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The Evolution of Coordinated Cooperative Behaviors

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The Evolution of Coordinated Cooperative Behaviors

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To my parents.

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The Evolution of Coordinated Cooperative Behaviors

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Cooperative behaviors are useful to many species of animals. Predators may team up to hunt large prey that they cannot catch on their own, while prey can herd together for defense. This dissertation focuses on understanding the environmental factors and cognitive architectures underlying the evolution of coordinated cooperation. An agent-based neuroevolutionary simulation of an ecosystem containing teams of predators and prey was built, modeling the environment of spotted hyenas. Communication, prey-capture rewards and reward-sharing strategies were found to determine whether cooperative hunting behaviors emerged. This simulation was extended to more complex cooperative behavior, that of coordinated mobbing. Through careful coordination, a large number of spotted hyenas can attack a group of lions and successfully steal a kill, even though lions are much stronger. The computational model developed in this dissertation helped understand how spotted hyenas are able to perform this complex cooperative task and how mobbing behaviors evolved. Many factors that were observed affecting lion-hyena interaction and rates of lion-mobbing in nature were also discovered using the model. This model was then used to make predictions about real-life hyena behaviors during mobbing events, which may be verified in the field in future. These results and predictions lead to general insights into how coor-

dinated cooperative behaviors arise in humans and animals. Such insights in turn should prove useful in building cognitive architectures and team strategies for artificial agents in the future.

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Chapter 1

Introduction

Animals, including humans, collaborate in nature to perform various tasks. Cooperative behaviors benefit the group by helping them achieve rewards that would not be possible for an individual to achieve alone. Predators cooperate to hunt prey that are stronger and faster than them, and prey may cooperate to defend themselves against predators (Packer and Ruttan, 1988; Penzhorn, 1984). For example, the spotted hyenas of Eastern Africa form teams to both hunt and to defend themselves (Holekamp et al., 2012). Developing simulations to study and replicate coordinated strategies observed in nature will help construct cooperative teams of robots and video game agents with complex behaviors in the future. These simulations can also be used to study how such such behaviors first emerged in animals and what factors influenced their evolution. The goal of this dissertation is to build such a computational model based on the hunting, social and lion-mobbing strategies of spotted hyenas (*Crocuta crocuta*).

1.1 Motivation

A major goal in AI is to develop intelligent behaviors that appear natural and believable. Extending complex cooperative animal interactions to, e.g., autonomous game playing agents or a team of robots is challenging. The approach taken in this dissertation is to draw motivation from nature in designing such behaviors.

In nature, animals may cooperate with their conspecifics (members of the same species) while simultaneously competing with conspecifics or other species for resources and territory. If this system can be modeled in simulation, then it can be used to create realistic non-player characters in video games that adapt quickly to match the abilities of human players. The emergence of simultaneous cooperative and competitive behaviors in teams of agents in a complex, dynamic environment is studied in Chapter 4. Competitive coevolution between teams leads to an arms race that, if sustained for a long time, produces innovative and sophisticated behaviors.

Hyenas generally hunt individually for small prey like gazelles, but once in a while, they team up to hunt larger prey. This kind of dynamic behavior-switching would be very useful for robotic teams that have to decide which of several different tasks require the most attention at any given point of time. The predator-prey environment is used in Chapter 5 to determine what environmental factors affect the evolution of cooperation and behavior-switching in the simulation of predatory behaviors of hyenas. One of the objectives was to discover the minimum amount of communication necessary to evolve cooperative hunting.

In order to use behaviors evolved for one task (domain-specific intelligence) to solve new problems, agents require domain-general intelligence. This general intelligence has been observed in several animals, but the factors affecting the extent to which general intelligence evolves in a species can be studied only in simulation, the development of which was the goal of Chapter 6. Such a simulation may also be able to help us understand the directions that evolution of intelligence will take in the future.

In addition to cooperative hunting, hyenas also participate in coordinated mobbing of lions, which is a sufficiently complex task that it indicates the emergence of near-general intelligence. Lions are larger and stronger than hyenas, and therefore the hyenas experience fear when facing lions. They need to cooperate in large numbers to overcome their fear and attack the lions. The computational model of lion-hyena interaction developed in Chapter 7 can help understand the evolution of mobbing behaviors. It may be used to evolve strategies in video game characters to overcome powerful adversaries or solve problems that involve high risk.

The roles of individual hyenas in lion-mobbing has not been studied in nature or in simulation, but it is clear that such individualistic traits play an important part in the precisely coordinated task. Modeling these traits in simulation helps understand the importance of different roles in cooperative robot teams and in video game characters. Furthermore, multiple emotions, such as fear and affiliation towards teammates, affect the willingness of hyenas to attack lions. Preliminary experiments were designed and run in Chapter 8 to analyze the contribution of individualistic traits and emotion inputs to the actions of the team as a whole. The cost of injury and death as an influence on mobbing and interaction rates was also tested in Chapter 8.

The work done in this dissertation will make it possible to evolve a cognitive architecture that is able to reproduce all the cooperative, complex behaviors exhibited by hyenas. In the future, it can be used to study what evolutionary stepping stones led to such behaviors and cognitive function in general. It can also be used to develop intelligent, adaptive video game characters or to build robotic teams that can coordinate their actions and cooperate to perform complex tasks.

1.2 Challenges

The components of successful cooperation are not easily discovered or analyzed. Primates exhibit many cooperative strategies, but they are hard to study because many of them are learned instead of being inborn or instinctive. Therefore, these behaviors are flexible and complex. On the other hand, less intelligent animals may not engage in sophisticated cooperative behaviors. Spotted hyenas are thus an appropriate species to study: even though their social and hunting behaviors are complex and cooperative, they are instinctive. They are less plastic than those of primates, and therefore easier to model (Holekamp et al., 2000; Holekamp, 2007).

In Chapter 4, a predator-prey system is built to study the emergence of simultaneous competition and cooperation in opposing teams. Existing neuroevolutionary techniques were found insufficient to sustain an arms race between predators and prey. A new neuroevolutionary architecture called Multi-Component ESP was developed to deal with this issue. It consists of multiple hierarchical layers of neurons and subnetworks, which in turn had to cooperate and compete in order to create the best neural networks for the task. The right network inputs and methods of communication necessary to evolve coordinated hunting strategies had to be discovered for this predator-prey simulation to work.

In order to evolve dynamic behavior-switching in simulated predators, Chapter 5 extended the previous predator-prey system to include different types of prey. The predators had to decide between hunting small prey individually or evolving cooperation to hunt larger prey as a team. The environmental constraints under which cooperation emerges in the predator team had to be discovered in order to apply this process to video game agents that can adapt to complex, dynamic environments.

Several animals possess general intelligence, which is the ability to use skills learned or evolved for other tasks to solve an entirely new problem. The study of the emergence of general intelligence is difficult because a simple task is initially needed. Neural networks should be evolved to perform this training task and then be introduced to a new task that is related to the first. Furthermore, the basic neural networks used in Chapter 6 had to be designed in such a way as to imitate the brains of real-life animals. To solve this problem, neural network connection densities were considered to represent the interactions among various brain processes in animals. The simple training task chosen was a handwritten digit recognition problem, which is a benchmark problem for neural networks.

A particularly challenging cooperative behavior that hyenas exhibit is lion mobbing. Lions are bigger and stronger than hyenas, but hyenas sometimes gather in large numbers and attack the lions, leading to the hyenas obtaining their kill. This behavior involves extreme risk for the hyenas and thus, it may be considered as evolutionarily complex and novel. The computational model developed in Chapter 7 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 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.

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, the different roles of individual hyenas are also hard to replicate in simulation when not much about these roles has been observed in nature. Preliminary experiments were designed in Chapter 8 to incorporate both emotions and individualistic traits. They did not result in realistic mobbing behaviors, so this aspect of the study is still future work.

1.3 Approach

Spotted hyenas are among the largest carnivores in Africa, and they live in large clans with complex hierarchical structure. A hyena typically hunts large prey like antelope on its own. Occasionally, however, hyenas team up to hunt prey like zebras, which are harder to catch because they defend themselves against predators. A clan may also fight for resources and territory with other hyena clans. A stronger and more united clan will win such fights and prosper.

The predator-prey task in Chapter 4 was set up on a toroidal grid environment with a team of predators and a team of prey. The agents cooperated within their teams, but competed across teams. Multi-Component ESP architecture was developed in order to control the predator and prey agents. This neuroevolutionary technique consisted of networks which had to cooperate to form a single agent. Teammates could not see one another but could see the members of the other team, and thus no communication was allowed among predators or prey.

Chapter 5 utilized the same toroidal grid environment and Multi-Component ESP architecture to investigate the factors affecting the evolution of cooperation within the predator team when given a choice between prey that must be caught using cooperative hunting and prey that can be caught individually. In this simulation, the prey did not evolve but had the fixed behavior of fleeing from the nearest approaching predator. This deterministic prey behavior helped in focusing on the evolution of cooperation in predators alone. The effects of reward structure, net return from capture of various kinds of prey, and coordination mechanism in predators were studied.

In animals, brain structure and interconnection between brain processes impact the development of different behaviors. van der Maas et al. (2006) hypothesizes that more interaction or interconnection among brain processes leads to more general intelligence. The emergence of general intelligence was simulated in Chapter 6 using neural networks with different connection densities, which represented interaction among brain processes. The training task was the recognition of handwritten digits along with their mirror images. Only the mirror images of digit 7 were withheld from the training set and were instead used in the test task. The neural networks should be able to use their knowledge of mirror images, gained from the training task, to recognize the mirror image of 7 correctly. The effects of different connection densities as well as those of prolonged evolution on the training task were studied.

A computational model was built in Chapter 7 to study lion-hyena interactions and the evolution of mobbing behaviors. The toroidal environment from Chapter 4 was reused, but the NEAT neuroevolutionary algorithm was used for the hyena agents. For each simulation, a single hyena was chosen from the population and cloned to form the team. Several environmental factors such as number of hyenas, number of lions, presence of adult male lions and prey size were varied and tested for any effects on mobbing rates and probability of interaction.

Chapter 8 also used the computational model developed in Chapter 7 to test the roles of individual hyenas. The hyenas most inclined to attack lions (aggressive hyenas) and those most likely to avoid the lions (diffident hyenas) were cloned and used in different proportions to form the hyena team. The second part of this chapter included simple fear and affiliation emotion inputs in addition to sensory inputs in hyena neural networks in order to discover the importance of emotions in mobbing.

1.4 Outline

This dissertation consisted of background and related work (Chapters 1-3), experiments and results (Chapters 4-8), and discussion and future work (Chapters 9-10).

Chapter 2 explores the biology behind the simulations in this dissertation. The observational and endocrinological data about spotted hyenas gathered by Dr. Holekamp and her colleagues is described in detail and the hypotheses behind cooperative hunting and mobbing are discussed.

Previous related work in computational modeling and neuroevolution is listed in Chapter 3.

The experiments in Chapter 4 simulating the predatory behavior of hyenas using neuroevolution showed that the hyena hunting team requires very little communication to coordinate its actions. The hyenas do not need to see or hear their teammates; they can navigate and perform their fixed actions just by watching the behavior of the prey (i.e. through stigmergy). A new neuroevolutionary architecture called Multi-Component ESP was developed in order to sustain competitive and cooperative coevolution in the predator and prey teams, leading to an extended arms race and the evolution of sophisticated behaviors.

In Chapter 5, the effects of different environmental factors on the dynamic behavior-switching of the predator team were studied. It was found that the reward structure, net return from prey and the coordination mechanism had significant impacts on the evolution of cooperation in team hunting.

The evolution of general intelligence was studied in simulation in Chapter 6. Increased neural network connection density was found to lead to the evolution of general intelligence for a simple handwritten digit recognition task. Prolonged evolution of neural networks past the point where their performance in a task plateaued was also found to have a positive impact.

A computational model was built in Chapter 7 to study lion-hyena interactions and the evolution of mobbing behaviors. Several environmental factors were discovered to affect mobbing rates and probability of interaction, including number of hyenas, number of lions, presence of adult male lions and prey size. These same conclusions were also drawn through observation of hyenas in nature.

Chapter 8 made some predictions about lion-hyena interactions using the computational model developed in Chapter 7. The first prediction was that a larger number of aggressive hyenas in the team led to increased interspecific interaction as well as higher rates of mobbing. The second was that as long as the emotions did not provide any extra information to the hyena that it could not get from sensory inputs, the frequencies of mobbing and interaction were not affected. This may change when sophisticated communication is introduced into the system.

Chapter 9 discusses the importance of the various projects explored in this work and the directions that future work may take, including the modeling of social structure of hyenas, the discovery of the stepping stones that led to the emergence of intelligence in hyenas, and the design of intelligent, adaptive video game characters and robot teams using the cognitive architecture built for hyenas.

Chapter 10 summarizes the contributions of this dissertation and presents the overall conclusion that the computational model built in this dissertation to study cooperative behaviors of hyenas is accurate and useful, and can be used to make predictions about lion-hyena interactions.

Chapter 2

Biological Background

Spotted hyenas have predominantly instinctive behaviors that are not very plastic when compared to those of primates. Most of these behaviors are specific to the challenges they face in everyday life and, therefore, are common to many predatory species in similar habitats. But coordinated mobbing of lions is a much more complex behavior than cooperative hunting, for instance, and can be considered a novel evolutionary step.

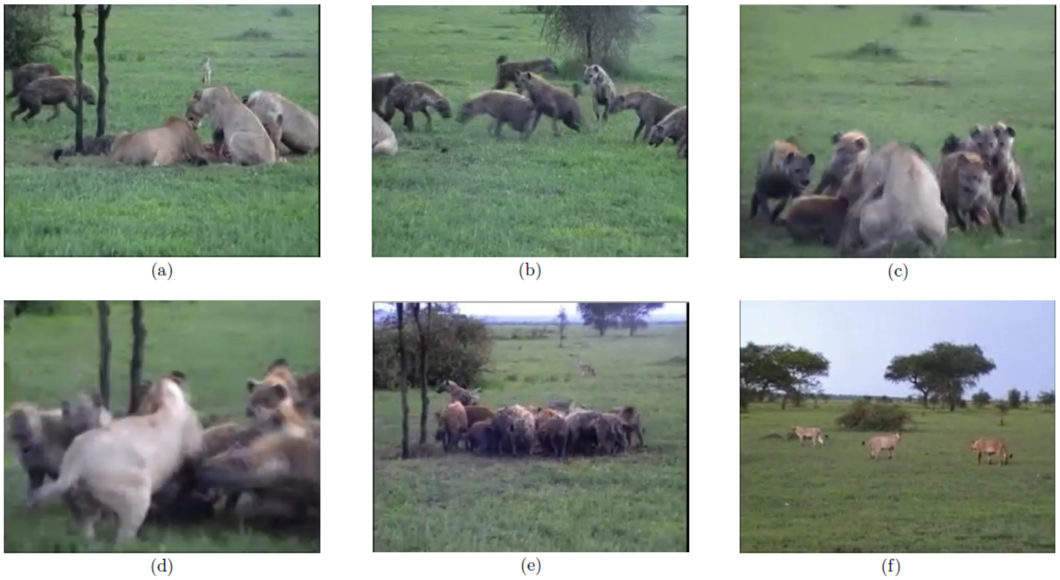
2.1 The Spotted Hyena

Spotted hyenas (*Crocuta crocuta*) are apex predators, and typically hunt small and large prey such as gazelles and wildebeest individually. However, they also sometimes demonstrate sophisticated team hunting behaviors, cooperating to hunt zebras (Holekamp et al., 1997; Kruuk, 1972). Zebras display aggressive antipredatory behaviors such as herding and kicking and, therefore, are rarely caught by a single hyena. The rewards from a team hunt are not distributed equally but depend upon the social rank of an individual. Hyenas may use vocal, visual and tactile signals to communicate during the hunt as well as during other social interactions (Kruuk, 1972; Henschel and Skinner, 1991; Holekamp et al., 2007; Mills, 1990), but they typically coordinate their hunting using stigmergy, or clues from the environment (Holekamp et al., 2000).

Hyenas live in matriarchical clans of up to 120 animals with several lineages (Kruuk, 1972; Holekamp and Smale, 1993; Engh et al., 2005; Holekamp et al., 2007). They have a hierarchical social structure where dominance is asserted not by strength, but through inherited social ranks. A hyena's rank within its clan is closely related to the rank of its mother and rarely changes during its lifetime (Holekamp and Smale, 1993). A higher social rank means more privileges including more food, better shelter, more offspring, etc. (Holekamp et al., 1996). As a result, low-ranked hyenas have to hunt far from the center of the clan territory to eat. Issuing a physical challenge to assert dominance is very rare; usually a low-ranked hyena will simply defer to its higher-ranked clanmates in all matters. It is not entirely clear how this ranking system evolved in hyenas or why it persists even while seeming counterproductive to the fitness of individual hyenas. One hypothesis is that the ranking system helps the hyena clan avoid internal struggles that would result in damage, and thereby stay strong in case there is a fight with another clan for resources and territory.

Hyenas share their habitats and resources with other powerful predators such as lions (*Panthera leo*). Because lions are larger and stronger, in any competition between hyenas and lions, lions are expected to win. However, large numbers of hyenas will occasionally gather to mob lions and drive them away in order to gain or retain control over a prey carcass (Watts and Holekamp, 2008). Mobbing refers to two or more hyenas coordinating a charge against one or more lions, and 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).

The mobbing scenario unfolds in the following manner (Figure 2.1). First, hyenas that are close to the lions (which possess the kill) start emitting loud whoop vocalizations that attract other hyenas to the scene. After sufficiently large numbers of hyenas converge



(a) (b) (c) (d) (e) (f)

Figure 2.1: **A typical sequence of events in coordinated mobbing behavior.** (a) A few hyenas circling the lions at a kill start vocalizing to attract other hyenas to the scene. (b) Once present in high enough numbers, the hyenas engage in affiliative behaviors: approach, greeting, low vocalizations. (c) Once sufficiently excited emotionally, the hyenas form a shoulder-to-shoulder mob, vocalizing loudly as they approach the lions. (d) The lions flee in response. (e) The vocalizations stop and the hyenas gain access to the kill. (f) The lions exit the scene and leave the kill to the hyenas. A two-minute video of this behavior is available at `http://nn.cs.utexas.edu/?LionsVsHyenas`.

to the spot and the right odds ratio for mobbing is reached, the hyenas begin communicating through sound, touch and greeting: low vocalizations, rubbing, moving towards the lions. Most of these behaviors are affiliative, forming a strong bond between them, and exciting them to act together. They coordinate arousal of multiple team members in preparation for an attack on the lions (Nocera and Ratcliffe, 2009; Replogle, 2011; Sumner, 1982; Wheatcroft and Price, 2008). Once a sufficiently high number of hyenas has reached this emotionally charged state, they mob the lions simultaneously, still vocalizing, chasing the lions away from the kill through an opening left for them (Figure 2.1). Once the lions flee, the scene becomes almost silent.

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). A lion-hyena encounter was said to have occurred when the hyenas and lions approached within 200 meters of one another, while a lion-hyena interaction occurred when they were within 10 meters of one another. 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). The conclusions they reached were:

1. Lions and hyenas interacted more frequently at fresh kill sites than at sites with carcasses older than 24 hours. Mobbing rates were also highest at a fresh kill. Mobbing could also occur at den sites to protect hyena cubs located there from the lions, but the frequency of mobbing at den sites was much lower than that at kill sites.
2. The probability of lion-hyena interaction 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. Male lions are more likely to initiate interaction by approaching the hyenas (Elliott and Cowan, 1978). However, they can also better protect the kill from hyenas because they are larger and stronger than female lions (Cooper, 1991; Kissui and Packer, 2004).
4. The probability of interaction increased as the number of hyenas present increased.
5. Local prey availability did not significantly impact the probability of interaction. Consequently, it could be concluded that lion-hyena interactions were independent of large-scale environmental factors and were more situational, i.e. they occurred whenever hyenas and lions were within sight of a kill.

6. Possession of the kill at the beginning of an interaction by a species was positively correlated with retention or acquisition of the kill at the end.
7. A successful lion-mobbing event could be predicted by an increase in the number of hyenas gathered on the scene.
8. 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.

Local prey availability was found not to affect the interaction and mobbing probabilities (Conclusion 5 above), and hence, was not modeled in the experiments in Chapter 7. This decision also allowed the experiments to focus more on the lion-mobbing behaviors than on hunting behaviors. Conclusion 6 refers to kills being in the possession of either hyenas or lions at the beginning of an encounter, but in this dissertation, the lions were always in possession of the kill at the beginning of each simulation. Mobbing behaviors are more interesting and complex when hyenas have to attack lions and obtain the kill from them. Conclusion 7 above states that a mobbing event was preceded by a sudden increase in the number of hyenas on the scene. Since extra hyenas could not be recruited to the scene in simulation, and all hyenas participating in mobs needed to be present in the environment from the beginning, this conclusion was not tested in the experiments in this dissertation. All the other conclusions from the observational data were tested in simulation in Chapter 7.

In addition to visual observations, Dr. Holekamp and her students also collected regular samples, including fecal samples from various hyenas at various times of the day. In the future, Dr. Holekamp's group plans to analyze these samples to measure the levels of three different steroid hormones: glucocorticoid stress hormones (GCs), testosterone (T), and Progesterone (PROG). These three hormones affect emotions in different ways. Risk-averse and fearful individuals are expected to have higher levels of GC than bold individuals

(Montoya et al., 2012; Cockrem, 2007; Koolhaas et al., 1999; Porges, 1997). In humans, higher levels of T have been found to correlate with willingness to take risks, (Stanton et al., 2011; Stenstrom et al., 2011). T has also been found to suppress affiliative emotions and social bonding (e.g. Mehta et al. (2009); Wingfield et al. (1990); Mehta and Josephs (2011). In contrast, PROG increases affiliation motivation and bonding with conspecifics (e.g. Brown et al. (2009); Wirth and Schultheiss (2006); Young and Insel (2002). Thus, individuals may be predisposed toward certain actions and emotions because of certain hormonal levels. These hormones and their effects are listed in Table 2.1.

For most hyenas participating in lion-hyena interactions, data documenting the baseline (mean long-term average) hormone concentrations exists already, based on the regular collection of fecal samples. Thus, hormone measurements provide a window to the emotions that the hyenas have experienced in the past about 24 hours. They will thus serve as an endocrinological verification of the theory of what emotions are involved in the lion-hyena interactions. It is possible that the degree to which each individual takes risks, engages in affiliative behaviors, and communicates could be predicted using its endocrinological profile. These traits may prove very important to the role of each hyena in a mobbing event. In the future, it may be possible to match the hyena's emotional state to observed levels of hormones once that data becomes available.

Mobbing behavior allows the hyenas to achieve a very difficult goal using a cooperative strategy. Hunting strategies of hyenas are typically coordinated through stigmergy (Holekamp et al., 2000). Mobbing of lions is thus a more complex task requiring more sophistication on the part of the hyenas than they ever display in their other behaviors. Communication and emotions play an important part in accomplishing this coordination. Previous computational work has shown that if emotions are not involved, a simulated hyena team needs a leader to make decisions during mobbing (Solomon et al., 2012; Fairey and Soule, 2014), but this result has not been verified in real-life hyenas. What role social ranks of hyenas play in this process, whether there is a leader, and whether experience and other

Hormone	**Effect on fear**	**Effect on affiliation**	**Effect on sensitivity to communication**	**Effect on actions**
Glucocorticoids (GC)	More fear, less risk-taking	Less affiliation and social bonding	Less sensitivity to communication signals	Retreat from lions
Testosterone (T)	Less fear, more boldness and risk-taking	Less affiliation and social bonding	Less sensitivity to communication signals	Approach the lions
Progesterone (PROG)	More fear, less risk-taking	Stronger affiliations and bonding	More sensitivity to communication signals	Cooperate with clanmates

Table 2.1: **The three steroid hormones being measured in hyenas and their effects.** The three hormones have a primary effect on two emotions: fear and affiliation to the team. These emotions then affect how sensitive the individual is to communication, and what actions it is likely to take.

individual differences matter are unknown at the moment, but are a subject of a parallel study conducted by Dr. Holekamp and her colleagues. Based on such detailed characterization of the behavior and its participants, the goal of this dissertation was to understand the cognitive processes that result in this behavior using a computational model to simulate lion-hyena interactions. Since mobbing frequency is higher at kill sites than at den sites, only kill sites were modeled in this work. The lions were always in possession of the kill at the beginning of every simulation, and all the hyenas necessary to form a mob were assumed to already be on the field since communication for recruiting hyenas from far away was not included in the computational model.

2.2 General Intelligence

When designing a cognitive architecture for a particular task, it is important to understand how different arrangements of modules within the brain affect the behaviors of the agent. Animals in their natural habitat face many different kinds of problems for which special abilities may be required. Indeed, all species exhibit specialized cognitive skills that are essential for their survival. These skills fall under the realm of *domain-specific intelligence*, and may be activated or inhibited by specific circumstances arising in the environment. Each ability is thought to be controlled by a particular module or area of the brain (Cosmides and Tooby, 2002). Thus, many animal species excel in solving certain problems, but not others.

In contrast to domain-specific intelligence, *domain-general intelligence* is the ability of an individual to solve new problems. Some animal species, for example, rodents (Matzel et al., 2011) and primates (Reader and Laland, 2002), possess an underlying cognitive mechanism that helps them with associative learning and general problem-solving. Evolutionary biologists and behavioral ecologists have posited that domain-general intelligence consists of several linked domain-specific abilities (Cosmides and Tooby, 2002). It has also been hypothesized that general intelligence emerged from domain-specific capabilities evolving under complex evolutionary pressures. Primatologists argue that these pressures were specifically the complex social structures and labile social interactions required of primates (Dunbar, 2003; Byrne and Whiten, 1989).

Primates are well known to be superior to most other animals in terms of behavioral flexibility and ability to solve problems (Byrne and Whiten, 1989; Tomasello and Call, 1997). Moreover, they live in structurally complex groups. Therefore, social cognition seems to be related to general intelligence, implying that all animal species that live in similarly large and complex societies should possess primate-like cognitive abilities. However, this prediction is not always true. For example, the societies of spotted hyenas (*Crocuta crocuta*) are remarkably like those of cercopithecine primates such as savanna baboons (*Papio anubis*) with respect to size, composition, structure, and patterns of competition and cooperation (Holekamp et al., 1999, 2012). A host of studies have found that spotted hyenas and baboons have converged with respect to social cognition (Holekamp et al., 2007; Benson-Amram et al., 2011), but there is no evidence that their domain-general intelligence has converged. This result indicates that there may be some fundamental differences in the way the brain structures and cognitive faculties of different species have evolved.

