EXPERIMENTAL INVESTIGATIONS OF COGNITIVE ABILITIES IN A SOCIALLY COMPLEX MAMMAL, THE SPOTTED HYENA (*CROCUTA CROCUTA*)

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ABSTRACT

EXPERIMENTAL INVESTIGATIONS OF COGNITIVE ABILITIES IN A SOCIALLY COMPLEX MAMMAL, THE SPOTTED HYENA (*CROCUTA CROCUTA*)

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The evolution of intelligence is a topic that has fascinated us ever since Charles Darwin first proposed that humans share many mental traits with other animals, and that the differences in cognitive abilities between humans and other animals are a matter of degree, not kind. Currently, the leading theory to explain the evolution of intelligence is the Social Intelligence Hypothesis (SIH), which posits that complex cognitive abilities evolved due to selection pressures associated with life in complex societies. This hypothesis was originally conceived to explain the evolution of intelligence in primates, and most work on this topic has focused on primates. However, if the SIH is correct, then many of the cognitive abilities observed in primates should also occur in non-primate mammals that live in primate-like societies.

In this dissertation, I test this prediction of the SIH by experimentally investigating several previously unexamined cognitive abilities of spotted hyenas (*Crocuta crocuta*) and then comparing the results of these studies to those from primate systems. Spotted hyenas are an ideal system for testing the SIH as they share many life history traits with cercopithicine primates including complex, stable, and hierarchical societies. Spotted hyenas and primates last shared a common ancestor 90-100 million years ago. Thus, similar cognitive abilities in these taxa could be attributed to convergent evolution and would provide important support for the SIH.

Spotted hyenas live in fission-fusion societies in which individuals travel, rest, and forage in subgroups that change frequently in size and composition. Numerical imbalances during intergroup conflicts can be more extreme in these societies when compared to more cohesive social groups. Thus, an ability to assess numerical advantage should be highly advantageous for individuals in fission-fusion societies. I used playback experiments to test whether spotted hyenas follow predictions of game theory and assess numerical advantage when presented with calls from varying numbers of simulated intruders. As predicted, hyenas responded more cautiously when they were outnumbered and were more willing to take risks when they had the numerical advantage. Additionally, hyenas showed comparable abilities to those demonstrated in chimpanzees and African lions, both of which live in fission-fusion societies.

I then examined technical intelligence and learning in both wild and captive spotted hyenas by investigating their responses to a novel technical problem. These experiments illuminated the role of the diversity of initial exploratory behaviors, persistence and neophobia in determining innovative problem-solving success. I found that individuals who exhibited a wider range of exploratory behaviors when first confronted with the novel problem, and who approached the novel object faster, i.e., were less neophobic, were more successful in solving the problem. Hyenas showed trial-and-error learning and became significantly faster at solving the problem as they gained experience with it. Lastly, I experimentally demonstrated that spotted hyenas learn from watching conspecifics solve a novel technical problem and that they use the same, relatively simple, mechanism of social learning as vervet monkeys and macaques.

These experiments inform our understanding of the cognitive abilities of hyenas. Moreover, comparing these studies to those from primates helps us understand the selection pressures that have shaped the evolution of intelligence. Generally, these results support the SIH by providing evidence that primates and carnivores with similarly complex social systems have evolved similarly complex social, technical and numerical cognitive abilities.

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I was fortunate to attend Cornell University as an undergraduate and was able to learn from some of the most eminent biologists in the country. In particular, Tom Gavin, Kelly Zamudio, and Harry Greene introduced me to the wide diversity of life on this planet. I fondly remember tromping through the woods in Tom's field biology class and watching the great salamander and newt migrations to breeding ponds with Kelly. I will never be able to look at a snake and not think of Harry and his passion for these animals. Harry has always been incredibly supportive of my career, and I have really enjoyed our many conversations.

