Factors that Affect the Evolution of Complex Cooperative Behavior

Padmini Rajagopalan[1], Kay E. Holekamp[2] and Risto Miikkulainen[1]

[1]The University of Texas at Austin, Austin, TX 78712
[2]Michigan State University, East Lansing, MI 48824
padmini@cs.utexas.edu

Abstract

Collaboration in order to perform various tasks such as herding or hunting is frequently seen in nature. Cooperative behaviors benefit the group by helping them achieve rewards that would not be possible for an individual to achieve alone. In addition to cooperative hunting, spotted hyenas also participate in coordinated mobbing of lions, which is a complex behavior that is still believed to be genetic. Lions are larger and stronger than hyenas, and therefore the hyenas need to cooperate in large numbers to overcome their fear and attack the lions. Individualistic hyena traits and other factors that may affect the frequency or success of lion-mobbing have not been studied in simulation before. Furthermore, multiple emotions, such as fear and affiliation towards teammates, affect the willingness of hyenas to attack lions. The computational model of lion-hyena interaction developed in this work can help understand the evolution of mobbing behaviors. It may be used in the future to evolve strategies in video game characters to overcome powerful adversaries or solve problems that involve high risk.

Introduction

Complex cooperative behaviors are hard to model in simulation, whether they be hard-coded or learned. In previous work, collaboration had to be evolved through coevolution, or other such means (Uchibe and Asada, 2006; Yong and Miikkulainen, 2009; Rawal et al., 2010). It is, therefore, helpful to examine how cooperative behaviors emerge in nature, and what factors influence their successful evolution.

In nature, spotted hyenas frequently cooperate in teams in order to hunt for prey that is difficult to kill (Kruuk, 1972; Holekamp et al., 1997). This behavior has previously been modeled in simulation (Rajagopalan et al., 2011).

Less frequently, hyenas also gather in large numbers to attack lions and drive them away in order to gain possession of a kill. This lion-mobbing behavior is very complex and requires precise coordination to succeed. This is because lions are larger and stronger than hyenas and, therefore, are expected to emerge the winners in any lion-hyena interaction.

There are some limitations to the study of lion-hyena interactions in nature. The path that hyena behavior evolution took to reach its current state of sophisticated mobbing cannot be studied in real-life hyenas. This problem can be solved by developing a computational model that faithfully reproduces lion-hyena interactions and mobbing behaviors from nature. It can then be used to study the evolution of such behaviors as well as to make predictions about them. This paper describes how such a model was built.

Neuroevolutionary techniques were used to control a team of hyenas that were placed in various situations along with simulated lions in a field. The simulations showed that the factors observed in nature as affecting the evolution and success of mobbing behaviors also emerged in the computational model. In the future, these principles can also be used to build teams of artificial agents with complex cooperative behaviors.

Related Work

This section will first describe the biological background of lion-mobbing, after which the modeling of cooperation and the various neuroevolutionary techniques that are used to build such models will be reviewed.

Biological Background

Since spotted hyenas (*Crocuta crocuta*) and lions are both apex predators that compete for prey, resources and habitat, they come into conflict very frequently. Lions are much larger and more powerful than hyenas and are expected to win most such interspecific competitions. Hyenas are generally reluctant to engage with lions. Nevertheless, hyenas have sometimes been observed to exhibit a curious cooperative action where they band together to attack a group of lions in order to gain or retain access to a kill (Watts and Holekamp, 2008). Hyenas display other cooperative behaviors for hunting and for defense (Holekamp et al., 2012), but lion-mobbing is much more complex than these, and can be considered a novel evolutionary step. Mobbing is very dangerous for the hyenas (Trinkel and Kastberger, 2005; Kruuk, 1972). In fact, lions are the leading cause of death in many hyena populations (Cooper, 1991; Hofer and East, 1995; Trinkel and Kastberger, 2005). Consequently, hyenas can rarely displace lions from food unless the odds ratio (i.e. the ratio of hyenas to lions) is at least four to one (Kruuk, 1972).

Dr. Holekamp and her colleagues have been continuously monitoring spotted hyena clans in the Masai Mara National Reserve and Amboseli National Park in Kenya since 1988. They have made direct observations of seven different hyena clans and recorded over 500 hours of videos and detailed notes about more than 900 lion-hyena encounters (Lehmann et al., 2016). Dr. Holekamp's group used this data to construct a table that characterizes each such encounter along dimensions such as the number of hyenas present, the number of lions, whether mobbing occurred, and whether it was successful. Using this dataset, they then characterized all the lion-hyena encounters and assessed mobbing probabilities in Lehmann et al. (2016). Some of the conclusions they reached were:

1. Lions and hyenas interacted more frequently at fresh kill sites than at sites with older carcasses. Mobbing rates were also highest at a fresh kill.

