- Complete Collective detection[4]
- Behavioral Monitoring[5]

But these assumptions are not well supported by the literature
The first model to incorporate a dynamic group size was by Beauchamp[6] in 2017.

[4] McNamara, J.M., Houston, A., 1992. Evolutionarily stable levels of vigilance as a function of group size.

[5] Lima, S.L., 1987. Vigilance while feeding and its relation to the risk of predation

[6] Beauchamp, G., 2017. The spatial distribution of foragers and good patches can influence anitpredator vigilance

Life History

Assumptions

- Each individual reproductive success proportional to their foraging success.
- No senescence. At any time an individual has μ chance of dying.

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

where α is foraging rate and μ is risk of death.

Foraging

For a forager in a group of size N, using a foraging strategy F,

$$\alpha(F, N) = \frac{s_0}{(1 + aF)^{N-1}} \frac{F}{s_2 + F} \quad (2)$$

parameter	explanation
s_0	base foraging rate of a single individual
a	rate of intraspecific competition
s_2	Half saturation rate of foraging for a single individual

Risk of Death

For a forager in a group of size N, using a foraging strategy F,

$$\mu(F,N) = (1-(1-F)p_v)\left(1-(1-F)\frac{N}{C+N}p_v\right)^{N-1}\frac{p_0}{\sqrt{N}} \quad (3)$$

parameter	explanation
p_v	Probability of an individual seeing a predator
C	constant inversely related to reliability of information
p_0	risk of attack

Fitness function

Now we have a fitness function $w : [0,1] \times \mathbb{N} \to \mathbb{R}$

$$w(F,N) = \frac{\alpha(F,N)}{\mu(F,N)} \tag{4}$$

This allows us to think about a game with N individuals all trying to maximize fitness.

Fixed group size

Consider a population of individuals which always forage in groups of size N. In general they always forage at at the same rate F but there is rare innovation (at a rate ε). If the mutant uses a new foraging strategy u. We can modify slightly our fitness functions from above to get

$$\begin{aligned} w_r(u, F, N) &: [0,1] \times [0,1] \times \mathbb{N} \to \mathbb{R} \\ w_m(u, F, N) &: [0,1] \times [0,1] \times \mathbb{N} \to \mathbb{R} \end{aligned} \tag{5}$$

Invsibility

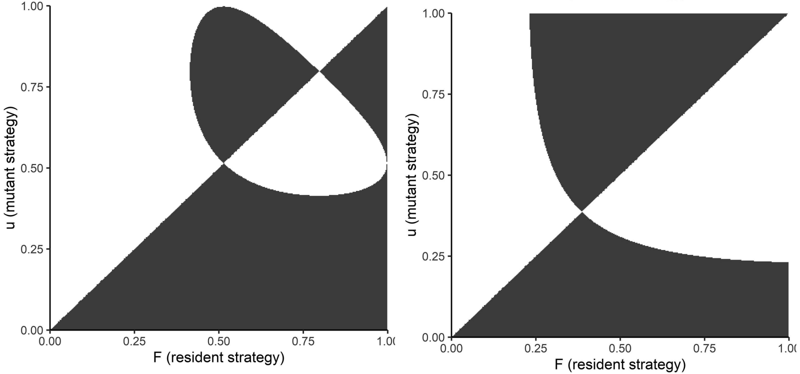
This is the basis of our investigation through pairwise invasion.

$$\Delta\tilde{w}(u, F; N) := w_r(u, F, N) - w_m(u, F, N) \quad (6)$$

Thus is $\Delta\tilde{w} > 0$ the mutant strategy cannot invade the resident population but if $\Delta\tilde{w} < 0$ the mutant strategy invades. Because the magnitude of the fitness differential doesn't matter, we just use

$$\begin{aligned}\Delta w(u, F; N) = F\xi(F, N)(1 - s_2 u)(1 - (1 - u)p_v) \\ - u\xi(u, N)(1 - s_2 F)(1 - (1 - F)p_v)\end{aligned} \quad (7)$$

Pairwise Invasion Surface



In the gray region, the residents resist invasion but in the white area mutant strategies invade.