The cooperative hunting behaviors of spotted hyenas may be thought of as domain-specific abilities, because the hyenas have evolved to perform them. But their coordinated lion-mobbing strategy is much more sophisticated than anything else the hyenas (or similar predatory species) can do. This fact seems to suggest that although domain-general intelligence is typically required to perform such complex cooperative tasks in any other species, this collaborative behavior is instinctive rather than learned in spotted hyenas. Coordinated mobbing is an extraordinarily complex and novel step in their evolution, which makes it important to understand how it comes about in their cognitive architecture.

General intelligence is most apparent in humans. There is a significant positive correlation between abilities in various cognitive tasks (van der Maas et al., 2006): A good score on one cognitive test predicts good scores on all other cognitive tests. This empirical phenomenon is called the *positive manifold*, and it is unlikely to result from a strictly modular brain (Figure 2.2). There are many theories regarding the origin of the positive manifold (van der Maas et al., 2006). One hypothesis is that there must be a single underlying mechanism in the brain on which general intelligence depends (van der Maas et al., 2006; Sternberg and Grigorenko, 2002). This factor is commonly denoted as g (Figure 2.2a). Another general intelligence model is called *mutualism* (van der Maas et al., 2006). In this model, the positive manifold arises from the interaction of multiple cognitive processes in the brain (Figure 2.2b). The extended mutualism model (Figure 2.2c) posits that g itself arises from the interaction between several latent cognitive mechanisms in the brain. These latent variables then influence the outwardly manifest variables that constitute general intelligence (van der Maas et al., 2006).

In Chapter 6, the mutualism model of emergence of the positive manifold was tested using neural networks. The general intelligence of the agent controlled by the neural network increased with increasing number of links between neurons, and in prolonged evolution.

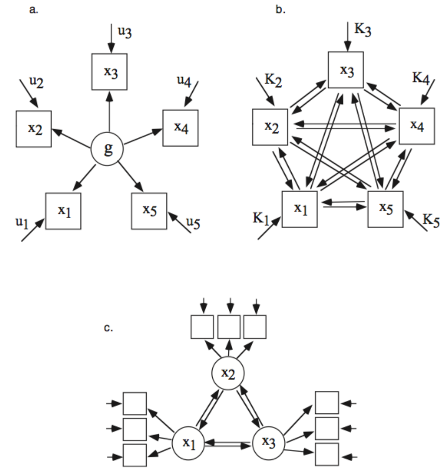


Figure 2.2: **Three models of the positive manifold.** (a) The standard *g* model, which shows the underlying *g* factor that influences all cognitive processes, (b) the mutualism model, showing the interaction between various mental mechanisms, and (c) the extended mutualism model, where only the latent processes interact. Squares and circles denote manifest and latent variables, respectively. Symbols x denote processes, u unique variances, and K resources (van der Maas et al., 2006). The mutualism model of the emergence of the positive manifold was tested and found viable in Chapter 6.

2.3 Conclusion

This chapter laid the foundation for all the simulations developed in later chapters. The spotted hyena is a truly unique animal which is on the brink of evolving general intelligence through the extremely complex task of lion-mobbing. The study of this cooperative task is very important and, therefore, a computational model was built for lion-hyena interactions. This model tried to replicate the hyena behaviors observed in the wild. Other cooperative behaviors such as team hunting were also simulated in this dissertation, and none of these experiments would have been possible without the biological base described in this chapter.

Chapter 3

Related Work

The predator-prey domain is a good abstraction for studying cooperation in nature. It can include multiple cooperating and competing agents that can be controlled in different ways. Neuroevolution is a learning algorithm that is commonly used for control tasks and open-ended problems. Thus, it is a good choice for the predator-prey domain as well. Each agent on the field is controlled by a neural network whose weights and topology are learned using evolutionary algorithms. If two or more agents are evolving at the same time, and interact with one another on the field, the process is called coevolution. Coevolution can lead to an arms race in competing agents, and collaborative behaviors in cooperating agents. These topics are reviewed in detail in this chapter.

3.1 The Predator-Prey Domain

A model of the cognitive architecture must be tested in a sufficiently complex environment. Since the hunting and lion-mobbing behaviors of hyenas are both complex in nature and possible to model through evolutionary algorithms, they are a good means to study evolution of cooperation. Therefore, the test environment should include multiple hyenas as well as other agents such as prey or lions. Such an environment can be formalized as the predator-prey domain.

In the predator-prey domain, predators chase and try to capture prey in a simulated environment. The domain is a special case of the well-known pursuit-evasion problem in mathematics and computer science. Pursuit-evasion problems are common in game agents. They pose a challenge for learning algorithms because the environment changes dynamically. The predator-prey domain is open-ended and requires continuous discovery of good behaviors on the part of both the predators and the prey. The agents in the simulation cannot adapt to this changing environment using a supervised training algorithm because the exact outcome of any single action of the agent is typically not known. The predator-prey domain can easily be extended to include multiple agents, teams of agents having similar goals and other more complex scenarios. Therefore predator-prey and pursuit-evasion tasks make a good testbed for many learning algorithms.

Predator-prey systems have previously been used to test existing learning algorithms and to construct new ones. These learning algorithms may then be used for problems in many different areas, such as video games, robot control and biological modeling. For example, Schrum and Miikkulainen (2014) used neuroevolution to create multimodal winning strategies for Ms.Pac-Man, where an agent takes on the role of both predator and prey at various points in the game. Similarly, Uchibe and Asada (2006) used genetic programming to control several soccer-playing robots. In chapter 7, the predator-prey domain was used to study the evolution of cooperation in hyena agents that are in a field with other agents such as prey and lions. The agent control method was based on neuroevolution, which will be discussed next.

3.2 Neuroevolution

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), robotic battle (Stanley and Miikkulainen, 2004) and Ms. Pac-Man (Burrow and Lucas, 2009; Schrum and Miikkulainen, 2014). Thus, neuroevolution is a natural choice for modeling the complex cooperative and competitive behaviors in teams of predators and prey.

Many different neuroevolution algorithms have been used for different tasks. The simplest algorithm consists of a fixed-structure network whose weights are evolved using a genetic algorithm. In this case, the chromosomes are strings of connection weights. Although this method works well in simple cases, it tends to lose diversity as the GA converges, encodes for the same solution in different ways (competing conventions), and requires too many parameters (connection weights) to be optimized simultaneously.

Enforced SubPopulations (ESP) is a more sophisticated neuroevolution method that is generally used to evolve fixed-structure two-layer networks and fully recurrent networks (Gomez and Miikkulainen, 1997). In ESP, it is not the string of connection weights that is evolved in a single population, but individual hidden neurons (a hidden neuron refers to a single node in the hidden layer of the neural network, or rather, a string of its incoming and outgoing connection weights). There is a separate population for each such hidden neuron and these populations all evolve in parallel. At the beginning of each generation, one neuron is selected from each population to construct the neural network. The resulting network is then evaluated and its fitness is equally distributed to its constituent neurons (Figure 3.1). This process is called a trial, and several trials may be conducted at every generation, picking a neuron at random from each population for each trial. If a specific neuron has undergone more than one trial, its fitnesses are averaged. Thus the ESP neuroevolutionary architecture itself is a good example of cooperative coevolution because the individual neurons are evolved to cooperate in order to form an efficient network. This process makes neuroevolution faster and more efficient, and helps establish cooperation among the components. The ESP algorithm preserves diversity (since a good network is made of

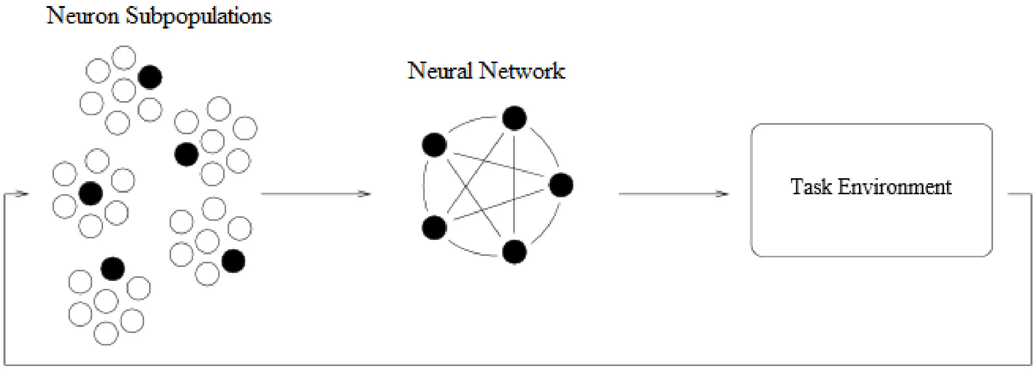


Figure 3.1: **The Enforced SubPopulations Method (ESP).** Each neuron is in its own subpopulation shown as clusters of circles. The network is constructed by selecting one neuron from each subpopulation at random. The fitness of the network in the task environment is then distributed equally to the neurons of which it is composed (Gomez and Miikkulainen, 1997). In this manner, neurons evolve to cooperate well in the network, resulting in an efficient search for a solution network.

several different types of neurons), avoids competing conventions by evolving each neuron separately, and divides the large search space into smaller subtasks, making it easier for evolution to discover optimal solutions. Other similar neuroevolution methods include the architecture used by Potter and De Jong (2000) for evolving subcomponents as a collection of cooperating species, SANE (Moriarty and Miikkulainen, 1996) for evolving neuron and network blueprints, and CoSyNE (Gomez et al., 2006) for evolving connection weights in separate populations.

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. NEAT includes mutations to add and delete both nodes and links. This technique was shown to be more effective than traditional neuroevolution methods that modify only the connection weights of neural networks (Stanley and Miikkulainen, 2002). To make crossover between two neural networks with different topologies possible, their links have to be lined up according to the nodes they connect. NEAT makes this lineup possible using a marker called a global innovation number that

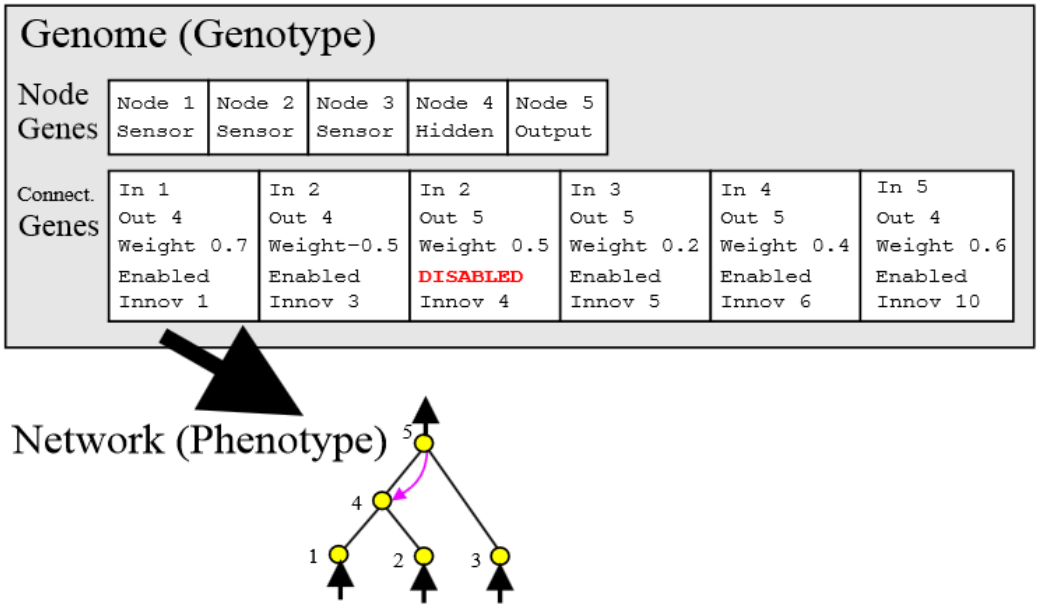


Figure 3.2: **A genotype to phenotype mapping in NeuroEvolution of Augmenting Topologies (NEAT).** There are three input nodes, one hidden, and one output node, and six connection definitions, one of which is recurrent. The third gene is disabled, so the connection that it specifies (between nodes 2 and 5) is not expressed in the phenotype (Stanley and Miikkulainen, 2002). NEAT allows the evolution of not only weights but also network topologies, which is necessary in many tasks.

records when each connection was formed in the population's history (Figure 3.2). Speciation is also used to nurture new innovations in network structure that might otherwise be lost due to their low initial fitnesses.

In Chapter 4, ESP was extended to the team level and shown to make predator-prey arms race possible. NEAT, in turn, was used in the general intelligence experiments that focused on network topology in Chapter 6. NEAT was also used in Chapter 7 and 8 when building a computational model to study lion-hyena interactions and mobbing events.

3.3 Coevolution

Since the goal of this dissertation was to study how various environmental factors and cognitive architectures affect the evolution of cooperation, two or more agents interact on the field at the same time. In the case of a hyena team hunting prey or interacting with lions, the prey or lion agents are also in the environment. The behaviors of these agents may be produced using a learning algorithm such as an evolutionary algorithm or reinforcement learning. When all these agents are evolved at the same time, they are said to be coevolved.

Coevolution is defined as the simultaneous evolution of two different populations whose fitnesses are measured based on their interactions with each other (Mitchell et al., 2006). In competitive coevolution, the two populations have opposing interests and the success of one population depends on the failure of the other. An arms race emerges as the coevolution progresses; each population evolves a little more at every step so as to defeat the other. Competitive coevolution is usually used to simulate the behavior of competing forces in nature, such as predators and prey. It can also be used as a method of improving the fitness of a single population by duplicating it and coevolving the two populations to outdo each other. After it was first described by Hillis (1990) as a host-parasite problem, competitive coevolution has been studied extensively by many researchers (Grefenstette and Daley, 1996; Mitchell, 2006; Mitchell et al., 2006; Pagie and Mitchell, 2002; Rosin and Belew, 1997). Mitchell (2006), in particular, compared competitive coevolution and plain evolutionary techniques. Competitive coevolution has many advantages: it does not get stuck at local optima as often, it can discover higher level strategies, it requires sparser training, and it preserves diversity over longer periods than regular evolution.

The arms race can be hard to sustain for extended periods because of three problems: over-specialization, red-queen dynamics and loss of gradients (Mitchell et al., 2006; Nolfi and Floreano, 1998). Over-specialization happens when the two competing populations learn to defeat each other easily but cannot generalize to new environments. Red-queen dynamics refers to stagnation caused by oscillation of the two populations among a set of states none of which is an improvement over another. Loss of gradients happens when evolution cannot proceed because all the population members are equally good at losing to or winning over members of the opposing population. Many attempts have been made to overcome these obstacles. For example, in spatial coevolution the hosts and parasites are distributed on a grid, and each of them interacts only with the hosts/parasites that are located close to it on the grid (Mitchell et al., 2006; Mitchell, 2006; Williams and Mitchell, 2005). Another way to avoid stagnation is to preserve the good behaviors of previous generations in an archive (often called Hall of Fame) so that diversity is not lost (Nolfi and Floreano, 1998; Rosin and Belew, 1997, 1995). Resource sharing, also known as competitive fitness sharing (Hillis, 1990; Pagie and Mitchell, 2002; Rosin and Belew, 1997), is another tactic where a population member is considered fitter if it defeats an opposing population member that few others have defeated.

In cooperative coevolution, different agents evolve to cooperate to perform a task. They share all the rewards and punishments of their individual actions equally. Cooperative coevolution is easier to achieve if the agents are components of the same system in which case they can learn different roles (Yong and Miikkulainen, 2009).

3.4 Modeling Cooperation

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 (Czirók and Vicsek, 2000; Reynolds, 1987; Seno, 1990). Cooperative behavior of micro-organisms like bacteria and viruses 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; Perez-Uribe et al., 2003; Waibel et al., 2006). For example, Perez-Uribe et al. (2003) studied the effects of group composition and level of selection in artificial ants. In general, ant-colony optimization (Dorigo et al., 1996; Iredi et al., 2001) is a probabilistic technique that can be used to model ants seeking shortest paths between their colony and a food source. At a higher level, the conflicting goals of individual versus team rewards were studied by Floreano and Keller (2009), focusing on the importance of relatedness (kin selection) in robotic agents.

Simultaneous cooperative and competitive coevolution was implemented in an experiment with soccer playing robots by Uchibe and Asada (2006). While they coevolved two cooperating players against one competing player, they did not simulate an environment comprising teams of agents. The multiple levels of cooperation and competition in teams of predators and prey would be closer to the complexity of such processes in nature. Furthermore, Uchibe and Asada (2006) used Genetic Programming to evolve decision trees for their agents but were not able to sustain an arms race. In contrast, neuroevolution was shown to previously support an arms race successfully in games (Stanley and Miikkulainen, 2004).

With the goal of understanding cooperation in predator-prey domains, Yong and Miikkulainen (2009) extended the ESP neuroevolution method to the level of networks (Figure 3.3). In their Multi-Agent ESP architecture, three neural networks were evolved in parallel to control three predators for the prey-capture task. These predators had to evolve to cooperate to capture a single non-evolving, fixed-behavior prey that none of them could catch on their own. Yong and Miikkulainen showed that this approach is more efficient than evolving a single central controller for all predators. Also, they found that cooperation is most efficient through role-based responses to the environment (i.e. through stigmergy), rather than direct communication between the agents.

In this dissertation, the Multi-Agent ESP architecture was further extended to include cooperative coevolution of subnetworks within an agent network. Multiple predator and prey agents were evaluated on the field to study simultaneous cooperative and competitive coevolution. In a separate experiment, the factors affecting the evolution of cooperative hunting were also analyzed. In addition, the evolution of general intelligence was studied

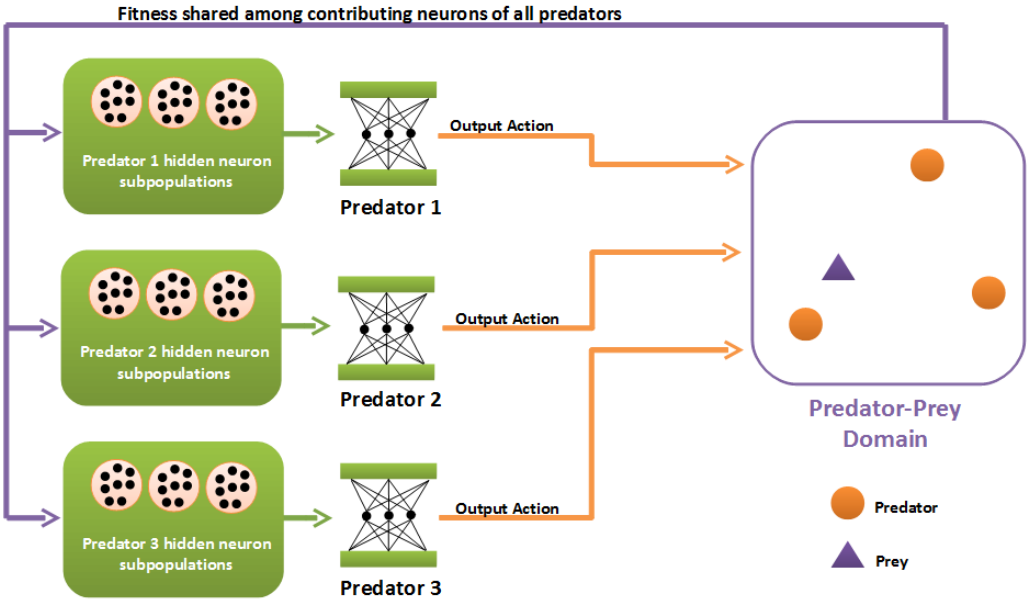


Figure 3.3: **Multi-Agent ESP architecture.** The circles are predators and the triangle is the prey. Each predator agent is controlled by a single neural network consisting of several hidden neurons. Each neuron in the hidden layer is drawn from its own subpopulation. Predator neural networks are evaluated in the domain at the same time, and fitness for the team is passed back to the participating neurons (Yong and Miikkulainen, 2009). This architecture leads to each agent evolving fixed roles as part of a coordinated strategy for the team.

using variations of the NEAT neuroevolution technique. NEAT was also used to model lion-hyena interactions and to study the evolution of lion-mobbing in hyenas. Although lion-mobbing has been simulated before in Solomon et al. (2012), that work studied the effect of different methods of communication and concluded that having a single leader to make all mobbing decisions for the hyena team resulted in the most effective coordination. In nature, however, the individual roles of different hyenas has not yet been studied, and hence the computational model developed in this dissertation involved identical hyena agents with no pre-assigned leader.

3.5 Conclusion

This chapter presented background material and previous work in the simulation of intelligent, adaptive agents participating in competitive and cooperative tasks. This body of related work will serve as the foundation for the development of the computational model to study the emergence of complex cooperative behaviors in this dissertation.

Chapter 4

Teams of Predators vs. Teams of Prey

The main goal of the experiments in this chapter was to sustain simultaneous cooperative and competitive coevolution in a complex environment that included teams of predators and prey. This first set of experiments extended the work of Yong and Miikkulainen (2009) to coevolution of predators and prey. One of the objectives was to understand how complex behaviors could evolve in such changing environments.

4.1 Hypotheses

In the simulation environment, a team of predators was placed opposite a team of prey. The predators had to cooperate to catch the prey, which required high-level cooperative strategies to evolve. Similarly, the prey could collaborate to evade the predators more effectively, for instance by fleeing in two opposite directions. In addition to cooperative behavior, predators and prey competed, and continually coevolved to exploit the weaknesses of each other.

The work in this chapter was previously published in Rawal, Aditya, Padmini Rajagopalan, and Risto Miikkulainen. "Constructing competitive and cooperative agent behavior using coevolution." In *Proceedings of the 2010 IEEE conference on computational intelligence and games*, pp. 107-114. IEEE, 2010. Aditya Rawal and I contributed equally to the conception of the research problem, experiment design and coding, analysis of results, and drafting of the paper. Risto Miikkulainen, our supervisor, advised us on research and revised the paper draft critically for important intellectual content.

Two hypotheses were tested in this chapter:

1. *Can an arms race be sustained in an environment with simultaneous cooperative and competitive coevolution?*

   Although it can be hard to sustain coevolution as discussed in Chapter 3, the predators and prey should not get stuck at local optima but continue to discover increasingly complex strategies to counter each other.

2. *Can cooperative and competitive behaviors like herding and baiting emerge in predators and prey in such conditions?*

   The predators need to cooperate and surround a prey before catching it. An interesting question is whether the predators can group or herd the prey together to make them all occupy the same position before catching them simultaneously. Similarly, the prey can cooperate to escape the predators by, for example, fleeing in two different directions.

4.2 Experimental Setup

The world in this simulation was a discrete toroidal environment with three evolving predators that tried to catch two evolving prey. The predators were aware of prey positions and the prey were aware of predator positions. However, there was no direct communication within the prey or predator team. The prey and predator agents all moved at the same speed and so the predators could not catch the prey if they used a greedy strategy of just following the prey around. A time limit was placed on the simulation to make sure that the predators did not keep moving at random and capture the prey by accident. Instead, they needed to surround the prey from different sides so that the prey did not have anywhere to escape.

Throughout the study, there were three predators that formed a team that had to cooperate to catch the prey. Each predator had as its inputs the *x*- and *y*-offset distances of all the prey from that predator. Similarly, each prey had as its inputs the *x*- and *y*-offset distances of all the predators from that prey. The output neurons represented different actions that a prey or predator agent could take. Each prey had only four possible output actions in each time step (move east, west, north, or south) and the predators had five (move east, west, north, south, or idle). To evolve blocking strategies in predators, the idle action was often important. The predator fitness was higher if a predator team caught both prey together rather than one by one. Such a fitness function encouraged herding of prey. The average distance of the predators from the prey was also included in the fitness function to help score predator teams that did not catch any prey. This fitness component discouraged random predator movements and provided a smooth gradient. More specifically,

$$Z_{\text{predator}} = \begin{cases} 25 & \text{if both prey caught,} \\ \\ \frac{20m}{n} + 2m + \frac{20d}{n} & \text{otherwise,} \end{cases}$$

where m was the number of prey caught, n was the total number of prey, and d was the normalized sum of distances from the predator to each of the prey at the end of the simulation.

Using a prey fitness function complementary to the predator fitness function (i.e the higher the predator fitness, the lower the prey fitness) (Hillis, 1990), did not result in good evasion strategies for prey. Instead, prey fitness was defined to be proportional to its lifespan. Even if one of the prey was captured, both prey were punished although less severely than if both were captured. If both prey survived until the end of the simulation, they were assigned the highest possible fitness. The simulation was limited to a maximum of 150 time steps so that the predators would have a finite amount of time in which to capture the prey. More specifically,

$$Z_{\text{prey}} = \begin{cases} 25 & \text{if neither prey caught,} \\ 12.5 & \text{if one prey caught,} \\ \frac{12.5\rho}{R} & \text{if both prey caught,} \end{cases}$$

where ρ was the number of time steps for which at least one prey remained alive, and R was the maximum possible number of time steps. The best predator and prey teams from each generation were saved in a Hall of Fame, and used during crossover in later generations.

The environment for the predator-prey tasks was a 100×100 toroid without any obstacles. The prey and predators could move in four directions: east, west, north and south. They moved one step at a time, and all the agents in the world took a step simultaneously. A predator was said to have caught a prey if it moved into the same location in the world as the prey at the same time. The following parameter settings were typically used: Each neural network was feedforward with a single layer of 10 hidden neurons and sigmoidal activation functions. Each subpopulation consisted of 100 neurons; each neuron (or a chromosome) was a concatenation of real-valued numbers representing full input and output connections of one hidden unit. During each evolutionary generation, 1,000 trials were run wherein the neurons were randomly chosen (with replacement) from their subpopulations to form a neural network. In each trial, the team was evaluated six times. The prey and predators started at random locations each time so that neither of them had an advantage over the other. The fitnesses over the six evaluations were averaged, and assigned to all the neurons that constituted the network. After the trials, the top 25% of neurons within each subpopulation were recombined using one-point crossover. The offspring replaced the bottom 50% of the neurons in the corresponding subpopulation, and they were then mutated with a probability of 0.4 on one randomly-chosen weight on each chromosome, by adding a Cauchy-distributed random value to it. Small changes to these parameters led to similar results.

4.3 Multi-Component ESP

In initial experiments, each prey and predator was controlled by a single neural network and fitness shared within a team through Multi-Agent ESP architecture (see Chapter 3). The experiment did not result in evolution of smart strategies on the part of predators. This outcome in turn implied that the prey were not required to learn any effective evasive behaviors. This stagnation seemed to result from overwhelming amounts of input information to each agent. However, just increasing the number of hidden neurons in each agent's neural network did not yield improved results. This outcome suggested that the components within the existing Multi-Agent ESP architecture (hidden neurons) were not able to effectively cooperate to decompose the task.