It was my first animal behavior course at Cornell University that opened my eyes to the possibility of a career studying the behavior of wild animals. After attending the first fascinating lecture in that course, I changed my career plans from pre-med to graduate studies in Zoology, and I've never looked back. I thank my professors in that course, Paul Sherman and Tom Seeley, for giving me my first glimpse of the fascinating world of animal behavior. Paul Sherman became my mentor at Cornell. He suffered through my first PowerPoint presentation, educated me on the importance of levels of analysis, encouraged me when I shared my dreams of studying the behavior of wild elephants, advised me on graduate programs, and helped me to get one of my first field jobs. I owe a great debt of thanks to all my professors from Cornell and hope to pay it back by giving the same encouragement to my future students.

Upon graduating from Cornell, I spent three years working on various research projects

before starting graduate school. Kevin Pilz took a chance on an eager undergraduate and helped me to get some very valuable first research experience. Erik Patel offered me an opportunity of a lifetime, studying an endangered lemur in Madagascar, and it was this project that gave me a love for fieldwork. Stacy Rosenbaum and Lisa Kelley shared in all of the highs and lows of that life-changing experience, and I will never forget their friendship. John Hoogland taught me the science of fieldwork. Jack Bradbury and Greg Budney introduced me to the incredibly rich world of animal communication and gave me valuable training in recording and analyzing vocalizations. I thank all of the staff at the Macaulay Library at the Cornell Lab of Ornithology. I particularly want to thank Melissa Groo for introducing me to Joyce Poole and helping me to realize my dream of studying elephants in the wild. Joyce Poole and Petter Granli introduced me to Kenya and to the wonders of Amboseli National Park. They were kind enough to invite me into their home, and I will never forget the year I spent working with them on ElephantVoices. I also want to thank Cynthia Moss, Harvey Croze, Soila Sayialel, Norah Nijraini, Katito Sayialel, and Purity Wanjiko for letting me stay in their camp in Amboseli, use their office in Nairobi and join them on their observations of the elephants.

I was first introduced to the fascinating and bizarre world of spotted hyenas during my year in Amboseli. Jaime Tanner, Heather Watts and Wes Dowd would often let me accompany them on their hyena observation sessions, and it was their enthusiasm for hyenas and their high praise of Kay Holekamp and her lab at Michigan State University that led me to do my Ph.D. with Kay. I am very grateful to Kay for the many opportunities she has provided to me. I greatly admire Kay's brilliant scientific work and her commitment to her students, and I feel very fortunate to have had her as an advisor. Due to Kay's mentorship, I have grown into a much better scientist, writer, and teacher. I thank her for the time she has devoted to my education, and I only hope that

I can have the same impact on my future students that she has had on me.

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GENERAL INTRODUCTION

The field of animal cognition is the study of the “mechanisms by which animals acquire, process, store, and act on information from the environment” (Shettleworth, 2009). It encompasses concepts such as perception, learning, memory, decision-making and problem-solving (Shettleworth, 2009). Psychologists and biologists have historically studied animal cognition using two distinct approaches. Traditionally, psychologists were interested in testing whether or not captive animals possess human-like cognitive abilities, and if so, determining how they accomplish specific tasks (Shettleworth, 2009). Psychologists were most concerned with ensuring internal validity and thus were not as likely to choose study animals based on their evolutionary relationships as were biologists (Shettleworth, 2009). In contrast, ethologists and behavioral ecologists were focused more on wild animals. Specifically, they tended to follow Tinbergen’s (1963) four levels of analysis (mechanism, development, functional, and evolutionary history) when questioning why wild animals behave in the way they do (Shettleworth, 2009). However, in the last 30 years a combination of the two approaches has emerged into what is now referred to as the study of comparative cognition (Kamil, 1987; Shettleworth, 2009). Psychologists have become more interested in studying ecologically meaningful cognitive abilities and in choosing study species based on shared evolutionary histories. On the other hand, biologists have become more interested in understanding the cognitive processes underlying behaviors observed in the wild and in using the experimental techniques pioneered by psychologists to investigate how animals perceive their environment, learn about their environment, and solve ecologically important problems (Shettleworth, 2009).