2. Lion-hyena interaction probability increased with increasing prey size.

3. The presence of adult male lions at the kill site increased the probability of interactions but decreased the probability of successful mobbing.

4. The interaction probability increased with number of hyenas present.

5. Local prey availability did not significantly impact the probability of interaction.

6. Mobbing increased the probability that hyenas would acquire food from a lion-controlled kill site. Thus, the evolution of cooperation in hyenas has increased their overall fitness.

The goal of this work was to understand the cognitive processes that result in mobbing behavior using a computational model to simulate lion-hyena interactions. All the conclusions from the observational data listed above were tested in simulation.

Simulations of Cooperative Behavior

A significant body of work exists on computational modeling of cooperation in nature. For instance, flocking behaviors of birds and shoaling of fish have been modeled extensively using rule-based approaches (Reynolds, 1987; Seno, 1990), while cooperative behavior of micro-organisms has been modeled with genetic algorithms (Kubota et al., 1996; Roeva et al., 2007). Ant and bee colonies have been the subject of many studies involving evolutionary computation as well (Dorigo et al., 1996; Waibel et al., 2006).

More complex cooperative behaviors in teams have also been studied in computation before. Yong and Miikkulainen (2009) used neural networks to control and evolve the behaviors of three predators cooperating to catch a prey. Simultaneous cooperative and competitive coevolution was implemented in teams of predators and prey by Rawal et al. (2010), while dynamically changing hunting behaviors of hyenas were modeled in Rajagopalan et al. (2011).

Previous computational work also studied the effect of different communication strategies in mobbing, evolving the behaviors as a set of rules (Solomon et al., 2012; Fairey and Soule, 2014). The results showed that having a single leader to make all mobbing decisions for the hyena team resulted in the most effective coordination. But this result has not been observed in nature, and therefore, this will not be an assumption in this work.

Neuroevolution of Behavior

Neural networks and evolutionary computation may be combined into a learning algorithm that can be used to solve difficult sequential decision tasks with continuous state and action spaces, and partially observable states. Neuroevolution has previously been used to discover dynamic and intelligent behavior in autonomous agents. For example, it has been used in simulated robot soccer (Whiteson et al., 2005), and Ms. Pac-Man (Burrow and Lucas, 2009; Schrum and Miikkulainen, 2014). Neuroevolution has also been used in previous modeling of predators and prey (Yong and Miikkulainen, 2009; Rawal et al., 2010) as well as in the evolution of cooperative hunting behaviors in simulated hyenas (Rajagopalan et al., 2011). Thus, neuroevolution is a natural choice for modeling the complex cooperative behavior of lion-mobbing.

NeuroEvolution of Augmenting Topologies, or NEAT (Stanley and Miikkulainen, 2002), is a neuroevolution technique that optimizes not only the connection weights, but also the topology of a neural network. This technique was shown to be more effective than traditional neuroevolution methods that modify only the connection weights (Stanley and Miikkulainen, 2002). Speciation is also used to nurture new innovations in network structure that might otherwise be lost due to their low initial fitnesses. NEAT was used in this work when building a computational model to study lion-hyena interactions.

Experimental Setup

The hyena agents were placed on a 100×100 toroidal grid without any obstacles, where they could move east, west, north or south. A group of non-evolving lions already in possession of the kill were fixed at a location, and had the deterministic behavior of killing any hyena that came within a certain number of steps from them, i.e. the *interaction radius*, with a certain *kill probability*. Whenever a hyena moved closer than the interaction radius, it was said to be interacting with the lions. Then, it could either be killed or

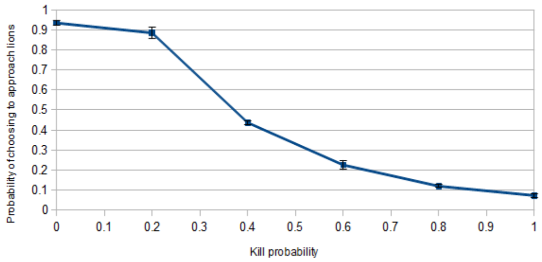

Figure 1: Interaction probability when kill probability is fixed. The *x*-axis has kill probability and the *y*-axis is the probability that the hyena approaches the lions, averaged over ten runs. The fixed value of the kill probability during each run had to be discovered by the hyena through evolution. The probability of approaching lions decreased as the kill probability increased.

be part of a successful mobbing event. The goal of the simulated hyenas was to mob the lions with enough teammates to drive them away and obtain the kill for themselves. An example of a successful mobbing behavior in simulation has been uploaded at http://nn.cs.utexas.edu/?mobbingfactors.