To solve this problem, a new neural network architecture was developed. Another hierarchical layer was added to the Multi-Agent ESP architecture bringing cooperatively coevolving components to the agent level. In this architecture, called Multi-Component ESP (Figure 4.1), each individual agent was split into multiple neural networks. Each component sensory neural network of a single predator agent had *x*- and *y*-offset distances of one prey as its input. The output values from each network of an agent were given as input to a combiner neural network. The outputs of the combiner network represented the confidence values of five possible predator actions. Similarly, each prey consisted of several component neural networks (one sensory network to track each predator, and one combiner network). Fitness was shared between the multiple neural networks within an agent through the Multi-Agent ESP architecture. At a higher level, each team of agents also shared fitness in a similar fashion. Thus there were multiple levels of coevolution in this neuroevolution technique: cooperative coevolution among the hidden neurons of each network, cooperative coevolution among the various networks of a single agent, cooperative coevolution among agents in a team, and competitive coevolution across teams.

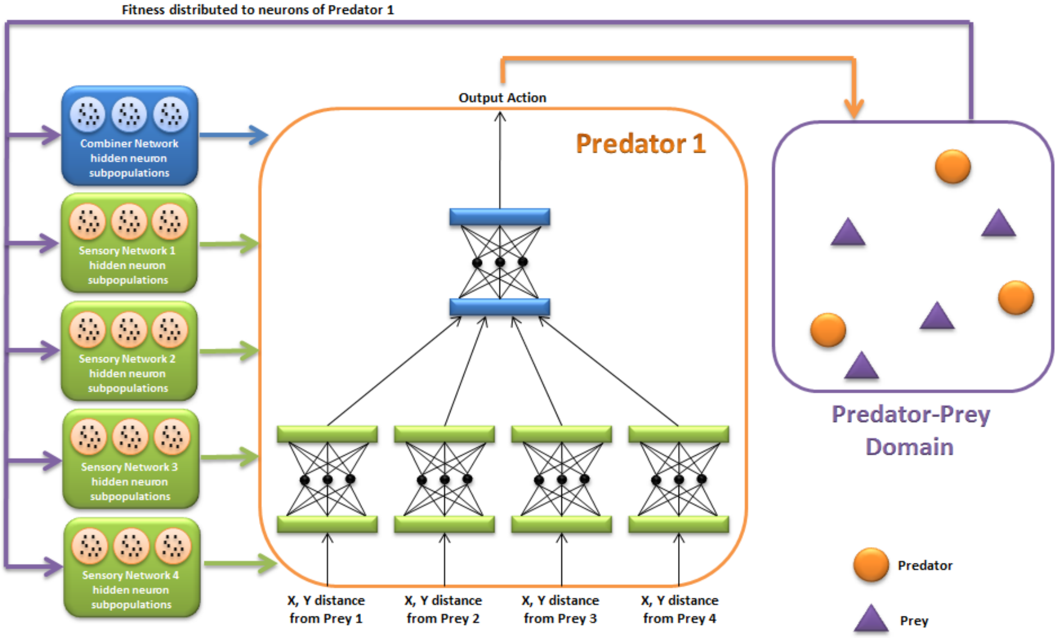
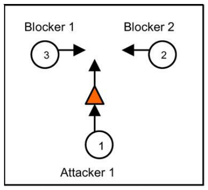


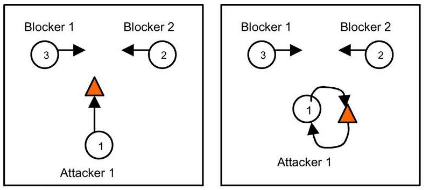
Figure 4.1: **Multi-Component ESP in the predator-prey domain for a predator agent.** A single predator agent is composed of five neural networks (a similar architecture can be used to implement a prey agent). Four of these sense the four prey agents. Their outputs are given to a fifth combiner network that outputs the next move for that predator. Each network is evolved in a separate ESP process, where one subpopulation is evolved for each of the neurons in the network. The predator is evaluated in the domain simulation with prey and other predator agents. Its fitness is distributed equally among all the networks and among all the neurons that participated in it. In this manner, evolution can discover neurons and networks that cooperate well to form an effective agent.

4.4 Results and Discussion

With this multi-component network architecture, coevolution was successfully sustained. The success rate of prey and predators alternated in cycles and new behaviors emerged in each phase (Figures 4.2, 4.3 and 4.4; Videos of these behaviors are at `nn.cs.utexas.edu/?armsrace`). In experiments with a single prey agent, initially in generations 50-75, the prey evolved only a greedy fleeing strategy, where it moved away from the closest approaching predator. Simple predator behavior was enough to catch the prey in this case. Two predators blocked the prey and the third approached it from the third direction (Figure 4.2: Phase 1, and Video 1). The success rate of the predators was high in this phase.

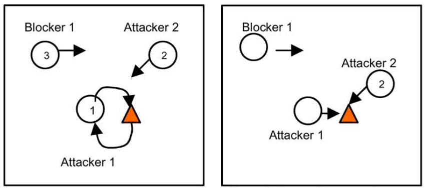


Phase 1, generations 50-75: Prey gets caught by Predators using simple strategy



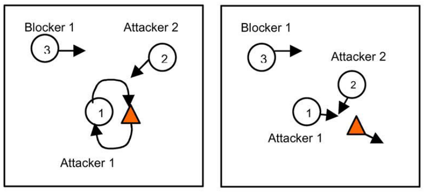
Phase 2, Frame 1, **generations 75-100**: Prey waits for Attacker 1 to come close

Phase 2, Frame 2, **generations 75-100**: Prey moves around by switching between fixed states



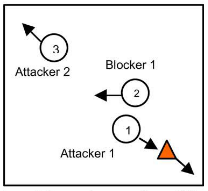
Phase 3, Frame 1, **generations 100-150**, Blocker 2 takes the role of attacker and move towards the prey

Phase 3, Frame 2, **generations 100-150**: Prey gets caught by two converging predators



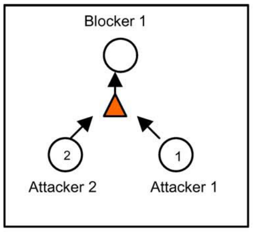
Phase 4, Frame 1, **generations 150-180**: Prey waits for Attacker 1 and 2 to converge

Phase 4, Frame 2 , **generations 150-180**: Prey moves away once the predators converge

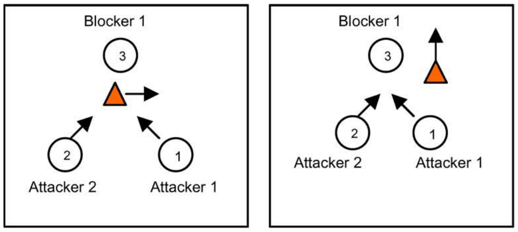


Phase 5, Frame 1, **generations 180-200**: Blocker 3 takes the role of Attacker 2 and Attacker2 becomes Blocker 1

Figure 4.2: **Arms Race in Team of Predators vs. Single Prey: Phases 1 to 5.** Each predator agent (circle) assumed the role of either an attacker or blocker. The role of an attacker was to chase the prey (triangle), while the blocker moved in a localized area to obstruct the prey's path. The predator-prey arms race emerged in phases. In phase 1, predators won using simple strategies, but phase 2 saw the prey evading the attacking predators by running in circles. In phase 3, two predators attacked the prey while the third acted as blocker. The prey evolved to flee the attacking predators in phase 4. The predator agents evolved to dynamically switch roles during a single run in order to counter this behavior of the prey in later generations (phase 5). The subsequent phases (6 to 9) are shown in Figure 4.4.

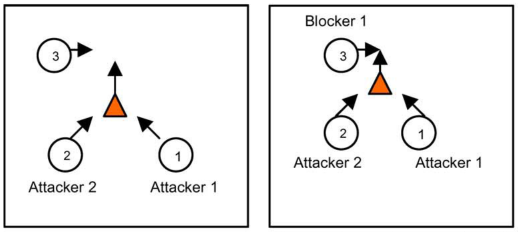


Phase 6, Frame 1, generations 200-250: Prey gets caught by Blocker 1 in its way



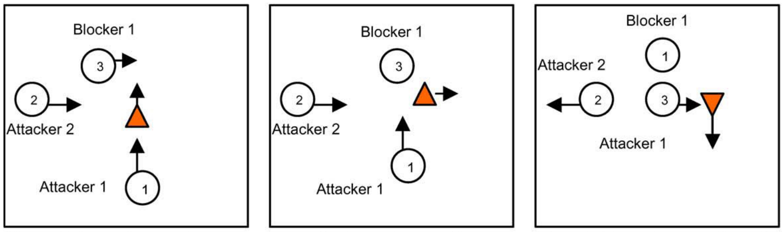
Phase 7, Frame 1, generations 250-300: Prey avoids the Blocker 1 by first making a move towards east (Sidestepping)

Phase 7, Frame 2, generations 250-300: Second, the prey goes around the Blocker 1 by moving north (Sidestepping)



Phase 8, Frame 1, generations 320-360: Blocker 1 positions itself away from the path of the prey, and approaches it by moving east

Phase 8, Frame 2, generations 320-360: Blocker 1 captures the Prey in its path



Phase 9, Frame 1, generations 400-450: Prey approaching the Blocker 1

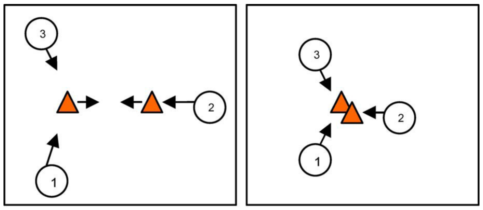
Phase 9, Frame 2, generations 400-450: Prey moves east to avoid Blocker 1

Phase 9, Frame 3, generations 400-450: Prey moves south to avoid Attacker 2 approaching from its right

Figure 4.3: **Arms Race in Team of Predators vs. Single Prey: Phases 6 to 9.** In phase 6, the prey was caught by two attackers and a blocker switching roles dynamically. The prey then evolved to sidestep the blocker in phase 7. To counter this behavior, the blocker stayed away from the prey, attacking it at the last moment (phase 8). In phase 9, the prey evolved to reverse its direction whenever an attacker moved directly towards it. Thus, the predator and prey agents kept evolving to defeat each other in turn, and an arms race emerged. Videos of these behaviors can be found at `nn.cs.utexas.edu/?armsrace`.

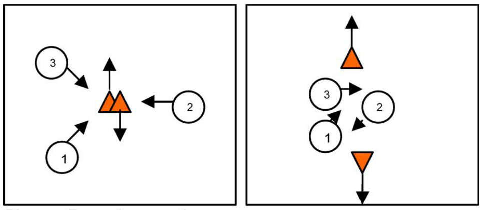
At generations 75-100, the prey evolved to selectively use the option of fleeing from the closest predator, and sometimes went around in a small circle with the closest predator on its tail (Figure 4.2: Phase 2 and Video 2). At this stage, the other predators too moved between fixed positions without making any new move to catch the prey because they were acting as blockers. The prey survived more often and therefore had high success rate in this phase. For generations 100-150, the predators learned to avoid this deadlock (Figure 4.2: Phase 3 and Video 3). Two of them now approached the prey from opposing directions (acting as attackers) and the third one assumed the role of blocking. The predators are more successful in this phase of the arms race. In the next phase (generations 150-180), the prey demonstrated intelligent baiting behavior by waiting for the two predators to converge towards it before moving away in a direction opposite to that of the predators (Figure 4.2: Phase 4 and Video 4). Since the third predator, the blocker, remained mostly stationary, the prey could easily dodge it. To counter this move, the predators learned to switch roles dynamically in generations 180-200 (Figure 4.2: Phase 5 and Video 5). The blocker also started to follow the prey when it tried to escape. In generations 200-250, the prey was captured often by two attackers and one blocker (Figure 4.3: Phase 6). In generations 250-300, the prey learned to avoid the blocker by sidestepping as it crossed the blocker's path (Figure 4.3: Phase 7 and Video 6). The blocker countered this action (in generations 320-360) by not blocking the path of the prey directly. It stayed a couple of steps away from the straight-line path of the prey and then moved towards it (in a direction perpendicular to the prey) as soon it came within a catchable distance (Figure 4.3: Phase 8 and Video 7). In the next phase (generations 400-450), the prey learned to reverse its direction so that it could avoid both the attackers and the blocker Figure 4.3: (Phase 9 and Video 8).

These observations demonstrated that the multi-component network architecture was successful in sustaining an arms race. This idea was next applied to teams of predator and prey agents to help sustain simultaneous cooperative and competitive coevolution. When coevolving three predators versus two prey, the scenario was more complex than that



Phase 3, **Frame 1**, **generations 150-200**: Predators surround the prey to herd them

Phase 3, **Frame 2**, **generations 150-200**: Prey are herded and caught simultaneously



Phase 4, **Frame 1**, **generations 250-300**: Prey bait the predators by first moving the close to each other

Phase 4, **Frame 2**, **generations 250-300**: Prey scatter in different directions to disturb predator group formation

Figure 4.4: **Arms Race in Team of Predators vs. Team of Prey.** In the beginning, predators and prey behaved very similarly to the ones in the previous experiment with a single prey. Later, predators started herding the two prey together before capturing them (phase 3). Prey then evolved to scatter at the last moment to escape the predator agents in phase 4. Thus arms race as well as cooperation within teams evolved in both predators and prey. Videos of these behaviors can be found at `nn.cs.utexas.edu/?armsrace`.

of a single evolving prey. There were multiple predators and prey on the field simultaneously and thus there were more factors that affected the evolution of both teams. The hierarchical structure of the Multi-Component ESP architecture made it possible to distribute roles effectively, which in turn allowed both populations to adapt to the continuously changing environment. The predators had to choose between two alternatives: catching the prey one by one or herding them together. Herding of prey is a complex behavior especially because the predators have to sacrifice the immediate gain of catching a single prey to achieve better efficiency by catching them together.

The coevolution of a team of three predators and a team of two prey was begun from scratch. In the beginning (generations 0-25, Phase 1) when predators had not yet learned high-level pursuit behaviors, they unsuccessfully attempted to herd the prey before capture. The prey easily evaded the predators during this time. At generations 25-50 (Phase 2), predators first attempted to herd the prey, but if their pursuit failed, they switched to catching the prey one at a time. At this point most of the behaviors observed in the single prey scenario (like dynamic role switching in predators and baiting by the prey) also evolved. At generations 150-200, predators were able to succeed in herding the prey and capturing them simultaneously (Figure 4.4: Phase 3 and Video 9). To counter herding (generations 250-320), the prey evolved to scatter in different directions just before the predators converged on them (Figure 4.4: Phase 4 and Video 10). One reason for this last-minute scattering could be that once the predators have almost converged, they are all roughly in the same location, making it easier for the prey to evade them. In this manner, behaviors coevolved in cycles, resulting in complex final behaviors for both predators and prey.

4.5 Conclusion

The experiments in this chapter showed that it was possible to sustain coevolution of teams of competing and cooperating agents. This result was made possible by a new architecture, Multi-Component ESP, that consists of cooperating components. The conclusion was that complex behaviors could emerge as a result of changing environments such as those provided by coevolution. In the next chapter, this architecture will be used to study the factors that affect whether cooperation emerges or not.

Chapter 5

The Role of Reward Structure, Coordination Mechanism and Net Return in the Evolution of Cooperation

The previous chapter showed that complex cooperative and competitive behaviors could emerge as a result of coevolution of teams of agents. In those experiments, cooperation always emerged within the team and competition across teams. But in nature, animals may sometimes compete with their groupmates and sometimes cooperate with them. As mentioned previously, spotted hyenas demonstrate sophisticated hunting behaviors, often catching prey such as antelope individually (competing with clanmates) and sometimes

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The work in this chapter was previously published in Rajagopalan, Padmini, Aditya Rawal, Risto Miikkulainen, Marc A. Wiseman, and Kay E. Holekamp. “The role of reward structure, coordination mechanism and net return in the evolution of cooperation.” In *Proceedings of the 2011 IEEE conference on computational intelligence and games*, pp. 258-265. IEEE, 2011. Aditya Rawal and I contributed equally to the conception of the research problem, experiment design and coding, analysis of results, and drafting of the paper. Risto Miikkulainen, our supervisor, and Kay Holekamp advised us on research and revised the paper draft critically for important intellectual content. Marc Wiseman analyzed biological data to characterize the behaviors of spotted hyenas, which provided ideas for our research.

coordinating to hunt zebras, which they cannot catch alone (cooperating with clanmates). The factors that lead to evolution of cooperation when it is not strictly necessary for survival need to be analyzed. This behavior-switching of hyenas offers a good domain for studying the constraints under which cooperation emerges in a team of simulated agents.

5.1 Experimental Setup

A team of predators (simulated hyenas) was evolved using cooperative coevolution to capture fixed-behavior prey. Multi-Component ESP was used as the neuroevolution technique for the predators. The predators were aware of prey positions and the prey are aware of predator positions. Direct communication among predators (in terms of knowledge of other predators' positions) was also introduced in some cases. In all other cases, the predator agents could sense only prey movements and had to use that to coordinate their actions through stigmergic communication. There was no direct communication among the prey. Each predator had as its inputs the *x*- and *y*-offsets of all the prey from that predator. In the case of communicating predators, they also got as input the *x*- and *y*-offsets to the other predators. When fitness rewards from prey capture were shared, all the predators gained fitness even when only one of them actually caught the prey. In cases with individual fitness, only the particular predator that captured the prey got the reward.

There were two types of prey in the environment: a smaller prey (gazelle) that moved with 0.75 times the speed of the predator and a larger prey (zebra) that had the same speed as the predator. The prey behaviors in these experiments were hard-coded and did not evolve. Each prey simply moved directly away from the current nearest predator. The predators could therefore catch the smaller prey individually, but could not catch the larger prey by just following the prey around, because their grid world was toroidal. The predators had to surround a zebra from different directions before they could catch it. In cases where both types of prey existed in the field simultaneously, the predators needed to decide whether to catch the small prey individually or to coordinate and hunt the larger prey together. The larger prey resulted in higher reward than the smaller prey, and the relative reward amounts could be varied.

5.2 Hypotheses

The following hypotheses about the evolution of cooperative behaviors in hyenas were tested in the simulations:

1. *Sharing the fitness reward is an incentive for the predators to cooperate.*

   If only the predator that catches a prey gets the reward, there is no reason for the other predators to help in the capture. If they all share the rewards, there is a benefit to cooperation, and it should emerge in evolution.

2. *If cooperation is easy to establish, e.g. through communication, it is more likely to emerge.*

   Evolving to cooperate just through stigmergy (sensing of clues from the environment) is a difficult task. If the predators can communicate directly (i.e. by sensing each others' positions), the cost of cooperation is significantly lower because it becomes easier for the predators to coordinate their actions. Cooperation is thus more likely to emerge.

3. *Evolution of cooperation depends on payoff upon prey capture.*

   Hyenas can both communicate and share fitness rewards, but they still typically hunt on their own. Perhaps the energy necessary to coordinate their hunting behaviors to catch larger prey is not off-set by the higher rewards they get upon catching it. If the reward was higher, cooperation would be more likely to emerge.

Expt. No.	**Reward Structure**	**Coordination Mechanism**	**Number of Prey**	**Reward for Catching Each Prey**	**Results**
1	Individual	Stigmergic	4 Zebras	150	Little cooperation, evolves slowly
2	Shared	Stigmergic	4 Zebras	150	Systematic cooperation, evolves early
3	Individual	Direct communication	4 Zebras	150	Improved cooperation, evolves gradually
4	Shared	Direct communication	4 Zebras	150	Effective, fast cooperation
5	Gazelle: Individual, Zebra: Shared	Direct communication	4 Gazelles, 1 Zebra	Gazelle: 100, Zebra: 150	Cooperation does not evolve, gazelle-hunting preferred
6	Gazelle: Individual, Zebra: Shared	Direct communication	4 Gazelles, 1 Zebra	Gazelle: 100, Zebra: 450	Cooperation evolves, zebra-hunting preferred

Table 5.1: **Setup and results of the experiments comparing the evolution of cooperation with different reward structures, coordination mechanisms and net returns from prey.**

5.3 Factors Affecting the Evolution of Cooperation

Three parameters were progressively modified in these experiments (Table 5.1): (1) whether only the individual actually catching the prey receives the fitness, or whether it is shared by all individuals, (2) whether the predators can observe one another or not (direct vs. stigmergic communication), and (3) the size of the fitness reward from catching a prey. These experiments were used to contrast the role of each of these parameters in the evolution of cooperation. The first experiment, i.e. the control experiment, included noncommunicating predators with individual fitness, and the goal was to catch more zebras. The second experiment added shared fitness rewards, while the third experiment added communication

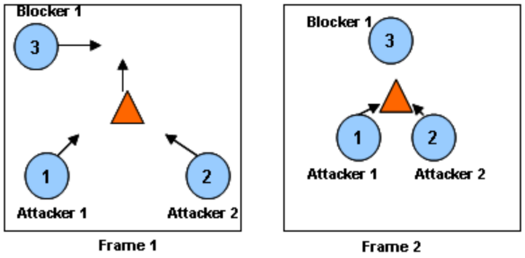

Figure 5.1: **Collaboration during a zebra hunt (frequently observed in Experiments 2, 3 and 4).** Two predators assume the role of attacker and chase the prey towards the third predator, which acts as blocker (Frame 1). They surround the prey from three directions and capture it (Frame 2). Videos of this behavior and those shown in Figures 5.2-5.4 are at `nn.cs.utexas.edu/?cooperation`.

instead. The predators in the fourth experiment both communicated and shared fitness rewards. The fifth and the sixth experiments included gazelles on the field and the size of the reward for catching them vs. zebras was varied.

In each study, there were three predators; the number of prey varied from experiment to experiment. In Experiments 1 through 4, there were four zebras, and each one gave a fitness of 150 points to each of the three predators upon capture. In Experiments 5 and 6, there were four gazelles and one zebra, and each gazelle gave a fitness of 100 to the predator that caught it. In Experiment 5, catching the zebra gave a reward of 150 points to each predator, while in Experiment 6, this reward was increased to 450 points. As before, the output neurons represented different actions that a predator agent could take. Each prey had four possible actions in each time step (move east, west, north, or south) and the predators had five (move east, west, north, south, or idle). The simulation setup was otherwise similar to that in the previous chapter.

5.4 Results and Discussion

Overall, the results showed that communication among the predators, reward distribution when a prey is caught, and net return from capturing a prey are important factors in the

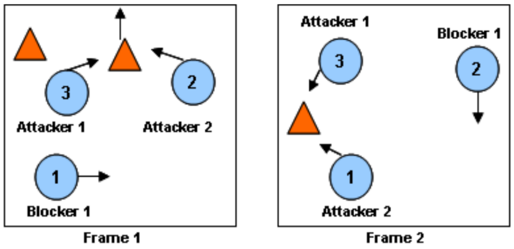

Figure 5.2: **Role switching between the hunting of two prey (Experiment 4).** The predators assume certain roles (attackers, blocker) while hunting a prey (Frame 1). These roles can change when hunting the next prey (Frame 2).

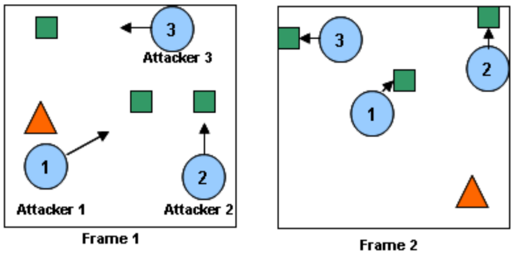

Figure 5.3: **No cooperation with low reward (Experiment 5).** When the net return from capturing a zebra is low, the predators prefer chasing the slower gazelles (depicted as squares; Frame 1). They successfully catch them on their own (Frame 2).

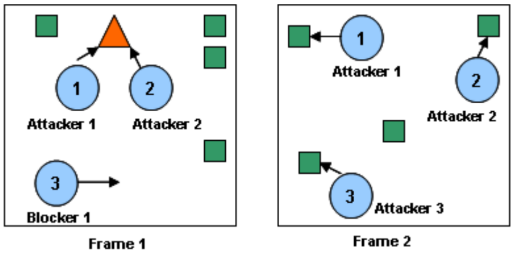

Figure 5.4: **Cooperation emerges with high enough reward (Experiment 6).** When the net return from capturing a zebra is high enough, the predators evolve to cooperatively hunt the zebra first (Frame 1). After the zebra is captured, they return to hunting gazelles individually (Frame 2).

