Introduction

Animals of many species respond to a perceived predator with some sort of vocalization. These alarm calls are usually thought to be directed towards the predator or other members of the caller’s own species, but alarm calls can also be heard by members of other species that happen to be present. Other species’ alarm calls can contain valuable information about the presence of shared predators. Though some species have an innate capacity to recognize other species’ alarm calls, they can also be learned from experience (Magrath et al. 2014). For example, superb fairy-wrens (*Malurus cyaneus*) have only been found to respond to miner (*Manorina melanocephala*) alarm calls in places where miners are also present, suggesting that the fairy-wrens learn to respond to the miners’ alarm calls (Magrath & Bennett 2011). Similarly, gray squirrels (*Sciurus carolinensis*) have been found to respond more strongly to the familiar alarm call of the American robin (*Turdus migratorius*) than to alarm calls made by the unfamiliar New Holland honeyeater (*Phylidonyris novaehollandiae*) or even the common blackbird (*Turdus merula*), which is unfamiliar to the gray squirrel, but whose alarm call is structurally similar to that of the American robin (Getschow et al. 2013).

Learning to attend to other species’ alarm calls is not an easy feat. Predators are necessarily uncommon relative to their prey and even if two species share all the same predators, alarm calls are not necessarily reliable. Animals should not respond to every alarm call they hear, despite the advantages of responding to an alarm call when there is danger, because while responding to an alarm call, the animals is not foraging or doing other things that increase its fitness. If an animal hears an alarm call, but does not see the predator, that will make it less likely to respond to the alarm call in the future. Between false alarms and infrequent opportunities for conditioning, learning through experience alone may not be enough, especially because each encounter with a predator may be the individual’s last. Therefore, some animals not only learn to attend to other species’ alarm calls based on their own experience with alarm calls and predators, but also by paying attention to other members of their own speices’ responses. For many species, it is more likely that a member of the same species will be present than a predator, so by learning from the responses of members of their own species, even false alarms can be opportunities for conditioning. However, because social learning makes it easier for an individual to learn to respond to a new alarm call, it also increases the likelihood that they will respond to a false alarm and waste time that could be spent foraging. Other indivdiuals may also not necessarily respond to the alarm call correctly, so social learning may perpetuate misinformation (Magrath et al. 2014).

Whether members of a given species learn other species’ alarm calls individually or also attend to the responses of others likely depends on a wide variety of factors, such as the frequency of predators, members of other species, and members of the same species, as well as the relative costs of taking time away from foraging and not attending to a predator. To learn to associate an alarm call with a predator, the individual must see the predator and hear an alarm call in close proximity. If the individual hears the alarm call, but does not see the predator, that diminishes their association between the alarm call and the predator and makes them less likely to respond to it in the future. Therefore, the amount of learning from individual experience alone in a given time frame is equal to:

*learning* = *learning rate* \* *frequency of predator* \* *frequency of accurate alarm*

- *extinction rate* \* *frequency of false alarm*

Alternatively, individuals that are capable of social learning not only learn to associate the alarm call with a predator when there is a predator present, but also learn from seeing other individuals of their own speices fleeing. If the individual hears an alarm call and neither a predator nor a member of the same species is present, or if a member of their own species is present but does not respond to the alarm call, then that will still interfere with their learning, however the combinaton of the two is much less likely. The amount of learning from a combination of individual experience and social learning in the same time frame is equal to:

*learning* = *learning rate* \* *frequency of predator* \* *frequency of accurate alarm*

*+ learning rate \* frequency of predator \* frequency of accurate alarm \* frequency of others’ response*

+ *learning rate* \* *frequency of false alarm* \* *frequency of response*

- *extinction rate* \* *frequency of false alarm* \* (1 - *frequency of response*)

Agent-based models can be used to make predictions about how different environmental conditions select for different behavioral strategies. They are especially useful in cases where the one individual's behavior relies on the behavior of others. Agent-based models have been used to form hypotheses about whether social learning should be favored in foraging contexts (Rendell et al. 2010). I will use a similar evolutionary tournament-style agent-based model to predict what conditions should favor social learning of alarm calls. If that is successful, I may create further models to form hypotheses about how animals learn to distinguish between different types of alarm call that vary in how useful they are to the eavesdropper or what type of response they require. I may also model the evolution of alarm calling and responding to alarm calls in general. That could branch into looking at deceptive alarm calls, where a species with usually reliable alarm calls occasionally raises a false alarm on purpose to steal food or other resources from members of another species.

Methods

I will create a model composed of a population of agents foraging and responding to alarm calls, predators, and in some cases, each other. First I will compare the performance agents with and without social learning in an environment where they do not encounter any other agents (the presence and response of other agents will be determined randomly based on a set probability). If that is successful, then I will go on to compare the evolutionary success of multiple agents in the same environment over multiple generations. Each agent will be composed of a small neural network which will take the presence or absence of an alarm call as input and output a response - either foraging or fleeing. Agents will have some probability of detecting alarm calls, predators, and the responses of other individuals, as well as a probability of falsely detecting them when absent. Agents with no capacity for social learning will not be able to detect the responses of other agents. Each time-step in the model, each agent will feed the current state of the environment (the presence or absence of an alarm call) forward through its neural network. Agents will generate their responses by taking a softmax over the activations of their output neurons. Then the agents will receive reinforcement, which will be backpropagated through their neural network. If the agent detects a predator or another individual fleeing, then it will receive reinforcement to flee and not forage. Otherwise, the network will receive reinforcement to forage and not flee.

The multi-agent simulation will be run for several generations. The higher an individual’s fitness is, the more likely it will be to reproduce, creating more individuals that use its learning strategy. In a later stage of the project, I may introduce mutations where different individuals receive differing degrees of reinforcement for foraging, fleeing when exposed to a predator, and fleeing when they observe other agents fleeing. Individuals gain fitness each time-step they spend foraging. However, when a predator is present, there will be a chance that the predator will kill each individual, which will be higher for individuals that are foraging instead of fleeing. All individuals that are killed will not be available for reproducing at the end of the round. I may simulate populations that reproduce on multiple occasions with opportunities to gain fitness and die between them as well as those that reproduce only once. I may also enable individuals to be injured instead of killed, so that predation can decrease an individual’s fitness without killing them.

References

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