The hyena population was evolved using the NEAT algorithm (Stanley and Miikkulainen, 2002). For each simulation, a hyena was picked from the population and cloned to create the team members. Each hyena in the population was evaluated five times, and each experiment was run ten times. The fitness, mobbing probability and lion-hyena interaction probability were averaged across these ten runs.

A hyena:lion ratio of 4:1 is necessary for a successful mobbing event to take place (Kruuk, 1972). The kill probability in the simulation depended on the number of hyenas and lions, but it came into play only when a hyena entered the interaction circle of the lions.

In addition to mobbing reward given to successful mobbers, a survival reward was given to those hyenas that survived until the end of the simulation regardless of whether they participated in a mobbing event. This represented reward from hunting in real-life hyenas, and provided a fitness gradient for the evolution of the hyena neural networks.

In the following section, several experiments were designed to build and test a computational model for lion-mobbing. Representations of various parameters from the real world were gradually introduced and tested.

Using a Computational Model to Characterize Lion-Hyena Interactions

In the following experiments, various parameters were carefully and systematically tested in order to reproduce the hyena behaviors seen in nature.

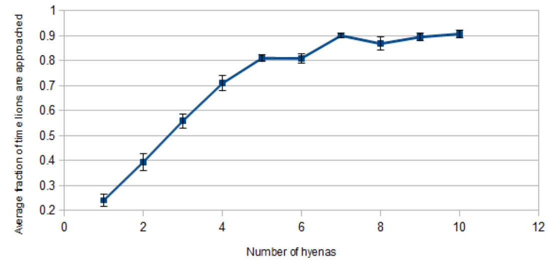

Figure 2: Interaction probability when number of hyenas varies dynamically. The number of hyenas is on the *x*-axis, and the *y*-axis is the probability of the hyena approaching the lions, averaged over ten runs. The number of lions was kept fixed at two. The numbers of hyenas and lions were given as input to the neural network, but the kill probability had to be calculated. The probability of approaching lions increased with number of hyenas.

Preliminary Experiments to Calculate Kill Probability

Initial experiments consisted of a single time step in which hyena agents decided whether to approach the lions, and were immediately rewarded. The number of clones created for each simulation run was chosen at random from [1, 10]. If the number of hyenas was more than four times the number of lions, the kill probability decreased to 0 and they could successfully mob the lions. Otherwise, it was equal to the normalized ratio of number of lions to number of hyenas.

More specifically,

$$K = \begin{cases} 0 & \text{if } H \leq 4L \\ \frac{\frac{L}{H} - 0.25}{0.75} & \text{if } H > 4L \end{cases}$$

where K was the kill probability, L was the number of lions, and H was the number of hyenas.

The numbers of lions and hyenas were not known to the hyena. However, both these numbers (and hence, kill probability) were kept fixed during an experiment run, so the hyena population could discover the kill probability through evolution. If the team of hyena clones chose to approach lions and were killed, they received a reward of $-10,000$ points. If they approached lions but were not killed, they got 1000 points. If they chose to stay away from the lions, a survival reward of 100 points was given to them. As expected, the fraction of time they chose to approach the lions decreased as the kill probability increased (Figure 1).

In the second experiment, the hyena neural network received as input the numbers of hyenas and lions, and had to calculate the current kill probability. The actual number of

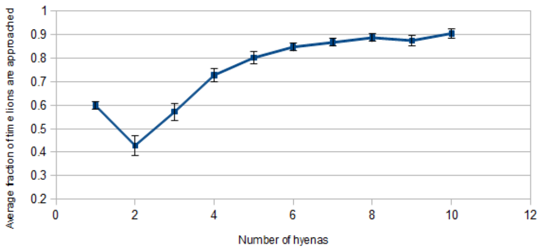

Figure 3: Interaction probability when lion-hyena distances are given. The *y*-axis shows the average probability of approaching the lions. The number of lions was kept fixed at 2. The absolute lion-hyena distances were given as input, but the number of hyenas was not. The probability of approaching lions generally increased with number of hyenas except for a small bump when number of hyenas was 1.

lions was kept fixed at 2. The number of hyenas in each run was chosen randomly between 1 and 10.

While the probability of approaching lions decreased with decreasing numbers of hyenas, it never reached 0 (Figure 2). Fewer hyenas in the environment lead to lower odds for a successful mob, and therefore the hyenas evolved to avoid the lions instead of getting killed. This behavior has also been observed in real-life hyenas (Lehmann et al., 2016).