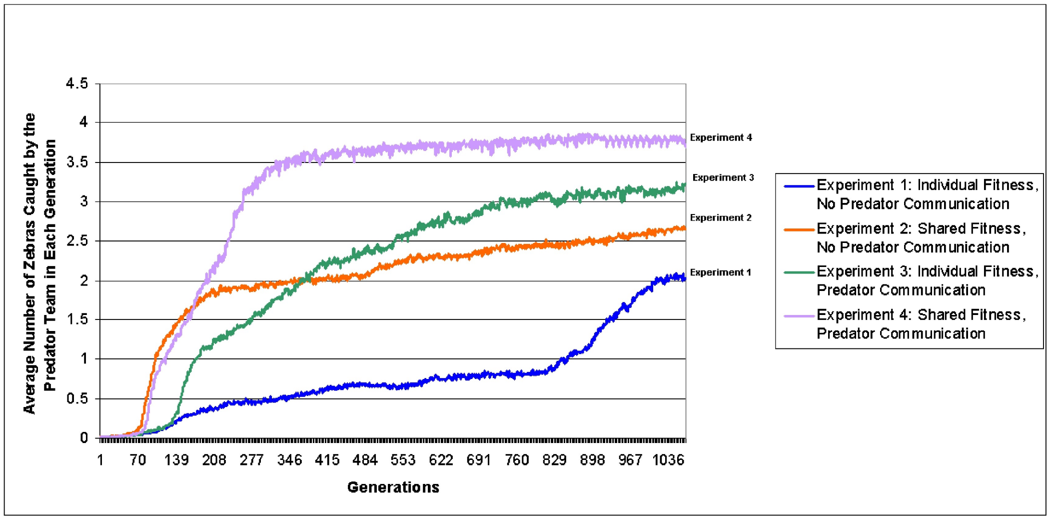

Figure 5.5: **Average number of prey (zebras) caught (out of four possible) in Experiments 1, 2, 3 and 4.** The total number of prey caught by the three predators was averaged over 6000 trials for each generation. Cooperation is slow to evolve with individual rewards and without communication, and is less efficient when it does (Experiment 1). Reward sharing results in faster and more effective evolution of cooperation (Experiment 2). Knowledge of positions of other predators makes it easier to evolve coordinated hunting strategies (Experiment 3). Evolution of cooperation is strongest when reward sharing and communication are combined (Experiment 4). These results show that communication and reward sharing are distinct but important factors that affect the evolution of cooperation in a team of predators.

evolution of coordinated hunting, as hypothesized (Figures 5.1 to 5.4; Table 5.1). Example videos of evolved behaviors are shown at `nn.cs.utexas.edu/?cooperation`. When the predators neither communicated nor shared fitness, they performed very poorly on the prey-capture task. Initially, they did not evolve to cooperate to catch the prey, and the prey easily eluded any individual predators. No predator knew where the other predators were, and there was no fitness incentive to cooperate when it sensed (through stigmergy) other predators hunting the same prey (Video 1). Eventually, the predators did evolve to coordinate through stigmergy, but this behavior was neither easy nor efficient. Once fitnesses were shared, the predators had a direct incentive to collaborate, and they quickly evolved specific roles to cooperate to catch the prey. These roles were rigid enough to not require communication. The predators acted like a well-trained team that knew exactly how each

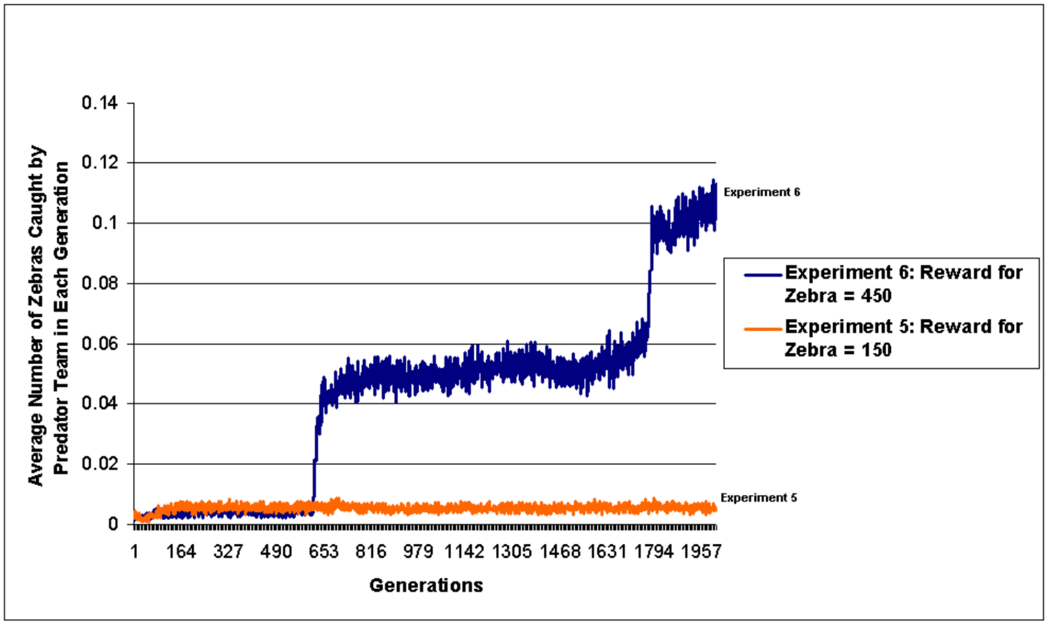

Figure 5.6: **Average number of zebras caught in Experiments 5 and 6.** The total number of prey (out of one possible) caught by the three predators was averaged over 6000 trials for each generation. When the payoff on capturing a zebra is low with respect to the difficulty of catching it (Experiment 5), the predators prefer to hunt the easy-to-catch gazelles individually. When the net return for capturing the zebra is high enough (Experiment 6), the predators evolve to discover cooperative strategies to hunt it. These results show that the net return from catching zebras should be high enough to overcome the cost of evolution of cooperation.

team member would behave in any given scenario: Usually one team member stayed in place while the other two chased the prey towards it (Figure 5.1, Video 2).

When comparing the control experiment to predators that could communicate, predators were again found to evolve cooperation much faster (Figure 5.1, Video 2). Communication makes it easier for a predator to sense what the other predators are doing and act accordingly, thus reducing the cost of evolving to cooperate. Further, as expected, evolution of cooperation was strongest in predators that both communicated and shared fitness rewards. While the non-communicating predators developed fixed roles, communication allowed them to adapt to the current situation (Yong and Miikkulainen, 2009). These predators also had more flexible behaviors, i.e. they could change roles in the middle of the hunt

(Figure 5.2, Video 3).

It is interesting to note that this result directly contradicts that of Yong and Miikkulainen (2009). They found that adding communication to predators that already shared fitness rewards made the evolution of cooperation more difficult and less robust; role-based cooperation based on stigmergy was more efficient. However, their experiment had only a single prey, which means the stigmergic signals based on its behavior are easy to interpret. All the predators attempted to capture the same prey, therefore the movements of this prey could be easily used to infer what the other prey are doing. In the above experiments, in contrast, all four prey responded to the three predators simultaneously, which made it hard to infer which ones were being closely chased and which ones were not. Such ambiguity made cooperative strategies harder to evolve, and very hard using stigmergy alone.

With two different types of prey, whether cooperation evolved or not depended on the value of the prey relative to the difficulty of catching it. When the zebra reward was not much higher than the gazelle reward, the predators did not evolve cooperation, preferring to catch gazelles on their own (Figure 5.3, Video 4). The reward for catching the zebra was much higher in Experiment 6, and the predators evolved to cooperate to catch it first (with some interference from nearby gazelles; Figure 5.6). Once the zebra was caught, the predators returned to hunting the gazelles individually (Figure 5.4, Video 5). Thus, increasing the net return on the zebra led to multiple (i.e. both individual and cooperative) hunting strategies in the predators. This result was important because it suggested that cooperative strategies include individual strategies as a special case. These results therefore showed how reward structure, coordination mechanism, and net return interact in producing cooperative behavior.

These simulations lead to insights into cooperation in nature. For instance, the predators in Experiment 3 (individual rewards with communication) evolved cooperative hunting strategies efficiently, but they did not have any fitness incentive for cooperation. Instead, they used one another to improve individual fitness. Is this real cooperation? In biological literature, a cooperator is defined as an individual who pays a cost for another individual to receive a benefit (Nowak, 2006). This is a useful working definition in artificial settings as well. Thus in Experiment 3, though not all the predators gained by coordinating their behaviors, they still cooperated.

Interestingly, a similar situation arises in spotted hyenas as well. As mentioned in Chapter 2, hyenas have a complex social structure that is based on hereditary social ranking (Holekamp et al., 2007). Higher-ranked hyenas have more offspring and are given a bigger share of the prey that is caught through cooperation. Rewards are thus not shared equally, but higher ranked hyenas use lower ranked hyenas to gain individual fitness.

5.5 Conclusion

The experiments in this chapter confirmed that predator coordination mechanism, reward structure, and net return on prey capture are important factors in the evolution of efficient cooperative hunting behaviors. When hyenas survive on gazelles, they do not need to cooperate. However, if the zebras are available and desirable enough, they will. These results are intuitive, but this is the first time easily replicable experiments were constructed to verify them. Therefore, they serve as a foundation for building more complex behaviors such as lion-mobbing.

Chapter 6

Evolution of General Intelligence

As stated in Chapter 2, brain structure and the interconnections between brain modules are important for the development of different behaviors. Spotted hyenas have evolved to hunt cooperatively, and this skill is a domain-specific ability. But cooperative lion-mobbing is a strategy that, while still evolved and not learned, is much more sophisticated and complex. Primates, which do exhibit such cooperative behaviors, require domain-general abilities to coordinate them. This fact seems to suggest that spotted hyenas are close to evolving general intelligence with coordinated mobbing as a sophisticated and complex behavior. Therefore, it is essential to understand how different cognitive architectures influence the evolution of such domain-general intelligence. This understanding will help in the design of a brain model for coordinated cooperative behaviors in Chapter 7.

The work in this chapter was previously published in Rajagopalan, Padmini, Kay E. Holekamp, and Risto Miikkulainen. "The Evolution of General Intelligence." In *Proceedings of the International Conference on the Simulation and Synthesis of Living Systems (ALIFE)*, pp. 63-70. 2014. I was responsible for the conception of the research problem, experiment design and coding, analysis of results, and drafting of the paper. Risto Miikkulainen, my supervisor, and Kay Holekamp advised me on research and revised the paper draft critically for important intellectual content.

6.1 Hypotheses

In the experiments in this chapter, neuroevolution was used to evaluate the theory of mutualism in the evolution of general intelligence (Figure 2.2). Neural networks represented the brains, and the neurons in them represented the cognitive mechanisms that interact to produce general intelligence. Experiments were set up to test the following hypotheses:

1. General intelligence should increase with the connection density.

Theories from differential psychology claim that more interaction between the various modules in the brain that have evolved for specific tasks results in higher domain-general intelligence (van der Maas et al., 2006). In the simulations in this chapter, a neural network with more connections between its neurons is expected to have perform better in the testing phase.

2. General intelligence should increase with extended evolution.

As stated in Chapter 2, performance in various cognitive tasks are found to be positively correlated with one another. If neural networks are evolved past the point where their performance in the known tasks has plateaued, they evolve to be more diverse, robust and efficient in these tasks (Watson et al., 2011; Lehman and Stanley, 2010). They are more resilient to changes in network function (such as mutations), and should be more resilient to changes in the input as well, and thereby more general. As a result, their performance in the testing phase should improve with prolonged evolution on the first task.

6.2 The Handwritten Digit Recognition Task

The recognition of handwritten digits, a well-known benchmark problem for neural networks, was chosen as the cognitive task, adapted for a test for domain-general intelligence. The inputs were not only the images of the digits, but also their mirror images. The mirror image of a single digit, 7, was left out of the set of inputs used during evolution and only used as a test input. The digit 7 was chosen for this purpose because the mirror image of

```
0 1 1 1 1 1 1 0
0 0 0 0 0 0 1 0
0 0 0 0 0 1 1 0
0 0 0 0 0 1 0 0
0 0 0 0 1 1 0 0
0 0 0 1 1 0 0 0
0 0 1 1 0 0 0 0
0 0 1 0 0 0 0 0
```

Figure 6.1: **Bitmap representation of a handwritten digit.** An example of the 8×8 bitmap encoding the image of a single digit, 7. The 1's represent black and the 0's represent white. This bitmap is concatenated into a 64-bit vector, which is given as input to the neural networks. Note that mirror images of the digits cannot be produced by interpolation between examples. Generalization to mirror images therefore requires higher level cognitive manipulation, which can be used as a test for general intelligence.

7 is not easily confused with other digits, and 7 is distinct from its mirror image (unlike 0, 1 or 8). If the neural network had evolved a general ability to recognize that some of its inputs were mirror images of other inputs, it should be able to recognize the previously unseen set of mirror images of digit 7 as well. Note that this level of general behavior is distinctly different from the usual generalization in neural networks, which is based on interpolation between known examples: mirror images do not result from interpolation, but from high-level cognitive manipulation. The performance during the testing phase is thus a good measure of the extent to which general intelligence has evolved in a neural network.

The handwritten digits were obtained from data stored in the NIST database. These images are taken from real-world data and therefore contain several noisy and distorted examples. The image of each digit was converted into an 8×8 bitmap representation, where 0 represents white and 1 represents black (Figure 6.1). The bits in the bitmap were then concatenated into a 64-bit vector, which was used as a single input to the neural network.

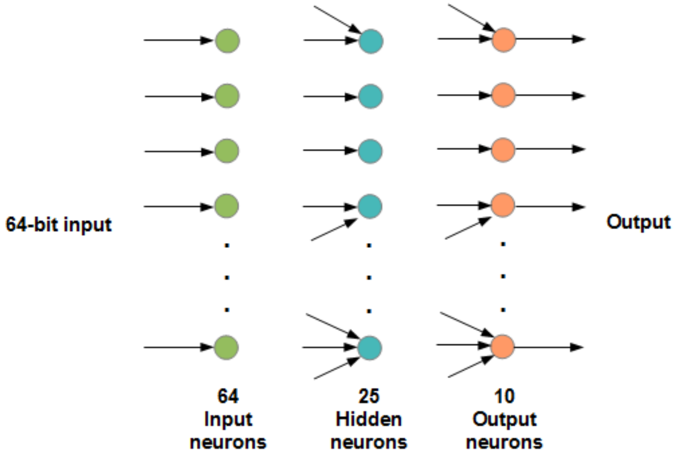

Figure 6.2: **The network topology for the handwritten digit recognition task.** There are 64 input nodes, 25 hidden neurons and ten output nodes. The connections between them are initially added at random based on the required connection density, but remain fixed thereafter. This more complex task and fixed-density architecture allowed testing the hypotheses about connectivity and prolonged evolution reliably.

Therefore, the neural networks in these experiments comprised 64 input nodes and 10 output nodes, representing a digit from 0 to 9. The digit corresponding to the node with the maximum value of output was considered the answer of the neural network to that particular input. The number of hidden neurons in each neural network was fixed at 25 (Figure 6.2). The number of distinct handwritten digit images shown to the networks during evolution was 5687, and the number of mirror images of 7 shown during the testing phase was 299. The fixed topology of the neural networks meant that the effect of connection density on the testing phase performance could be easily measured. The second hypothesis, that the extent of prolonged evolution influences test performance, could also be verified by varying the number of generations for which the neural network was evolved after it had already evolved to recognize the inputs shown during evolution.

6.3 Using NEAT to Evolve General Intelligence

The NEAT algorithm (Stanley and Miikkulainen, 2002) was used to evolve the neural networks. It is easy to manipulate the connectivity of networks in NEAT by changing the probability of adding new links, which made it a natural choice for this particular study. However, initial experiments showed that the topology-modifying capabilities of the NEAT algorithm resulted in final networks that were similar in connection density, despite having vastly different probabilities of adding links during evolution. Apparently, the NEAT algorithm is capable of adding links as needed for different network structures regardless of the probability of adding links. To avoid this problem, in the main experiments, the topologies of all the networks were fixed and only the connection weights were evolved. The networks had a single hidden layer with 25 neurons, and with sigmoidal activation functions. The connections were feed forward and selected randomly among the full set of connections with probabilities from 0.15 to 1.0. Twenty trials of each experiment were run for each population and their results were averaged. The connection density remained the same between trials, but the individual connections could be different. The population consisted of a single species of either 30 or 100 individual neural networks. This number and the number of species changed during the program's execution as part of the NEAT algorithm. Fitness was defined as the percentage of inputs for which the correct output was produced.

The results of these experiments are shown in Figures 6.3 and 6.4. As predicted, the test performance increased with increasing connection density of the neural network. After 65% density, however, the test performance started to decrease again. At the same time, the fitness on the training inputs also decreased, indicating that the decrease was not due to overfitting, but probably from the difficulty of evolving large numbers of connection weights.

In the prolonged evolution experiment, evolution was continued beyond the 100 generations needed for networks with the optimal connection density (65%) to learn the training inputs. During this time, there was no significant increase in fitness over the training

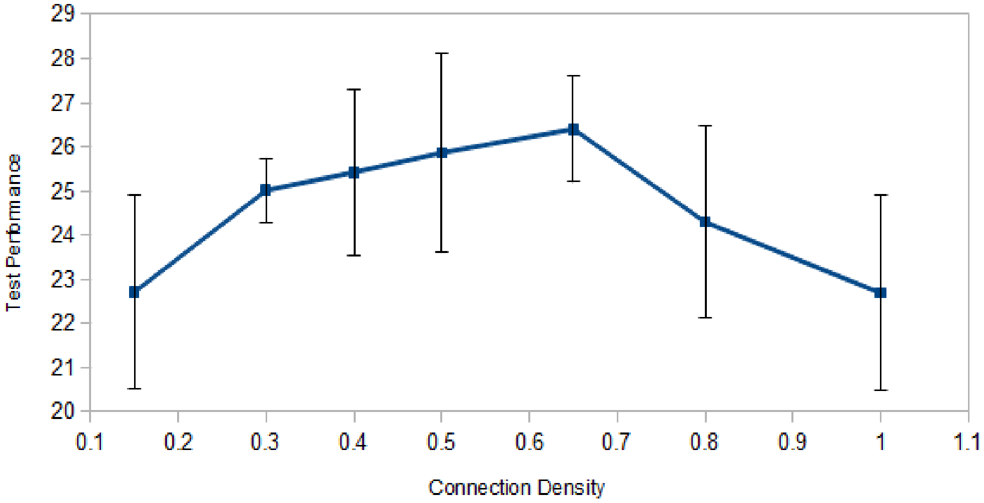

Figure 6.3: **The average performance on the test phase after evolving the network for 100 generations on the other inputs.** Connection density fraction is on the *x*-axis and percentage of test inputs (mirror images of digit 7) the neural network identified correctly on the *y*-axis. The performance increases with increased connectivity up to a point, indicating more general intelligence.

inputs. However, the performance on the mirror images of 7 increased significantly (Figure 6.4). Note that the fitness at point 0 on the *x*-axis, corresponding to 100 generations of evolution (i.e. the point where stagnation was just reached) is the same as the fitness for point 0.65 in the Figure 6.3. The same results were obtained with initial population sizes of both 30 and 100. Thus, these results confirm that both denser connectivity and prolonged evolution result in networks that implemented more general solutions.

6.4 Discussion

From a machine learning perspective, more connections in a neural network and prolonged training should result in overfitting, i.e. the network should not be able to generalize as well. It is interesting that the opposite effect is observed in these experiments: more connections and prolonged evolution results in more general behavior. The likely reason is that the task

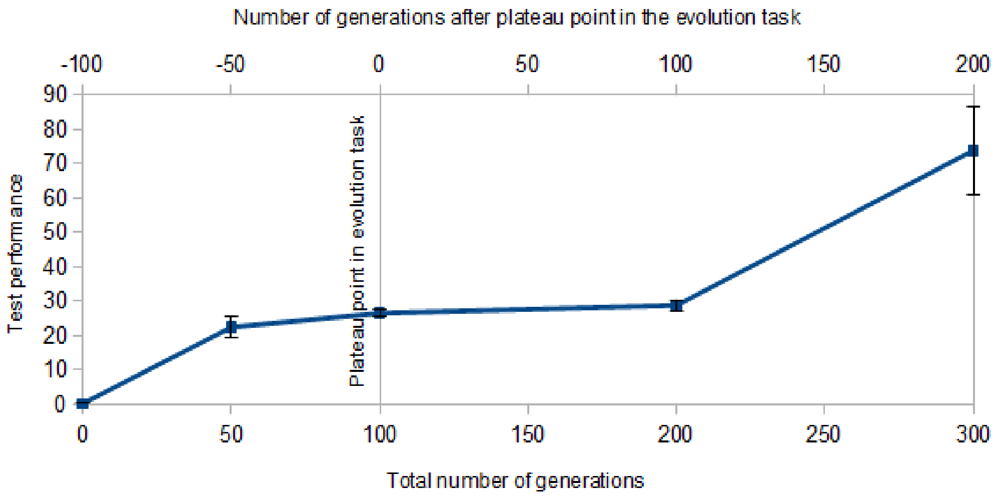

Figure 6.4: **The average test performance of neural networks with connection density 65% after evolution for 50, 100, 200, and 300 generations on the training inputs.** The training fitness usually plateaued at around 100 generations of evolution. The total number of generations is on the x-axis below the plot and the number of generations after fitness stagnation is on the x-axis above the plot. The percentage of test inputs the neural network identified correctly is on the y-axis. The performance on the test input increases with prolonged evolution, indicating more general intelligence.

in these experiments is not to simply interpolate between training examples (as is usually done in machine learning experiments), but to extend the behavior to a new class of examples. Such a task is cognitive, and indeed the result is different. Obviously the task is still limited and it is difficult to demonstrate extensive general intelligence in it. But the fundamental property of general intelligence is the ability use behaviors in a novel context, and thus it can be argued that the results indicate not just a generalization of neural networks, but the signature of general intelligence.

One significant insight gained from the above simulations is that the neural network architecture, the training algorithm, and the cognitive task employed to test general intelligence are all important. Further work is necessary to determine which combinations are most conducive to general intelligence. The main advantage of NEAT is that it evolves the neural network structure, but since it is the level of interaction between many specialized modules that is being studied, a fixed-structure neuroevolution algorithm such as Multi-Component ESP (Gomez and Miikkulainen, 1997; Rawal et al., 2010) may be more beneficial. Different subnetworks of the same network can be evolved to perform different tasks, and their interconnections can be varied while the whole network is tested on a new domain-general task.

6.5 Conclusion

The work in this chapter helped in understanding how a cognitive architecture for a task that is complex, involves cooperation, and requires general intelligence could be built. The interconnections between various brain modules can be varied in a systematic fashion to produce differences in the ability to perform such a task. Denser connectivity and prolonged evolution resulted in neural networks that implemented more general solutions and therefore, more general intelligence.

Chapter 7

Interspecific Competition Between Hyenas and Lions

To evolve complex cooperative behaviors, the right cognitive architecture needs to be designed and built for the agents. In Chapters 4 to 6, various cooperative behaviors such as team hunting and evasion were achieved with different neural network architectures. Changes in communication systems and differing rewards from prey were enough to sway the preferences of the hyena team from hunting individually to cooperative hunting. This behavior was still simple in that there was little cost to it. It becomes more complex when the individuals are initially adverse to doing it and have to be persuaded to participate by their teammates. A particularly challenging such behavior is lion mobbing, as was seen in Chapter 2.

There are, however, 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, and therefore, there is no way of knowing what steps it may take in the future. Any predictions about hyena behaviors are hard to make unless such a behavior has already been observed. These problems can be solved by developing a computational model that faithfully reproduces lion-hyena interactions and

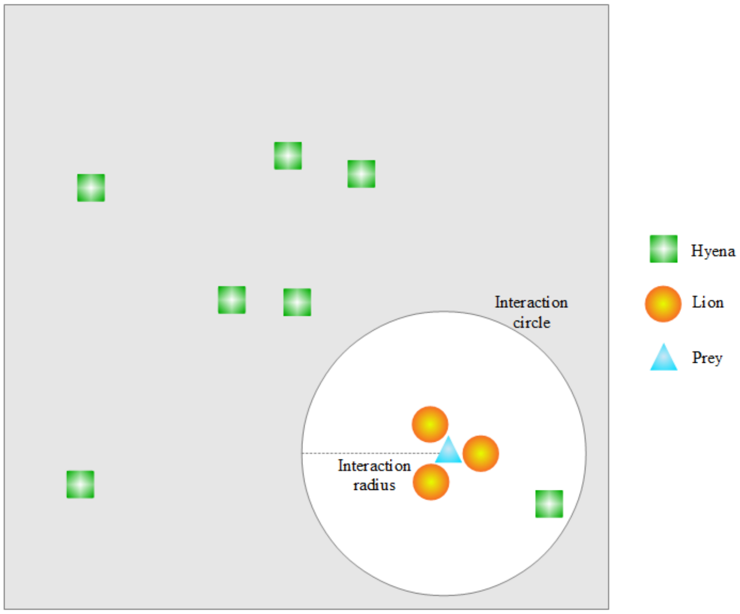

Figure 7.1: **The simulation environment with multiple hyenas and lions.** This figure shows a toroidal grid environment where a group of lions in possession of a kill is placed at a random location. The hyenas are also placed at random locations on the grid, but unlike the lions, they are mobile: They can move east, west, north or south. If a hyena enters the interaction circle, it may be killed. If a sufficiently large number of hyenas is within the interaction circle, they can mob the lions and drive them away from the kill. As in nature, the hyenas need to precisely coordinate their attack on the lions in order to conduct a successful mobbing event. Instead, if they approach the lions one by one, they will be killed.

mobbing behaviors from nature. It can then be used to study the evolution of such behaviors as well as to make predictions about them. The rest of this chapter describes how such a model was built and the results of experiments conducted using this model.

7.1 Experimental Setup

Hyenas lack a theory of mind (Holekamp et al., 2007), so cooperative mobbing strategies are likely not a result of rational thought or prior planning. Instead, they are instinctual behaviors, and therefore more fixed and predictable, and can be more easily studied than similar behaviors of more intelligent animals. Neuroevolution is therefore an appropriate method to model them: Behaviors emerge in neural networks that are evolved rather than trained during an individual's lifetime.

The predator-prey environment used in Chapters 4 and 5 was re-used for the lion-mobbing task (Figure 7.1). Thus, 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 lions was assumed to already be in possession of the kill. Therefore, they were fixed in place on the kill site. The lions did not evolve 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 approached the lions and moved closer than the interaction radius, it was said to be interacting with the lions. At this point, it could either be killed (according to the kill probability) or be joined by its teammates in a successful mobbing event. If the mobbing event failed, which could happen if there were fewer hyenas than four times the number of lions, all the hyenas that participated in the mob had a high probability of being killed. The goal of the simulated hyenas was to mob the lions with enough teammates to drive them away and obtain the kill for themselves. The lions were in possession of the kill at the outset and had a fixed position as well as behavior, which made it possible to focus the study on the evolution of hyena behaviors exclusively.

No conclusive data exists about individualistic behaviors of real-life hyenas, and these behaviors may depend on several factors such as social rank, current emotions and baseline hormone concentrations, whose modeling is outside the scope of this dissertation. Hence, in the experiments described in this chapter, all the hyenas on the field at a given time were assumed to react in exactly the same way to all external stimuli. To enforce this assumption, all the hyena agents in a team during a simulation were clones and, therefore, could not be evolved using Multi-Component ESP. Instead, they were evolved using the NEAT algorithm (Stanley and Miikkulainen, 2002) instead, which helped ensure diversity in the population. For each simulation, a hyena was picked from the population and cloned to create the team members. The fitnesses of all the clones were added up at the end of the simulation and assigned to that hyena. Each hyena neural network in the population was evaluated five times, and the fitness of the individual hyena was averaged across these five trials. Furthermore, each experiment was run ten times and the highest fitness attained at each generation, the probability of successful mobbing and the probability of lion-hyena interaction were averaged across these ten runs.

In the real world, a single lion can seriously harm or kill up to four hyenas and therefore a hyena:lion ratio of 4:1 is necessary for a successful mobbing event to take place (Kruuk, 1972), and this was another assumption built into the computational model. The kill probability depended on the number of hyenas and number of lions on the field, but it came into play only when a hyena got within a certain distance from the lions, the interaction radius. The hyena neural network, therefore, received as input the number of lions and hyenas as well as the distances of itself and all its teammates from the lion group.

Dr. Holekamp's group concluded that mobbing leads to better fitness for the hyenas (Lehmann et al., 2016). This conclusion was built into the model by assigning high fitness rewards to hyena teams that mobbed lions successfully. Since Lehmann et al. (2016) also found that local prey availability did not affect lion-hyena interaction or mobbing rates, no simulated gazelles were included in the environment for the hyenas to hunt directly, except in the preliminary experiments. Instead, a separate reward was given to those hyenas that survived until the end of the simulation regardless of whether they participated in a mobbing event. This reward represented the prey that real-life hyenas catch on their own regardless of whether they mob lions. However, they can only do that if they survive mobbing events. The survival reward also provided a fitness gradient for the evolution of the hyena neural networks.