Results of Pairwise Invasion

The curves on which $\Delta w(u, F, N) = 0$ are called isoclines.

$$S(u, F; N) = \lim_{(y,x)\to(u,F)} \frac{\Delta w(y, x; N)}{(x - y)} \tag{8}$$

We are assured that this is a polynomial and that the zeros of S are zeros of Δw.

$$\begin{aligned} \mathcal{I}_1 &= \{(u, F) \in [0, 1]^2 | u = F\} \\ \mathcal{I}_2 &= \left\{(u, F) \in [0, 1]^2 | S(u, F; N) = 0\right\} \end{aligned} \tag{9}$$

When Now consider restricting $S(u, F; N)$ onto $\mathcal{I}_1$.

Results of Pairwise Invasion

For very small innovations of size δ , we can say that when $S(F+\delta, F; N) > 0 \to \Delta w(F+\delta, F; N) < 0$ so strategies of increased foraging can invade but strategies of decreased foraging do not invade. Likewise when $S(F+\delta, F; N) < 0 \to \Delta w(F+\delta, F; N) > 0$ so strategies of increased foraging cannot invade. To make this more clear let

$$P(F; N) := S(F, F; N) = \lim_{(x,y)\to(F,F)} \frac{\Delta w(y, x; N)}{(x-y)} \tag{10}$$

Results of Pairwise Invasion

So if $P(F;N) > 0$ increased foraging strategies invade and when $P(F;N) < 0$ decreased foraging strategies can invade.

$$\frac{dF}{dt} = \varepsilon \text{sign}(P(F;N)) \quad (11)$$

Dynamic Group Size

Group size can be controlled in two ways

- External - Individuals join a group if it increases their own fitness
- Internal - Individuals are added to the group if it increases the fitness of the group

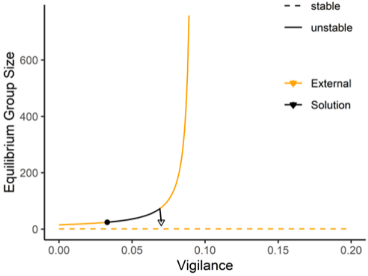
So we have two different ways to describe the change in group size

$$\begin{aligned} \frac{dN_E}{dt} &= \sqrt{N} - \xi(F,N)^{N-1} \\ \frac{dN_I}{dt} &= 1 + 2N\left(-\log(\xi(F,N)) + \frac{1-N}{\xi(F,N)}\frac{\partial}{\partial N}\xi(F,N)\right) \end{aligned} \tag{12}$$

Separation of Time Scales

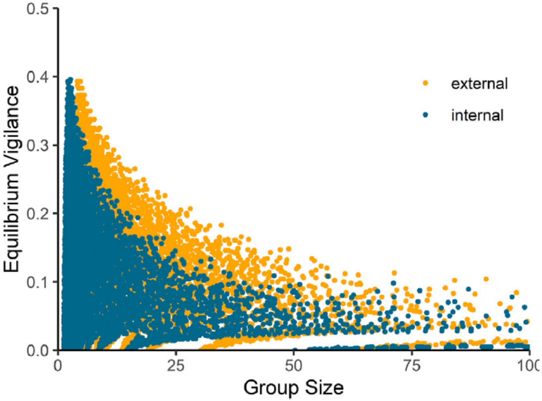
Initially we will require that the rate of fixation is far greater than the rate of mutation

$$\frac{dN_E}{dt} = \sqrt{N} - \xi(F, N)^{N-1}$$
$$\frac{dF}{dt} = \varepsilon \text{sign}(P(F; N)) \quad (13)$$



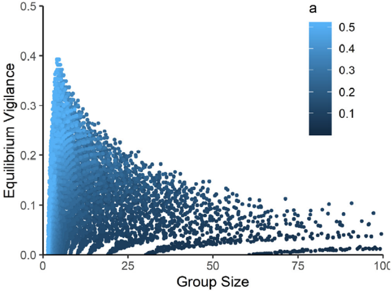
Entire Parameter Space

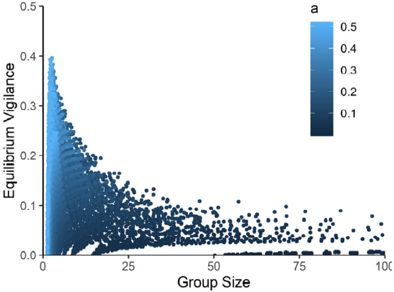
We search for equilibria across the reasonable parameter space.