In a third exploratory experiment, the hyena neural network received as inputs the distances of all other hyenas from the lions in addition to the number of lions (L) and its own *x*- and *y*-distances from the lions. The number of other hyenas was not an input. The other hyenas were virtual for now, so their distances were generated at random. Kill probability still depended only on the number of hyenas and lions, so the values of distances did not matter. However, the hyena had to evolve to count the number of distance inputs that were switched on and thus find out the number of other hyenas.

The probability of approaching the lion increased with increasing number of hyenas on the field with a small bump when there was only one hyena (Figure 3). When there were fewer hyenas than the *mob minimum*, it was unable to evolve to avoid the lions completely.

The next experiment had H non-virtual hyena clones instead of just one. Based on its inputs, each clone had to decide whether to attack the lions, which could lead to death, or avoid them, which gave smaller reward. The probability of interaction increased with increasing number of hyenas, just as stated in Conclusion 4 in the Biological Background section (Figure 4). The average maximum fitness reached for $H = 1$ and 2 was exactly equal to the survival reward, because H was below the mob minimum. But when $H = 3$ or 4, they chose to approach lions more often.

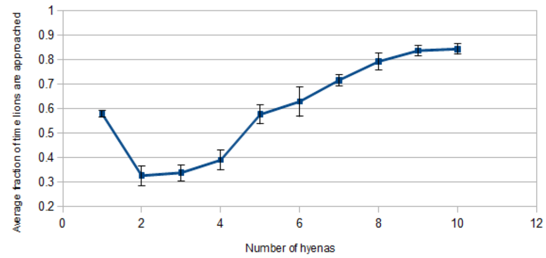

Figure 4: Interaction probability for multiple hyenas when lion-hyena distances are given. The number of lions was kept fixed at 2. The absolute lion-hyena distances were given as input to all the hyenas, but the number of hyenas was not. Each hyena had to make a decision whether to approach the lions. The average probability of approaching lions generally increased with number of hyenas, except for a small rise when there is a single hyena present.

Realistic Modeling of Lion-Hyena Encounters

The previous subsection paved the way for a multi-step simulation where the hyena clones could move around. Therefore, the number of time steps was increased to 500, and the hyenas could move east, west, north and south, or remain idle, represented by five output nodes. Each hyena neural network received a continuous input of the distances of itself and the other hyenas from the lions. The number of lions was fixed at 1. At every time step, if a hyena was within 10 steps (interaction radius) of the lion, kill probability came into play, which depended on how many hyenas were within the interaction circle (mob count). If a hyena was killed, it got a fitness penalty of $-10,000$ points and disappeared from the environment. For each time step that a hyena was within the interaction circle but did not die, it received a reward of five points, which represented the hyena feeding on the kill alongside the lions. If the mob count was greater than the mob minimum, the simulation was terminated with a mobbing reward of 10,000 points per hyena. At the end of the simulation, a reward of 100 points per hyena was given to all surviving hyenas. The inputs to the neural networks were the same as in the previous exploratory experiments, but now their values changed at every time step. The initial neural networks had 15 input-output neurons, 65 links and no hidden layer. The final evolved networks had around 130 neurons and around 400 links.

The results showed that the hyenas did not mob the lion successfully in most cases, but even the rare mobbing successes raised their average highest fitness above survival reward. More hyenas approached the lion even if they did not end up mobbing it. When the number of hyenas was less than the mob minimum, the best hyena teams evolved to avoid the lions altogether to stay alive and collect their survival reward. In general, the interaction probability in-

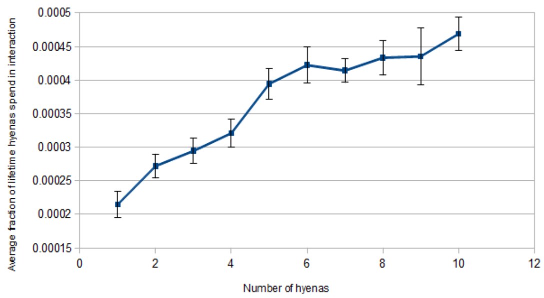

Figure 5: Interaction probability for hyenas in a 500-time-step simulation. The *x*-axis has number of hyenas, and the *y*-axis represents the average interaction probability, i.e. fraction of time the hyenas were within the interaction circle. The number of hyenas was not given as input, but the absolute lion-hyena distances were. The average interaction probability increased with number of hyenas.