In the following sections, several experiments were designed to build and test a computational model for lion-hyena interactions and lion-mobbing. The preliminary experiments had a basic environment where a few hyena agents had to choose between approaching lions and hunting gazelles. This environment was a simple extension of the task in Chapter 5, where the predator team had to choose between cooperating to hunt large prey or hunting small prey individually. In later experiments, representations of various parameters from the real world were gradually introduced and tested, including a kill probability that was based on the ratio of number of hyenas to number of lions, a mobbing reward, a fitness penalty for death or injury, and a survival reward that gave extra fitness to surviving hyenas.

7.2 Preliminary Experiments

In order to build the eventual computational model for simulating lion-hyena interactions and mobbing behaviors, some preliminary experiments were designed with simple neural networks. The hyenas in these experiments were stationary and had the simple decision of approach lions vs. hunt gazelles to make. No actual movement was undertaken by the hyena, and the simulation lasted for a single time step. These preliminary experiments helped determine the inputs and outputs that were most useful to the hyena neural network in order to make its decision regarding approaching lions.

7.2.1 Simplified Task with Single Time Step

In the preliminary experiments, the hyena neural networks were simple with no inputs at all except for a bias. The neural network had two output nodes, which represented the choice of hunting gazelles or approaching lions. The node with the higher output value was taken to be the choice that the hyena had made. The decisions made by the hyena were only symbolic because the hyena did not move around in the environment, but was rewarded immediately after it chose to hunt gazelles or approach lions; the simulation ended immediately after that. The reward for choosing to hunt gazelles was 100 fitness points. The kill probability, which applied only if the hyena decided to approach the kill site, was systematically varied from 0.1 to 0.9 in increments of 0.1. If the hyena did not die after having chosen to approach the kill site, it received a small reward that represented its feeding on the kill. This reward was varied from 100 to 1000 points in 100-point increments in different experiments. In contrast, if a hyena died, its fitness was decreased by 10,000 points. This simulation always consisted of a single time step. Since the environment did not vary during a simulation, each hyena individual from the population was only tested once in each generation. Running multiple trials did not lead to different results.

Thus, there were 90 experiments with different rewards from feeding on kill and different kill probabilities. Each of these 90 experiments was run 10 times and the final fitnesses averaged over these 10 runs. The reward from feeding on kill and the kill probability did not vary within a single experiment run. The average probabilities with which the hyenas chose to approach the lions or hunt gazelles in each experiment were recorded. As expected, if the reward from feeding on the kill was higher than that from gazelle-hunting, and the kill probability was low, the hyenas chose to approach lions more frequently. This frequency decreased with decreasing reward from feeding on kill as well as with increase in kill probability.

7.2.2 Mobbing vs. Individual Hunting

In this subsection, the environment was extended to include mobile hyena and prey agents. Four clones of the hyena chosen from the population each time were placed at random locations in the environment. There were also four gazelles that had the fixed behavior of moving directly away from the nearest hyena, and one stationary kill site that represented lions feeding on a kill. The kill was a larger prey, and it gave more reward than a gazelle. The neural network representing each hyena received as input its x- and y-offsets from each of the gazelles and the other hyenas on the field. It also received the x- and y-offsets from the kill site at each time step.

The interaction radius was five steps and the kill probability was 0 or 1, depending on the number of hyenas within the interaction circle. If the number of hyenas within the interaction radius was less than necessary for a mob (the *mob minimum*), they were killed instantaneously. The hyena team was given a fitness penalty of $-10,000$ points and the simulation was terminated. In contrast, if the number of hyenas moving into the interaction circle simultaneously was sufficiently high (i.e. more than the mob minimum), they were considered to have successfully mobbed the lions, and thus received a reward of 10,000 points. The simulation did not stop at this point, so that they could continue to hunt gazelles. Each gazelle gave a fitness of 100 points when caught, which was again shared by the cloned hyenas. The simulation lasted for 500 time steps unless prematurely terminated by a hyena death.

The results from these experiments showed that the highest average fitness achieved decreased with increasing number of hyenas needed to form a mob (Figure 7.2). There was greater overhead involved in evolving more hyenas to attack the lions simultaneously. Any accidental approach of fewer hyenas at the kill site caused them to lose fitness and the simulation to be stopped instantly. In contrast, when the mob minimum was just two, the other two hyenas could continue hunting gazelles. There was also a lower probability of the hyenas getting killed if fewer of them needed to be within the interaction circle, thus leading to higher fitness.

7.3 Using a Computational Model to Characterize Lion-Hyena Interactions

The preliminary experiments in the previous section were a good foundation for building a computational model to study lion-hyena interactions and the evolution of successful mobbing behaviors. However, since the tasks in those experiments were simple, the model is not yet very realistic in its portrayal of hyenas. This section expands the previous experiments to include more features from nature, including tracking distances of hyenas from lions, having kill probability be dependent on the ratio of number of hyenas to number of lions and having more hyenas in the environment than just four. The various parameters

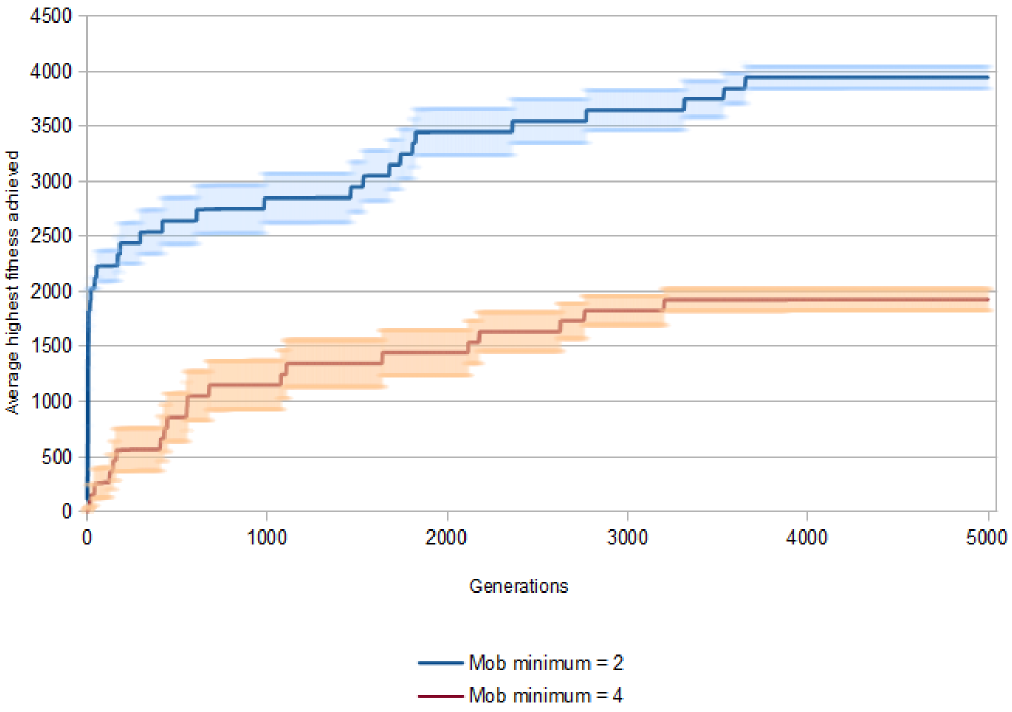

Figure 7.2: **Average highest fitness attained at each generation with two different mob minimums.** The *x*-axis on this graph is the number of generations for which the experiments were run and the *y*-axis represents the highest fitness attained by any individual so far, averaged over 20 runs. The mob minimum for the first experiment was two, while the mob minimum for the second experiment was four, which was equal to the number of hyenas on the field. The average highest fitness achieved, plotted here with transparent error bars, was significantly higher when mob minimum was lower. This result shows that mobbing behaviors are easier to evolve when the mob minimum is lower because it requires less precise coordination and presents a smaller overhead.

were carefully and systematically tested in order to reproduce the hyena behaviors seen in nature. The goal was to match the empirical characterization of behaviors reviewed in Chapter 2. To recap, the following were the conclusions from observational data as stated in Lehmann et al. (2016):

1. Interaction frequency was higher at fresh kill sites.

2. Interaction probability increased with increasing prey size.

3. Presence of male lions increased the interaction probability but also increased the number of hyena deaths.
4. Interaction probability increased with increasing number of hyenas.
5. Local prey availability did not significantly impact the probability of interaction.
6. Possession of kill at the beginning of an interaction was positively correlated with retention or acquisition of the kill at the end.
7. A successful lion-mobbing event could be predicted by an increase in the number of hyenas gathered on the scene.
8. 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.

Subsections 7.3.1 and 7.3.2 describe exploratory experiments with stationary hyenas in single-time-step simulations that were used to determine whether the hyena neural network could evolve to discover the kill probability using the number of lions, the number of hyenas and the distances of all hyenas from the lions. The experiments in Subsection 7.3.3 aimed to match Conclusion 4 from Chapter 2, i.e. that interaction probability increases with increasing number of hyenas. Subsection 7.3.4 explored the parameter changes necessary to bring about successful mobbing behaviors that could be productive to the hyena team (Conclusion 8 from Chapter 2), and thus helped gain insight into the environmental factors that affect mobbing. Conclusion 3 from Chapter 2 states that the presence of adult male lions increase interaction probability and hyena death probability, and this conclusion was verified in simulation in Subsection 7.3.5. Prey freshness and prey size from Conclusions 1 and 2 were combined into a single factor, prey desirability. In Subsection 7.3.6, prey desirability was shown to affect interaction probability, just as in nature. According to Conclusion 5 from Chapter 2, local prey availability does not affect interaction rates, and therefore, this conclusion was not modeled in simulation. Instead, a small reward was given to all hyenas at the end of each simulation, which represented a gazelle-hunting reward. Conclusions 6 and 7 were also not modeled in this dissertation; instead, lions were always placed in possession of the kill at the beginning of each simulation, and all the hyenas required to form a mob were already present in the environment.

7.3.1 Large Numbers of Hyenas in the Environment

There were only four hyenas at any given time on the field in the preliminary experiments from the previous subsection. Each hyena tracked the distances of itself in both x- and y-directions from all the other hyenas, the four gazelles and the group of lions at the kill site. In nature, a lion should be able to fend off and seriously injure or kill up to four hyenas by itself. Therefore, to model a realistic mobbing event, more than four hyena agents per lion should be in the environment simultaneously. The neuroevolutionary architecture used in the preliminary experiments is not scalable to such a large number of hyenas, nor is it amenable to dynamically changing numbers of hyenas on the field.

A different set of experiments was specifically designed to allow such scalability. First, a limit was set on the maximum number of hyena clones that could exist on the field at once. The kill probability should depend on the ratio of the number of hyenas to the number of lions, and so, if the number of hyenas was varied dynamically, the number of lions could be fixed at one or two and did not need to change during a single experiment run. Using the mob minimum of four hyenas per lion, the maximum number of hyenas was set to 10. Second, the gazelles were removed and replaced with a direct reward given to the hyenas when they chose to avoid lions. In this way, the hyenas did not need to evolve to hunt individually and the experiments could focus on evolving mobbing behaviors.

The number of hyena clones created for a simulation run was chosen at random for each hyena individual from the population. The kill probability depended on both number of hyenas and number of lions. Initially, the hyenas did not move around, and the simulation consisted of a single time step in which all hyenas decided whether to approach the lions or avoid them. If the number of hyenas was more than four times the number of lions, the kill probability reduced 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.

At first, the only input given to the hyena neural network was a bias; the numbers of lions and hyenas in the simulation were not known to the hyena. However, both these numbers (and hence, kill probability as well) were kept fixed during an experiment run, so the hyena population could discover the specific kill probability used in that run 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 gazelle reward of 100 points was given to them. This reward was kept small so that the hyenas did not come to rely solely on it instead of evolving mobbing strategies. As expected, the fraction of time they chose to go approach the lions decreased as the kill probability increased (Figure 7.3).

In order to be able to change the number of hyenas and the number of lions dynamically during a simulation, the hyena neural network received these two numbers as input in the next experiment so that it could calculate the current kill probability. The actual number of lions was kept fixed at 2 since the kill probability could be varied by just changing the number of hyenas. The number of hyenas was chosen randomly between 1 and 10 before each simulation. Since all the hyena clones received identical inputs, their responses would

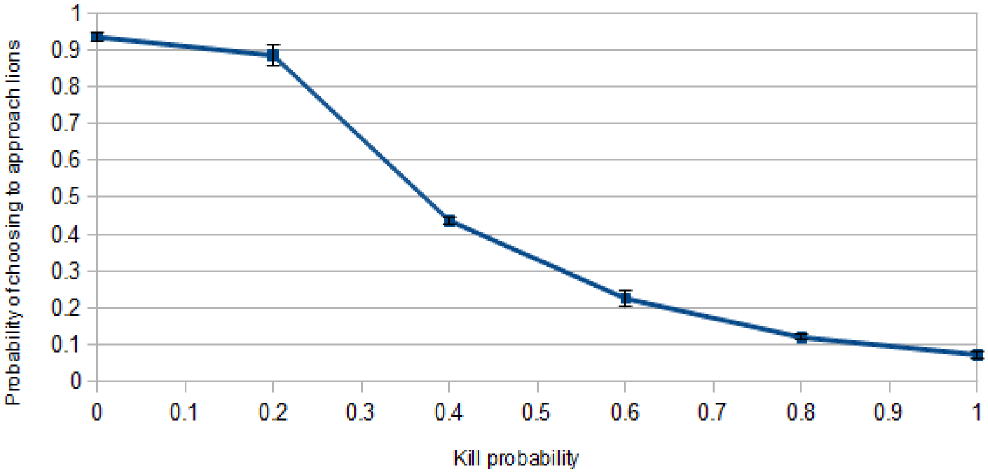

Figure 7.3: **Interaction probability comparisons for stationary hyena in a single time step simulation when kill probability is fixed during an experiment.** The x-axis on this graph shows the kill probability for that experiment and the y-axis represents the probability of the hyena choosing to approach the lions instead of avoiding them, averaged over ten runs. The kill probability remained at a fixed value during a single experiment run and had to be discovered by the hyena through evolution. The average probability of choosing to approach lions decreased as the kill probability increased. Thus, the hyena has discovered kill probability through evolution. This ability will be useful in the rest of the experiments in this chapter.

all be the same too. Therefore, in actuality, only one hyena neural network needed to be activated. The other hyenas were virtual constructs.

In the final generation, the number of hyenas was set to different values in different experiments, and the highest fitness achieved, the probability of choosing to approach lions, and the fraction of time the hyenas got killed were recorded. The hyenas were found unable to connect lower hyena-lion ratios with failure and certain death. While the probability of approaching lions decreased with decreasing numbers of hyenas even when kill probability was constant, it never reached 0 (Figure 7.4). 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. Avoidance of lions when there are fewer hyenas present has also been observed in real-life hyenas by Dr. Holekamp's group (Lehmann et al., 2016).

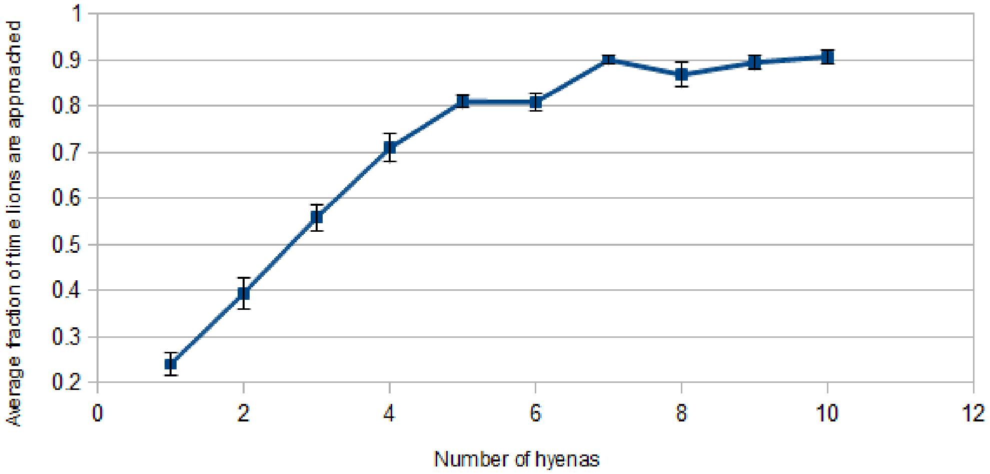

Figure 7.4: **Interaction probability comparisons for stationary hyena in a single time step simulation when number of hyenas varies dynamically during the experiment.** The x-axis on this graph shows the number of hyenas in the last generation and the y-axis represents the probability of the hyena choosing to approach the lions instead of avoiding them, averaged over ten runs. The number of hyenas was a randomly chosen integer from [1, 10], while the number of lions was kept fixed at two. Both the number of hyenas and the number of lions were given as input to the hyena, but the kill probability was not given and had to be calculated by the neural network. The average probability of choosing to approach lions increased as the number of hyenas increased, in accordance with Conclusion 4 from Chapter 2. This result shows that the hyena evolved to calculate the kill probability from number of hyenas and number of lions.

7.3.2 Taking Distances From Lions Into Account

In nature, hyenas are free to move around and to coordinate their actions to instigate an attack on the lions en masse and obtain the kill for themselves. This means that, eventually, the kill probability should depend not only on the number of hyenas and lions, but also the distances of the hyenas from the lions. To this end, in an exploratory experiment, the single non-virtual hyena neural network received as inputs the absolute combined distances (absolute x-offset + absolute y-offset) of all other hyenas from the lions instead of receiving just the number of hyenas (H) as before. Only sum of absolute distances mattered because the lions were stationary and did not need to be attacked from several different directions

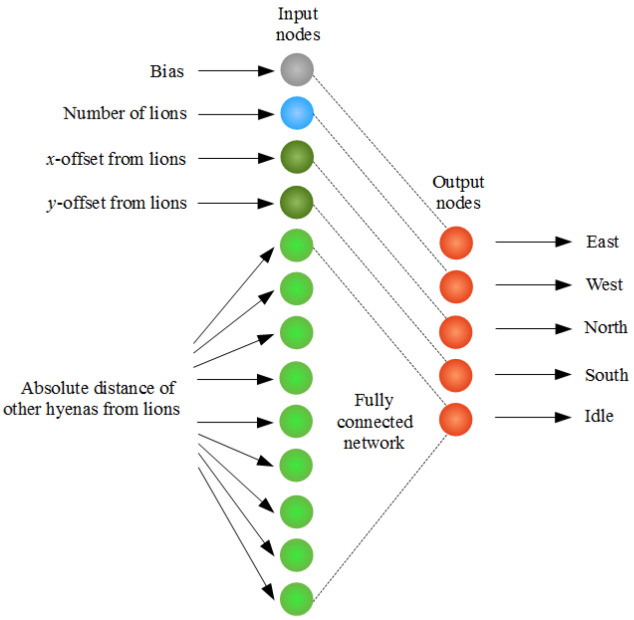

Figure 7.5: **Initial hyena neural network structure for the lion-mobbing task.** The image shows the inputs and outputs; the hidden nodes were evolved by NEAT. Each hyena received its own distances in the x- and y-directions from the lions at each time step. It also received the absolute distances of all other hyenas from the lions, where the maximum possible number of hyenas at any given time in the simulation was 10. If there were fewer than ten hyenas, the nodes corresponding to the absent hyenas were given an input of -1. Other inputs to the neural network were the number of lions and a bias. The initial network had no hidden neurons and was fully connected, i.e. all input nodes were connected to all output nodes. The five output nodes represented the five actions the hyena could take at every time step: move east, west, north or south, or remain stationary. The hyena had to calculate the kill probability at any given point in the simulation using the number of lions and number of hyenas that were within the interaction circle. Based on the kill probability and its own distance from lions, it had to decide whether to approach lions or avoid them.

at once, unlike the prey in Chapters 4 and 5. These distances were generated at random for now, as the other hyenas were still virtual. Also given as input to the hyena were the x- and y-offsets of itself from the lions, and the number of lions (L). Thus, the number of input neurons was 13, with one for bias, two for its own x- and y-offsets from the lions, one for the number of lions and nine for the distances of the other hyenas from the lions (see Figure 7.5). The maximum number of hyenas was set to 10, and if H hyenas were present on the field, the inactive $9 - (H - 1)$ input neurons that should have received the distances of the missing hyenas from the lions instead received input value -1. Individual x- and y-distances from lions had integer values between -50 and 50 because the environment was a 100×100 toroidal grid. The combined distances of the other hyenas from the lions could take integer values between 0 and 100. Kill probability still depended only on the ratio of number of hyenas to number of lions. So the values of distances did not matter now and the results should be the same as in the previous experiments, where only number of hyenas was given as input to the neural network. The hyena neural network should learn to count the number of inputs that were switched on and act accordingly. It should also learn to ignore its own distances from lions for now. As before, the number of hyenas varied from 1 to 10 during an experiment run, but was fixed to a single value in the last generation so that probability of approaching lions, fraction of time the hyenas got killed, and the highest fitness achieved could be recorded.

The results from this exploratory experiment (Figure 7.6) did look very similar to those of the experiments from the previous section. As in those experiments, 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. When there were fewer hyenas than the mob minimum, it was unable to evolve to avoid the lions completely.

In a following experiment, therefore, H non-virtual hyena clones were created and placed at random locations on the field. 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. Since the hyenas could be at different locations on the field, each hyena received different inputs. Kill probability still depended only on the number of lions and the number of hyenas. Once again, this was a single time step simulation, where the hyenas received all input values at once, made a decision and were rewarded at once. The results from this experiment (Figure 7.7) were similar to the previous experiment in this section (Figure 7.6). If the kill probability was changed to depend not on the total number of hyenas in the environment, but on the number of hyenas that chose to approach the lions (as in nature),

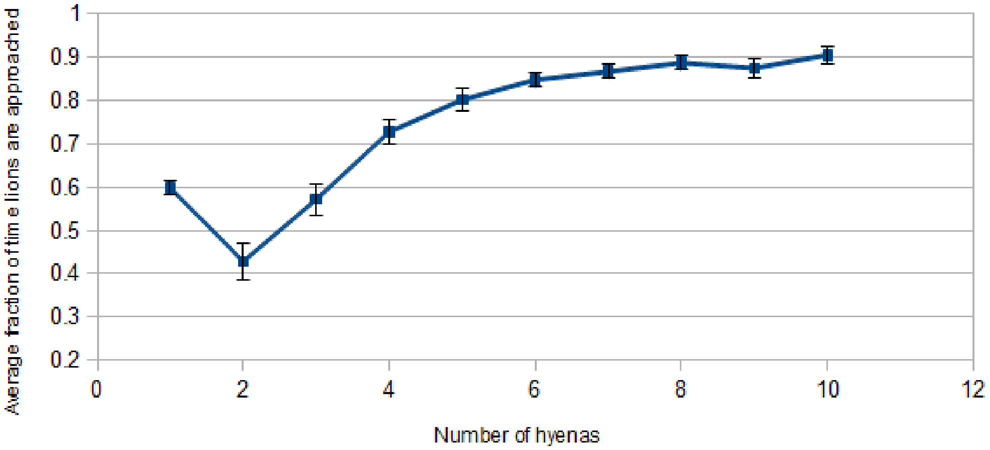

Figure 7.6: **Interaction probability comparisons for stationary hyena in a single time step simulation when absolute distances of the hyenas from the lions is given as input to the hyena.** The x-axis on this graph shows the number of hyenas in the last generation and the y-axis represents the probability of the hyena choosing to approach the lions instead of avoiding them, averaged over ten runs. The number of hyenas was a randomly varied between 1 and 10 for each simulation, while the number of lions was kept fixed at 2. The number of lions was given as input to the hyena, but the number of hyenas was not. The absolute distances of the hyenas from the lions were given as input. The average probability of choosing to approach lions generally increased as the number of hyenas increased with a small bump when number of hyenas was 1. This result was in accordance with Conclusion 4 from Chapter 2.

the probability of approaching lions remained more or less constant for higher numbers of hyenas. This result could be because the total number of hyenas did not directly relate to the kill probability now. Even with 10 hyenas on the field, only a few of them may have chosen to approach lions. The probability of approaching lions decreased as the number of hyenas decreased further, as in previous experiments. The average maximum fitness reached for $H = 1$ and 2 was exactly equal to the gazelle reward, because H was below the mob minimum, so they evolved not to choose that. But when $H = 3$ or 4, they could still mob the lions successfully if all the hyenas decided to approach the lions, so they tended to choose to approach lions more often. Therefore, the probability of interaction increased with increasing number of hyenas in the environment, just as stated in Conclusion 4 in

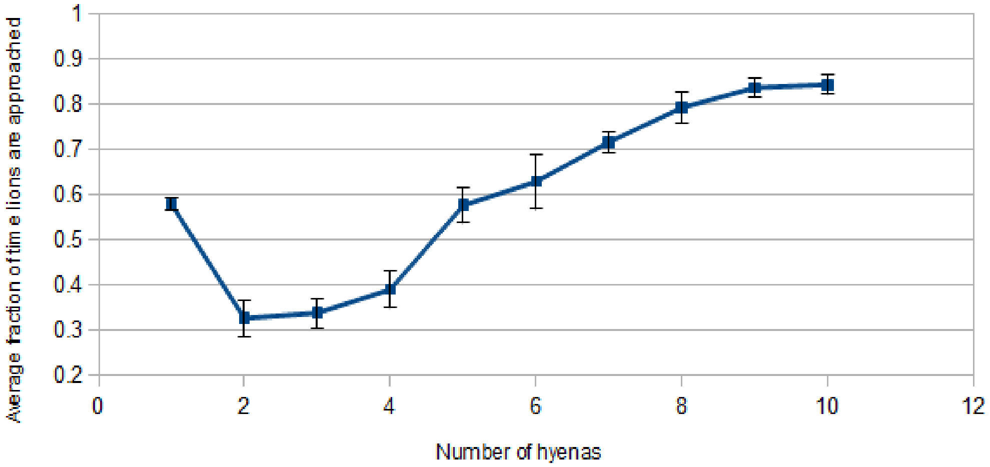

Figure 7.7: **Interaction probability comparisons for multiple non-virtual stationary hyenas in a single time step simulation when absolute distances of the hyenas from the lions is given as input.** The *x*-axis on this graph shows the number of hyenas in the last generation and the *y*-axis represents the probability of the hyenas choosing to approach the lions instead of avoiding them, averaged over ten runs. The number of hyenas was a randomly varied between 1 and 10 for each simulation, while the number of lions was kept fixed at 2. The number of lions was given as input to the hyenas, but the number of hyenas was not. The absolute distances of the hyenas from the lions were given as input to all the hyena neural networks. Each hyena could make an individual decision whether to approach the lions or not. The average probability of choosing to approach lions generally increased as the number of hyenas increased, except for a small rise when there is a single hyena present. At higher numbers of hyenas, this probability did not vary much.

Chapter 2.

