

Exploring conditions that select for the evolution of cooperative group foraging

Patrick B. Haley^{1,3}, Randal S. Olson^{2,3}, Fred C. Dyer^{2,3}, and Christoph Adami^{2,3}

¹The University of Texas at Austin, Austin, TX 78712

²Michigan State University, East Lansing, MI 48824

³BEACON Center for the Study of Evolution in Action, East Lansing, MI 48824

patrick.haley@utexas.edu, olsonran@msu.edu, fcdyer@msu.edu, adami@msu.edu

Extended Abstract

Many prey choose to live, forage, and reproduce in groups — this is one of the most readily-observed phenomena in biology. Group living is potentially costly (because of competitive interactions among other reasons), and the benefits that outweigh these costs are difficult to understand, as they may interact in complicated ways (Krause and Ruxton, 2002). Collective vigilance is one oft-cited benefit of grouping behaviors. This claim relies on the principle that at each moment in time prey must make a choice between two mutually exclusive actions: foraging for food or being vigilant to look for predators. Group foraging potentially allows individuals to increase their foraging efficiency — and therefore their fitness — by sharing the expensive task of looking out for predators. Since isolating such decision-making in biological systems is difficult (particularly on an evolutionary timescale), we use digital organisms to study how this decision is made by groups of prey under the threat of predation.

Decision making in groups can take two different forms. Most computational research has concentrated on homogeneous groups, where every agent has an identical method of making decisions, usually regarding movement (Ward et al., 2001). However, it is also possible for groups to be heterogeneous, with behaviors varying drastically among individuals. A group with both altruistic and selfish members would be an example of such heterogeneity.

Here, we explore the effects of this distinction between homogeneous and heterogeneous group composition in relation to the evolution of vigilance behaviors. In addition, we examine the impact of two reproductive strategies: populations are either iteroparous (reproducing repeatedly) or semelparous (reproducing a single time before they die), which should affect the intensity of selection on antipredatory traits that influence survival to reproductive maturity.

Methods As in previous work, agent fitness is determined in a disembodied simulation, where the agent's goal is to forage as much as possible while surviving predator attacks (Ruxton and Beauchamp, 2008). All agents are in the same group, and group size is varied between experiments to explore its effect. Fitness is equal to the number of updates spent foraging rather than being vigilant. When the simu-

lation is complete, a genetic algorithm generates the next population of genotypes. An agent's genotype codes for a Markov Network in which one output state is the decision to forage or be vigilant (Olson et al., 2013). Currently, this means vigilance levels are defined by probabilities, but future studies could consider more complex outputs (e.g. multiple interrelated strategies), or inputs from a visual system that provides a richer picture of the environment.

In the simulation, vigilance comes into play when a predator attacks. The rate of this attack is relative to the size of the group, so there is no dilution of the attack risk with increasing group size. When the predator appears, it randomly selects one of the prey as its target. The predator then waits for several turns (approximating the time required to close for an attack). If the target is vigilant at some point in this interval, it becomes aware of the predator and has a 90% chance of survival. If the target remains unaware but another prey is vigilant, the target has a 50% chance of survival (i.e., the threat is automatically communicated). If none of the prey are vigilant, the target has a 10% survival rate.

The fitness function can be varied in two ways. First, prey can be evaluated in either homogeneous or heterogeneous groups. In a homogeneous evaluation, one genotype is considered at a time, copies of its agent are made to fill the simulation, and the final fitness of all of these clones is averaged at the end. In a heterogeneous evaluation, genotypes compete against one another and the fitness an agent has at the end of the simulation is its fitness for that generation. Since differing genotypes can evolve to exploit the vigilance of others, thus lowering their own vigilance, we hypothesize that vigilance will be greater in homogeneous populations.