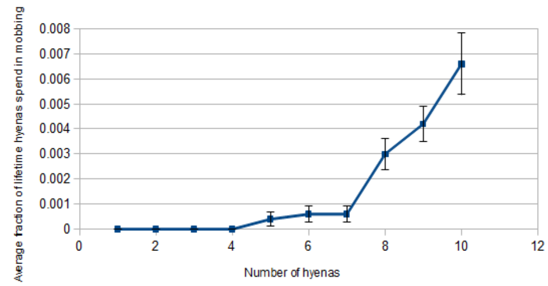

Figure 6: Successful mobbing probability for increased mobbing frequency. The *y*-axis represents the average mobbing probability. The interaction radius, mobbing reward and reward from feeding on the kill were all increased. A small survival reward was given to all surviving hyenas at the end of the simulation. The average mobbing probability was very low, but successful mobbing occurred more often than in previous experiments.

creased with increasing number of hyenas (Figure 5). Overall, this probability was low because when a hyena entered the interaction circle, it would either soon get killed, or successful mobbing would occur, ending the simulation.

While the mobbing frequency was very low, the interaction probability increased with increasing number of hyenas in the environment, which is in line with Conclusion 4 from the Biological Background section. Successful mobbing did evolve and, therefore, can be productive for the hyena team and increase its fitness as long as mobbing gives a net gain to the hyenas. This agrees with Conclusion 6.

Increasing the Frequency of Successful Mobbing

While the hyenas in the previous subsection did evolve to successfully mob the lions, they did so very rarely. To increase the frequency of mobbing, various parameter values were tested carefully and systematically. The reward for remaining alive within the interaction circle needed to be higher to encourage hyenas to approach the lions. The interaction radius also needed to be increased in order to allow hyenas to drive away the lions from a greater distance. But this meant that the probability of hyenas dying also increased, since the kill probability came into play once a hyena was within the interaction circle. The mobbing reward per hyena was increased, while the survival reward as well as the mobbing reward were given only to those hyenas that survived to the end of the simulation, unlike in previous experiments. This change helped hyenas evolve to coordinate their attack on the lions instead of charging them blindly. The survival reward needed to be low so that the hyenas did not avoid the lions altogether.

The result of these parameter changes was that the frequency of mobbing increased when compared to previous experiments (see Figure 6). In all cases where the number of hyenas was five or more (the mob minimum), the mobbing probability was non-zero. The average mobbing probability increased with increasing number of hyenas on the field. The fraction of time the hyenas spent within the interaction circle, also increased (compare Figures 5 and 7). The average interaction probability also increased with increasing number of hyenas. A surprising development, which is also observed in nature, was that even when they did not have the numbers to mob the lion, they still obtained some reward from moving into the interaction circle and feeding on the kill. But this meant that they did not all stay alive until the end of the simulation, and thus the team did not get the maximum possible survival reward.

Presence of Adult Male Lions

Dr. Holekamp's group found that the presence of adult male lions in the lion group led to an increase in the probability of the hyenas and lions interacting (Lehmann et al., 2016). Male lions are more likely to initiate the interaction themselves (Elliott and Cowan, 1978), but are also better able to protect their kill, leading to lower mobbing frequency (Cooper, 1991; Kissui and Packer, 2004). The computational model matched Conclusion 3 from the Biological Background section in the following experiments.

Since male lions instigate interspecific interactions with the hyenas, the presence of male lions could be represented by a larger interaction circle in the computational model. The male lions also end up killing or injuring more mobbing hyenas due to their strength. That fact would also true in the model when using a larger interaction circle, because any hyenas are more likely to step into the interaction circle if it is larger, and thus, they would be more likely to die.

In these experiments, the interaction radius was varied

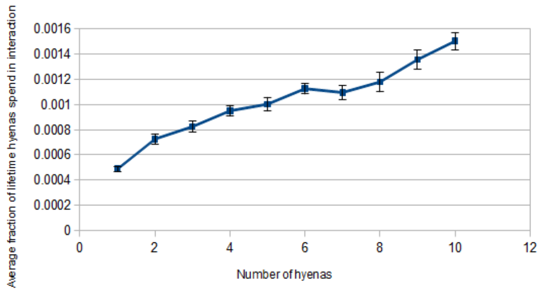

Figure 7: Interaction probability with increased mobbing frequency. The y-axis represents the average interaction probability, i.e. fraction of time the hyenas were within the interaction circle. The interaction radius, mobbing reward, and reward from feeding on the kill were all increased. There was also a small survival reward. The average interaction probability was higher than in previous experiments, and increased with number of hyenas.