7.3.3 Realistic Modeling of Lion-Hyena Encounters

The first step is to match Conclusion 4 from Chapter 2, i.e. that interspecific interaction probability increases as the number of hyenas on the field increases. Now that the above exploratory experiments had shown that the hyenas could calculate the kill probability with the almost the same accuracy in the case where they received the distances of their teammates from the lions as in the case where they directly received the number of hyenas on the field, the way was paved for an environment where the hyenas could move around and the simulation lasted for more than one time step. Therefore, the number of time steps was increased to 500, and the hyenas could move around the field, one step at each time step. They could move in four directions: east, west, north and south, or remain idle. Thus, the hyena neural network had five output nodes to decide on the direction in which to move at every time step. Each hyena neural network received a continuous input of the dynamically changing distances of itself and the other hyenas from the lions. The number of lions was fixed at 1 to allow for more mobbing possibilities. The interaction radius was set to 10. That is, at every time step, the positions of the hyenas were checked, and if a hyena was within 10 steps of the kill site, kill probability came into play. The kill probability depended on how many hyenas were within the interaction circle. Since these hyenas constituted a potential mob, their number was called the 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. This reward represented the hyena slowly feeding on the kill at the kill site. If the mob count was ever more than four times the number of lions, the lion was considered successfully mobbed, and the simulation was terminated with a mobbing reward of 10,000 points per hyena given to the team. At the end of the simulation, regardless of whether they mobbed the lion or not, a reward of 100 points per hyena was given to the team, which represented a reward from hunting gazelles. 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 results of these experiments showed that they mobbed the lion successfully in a very small number of cases, making their average highest fitness rise beyond gazelle-only reward (Figure 7.8). Not all hyenas were left alive at the end of the simulations, showing that more hyenas did choose to approach the lion even if they did not end up mobbing it. The fraction of time when successful mobbing occurred was still very low. In the cases where 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 gazelle reward. In

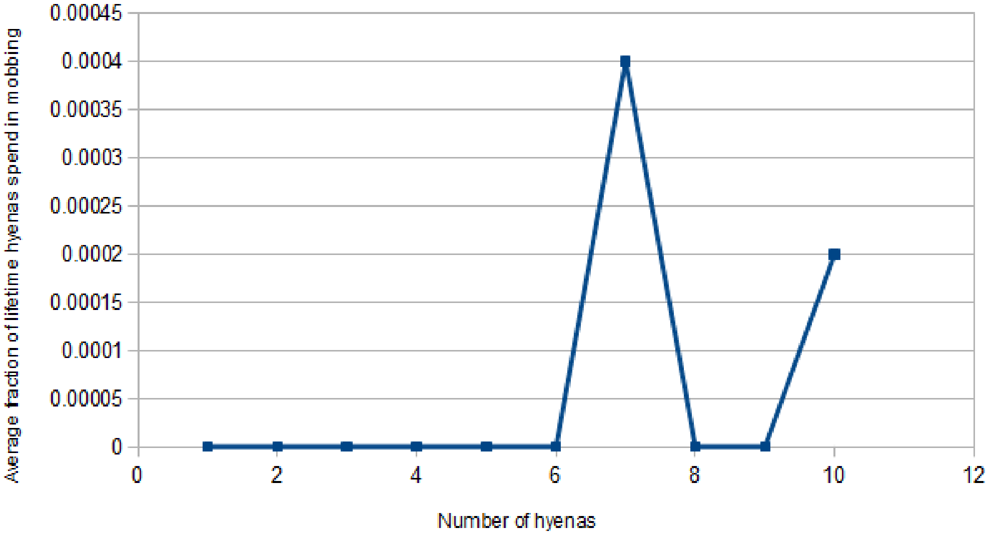

Figure 7.8: **Successful mobbing probability comparisons for multiple mobile hyenas in a 500-time-step simulation.** The *x*-axis on this graph shows the number of hyenas in the last generation and the *y*-axis represents the mobbing probability, i.e. fraction of time the hyenas successfully mobbed the lion, averaged over ten runs. The number of hyenas was a randomly varied between 1 and 10 for each simulation, while the number of lions was kept fixed at 1. The number of lions was given as input to the hyenas, but the number of hyenas was not. The absolute distances of the hyenas from the lions were given as input at each time step to all the hyena neural networks. Each hyena could make a decision whether to move east, west, north or south, or remain idle. The average mobbing probability remained at 0 for most cases. This result showed that the values of certain factors needed to be sufficiently high for mobbing to occur in simulation.

general, the interaction probability increased with increasing number of hyenas (Figure 7.9). Overall, the interaction probability values were very low because when a hyena entered the interaction circle, it would either immediately get killed, or successful mobbing would occur, which would end the simulation. The odds of the hyena surviving the interaction when no mobbing took place were very low, so not much of the hyena's lifetime was spent in the interaction circle.

While the mobbing frequency was very low, the average interaction probability of the hyena team increased with increasing number of hyenas in the environment, which is in

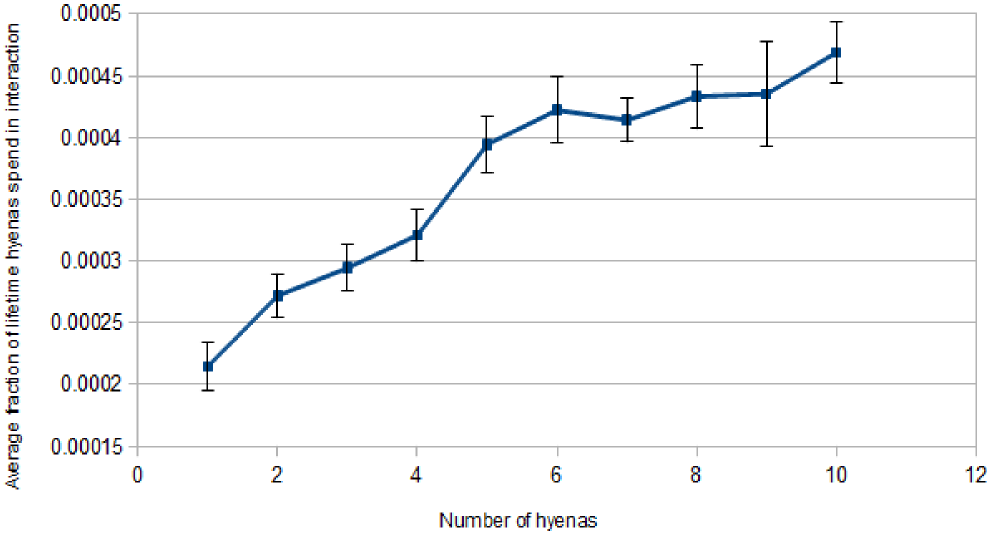

Figure 7.9: **Interaction probability comparisons for multiple mobile hyenas in a 500-time-step simulation.** The x-axis on this graph shows the number of hyenas in the last generation and the y-axis represents the interaction probability, i.e. fraction of time the hyenas were within the interaction circle, averaged over ten runs. The number of hyenas was a randomly varied between 1 and 10 for each simulation, while the number of lions was kept fixed at 1. The number of lions was given as input to the hyenas, but the number of hyenas was not. The absolute distances of the hyenas from the lions were given as input at each time step to all the hyena neural networks. Each hyena could make a decision whether to move east, west, north or south, or remain idle. The average interaction probability increased as the number of hyenas increased. This result corresponds to Conclusion 4 from Chapter 2.

line wit Conclusion 4 from Chapter 2.

7.3.4 Increasing the Frequency of Successful Mobbing

According to Conclusion 8 from Chapter 2, mobbing can be very productive for the fitness of the hyena team, but this was not observed in the experiments in the previous subsection. While the hyenas in the previous subsection did evolve to successfully mob the lions, the probability of a mobbing event was still very low, unlike in nature. To increase the frequency of mobbing, various parameter values were tested carefully and systematically. The

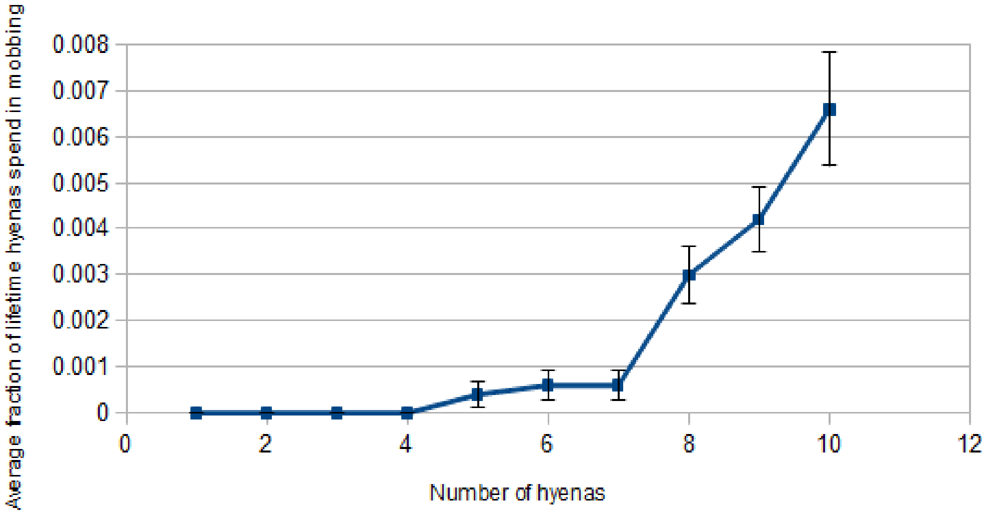

Figure 7.10: **Successful mobbing probability comparisons for simulation with increased mobbing frequency.** The x-axis on this graph shows the number of hyenas in the last generation and the y-axis represents the mobbing probability, i.e. fraction of time the hyenas successfully mobbed the lion, averaged over ten runs. 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 simulations. The average mobbing probability was very low, but successful mobbing occurred more often than in previous experiments. This result shows that mobbing can be productive for the hyena team and increase its fitness as long as certain parameters are set sufficiently high, i.e. as long as mobbing gives a net gain to the hyenas. Therefore, Conclusion 8 from Chapter 2 was verified in simulation in this experiment.

reward received by a hyena at each time step for remaining within the interaction circle without dying needed to be higher to encourage hyenas to approach close to 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 gazelle reward from the previous experiments was replaced with a survival reward given only to those hyenas that survived to the end of the simulation. This change helped hyenas evolve to coordinate their attack on the lions instead of charging them blindly by themselves and dying. The survival

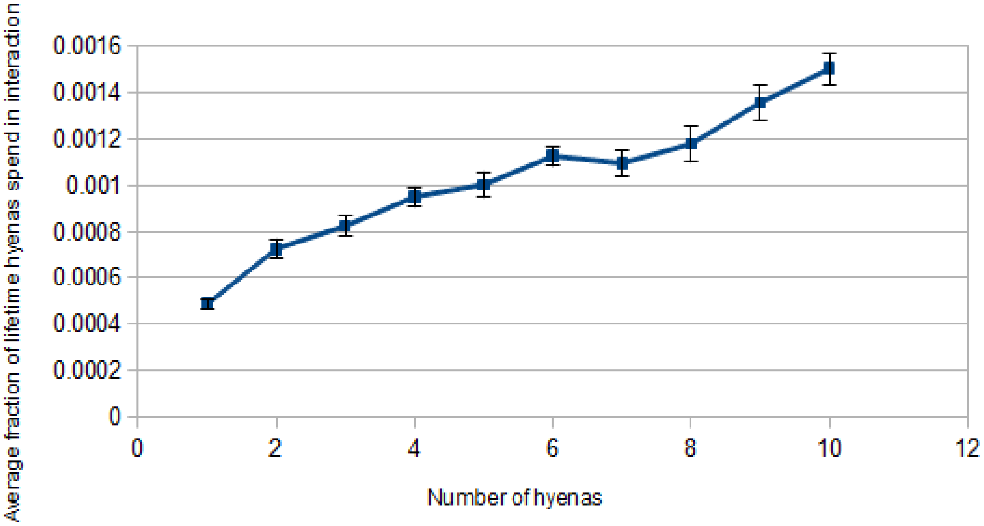

Figure 7.11: **Interaction probability comparisons for simulation with increased mobbing frequency.** The x-axis on this graph shows the number of hyenas in the last generation and the y-axis represents the interaction probability, i.e. fraction of time the hyenas were within the interaction circle, averaged over ten runs. The 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 simulations. The average interaction probability increased as the number of hyenas increased, just as in Conclusion 4 from Chapter 2. The average interaction probabilities were also higher than in previous experiments.

reward needed to be low so that the hyenas did not avoid the lions altogether in order to survive and claim it. The mobbing reward was also only given to hyenas that survived until the end.

The result of these parameter changes was that the frequency of mobbing increased when compared to the previous experiments (see Figure 7.10). 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 interacting with the lion, i.e. within the interaction circle, also increased (compare Figures 7.9 and 7.11). 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. Unlike in the previous experiments, they did not stop approaching the lion when the total number of hyenas was too low to form a successful mob.

It can hence be concluded that mobbing can be successful 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. Once they have evolved to mob lions successfully, they can fine-tune the process to be successful more and more frequently with relatively low cost. 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 (see Section 9.3 for more details).

7.3.5 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 Chapter 2 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.

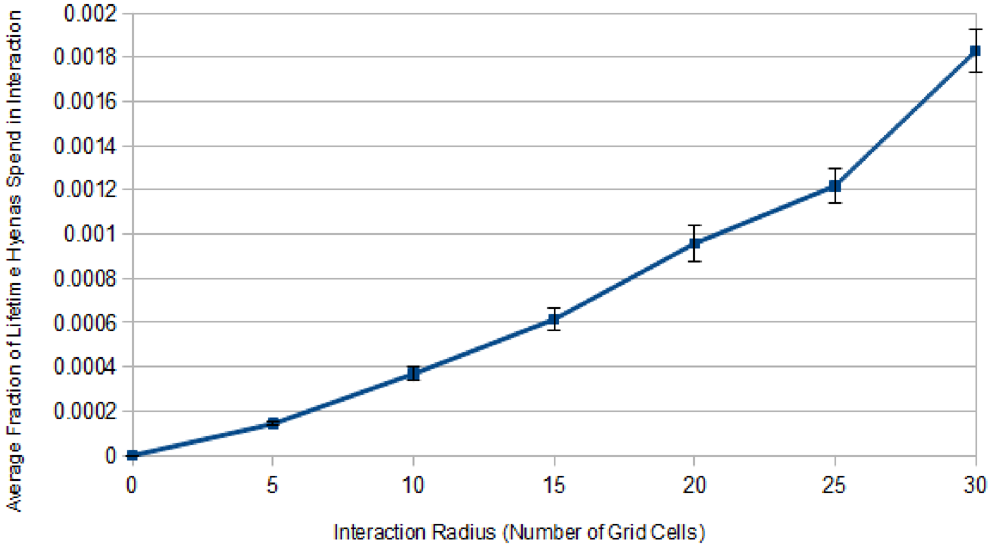

Figure 7.12: **Interaction probability comparisons for simulation with adult male lions present.** The *x*-axis on this graph shows the interaction radius in the last generation and the *y*-axis represents the interaction probability, i.e. fraction of time the hyenas were within the interaction circle, 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, which matches Conclusion 3 from Chapter 2.

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 randomly in the range 0 to 30 during the experiment run. This value was then given as input to the hyena neural network so that the hyenas could keep track of the current interaction circle size. In the final generations of separate experiments, the interaction radius was fixed at various values from 0 to 30 and the results compared. 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.

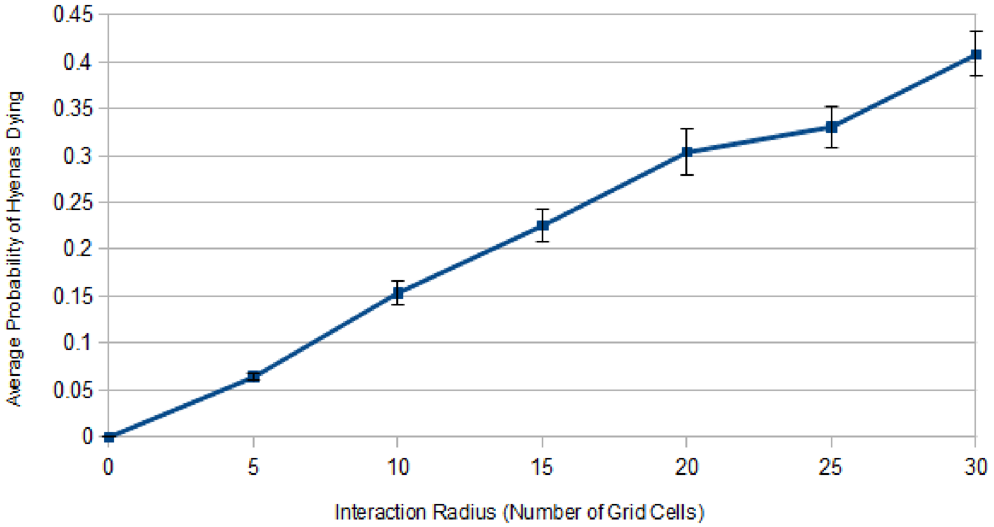

Figure 7.13: **Hyena death probability comparisons for simulation with adult male lions present.** The *x*-axis on this graph shows the interaction radius in the last generation and the *y*-axis represents the probability of the hyenas dying, averaged over ten runs. The numbers of hyenas and lions were 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 interaction radius increased. Therefore, the number of hyena deaths increased in the presence of male lions. This result is in accordance with Conclusion 3 from Chapter 2.

Just like in nature, the simulated hyenas did spend more of their time interacting with lions as the interaction radius increased, but they also got killed more frequently (see Figures 7.12 and 7.13). This result is in line with Conclusion 3 from Chapter 2, which states that presence of male lions increases the interaction probability, but also increases the number of hyena deaths. The reason for this is that male lions themselves initiate interactions with hyenas, but are also better able to injure or kill any hyenas that approach too closely.

7.3.6 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, by concluded in 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 Chapter 2). They also observed that the propensity of the hyenas for interspecific interactions with the lions increased with increasing prey size (Conclusion 2 from Chapter 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.

The prey desirability value in the computational model is represented by the mobbing reward, which is the reward that is received by each surviving hyena when a successful mobbing event has occurred. While varying this reward and comparing the results seemed to be very simple, 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 evaluated very carefully and systematically 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 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 7.14). This result is in line with Conclusions 1 and 2 from Chapter 2.

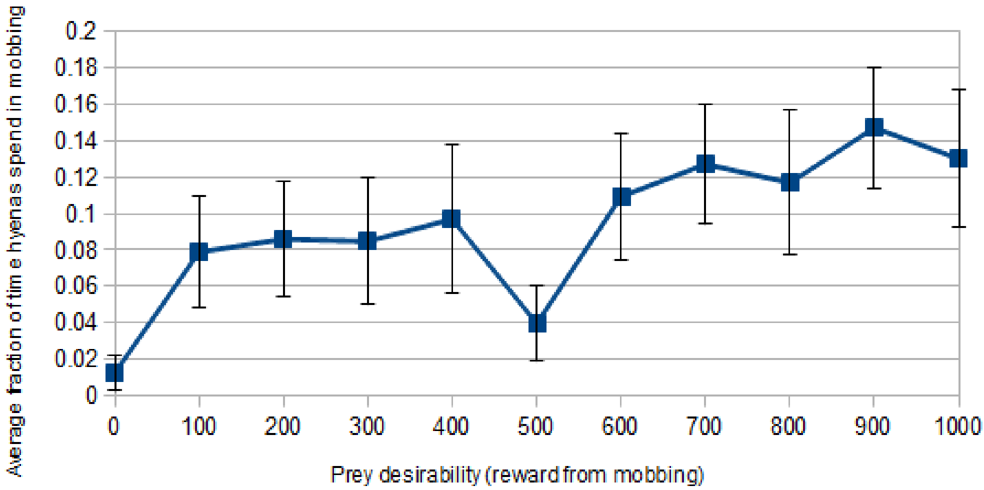

Figure 7.14: **Successful mobbing probability comparisons for different prey desirability values.** The *x*-axis on this graph shows the prey desirability value, which is equal to the mobbing reward, and the *y*-axis represents the mobbing probability, i.e. fraction of time the hyenas successfully mobbed the lion, averaged over ten runs. The survival reward given to all surviving hyenas at the end of the simulations was 5 points. The average mobbing probability showed a trend of increasing with increasing prey desirability. Thus, Conclusions 1 and 2 from Chapter 2 were verified in simulation.

7.4 Conclusion

The computational model built in this chapter 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 hasn't occurred. In order to replicate frequent mobbing behaviors as seen in nature, the values of these factors had to be very carefully and systematically varied. From the simulation experiments in this chapter, it could be concluded that mobbing and interaction frequencies increased when:

- Interaction radius was increased

- Mobbing reward was increased
- Reward given at the end of the simulation was decreased
- Reward from feeding on kill gradually while staying alive was increased
- Mobbing reward was given only to survivors, and
- Simulation-end reward was given only to survivors.

These parameters represented environmental factors in the real world which affect interspecific interaction probabilities and mobbing rates in hyenas. Out of the eight conclusions from observational data listed in Chapter 2, five were modeled successfully in simulation. The following are the conclusions that matched perfectly with those in Chapter 2:

1. The probability of interspecific interaction between lions and hyenas increased with increasing number of hyenas present. This result matches Conclusion 4 from Chapter 2.
2. Successful mobbing contributed positively to the overall fitness of the hyena team. While mobbing gave a large reward in the simulations, the artificial hyenas still had to evolve to coordinate their attack on the lions, and a fine balance of parameter values was necessary to bring about mobbing behaviors. This result matches Conclusion 8 from Chapter 2.
3. The probability of interaction 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 from Chapter 2.
4. The probability of interaction was higher when prey desirability was higher. In the case of hyenas in nature, prey desirability was a combination of freshness and size

of the kill, while in the computational model, it was represented by the value of the mobbing reward. This result matches Conclusions 1 and 2 from Chapter 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. Three such predictions are described in the following chapter.

Chapter 8

Computational Predictions on Coordinated Cooperation

Chapter 2 described the observational data on lion-hyena encounters gathered over 27 years, consisting of very detailed notes and hundreds of hours of videos. Dr. Holekamp's group used this dataset to characterize lion-hyena interactions, analyzing some environmental factors that influenced the rates of mobbing as well as the probability of interspecific interaction (Lehmann et al., 2016). These included prey size, presence of adult male lions, number of hyenas, number of lions and freshness of kill. The computational model developed in the previous chapter simulated lion-hyena interaction as well as lion-mobbing. Using the model, many of the same conclusions were reached regarding the factors affecting probabilities of interaction and mobbing as Lehmann et al. (2016). Therefore, various components in the model could now be changed systematically to make predictions about behaviors of hyenas during lion-hyena interactions. These behaviors may be verified in the field in the future, or may lead to a deeper understanding of how mobbing evolved in the spotted hyena and how it may evolve into more intelligent behaviors in generations to come.

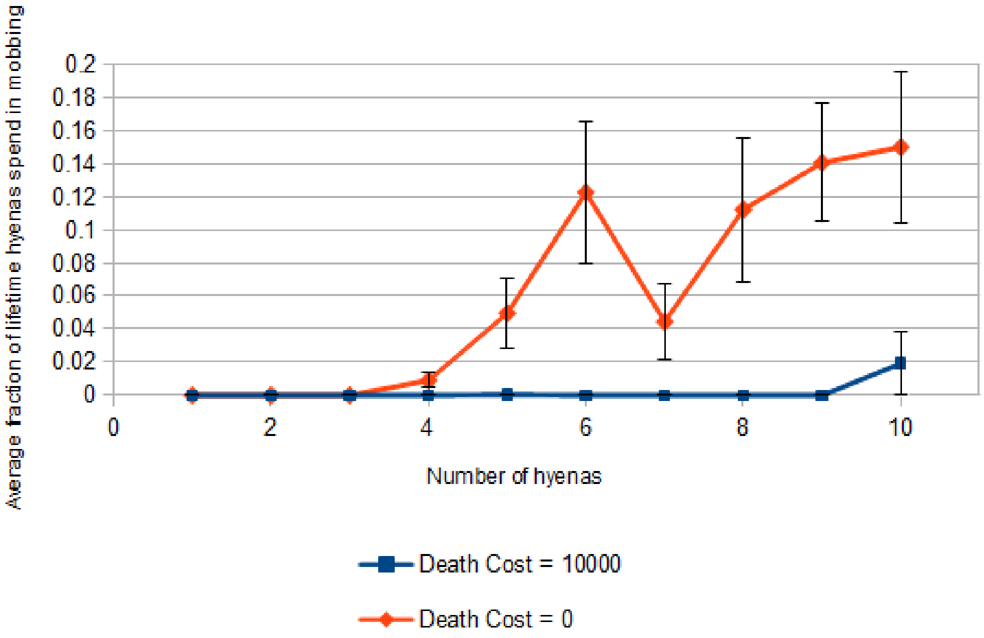

Figure 8.1: **Successful mobbing probability comparisons for simulations with and without death or injury cost.** The x-axis on this graph shows the number of hyenas in the environment and the y-axis represents the mobbing probability, i.e. fraction of time the hyenas successfully mobbed the lion, averaged over ten runs. The fitness penalty for the death of each hyena was 10,000 points in one experiment and 0 in the other. The average mobbing probability was significantly higher when death cost was 0. Mobbing did not occur in the case where death cost was 10,000 except for a few times when there 10 hyenas on the field. Therefore, mobbing probability decreases when death cost is high.

8.1 Injury and Death Cost

In the simulations in the previous chapter, all hyenas received a large fitness penalty upon getting killed while attempting to mob lions. This penalty was deemed necessary to encourage the hyenas to coordinate their actions precisely in order to mob lions. Without this precise coordination, the hyenas may approach the lions one by one and end up dying.