Intraspecific Competition

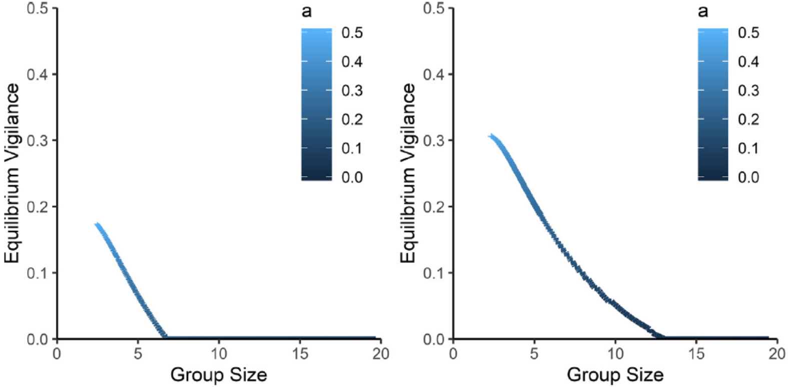
Now observe the trend we see when equilibria are colored by Intraspecific competition.





Intraspecific Competition

To see this relationship better, take a curve out of the parameter space $\{a, s_2 = 4, p_v = 0.75, C = 6\}$ and find the position of the associated equilibrium.



Proposed Mechanism

Therefore we have observed:

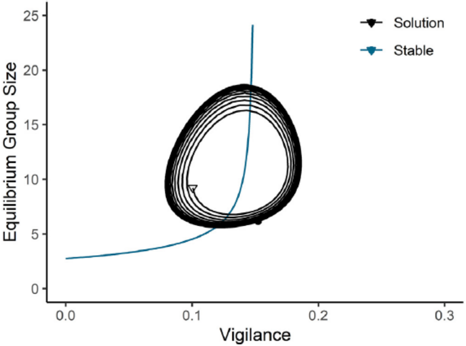
- Dynamic group size is crucial to the relationship between vigilance and group-size
- Varying intraspecific competition can lead to the observed negative trend.

So we may be propose that as a population breaks into groups over a heterogeneous landscape, variation in intraspecific competition result in differences in equilibrium group size and vigilance.

Weakened assumptions

Notice that the separation of time scales assumption is inappropriate for this setting because both vigilance and group size change in the behavioral time scale.

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



Future Direction

This relaxation of the separation of time scales assumptions requires more study. Pairwise invasion requires fixation to be much faster than mutation.

Acknowledgments

- This research was done in collaboration with Dr. Ian Hamilton at The Ohio State University.
- This Research was funded by The Ohio State Universities STEP Fellowship.

Work Cited

- Illius, A.W., Fitzgibbon, C., 1994. Costs of vigilance in foraging ungulates. Animal Behavior 47, 481–484.
- Sansom, A., Cresswell, W., Minderman, J., Lind, J., 2008. Vigilance benefits and competition costs in groups: do individual redshanks gain an overall foraging benefit? Animal Behavior 75, 1869–1875.
- Roberts, G., 1996. Why individual vigilance declines as group size increases. Animal Behavior 51, 1077–1086.
- McNamara, J.M., Houston, A., 1992. Evolutionarily stable levels of vigilance as a function of group size. Animal Behavior 43, 641–658.
- Lima, S.L., 1987. Vigilance while feeding and its relation to the risk of predation. J. Theor. Biol. 124, 303–316.
- Beauchamp, G., 2017. The spatial distribution of foragers and good patches can influence anitpredator vigilance. Behav. Ecol. 28 (1), 304–311.