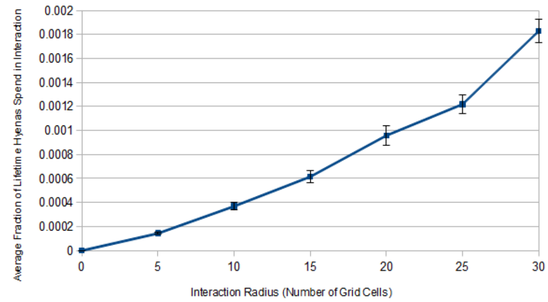

Figure 8: Interaction probability comparisons when adult male lions are present. The x-axis shows the interaction radius, and the y-axis represents the interaction probability, i.e. fraction of time the hyenas were within the interaction circle, averaged over ten runs. The numbers of hyenas and lions were kept fixed at 10 and 1, respectively. The interaction radius was varied dynamically between 0 and 30 steps. The average interaction probability increased as the interaction radius increased. Therefore, the frequency of interaction increased when there were male lions present.

randomly in the range 0 to 30 during the experiment run. This value was then given as input to the hyena neural network. The number of hyenas was fixed at 10 in all the experiments so that the comparisons between results would reflect only the changes in interaction radius.

Just like in nature, the simulated hyenas spent more of their time interacting with lions as the interaction radius increased, but they also got killed more frequently (see Figures 8 and 9). This result is in line with Conclusion 3 from the Biological Background section, which states that presence of male lions increases the interaction probability, but also increases the number of hyena deaths.

Prey Desirability

It makes intuitive sense that the desirability of the prey at the kill site should dictate whether the hyenas mob the lions to gain the kill, as concluded by Lehmann et al. (2016). Both interaction and mobbing rates were highest at a fresh kill site when compared to a kill site with an old carcass (Conclusion 1 from the Biological Background section). They also observed that the propensity of the hyenas for interspecific interactions with the lions increased with increasing prey size (Conclusion 2). The fitness boost from a successful mobbing had to be large enough to overcome the cost of injury or death while mobbing. In the experiments in this subsection, the freshness and the size of the prey were combined into one component, prey desirability. This component was represented by the mobbing reward in the simulations.

The simulated hyenas did not always behave in the same way as their real-life counterparts. If the initial mobbing reward was too low, the hyena team had a large overhead cost for evolving mobbing strategies and they simply avoided the lions altogether, preferring to collect the survival reward instead. On the other hand, if the initial mobbing reward was too high and the survival reward too low, they evolved successful mobbing behaviors that they could execute with minimal cost even if the mobbing reward decreased later in the experiment run.

The survival reward values for these experiments had to be chosen very carefully to come up with a situation where hyenas could dynamically choose to mob or avoid lions based on the prey desirability. Different values of survival reward were tested systematically with varying success. When the survival reward was 5 fitness points, there was a trend of successful mobbing probability increasing with increasing prey desirability (see Figure 10). This result is in line with Conclusions 1 and 2 from the Biological Background section.

Discussion and Future Work

The computational model developed in this work to study lion-hyena interactions used neural networks for the hyenas. One challenge was that neural networks do not fear the lions in the same way that real hyenas do. If they evolve a good mobbing strategy, they always use it. If the net return from mobbing is very low, they evolve to never mob the lions instead. In order to replicate mobbing behaviors from nature, various parameters such as mobbing and survival rewards, and probability of injury or death had to be fine-tuned very carefully and systematically. However, the resulting successful settings suggested principles that make such behaviors possible.

It can hence be concluded that mobbing can be success-

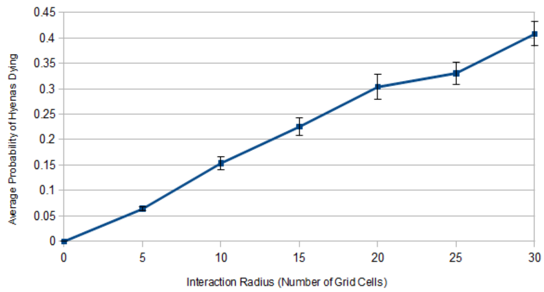

Figure 9: Hyena death probability comparisons when adult male lions are present. The x-axis shows the interaction radius, and the y-axis shows the probability of the hyenas dying, averaged over ten runs. The numbers of hyenas and lions were kept fixed at 10 and 1, respectively. The interaction radius was varied dynamically between 0 and 30 steps. The average death probability increased as the number of male lions increased, which is represented by increase in interaction radius.

ful without being counterproductive. Carefully coordinated mobbing leads to better overall fitness for hyenas because once they drive the lions away, there is no more danger. They also get a big fitness boost from eating the kill they wrested from the lions. These observations from computational simulation suggest that mobbing is possible and successful in specific circumstances, but not a very general and common ability. This may be the reason why mobbing is indeed rare, i.e. the spotted hyenas seem to do it, and not their closest relatives, the striped and brown hyenas.