In order to find out if the cost of injury or death during the mobbing event changes the propensity of the hyenas for mobbing, the fitness penalty of $-10,000$ points for each

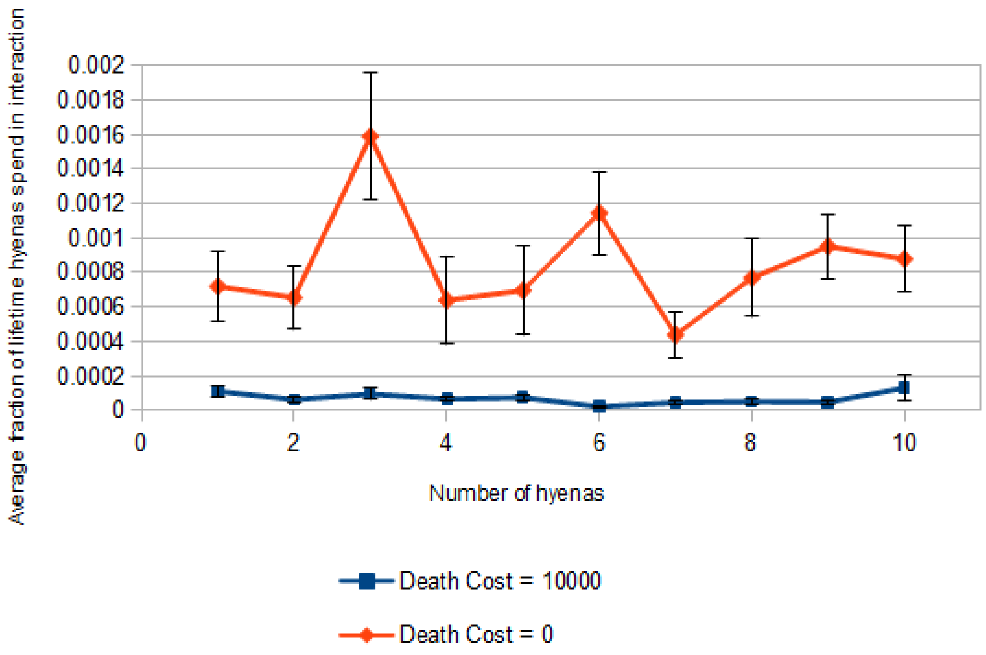

Figure 8.2: **Interaction probability comparisons for simulations with and without death or injury cost.** The *x*-axis on this graph shows the number of hyenas in the environment and the *y*-axis represents the interaction probability, i.e. fraction of time the hyenas spent interacting with the lion, averaged over ten runs. The fitness penalty for the death of each hyena was 10000 points in one experiment and 0 in the other. The average interaction probability was significantly higher when death cost was 0. Therefore, interaction rates increase when death cost is low.

hyena death was eliminated. The death of a hyena still negatively impacted fitness of the hyena team in an indirect way. If a hyena died, it could no longer participate in mobbing. This change in the number of hyenas reduced the probability of a successful mobbing event. Additionally, a dead hyena could receive neither mobbing reward nor survival reward, thus reducing the overall fitness of the team.

In this particular experiment, the lion was placed at the center of the environment, and the hyenas always started at specific positions that were equidistant from the lion. The mob minimum was four hyenas. It was observed that removing the injury or death cost for hyenas did increase the frequency of mobbing (Figure 8.1). The fraction of time the hyenas

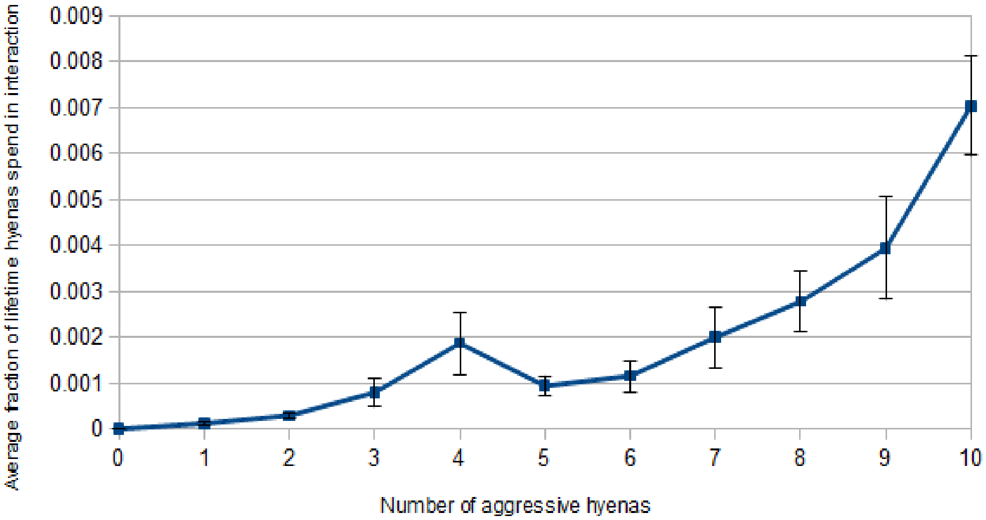

Figure 8.3: **The average probability of interaction for teams with different proportions of aggressive and diffident hyenas.** The number of aggressive hyenas is on the *x*-axis, and the probability of interaction between hyenas and lions, averaged over ten runs, is on the *y*-axis. The total number of hyenas in the hyena team was always ten, but the number of aggressive and diffident hyenas varied. The average interaction probability increased as number of aggressive hyenas increased, with a small but significant local maximum at four aggressive hyenas. The reason for this increase is that aggressive hyenas have a high tendency to approach the lions and interact with them.

spent interacting with the lions also increased, and this occurred even when mobbing did not occur (Figure 8.2). Thus, it was seen that elimination of the fitness penalty for death made the hyenas more likely to approach the lions and to conduct successful mobbing. In nature, reducing death costs could mean more altruism or group selection, where death and injury of an individual hyena are deemed cheap because they benefit the hyena clan as a whole.

8.2 Individual Roles in Mobbing

While the lion-hyena encounter dataset is undoubtedly very rich, all possible information has not yet been extracted from it. For instance, the roles of individual hyenas in interspecific interactions and in mobbing events have not yet analyzed. Different hyenas may react differently to highly complex situations, and the degree to which any one hyena may affect the outcome of a mobbing attempt, for example, is unknown. Do the hyenas have a leader who decides whether to attack the lions or retreat? Or is it like a democracy, where the majority vote decides the action taken by the whole group?

To study the question of the roles different hyenas play in lion-mobbing using the computational model, there had to be at least two hyenas that acted in distinctly different ways during a simulation. All the experiments in the previous chapter used clones of a single hyena to build the team that would interact with the lions during a simulation. However, different hyenas did exist in the population and were all used as templates to create clones for the lion-mobbing team. Some hyenas were inclined to participate in the mobbing, while others almost always avoided the lions.

A typical experiment from the previous chapter was run for 1000 generations with number of hyenas kept fixed throughout at 10, and number of lions at 1. They always started at fixed positions instead of random positions in the environment, with the lion in the center, and all ten of the hyenas equidistant from it in different directions outside the interaction circle. In the final ten generations, the individual hyenas that had the least and highest numbers of clones interacting with the lions throughout the simulation were saved in a hall of fame. They were only chosen from the last ten generations so that both types of hyenas had good fitness. For example, a hyena that had not yet evolved to recognize the lions and just idle was not ideal for the purposes of this task. At the end of the experiment, these two individuals, i.e. the most aggressive hyena and the most diffident hyena, were then cloned to form a new team. Different proportions of aggressive and diffident clones were used, and interaction probability, mobbing frequency, fitness, and probability of dying were recorded and averaged over ten trials.

The trend observed in all ten trials of the experiment was that the hyena team did not mob the lion or interact with it at all when the number of aggressive hyenas was 0.

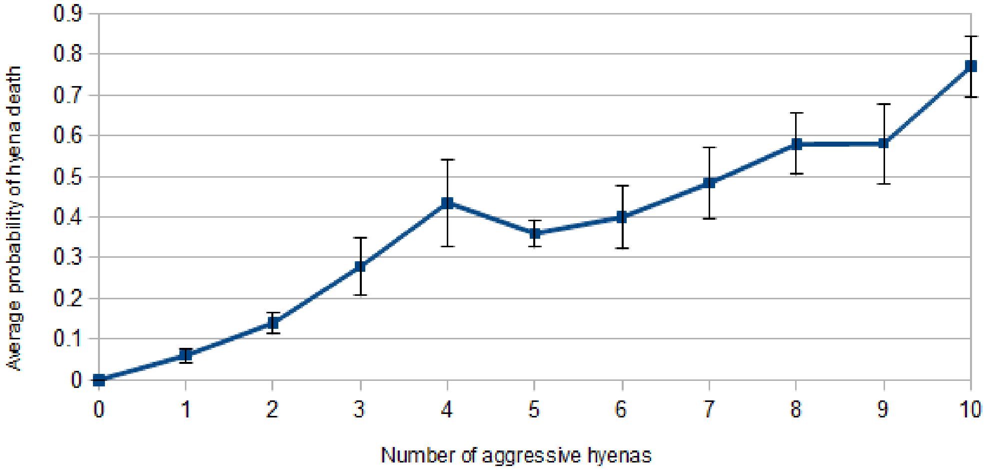

Figure 8.4: **The average probability of hyenas dying for teams with different proportions of aggressive and diffident hyenas.** The number of aggressive hyenas is on the *x*-axis, and the probability of hyenas dying, averaged over ten runs, is on the *y*-axis. The total number of hyenas in the hyena team was always ten, but the number of aggressive and diffident hyenas varied. The average probability of hyenas dying increased as number of aggressive hyenas increased, with a local maximum at four aggressive hyenas. This results shows that aggressive hyenas approach lions more frequently and, consequently, get killed.

Then, as the number of aggressive hyenas was increased and the number of diffident hyenas decreased, the frequency of interaction rose (Figure 8.3). The fraction of hyenas that died also increased with increase in number of aggressive hyenas, thus reducing their overall fitness. There were local maxima in interaction probability, death probability and team fitness when the number of aggressive hyenas was four, but the values dropped again when the number of aggressive hyenas increased (Figures 8.3, 8.4 and 8.5). This result was observed in spite of the fact that there was still no mobbing occurring (see Figure 8.7). The first instance of successful mobbing took place only when the number of aggressive hyenas reached 8. Therefore, the increase in fitness when there were four aggressive hyenas arose because the aggressive hyenas spent more time in the interaction circle, slowly feeding on the kill before getting killed themselves. After the number of aggressive hyenas increased

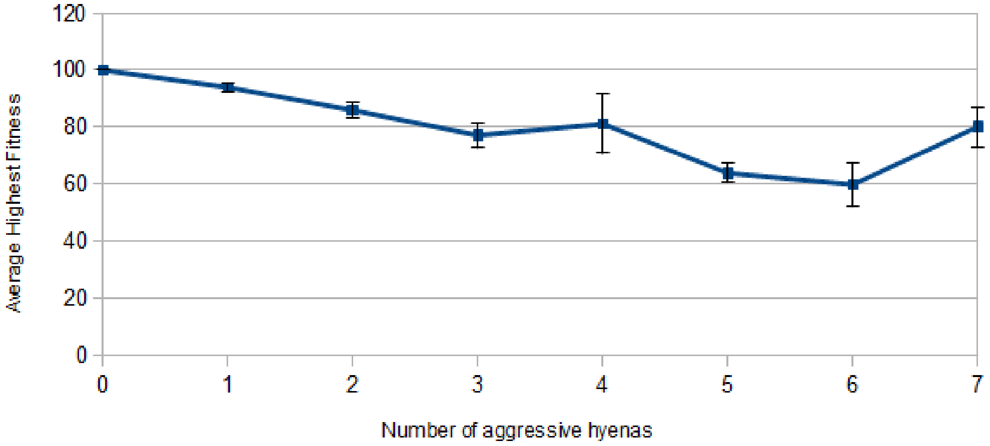

Figure 8.5: **The average probability of hyenas dying for teams with up to seven aggressive hyenas.** The number of aggressive hyenas is on the *x*-axis, and the highest fitness achieved, averaged over ten runs, is on the *y*-axis. The total number of hyenas in the hyena team was always ten, but the number of aggressive and diffident hyenas varied. Only teams with up to 7 aggressive hyenas are represented here. The average highest fitness achieved had a local maximum at four aggressive hyenas. The trend seen here is that fitness decreases with increasing number of aggressive hyenas. Aggressive hyenas approach the lions without coordinating their movements, which results in death for each of them, and lower fitness for the team as a whole.

to 8, the fitness climbed dramatically because successful mobbing was being conducted (Figures 8.6 and 8.7).

These results showed that the proportion of the hyenas that were more inclined to participate in mobbing and those that tended toward avoiding the lions was important in determining the probabilities of interaction and successful mobbing. A large number of aggressive hyenas resulted in more interaction with lions and more mobbing. But when they are fewer than a certain number, even when in majority, it was counterproductive to fitness because they attacked the lions by themselves without sufficient coordination and were killed, thus reducing the fitness for the team as a whole.

In order to observe how the presence of non-identical hyenas with different behaviors affected the tendencies of aggressive and diffident hyenas to approach lions, the above

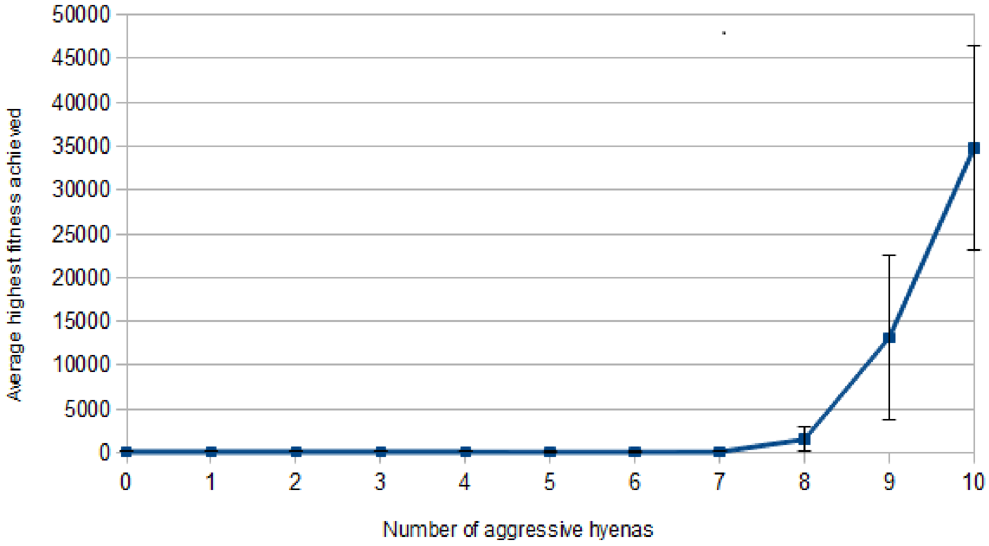

Figure 8.6: **The average probability of hyenas dying for teams with different proportions of aggressive and diffident hyenas.** The number of aggressive hyenas is on the *x*-axis, and the highest fitness achieved, averaged over ten runs, is on the *y*-axis. The total number of hyenas in the hyena team was always ten, but the number of aggressive and diffident hyenas varied. The average highest fitness achieved did not vary much initially as the proportion of aggressive hyenas increased, but it climbed steadily after the number of aggressive hyenas reached 7. This sudden fitness increase is because of successful mobbing events, which start occurring after the number of aggressive hyenas reaches 7.

experiment was rerun and the average distances of the diffident and aggressive hyenas from the lions were recorded and compared. In this experiment, all the hyenas started on the same location on the toroidal grid at the beginning of the simulation in order to eliminate noise from random initial positions. From Figure 8.8, it can be seen that the average distance of diffident hyenas decreased as number of aggressive hyenas increased. The aggressive hyenas had the least distance from lions somewhere in the middle. Hence, the diffident hyenas indeed changed their behavior significantly when there were many aggressive hyenas around, but the behaviors of aggressive hyenas were too noisy to draw clear conclusions from.

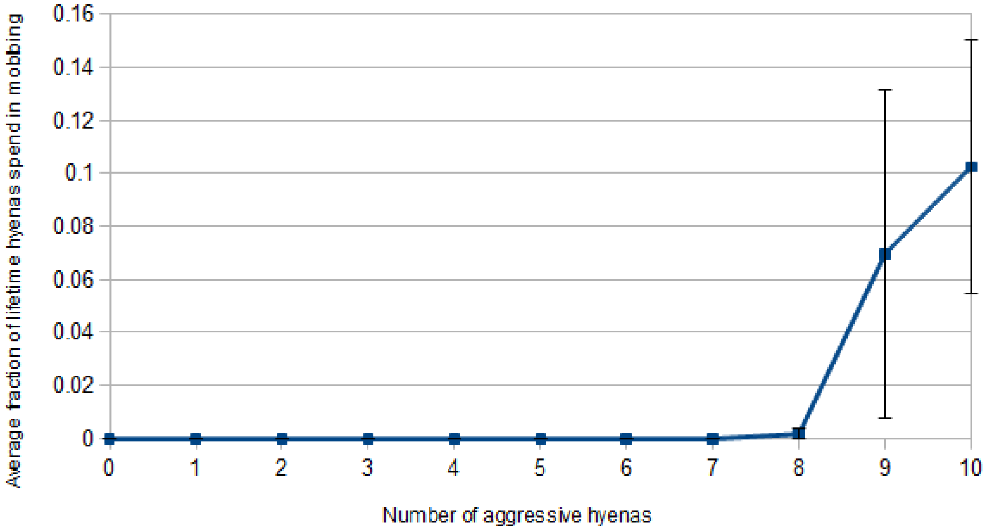

Figure 8.7: **The average probability of hyenas successfully mobbing lions for teams with different proportions of aggressive and diffident hyenas.** The number of aggressive hyenas is on the x-axis, and the probability of successful mobbing, averaged over ten runs, is on the y-axis. The total number of hyenas in the hyena team was always ten, but the number of aggressive and diffident hyenas varied. The average probability of successful lion-mobbing stayed at 0 when the proportion of aggressive hyenas was low, but it increased after the number of aggressive hyenas reached 8. Fewer aggressive hyenas did not conduct successful mobbing and tended to approach lions without any coordination, leading to more hyena deaths.

8.3 The Role of Emotions

Lion-mobbing is an unusual cooperative task for the hyenas in that it involves a high risk of death and injury, making it seem counterproductive to fitness. This is the reason why, in the previous chapter, the probability of mobbing remained low even though the simulated hyena team did manage to evolve successful mobbing behaviors. Any action that requires such extreme risk-taking induces fearfulness in its participants. The fear emotion in hyenas increases when a lion is sighted, but may not die down immediately if the lion goes away. Thus, the fear emotion engenders caution in the hyena when a lion is in the vicinity.

In nature, spotted hyenas engage in mobbing events more frequently than in sim-

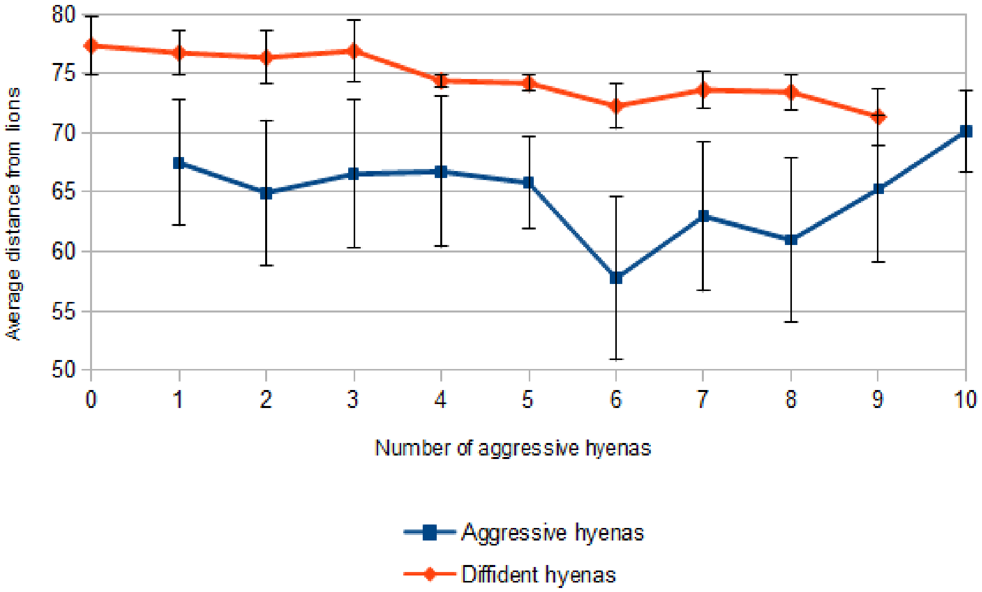

Figure 8.8: **The average distances of aggressive and diffident hyenas from lions with different proportions of aggressive and diffident hyenas in the team.** The number of aggressive hyenas is on the x-axis, and the average distance from lions, averaged over ten runs, is on the y-axis. The total number of hyenas in the hyena team was always ten, but the number of aggressive and diffident hyenas varied. The average distance of diffident hyenas from lions decreased as more aggressive hyenas were added to the team, but the average distance of aggressive hyenas was too noisy to draw any conclusions from.

ulation, indicating that more emotions play a role than just fearfulness. In the previous section, the proportions of aggressive and diffident hyenas in the team seemed to play a role in determining the mobbing probability. The aggressive hyenas could be said to be less fearful, while the diffident hyenas were more fearful of approaching the lions. However, with a sufficiently large number of hyenas, successful lion-mobbing is possible without too high a probability of injury or death. For the hyenas to be able to overcome their fear and attack the lions in precise coordination, they need to have a different emotion relating to number of other hyenas on the field with them. This emotion, affiliation with conspecifics, has been observed in real-life hyenas, which allows them to bond socially with one another.

Affiliation is also responsible for how hyenas excite themselves into a heightened state of emotion to mob lions. As seen in Chapter 2, Dr. Kay Holekamp and her group plan to analyze the hyena fecal samples they have collected for various hormone levels, which should give a good idea of the emotional states of the hyenas during mobbing events. These results can then be used to identify the role of different emotions in the execution of mobbing strategies.

In nature, emotion inputs provide additional information to the hyena neural network. This information supplements information received through sensory inputs. The emotions of a hyena along with its sensory inputs and constitute a state. The state in which a hyena finds itself at any given point in time determines its subsequent actions. The following set of experiments was set up within the computational model built in the previous chapter, augmenting the original hyena neural network with emotion inputs. There were mobile gazelles on the field that gave a fitness of 100 points each upon capture, just as in Section 7.3.2. The fitness of a hyena increased by 50 points for each time step during which it was on the same grid cell as the kill site, which represented the reward it got from slowly feeding on the kill before getting killed. Instead of having kill probability depend on the ratio of number of hyenas to number of lions, it was set very simply to $0.15 \times H$, where H was the number of hyenas present simultaneously at the kill site. The total number of cloned hyenas on the field had a fixed value of four. The hyenas could choose to either advance to the kill site and slowly feed on the kill, or hunt gazelles for food. They could also stop feeding on the kill at any time and exit the kill site. The sensory inputs to the hyena neural network consisted of the *x*- and *y*-offsets from the gazelles, the other hyenas, and the kill site at each time step. As seen in the previous chapter, hyena neural networks can evolve to discover the kill probability through evolution using information received through sensory inputs alone.

In the first experiment, the hyena neural networks had no emotion inputs and hence, it served as a control experiment. The hyenas in the second experiment were given a fear

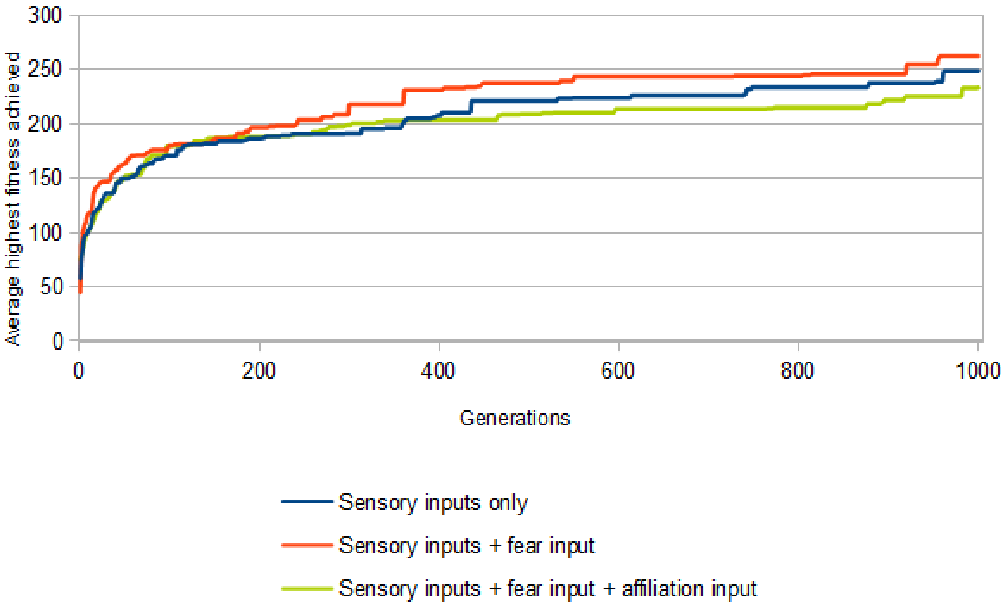

Figure 8.9: **The average highest fitness achieved at each generation for different neural network inputs.** On the *x*-axis is the generation number and the *y*-axis represents the highest fitness seen thus far in the experiment, averaged over ten runs. There was no significant difference in average highest fitness achieved when fear and affiliation emotion inputs were added to the hyena neural network.

input, which was a single real number. This number increased by $100-(x\text{-offset} + y\text{-offset})$ if the hyena was within 20 steps of the kill site, and decreased by half its value every time step. The fear input was hypothesized to decrease the amount of time hyenas spent feeding on the kill and increase gazelle-hunting.

In order for successful mobbing to occur, it is important for the hyenas to overcome the natural fear they have when facing a lion through emotions of affiliation with one another. To simulate affiliation, another real-number input was added to the hyena neural network in the third experiment. This input increased by $100-(x\text{-offset} + y\text{-offset})$ if another hyena was within 20 steps of itself, and also decreased by half every time step. The introduction of the affiliation input was hypothesized to increase the amount of time hyenas

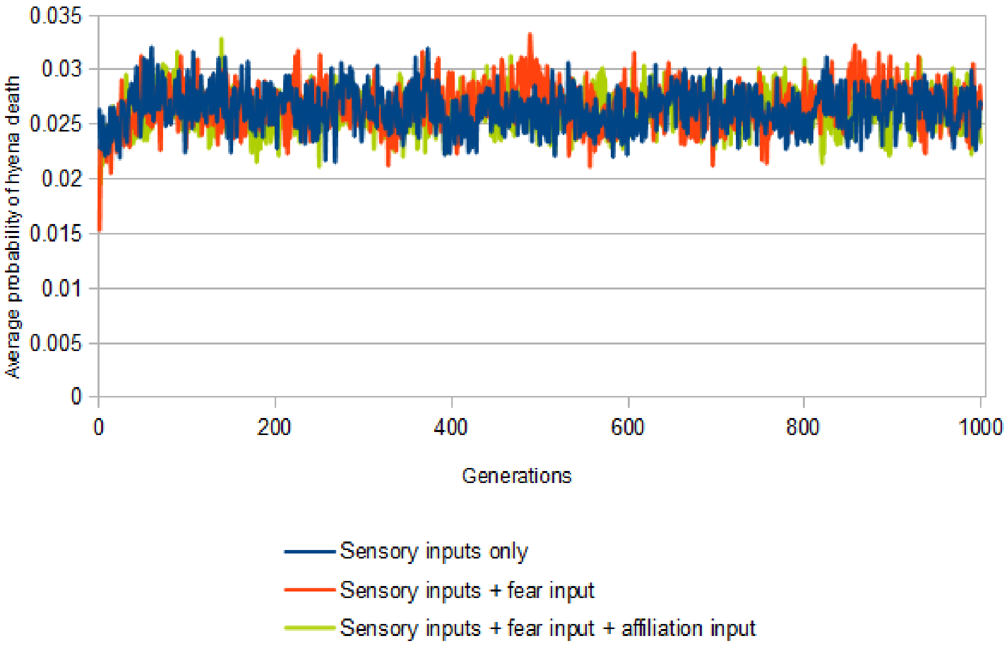

Figure 8.10: **The average fraction of hyenas that were killed in simulation during each generation for different neural network inputs.** The number of generations is on the *x*-axis, and the fraction of hyenas that died, averaged over ten runs, is on the *y*-axis. There was no significant difference in probability of death when fear and affiliation emotion inputs were added to the hyena neural network.

spent at the kill site, while also increasing the number of hyenas present on the scene.