The second method for varying fitness functions is reproductive method. In semelparous treatments, a prey that died during the simulation is assigned a fitness of zero for that entire simulation (i.e., only surviving agents are said to reach reproductive maturity). In iteroparous treatments, dead prey cease to forage but they do not lose the fitness they have acquired during their lifetime (i.e., reproduction is continually occurring in the group). We hypothesize that semelparous treatments select more strongly for survival, therefore they

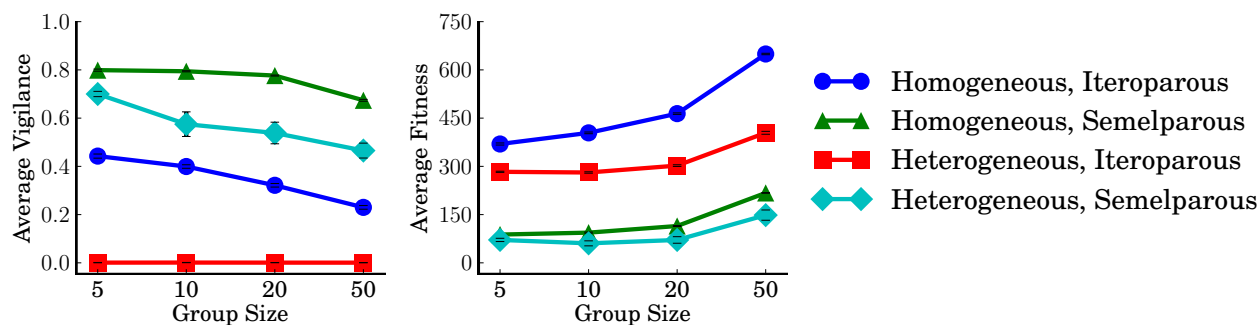


Figure 1: Semelparity and homogeneity select positively for vigilant behavior in prey without interfering with one another. Either treatment is sufficient to select for vigilance, but at least one is necessary. Fitness increases with group size while vigilance decreases, as predicted by the many-eyes hypothesis. Error bars are shown for 95% confidence intervals.

should produce higher levels of vigilance.

Results As shown in Figure 1, agents are more vigilant in semelparous treatments. This finding holds across both homogeneous and heterogeneous populations. In addition, homogeneous populations consistently evolve higher levels of vigilance than heterogeneous populations. We do not take this to mean that cooperative vigilance is impossible in heterogeneous groups, only that vigilance is a less stable strategy when genotypes compete against one another. This conclusion is supported by the evolution of vigilance in heterogeneous, semelparous populations, which shows that vigilance is possible outside of homogeneous conditions.

While homogeneity and reproductive strategy both select positively for vigilance, Figure 1 demonstrates that homogeneity plays the greater role. This can be seen from the lower evolved vigilance levels in the homogeneous, iteroparous populations compared to the heterogeneous, semelparous populations. Homogeneity and reproductive strategy also do not inhibit one another’s selective pressure, since the homogeneous, semelparous population evolves the greatest levels of vigilance.

It is possible that some prey could evolve to take advantage of the vigilance of others. Such cheaters would spend most of their time foraging. Naturally, this is only possible in the heterogeneous treatment. We would expect such genotypes, if they exist, to be characterized by significantly higher fitness and lower vigilance values. However, in all cases the most fit organism in the population had vigilance and fitness values closely matching that of the rest of the population. Thus, we posit that this experimental environment is not suitable for the evolution of a stable cheating strategy.

Our general finding that vigilance promotes survival in groups even when it entails a tradeoff with foraging aligns with observational evidence of animals (Lima, 1995), which show higher levels of vigilance in smaller groups. The inverse relationship between vigilance and group size and the

direct relationship between fitness and group size we observed fit the predictions made by one theory on the benefits of grouping, the many-eyes theory (Pulliam, 1973). Such patterns suggest that the advantages of vigilance are a major driver of group living, and may favor living in larger groups in spite of the costs of competition. So far we have not explored such variables as the dilution of predation risk by group size (we explicitly controlled this), the dilution of vigilance costs by relatedness, or the ability to vary levels of vigilance conditional upon an assessment of the risks, but our system provides a platform for exploring such variables.

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