The role of emotions such as fear and affiliation, as well the importance of individualistic traits in lion-mobbing has not been studied before. It is not clear exactly what information emotions provide to the hyenas and how they regulate behavior. As such, it is difficult to simulate emotion inputs to hyena neural networks. Similarly, a heterogeneous team will behave very differently from the homogeneous team employed in this work. The different roles of individual hyenas are hard to replicate in simulation when not much about these roles has been observed in nature. Therefore, computational modeling of emotions and individualistic traits in the context of lion-hyena interactions is still future work.

Conclusion

The computational model built in this paper was used to study lion-hyena interactions and the evolution of successful mobbing strategies. Several factors affected the evolution of realistic behaviors on the part of the hyenas, including interaction radius, mobbing reward, survival reward and reward from feeding on the kill gradually when mobbing has not occurred. In order to replicate frequent mobbing behaviors as seen in nature, the values of these factors had to be very

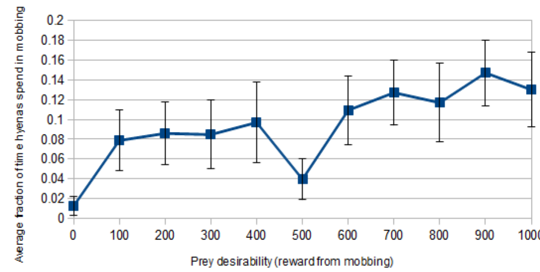

Figure 10: Successful mobbing probability comparisons for different prey desirability values. The x-axis shows the prey desirability value, which is equal to the mobbing reward, and the y-axis shows the mobbing probability, i.e. fraction of time the hyenas successfully mobbed the lion, averaged over ten runs. The survival reward was 5 points. The average mobbing probability showed a trend of increasing with increasing prey desirability.

carefully and systematically varied. From the simulation experiments in this work, it could be concluded that mobbing and interaction frequencies increased with increase in interaction radius, mobbing reward, and reward from feeding on kill gradually inside the interaction circle. These frequencies also increased when survival reward was reduced, and when mobbing and survival rewards were only given to survivors.

These parameters represented environmental factors in the real world that affect interspecific interaction probabilities and mobbing rates in hyenas. Out of the six conclusions from observational data listed in the Biological Background section, five were modeled successfully in simulation. The following are the conclusions that matched perfectly:

1. The probability of lion-hyena interaction increased with number of hyenas present. This result matches Conclusion 4.

2. Successful mobbing contributed positively to the overall fitness of the hyena team, although a fine balance of parameter values was necessary to bring about mobbing behaviors. This result matches Conclusion 6.

3. Interaction probability was higher when adult male lions were present, but the probability of death and injury for the hyenas was also greater. In simulation, the presence of male lions was represented by a larger interaction radius. This result matches Conclusion 3.

4. Interaction probability was higher when prey desirability was higher. In the computational model, prey desirability was represented by the mobbing reward. This result matches Conclusions 1 and 2.

Since the results discovered through simulation and those observed in nature were congruent, the computational model was deemed to be a faithful representation of real-life lion-hyena encounters. The next step then is to use this model to make predictions about hyenas in nature, which could be tested in the field in future. The behaviors simulated here can also be used to create complex cooperative behaviors in artificial agents in the future.

Acknowledgements

This research was supported in part by NSF grant DBI-0939454, and in part by NIH grant R01-GM105042.

References

Burrow, P. and Lucas, S. M. (2009). Evolution versus temporal difference learning for learning to play Ms. Pac-man. In *Proceedings of the IEEE Symposium on Computational Intelligence and Games (CIG 2009)*, pages 53–60.

Cooper, S. (1991). Optimal hunting group size: the need for lions to defend their kills against loss to spotted hyaenas. *African Journal of Ecology*, 29(2):130–136.

Dorigo, M., Maniezzo, V., and Colorni, A. (1996). Ant system: optimization by a colony of cooperating agents. *Systems, Man, and Cybernetics, Part B: Cybernetics, IEEE Transactions on*, 26(1):29–41.

Elliott, J. P. and Cowan, I. M. (1978). Territoriality, density, and prey of the lion in ngorongoro crater, tanzania. *Canadian Journal of Zoology*, 56(8):1726–1734.

Fairey, J. and Soule, T. (2014). Evolution of communication and cooperation. In *Proceedings of the 2014 conference on Genetic and evolutionary computation*, pages 169–176. ACM.