The highest fitnesses attained in each experiment were plotted in Figure 8.9. There did not seem to be any significant difference in the fitnesses achieved by the hyenas in the three experiments. This may be due to the fact that the hyena neural network evolved to predict the kill probability without the help of the emotion inputs. The fear and affiliation inputs did not directly influence the fitness outcome for the hyena and thus, they may have been ignored within the network. Something similar may be seen in Figure 8.10 as well, where the average fraction of hyenas that died per generation was plotted for all three experiments. The number did not vary significantly across experiments.

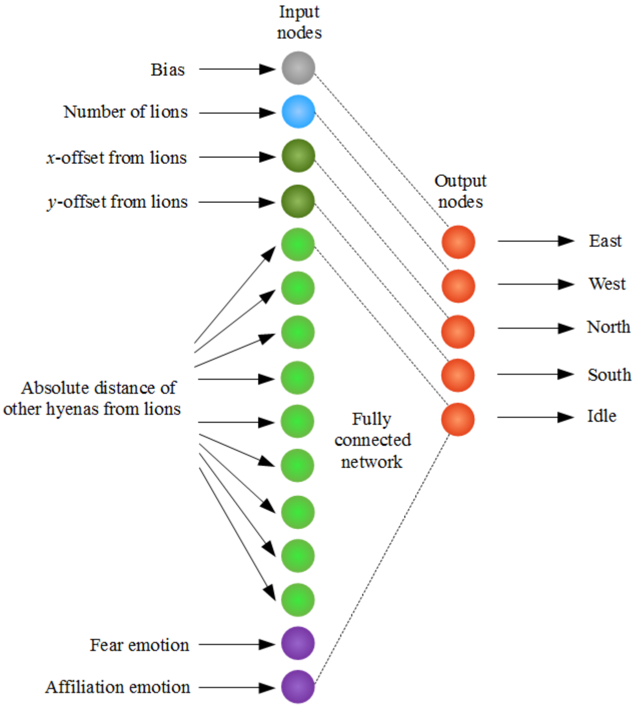

Figure 8.11: **Initial hyena neural network structure for the lion-mobbing task with additional emotion inputs.** Only input and output nodes are shown; the hidden nodes are evolved by NEAT and vary from network to network. Each hyena received its own distances in the x- and y-directions from the lions at each time step. It also received the absolute distances of all other hyenas from the lions, where the maximum possible number of hyenas at any given time in the simulation was 10. If there were fewer than ten hyenas, the nodes corresponding to the absent hyenas were given an input of -1. Two additional inputs representing fear and affiliation were also given to the hyena. Other inputs to the neural network were the number of lions and a bias. The initial network had no hidden neurons and was fully connected, i.e. all input nodes were connected to all output nodes. The five output nodes represented the five actions the hyena could take at every time step: move east, west, north or south, or remain stationary. The only difference from the neural network in the previous chapter is the inclusion of the two emotion inputs.

The results from these experiments suggested that when emotion inputs did not provide any extra information to the hyena neural network, they were ignored by the hyenas. To check what happens when sensory inputs were missing and the hyena had to get all its information about the environment through the emotion inputs, one more set of experiments was designed.

As in the previous section, the number of hyenas was kept fixed at 10 and the number of lions at 1. The hyenas were all placed in specific locations equidistant from the lion in the center of the toroidal grid environment at the outset of the each simulation. The interaction radius was 10 grid cells and the reward for moving into the interaction circle without getting killed was 10 points at each time step. The mobbing reward was 10,000 points and the survival reward was 10 points per surviving hyena.

The first experiment had only sensory inputs, and no emotion inputs for the hyena neural network. Therefore, it served as the control experiment. Sensory inputs to each hyena consisted of the distances in the x- and y-directions to the lion, the absolute distances of all other hyenas from the lion and the number of lions. The second experiment had a fear input in addition to sensory inputs, while the third experiment had both fear input and affiliation input along with sensory inputs. The final experiment had both emotion inputs, but no sensory inputs. Using the fear and affiliation input values in tandem, the hyena neural network should, in theory, have been able to determine whether it was within the interaction circle and whether sufficient numbers of its teammates were present nearby to mount an attack on the lion. The initial hyena neural network structure for this experiment is given in Figure 8.11.

The fear emotion value was set to $100-(x\text{-offset} + y\text{-offset})$ from the lion whenever the hyena was within 20 steps of the lion, but the value decreased by half at every time step when the hyena was not within 20 steps of the lion. Similarly, the affiliation emotion value for a hyena was set to $100 \times H$, where H was the number of hyenas within a 20-step radius from it, but the value was decreased by half at every time step when no hyenas were within 20 steps of it.

From Figures 8.12 and 8.13, it can be seen that the probabilities of interaction and successful mobbing decreased slightly when fear input was added, and even more when affiliation input was added. The differences were not significant, especially for interaction probability, but the trend is explained by the extra overhead required to process the additional network inputs, which may eventually have to be ignored altogether. This trend

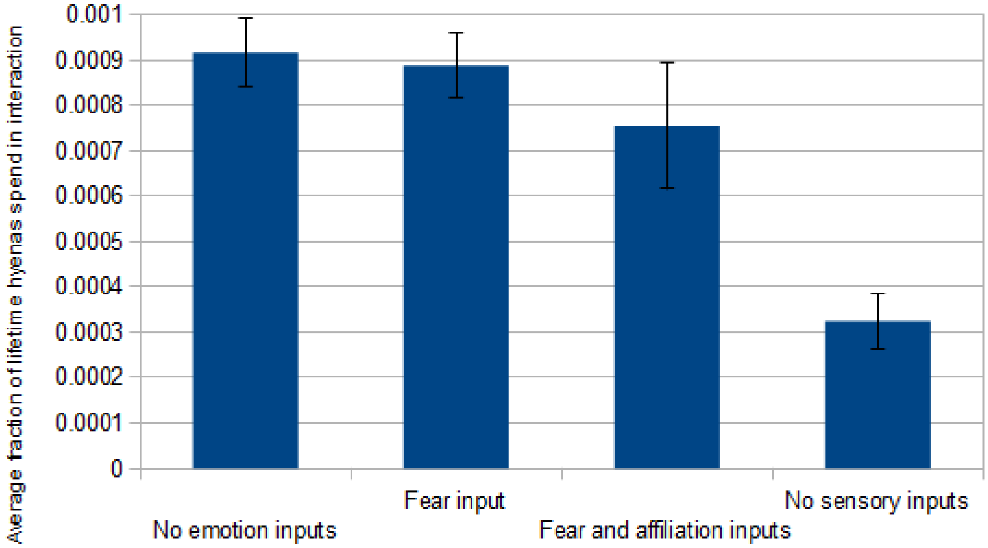

Figure 8.12: **The average probability of interaction with different sensory and emotion inputs.** The inputs which were given to the hyena neural network are on the *x*-axis, and the probability of interaction between hyenas and lions, averaged over ten runs, is on the *y*-axis. The average interaction probability decreased as additional inputs were added to the network. In the final experiment, where there there only emotion inputs and no sensory inputs, the average interaction probability was significantly lower. These results show that emotion inputs added extra overhead to the hyena neural network.

can be seen more clearly for average mobbing probability in the case where both fear and affiliation inputs are present in addition to sensory inputs (Figure 8.13).

The fourth case, where only emotion inputs were given to the network and no sensory input was present, resulted in a significantly lower interaction probability than all the previous experiments (Figure 8.12). The average mobbing frequency was also much lower than in the other cases (Figure 8.13). This decrease cannot be attributed to evolution overhead since there were only two inputs. However, it can be explained by the fact that the calculation of kill probability and the evolution of precise coordination to achieve successful mobbing were far more challenging when the only source of information about the environment were the emotion inputs. The sensory inputs give a direct accounting of the

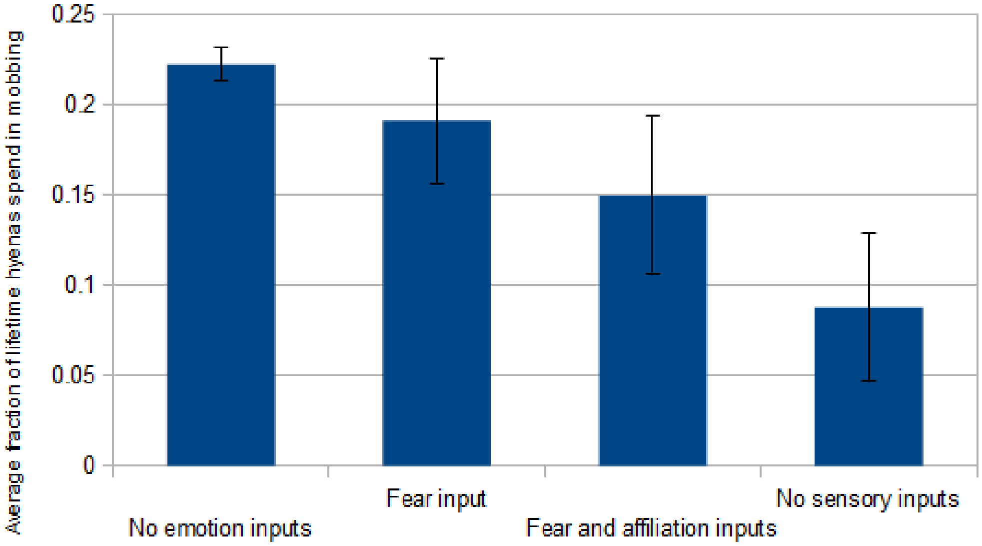

Figure 8.13: **The average probability of successful mobbing with different sensory and emotion inputs.** The inputs that were given to the hyena neural network are on the *x*-axis, and the probability of lion-mobbing, averaged over ten runs, is on the *y*-axis. The average mobbing probability decreased as additional inputs were added to the network. In the final experiment, where there were only emotion inputs and no sensory inputs, the average mobbing probability was much lower, but the difference was not significant. These results show that emotion inputs added extra overhead to the hyena neural network.

distances of various hyenas from the lion, which in turn could be used to count the number of hyenas close to or within the interaction circle. The number of lions was also given as input, and this number was used in the calculation of how many hyenas were required to form a large enough mob. On the other hand, the emotion inputs represented a vague feeling of nearness to lions or to other hyenas, giving rise to either fear or affiliation.

The probability of hyenas dying while attempting to mob lions was plotted in Figure 8.14. The average probability of dying decreased as more inputs were added, and it was significantly lower when both fear and affiliation inputs were present. This decrease may have been partly due to the evolutionary overhead of having two extra neural network inputs. The average interaction and mobbing probabilities decreased, and therefore the probability

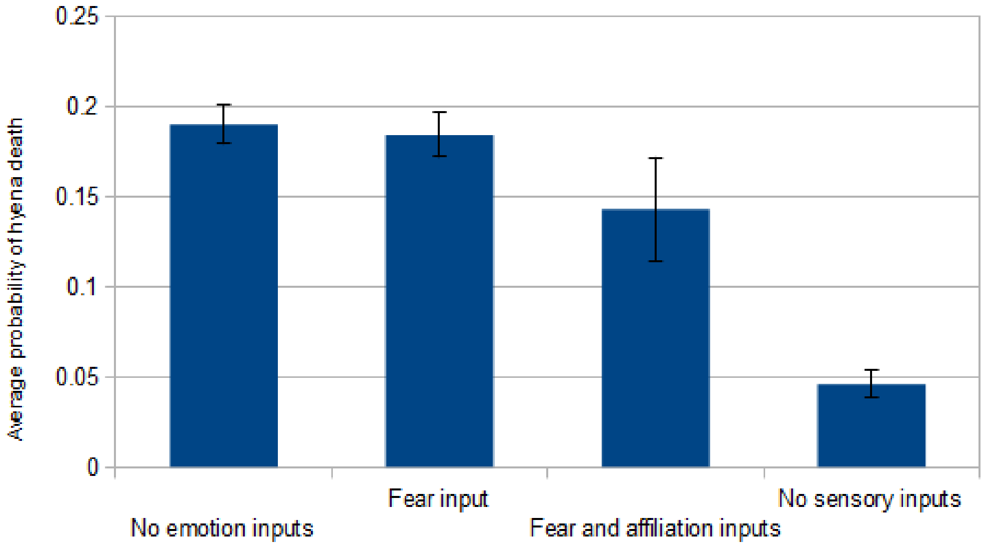

Figure 8.14: **The average probability of hyenas dying with different sensory and emotion inputs.** The inputs that were given to the hyena neural network are on the *x*-axis, and the probability of hyenas dying, averaged over ten runs, is on the *y*-axis. The average probability of death decreased as additional inputs were added to the network. In the final experiment, where there there only emotion inputs and no sensory inputs, the average probability of death was much lower, but the difference was not significant. These results show that emotion inputs added extra overhead to the hyena neural network.

of dying declined as well. The same reasoning holds true for the case when only emotion inputs and no sensory inputs were given to the hyena networks. The decrease in probability of dying may have been partly because of the emotion inputs directing the hyena to avoid the lion entirely while staying close to its conspecifics.

These results imply that extra emotion inputs are not necessary for successful mobbing behaviors to evolve as long as the hyena neural networks can calculate the kill probability through sensory inputs or can discover it through evolution. Emotions should present new information that cannot be obtained from sensory inputs. In any case, the precise coordination of a successful mobbing event was not modeled in this work, and affiliation as well as communication may play an important role in that process. Maybe emotions evolved because they are useful in other situations in the life of a hyena and have just been exapted for this task of lion-mobbing. It is also possible that fear and affiliation are not the only emotions to play important roles in lion-mobbing. Whether these results mean that sensory inputs such as number of lions, distance from lions and number of teammates are themselves representative of fear and affiliation emotions, or whether it means that an emotion is much more complex than just a single number that accumulates value over time and decays slowly without presenting any extra information to the hyena remains to be verified either in real hyenas or using the computational model.

8.4 Conclusion

This chapter made three predictions about lion-hyena interactions using the computational model developed in Chapter 7. The cost of injury or death for hyenas cannot be changed in nature. However, they could be adjusted or even eliminated entirely in simulation. The first prediction made in this chapter was that the removal of fitness penalty for death encouraged hyenas to interact more frequently with lions as well as to mob them successfully. In the second experiment, the hyenas most inclined to attack lions (aggressive hyenas) and those most likely to avoid the lions (diffident hyenas) were cloned and used in different proportions to form the hyena team. The second prediction was that a larger number of aggressive hyenas in the team led to increased interspecific interaction as well as higher rates of mobbing. The third part of this chapter included simple fear and affiliation emotion inputs in addition to sensory inputs in hyena neural networks in order to discover the importance of emotions in mobbing. The prediction was that as long as the emotions did not provide any extra information to the hyena that it could not get from sensory inputs, the frequencies of mobbing and interaction were not affected. This may change when sophisticated communication is introduced into the system. Emotions may be more than just simple numbers. Instead, they may be continuous sequences of information that are regulating the internal state of a hyena. The role of emotions and the importance of individualistic traits in lion-mobbing has not been studied before in nature, and therefore, are hard to predict or replicate.

Chapter 9

Discussion and Future Work

The computational model built in this dissertation simulated various cooperative behaviors of hyenas, including the extremely complex behavior of lion-mobbing. Five out of eight conclusions from observational data listed in Lehmann et al. (2016) and in Chapter 2 were matched in simulation. In the future, the remaining three conclusions may also be modeled.

9.1 The Role of Emotions and Communication in Mobbing

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. A such, it is difficult to simulate emotion inputs to hyena neural networks. Similarly, the different roles of individual hyenas are also hard to replicate in simulation when not much about these roles has been observed in nature. Preliminary experiments were designed in Chapter 8 to incorporate both emotions and individualistic traits, and they resulted in useful predictions that can be checked in nature. Eventually, Multi-Component ESP can be used to model individual hyenas in order to produce a role-based system where each hyena has a significant and distinct part to play in mobbing events. When there are far too few hyenas on the field than are required for a successful mob, no mobbing can occur. Similarly, when there are very large numbers of hyenas on the field, it does not matter how or when they attack the lions, because their attack is very likely to be successful. Therefore, the most interesting and fascinating social dynamics and behaviors should emerge in medium-sized groups of hyenas, somewhere in between these two extremes.

Emotions may play a larger role once communication is also introduced in the hyena team. They may also need to be represented in an entirely new way in the cognitive architecture of the simulated hyenas along with a purpose-built communication system to aid in lion-mobbing and other complex cooperative tasks. Preliminary work in simulating emotion inputs and communication signals in cooperative tasks has already been done by Rawal et al. (2012) and Rawal et al. (2014). The hormone-to-emotion and emotion-to-behavior mappings obtained from the endocrinological data described in Chapter 2 can be used to constrain this cognitive architecture.

In real-life hyenas, many kinds of vocal and tactile signals are very important in recruiting hyenas into the mob, raising their emotional level to a heightened state to overcome fear and to attack the lions all at once. Affiliation and fear affect the responsiveness of hyenas to these communication signals. Various modules such as those for perception, communication, emotions and decision-making should therefore be included in the eventual cognitive architecture for hyenas during cooperative tasks. This architecture can then serve as a starting point for further research in identifying the evolutionary steps that led to its development, and steps that evolution may take in the future, as well as research on understanding the social structure and interactions of the hyenas, both interspecific and intraspecific, in more detail. These potential future directions are described below.

9.2 Social Ranks in Hyena Society

As described in Chapter 2, hyenas live in large clans with complex social structures. The clan is matriarchal and consists of several matrilines, i.e. descendants of several females who may or may not be related to one another. A hyena has a certain rank associated with it from birth, and this rank is inherited from its mother. This rank never changes during its lifetime (unless there is a major upheaval within the clan). All the females are ranked above all the males in the clan. Males usually emigrate to a different clan shortly after reaching adulthood. This emigration places them at the bottom of the ranking system in the new clan. The rank is extremely important as everything in hyena society depends on it. Higher-ranked hyenas always get the first share of all food, and mate more often with the mate of their choice, and their offspring also get better feeding opportunities. As a result, higher-ranked offspring far outnumber lower-ranked offspring. There is no evidence to suggest how such a biased system evolved in nature or why it is sustained with hardly any fighting to challenge it based on physical strength. Although such a ranking system seems counterproductive to survival for the low-ranked hyenas, there must be some evolutionary advantage to it. The cognitive architecture developed for simulating complex cooperative behaviors like lion-mobbing may be of help in studying the early evolutionary processes that led to and maintain hereditary social ranking as well.

9.3 Studying the Early Evolution of Cooperation in Animals

Discovering and building the best cognitive architecture for lion-mobbing will result in a model that can be used to predict and replicate other complex cooperative tasks carried out by animals in nature. For example, spotted hyenas live in clans that are highly territorial. Occasionally, all the members of a clan cooperate to fight another clan over resources or territory. This behavior can be simulated by coevolving two clans of hyenas with the same cognitive architecture that will be developed for lion-mobbing. The part that social ranking plays in these large-scale battles can also be explored. It may also be possible in the future to study hyena brains and identify the parts corresponding to different modules in the cognitive architecture. This way, it may be possible to discover how the cognitive architecture is implemented in the brain.

A fascinating project would be to study the stepping stones in the evolution of the spotted hyenas that led to their current cognitive architecture. It is interesting to note that the three closest relatives of the spotted hyena, the brown hyena (*Hyaena brunnea*), the striped hyena (*Hyaena hyaena*) and the aardwolf (*Proteles cristata*), do not display such cooperative skills. All these species are scavengers or insectivores, and hunt alone, if at all. Only spotted hyenas hunt live prey, and only they sometimes team up and communicate to capture larger prey. Only spotted hyenas live in extensive clan-based societies with complex hierarchical structure with significant cooperation and competition. This pattern suggests that somehow their evolution has taken a different path, one with the emergence of social cognition and sophisticated cooperative strategies. This path may serve them well in the future. Once social structures start to form, there is a strong pressure for communication and recognition skills to emerge. The frontal lobe, which is involved in coordination, memory, planning and motivation, is already expanded in spotted hyenas compared to the other hyena species (Sakai et al., 2011). Moreover, spotted hyenas are already capable of recognizing conspecifics and detecting their emotional states through communication. Lion-mobbing thus indicates an emerging cognitive function that could lead to higher cognitive abilities in further evolution, including a theory of mind. Modeling such progress both in the past and in the future is a most interesting direction of future work.

The ultimate objective of using computational evolution to analyze an animal model is to extrapolate the results to more complex brains, including that of humans. This study could result in a computationally verified theory of how the interplay of communication, perception and emotions can lead to cooperative behavior. Such a theory would be useful in understanding how to ameliorate behavioral problems and suggest therapeutic measures. Such problems may include issues with cooperative tasks, communication, and excessive or flat emotions. This study may also help in understanding mob behavior and how to control it. In addition, the results should be useful for constructing teams of artificial agents or robots that can respond to the environment in a realistic way and cooperate to perform difficult tasks.

9.4 Conclusion

This chapter discussed the future directions that the research in this dissertation could take. One potential direction is the simulation of different emotions and sophisticated communication in hyenas during a mobbing event. Hyenas use different signals to call their conspecifics and to excite one another to a frenzy in order to mob the lions. Emotions play an important role in this process. Communication is also used to coordinate the final attack. Another future research area is the modeling of the complex social structure of hyenas to investigate the early evolution of social ranks and the factors that affect it. Ultimately the work from this dissertation may be extrapolated to more complex behaviors, including those of humans. It may also be used to construct realistic video game agents or robots that can cooperate to perform complex tasks.

Chapter 10

Conclusion

Spotted hyenas exhibit unusually complex cooperative behavior for their general level of intelligence. Their hunting behaviors formed the basis of the predator-prey environment and neuroevolutionary architecture constructed in Chapter 4, which was used throughout this dissertation for various simulated cooperative tasks. Observational data about their occasional coordinated attacks on lions to steal their kill helped in the creation of a computational model to replicate lion-hyena interactions as well as to make predictions about lion-mobbing behaviors not analyzed in nature. This final chapter discusses the contributions made in this work and concludes the dissertation.

10.1 Contributions

The focus of this dissertation was the evolution of complex cooperative behaviors and the project started with predator and prey teams in Chapter 4. The predator-prey task showed that it was possible to set up both cooperative and competitive coevolution in the same system simultaneously. This coevolution led to a sustained arms race between the predator and prey teams, and sophisticated cooperative predatory and evasive behaviors emerged. Additionally, this task also required the development of a new neural network architecture called Multi-Component ESP in order to build the role-based cooperative predator and prey teams.

Chapter 5 utilized the same toroidal grid environment and Multi-Component ESP architecture as in Chapter 4 to investigate the factors affecting the evolution of cooperation within the predator team when given a choice between prey that must be caught using cooperative hunting and prey that can be caught individually. It was found that the net return from capturing different prey, the way in which this reward is shared among the predator team and the method of communication played important roles in the evolution of cooperative hunting.

The Multi-Component ESP architecture is particularly useful when a limited number of agents have to act in specific roles in a cooperative task. The NEAT neuroevolutionary method is useful in optimization tasks because it is basically an evolutionary computation technique with neural networks as the individuals being evolved. Therefore, different neural network structures can be seen to affect evolution differently. Similarly, in animals, brain structure and interconnection between brain processes impact the development of different behaviors. van der Maas et al. (2006) hypothesized that more interaction or interconnection among brain processes leads to more general intelligence. This hypothesis was verified in Chapter 6 for a simple handwritten digit recognition task using neural networks with different connection densities. Prolonged evolution of neural networks past the point where their performance in a task plateaued was found to result in better performance in a different task, which was related to the training task. Thus, the prolonged evolution had a positive impact on the evolution of general intelligence in the handwritten digit recognition task.

The significantly more complex task of lion-mobbing requires precise coordination on the part of hyenas. This task is hypothesized to be on a very novel evolutionary step for the hyenas and therefore, a computational model was built in Chapter 7 to study lion-hyena interactions and the evolution of mobbing behaviors. Several environmental factors were discovered to affect mobbing rates and probability of interaction, including number of hyenas, number of lions, presence of adult male lions and prey size. These same conclusions were also drawn through observation of hyenas in nature.

Chapter 8 made three predictions about lion-hyena interactions using the computational model developed in Chapter 7. The first prediction concerned the effect of injury and death cost on mobbing and interaction rates. In the experiments designed for that prediction, the probalities of interaction and mobbing increased significantly with decrease in death cost. The second prediction was that a larger number of aggressive hyenas in the team led to increased interspecific interaction as well as higher rates of mobbing. Aggressive hyenas were those hyenas most inclined to attack the lions, while diffident hyenas were those inclined to avoid the lions. Further study of individual roles and traits of hyenas during lion-mobbing events needs to be conducted in nature and in simulation to understand the process better. The third part of this chapter aimed to verify the hypothesis that fear and affiliation emotions are necessary for the hyenas to develop efficient coordination for mobbing. The results of this experiment showed that as long as the emotions did not provide any extra information to the hyena that it could not get from sensory inputs, the frequency of mobbing and interaction was not affected. These results showed that emotions are not simple numbers but need to be modeled better in the future. They also play an important role in mobbing behaviors once communication is added to the model.

10.2 Conclusion

The evolution of complex cooperative behaviors in simulation helps in the study of such behaviors in nature, while observations of cooperative behaviors of animals in turn inform simulations. A computational model was built in this dissertation to study the evolution of sophisticated coordinated mobbing and other collaborative tasks, and to simulate realistic hunting behaviors and lion-hyena interactions. Endocrinological studies done on individual hyenas will help determine exactly what part communication and emotion play in these behaviors. Such characterization will make it possible to build a cognitive architecture that will include perception/communication, emotion, and decision-making modules whose interconnections will be discovered through neuroevolution. Such a cognitive architecture should lead to insights on how cooperation is established in animals and humans. In the future, it can be used to study what evolutionary stepping stones led to such behaviors and cognitive function in general. It can also be used to build robotic teams that can coordinate their actions and cooperate to perform complex tasks, or to develop intelligent, adaptive video game characters.

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