Hofer, H. and East, M. (1995). Population dynamics, population size, and the commuting system of serengeti spotted hyenas. *Serengeti II: dynamics, management, and conservation of an ecosystem*, 2:332.

Holekamp, K. E., Smale, L., Berg, R., and Cooper, S. M. (1997). Hunting rates and hunting success in the spotted hyena (crocuta crocuta). *Journal of Zoology*, 242(1):1–15.

Holekamp, K. E., Smith, J. E., Strelioff, C. C., Horn, R. C. V., and Watts, H. E. (2012). Society, demography and genetic structure in the spotted hyena. *Molec. Ecol.*, 21(3):613–632.

Kissui, B. M. and Packer, C. (2004). Top–down population regulation of a top predator: lions in the ngorongoro crater. *Proceedings of the Royal Society of London B: Biological Sciences*, 271(1550):1867–1874.

Kruuk, H. (1972). The spotted hyena: a study of predation and social behavior. *Wildlife Behavior and Ecology*, pages 315–325.

Kubota, N., Shimojima, K., and Fukuda, T. (1996). Virus-evolutionary genetic algorithm-coevolution of planar grid model. In *Fuzzy Systems, 1996., Proceedings of the Fifth IEEE International Conference on*, volume 1, pages 232–238. IEEE.

Lehmann, K. D. S., Montgomery, T. M., MacLachlan, S. M., Parker, J. M., Spagnuolo, O. S., VandeWetering, K. J., Bills, P. S., and Holekamp, K. E. (2016). Lions, hyenas and mobs (oh my!). *Current Zoology*.

Rajagopalan, P., Rawal, A., Miikkulainen, R., Wiseman, M. A., and Holekamp, K. E. (2011). The role of reward structure, coordination mechanism and net return in the evolution of cooperation. In *Proceedings of the IEEE Conference on Computational Intelligence and Games (CIG 2011)*, pages 258–265.

Rawal, A., Rajagopalan, P., and Miikkulainen, R. (2010). Constructing competitive and cooperative agent behavior using coevolution. In *Proceedings of the IEEE Conference on Computational Intelligence and Games (CIG 2010)*, pages 107–114.

Reynolds, C. W. (1987). Flocks, herds and schools: A distributed behavioral model. *ACM SIGGRAPH Computer Graphics*, 21(4):25–34.

Roeva, O., Pencheva, T., Tzonkov, S., Arndt, M., Hitzmann, B., Kleist, S., Miksch, G., Friehs, K., and Flaschel, E. (2007). Multiple model approach to modelling of escherichia coli fed-batch cultivation extracellular production of bacterial phytase. *Electronic Journal of Biotechnology*, 10(4):592–603.

Schrum, J. and Miikkulainen, R. (2014). Evolving multimodal behavior with modular neural networks in ms. pac-man. In *Proceedings of the Genetic and Evolutionary Computation Conference (GECCO 2014)*, pages 325–332. ACM.

Seno, H. (1990). A density-dependent diffusion model of shoaling of nesting fish. *Ecological Modelling*, 51(3):217–226.

Solomon, M., Soule, T., and Heckendorn, R. B. (2012). A comparison of a communication strategies in cooperative learning. In *Proceedings of the fourteenth international conference on Genetic and evolutionary computation conference*, pages 153–160. ACM.

Stanley, K. O. and Miikkulainen, R. (2002). Evolving neural networks through augmenting topologies. *Evolutionary Computation*, 10(2):99–127.

Trinkel, M. and Kastberger, G. (2005). Competitive interactions between spotted hyenas and lions in the etosha national park, namibia. *African Journal of Ecology*, 43(3):220–224.

Uchibe, E. and Asada, M. (2006). Incremental coevolution with competitive and cooperative tasks in a multirobot environment. *Proceedings of the IEEE*, 94(7):1412–1424.

Waibel, M., Floreano, D., Magnenat, S., and Keller, L. (2006). Division of labour and colony efficiency in social insects: effects of interactions between genetic architecture, colony kin structure and rate of perturbations. *Proceedings of the Royal Society B: Biological Sciences*, 273(1595):1815–1823.

Watts, H. and Holekamp, K. E. (2008). Interspecific competition influences reproduction in spotted hyenas. *Journal of Zoology*, 276(4):402–410.

Whiteson, S., Kohl, N., Miikkulainen, R., and Stone, P. (2005). Evolving soccer keepaway players through task decomposition. *Machine Learning*, 59(1-2):5–30.

Yong, C. H. and Miikkulainen, R. (2009). Coevolution of role-based cooperation in multiagent systems. *IEEE Transactions on Autonomous Mental Development*, 1(3):170–186.