In this dissertation, I present experiments that were inspired by the current field of comparative cognition. I implement experimental techniques pioneered by psychologists to answer questions regarding the mechanisms and functions of sophisticated cognitive abilities in both wild and captive populations of a socially complex, nonprimate mammal, the spotted hyena. I then compare the cognitive abilities of spotted hyenas to those of primates with similarly complex social systems in order to help elucidate the evolutionary drivers of intelligence.

Two major groups of hypotheses have been put forward to explain the evolution of complex intelligence. The first group of hypotheses focuses on ecological explanations for the evolution of intelligence and suggests that sophisticated cognitive abilities evolved due to complex physical environments, such as the need to remember when and where food will be available, known as the 'cognitive mapping hypothesis' (Milton, 1981), or the need to use tools to extract food from nuts or shells, known as the 'extractive foraging hypothesis' (Parker and Gibson, 1977). The second group of hypotheses, most notably the social intelligence hypothesis, posits that sophisticated cognitive abilities evolved due to life in complex societies, such as the need to recognize, respond appropriately to, and manipulate the actions of conspecifics (Byrne and Whiten, 1988; Humphrey, 1976; Jolly, 1966). The social intelligence hypothesis has gained favor through comparative primate research, which suggests that the evolution of complex intelligence has been more strongly driven by social than physical aspects of the environment (Amici et al., 2008; Byrne, 1994; Cheney and Seyfarth, 1990; Dunbar, 1992, 1995). Additionally, it has been postulated that challenges posed by conspecifics and other individuals often require the use of highly flexible and responsive cognitive strategies and cannot usually be solved by evolved 'rules of thumb' (Byrne and Whiten, 1988; Dunbar, 1998). It has also been proposed that these flexible cognitive strategies can more easily be applied to challenges in other domains, such as those posed by the physical environment, than more rigid mechanisms. Thus, selection for social dexterity may have led to the development of large brains and complex social intelligence, but it is likely that the resulting cognitive abilities are beneficial for solving problems in other domains as well (Byrne and Bates, 2007).

If the social intelligence hypothesis is correct, then many of the complex cognitive abilities observed in primates should also occur in non-primate mammals that live in primate-like societies (de Waal and Tyack, 2003; Schultz and Dunbar, 2006; Tomasello and Call, 1997). However, few studies have focused on testing complex cognitive abilities in nonprimates and this lack of data limits knowledge of the generality of the social intelligence hypothesis (Engh et al., 2005; Harcourt and Waal, 1992; Kamil, 1987). In this dissertation, I test the social intelligence hypothesis by investigating cognitive abilities of a socially complex non-primate mammal, the spotted hyena, and then comparing my results to those from primates with similarly complex social systems.

Spotted hyena societies are similar to those of cercopithicine primates in terms of group size, hierarchical structure, and patterns of competition and cooperation (Frank, 1986; Holekamp et al., 2007; Holekamp, 1999, 2007). Specifically, hyenas and cercopithicine primates live in stable social groups in which group members recognize each other individually (Benson-Amram et al., 2011; Holekamp, 1999) and cooperate to defend group territory (Boydston et al., 2001; Harcourt and Waal, 1992). In both taxa, females are philopatric whereas males disperse (Cheney and Seyfarth, 1983; Henschel and Skinner, 1987; Pusey and Packer, 1987; Smale et al., 1997). Social groups contain multiple adult males as well as several matrilines of adult female relatives and their offspring. Additionally, societies of both taxa are characterized by a strict linear dominance hierarchy, in which an individual’s social rank determines its priority of access to resources (East and Hofer, 2001; Frank, 1986; Tilson and Hamilton, 1984; Wrangham and Waterman, 1981). Juveniles inherit a rank directly below that of their mother (Holekamp and

Smale, 1991) and individuals in both taxa learn and acquire their rank using the same mechanisms, such as maternal support in agonistic interactions and coalition formation (Engh et al., 2000; Horrocks and Hunte, 1983). Given their remarkably similar social systems, similarities found in cognitive abilities in spotted hyenas and cercopithicine primates could be attributed to convergent evolution, and would support the social intelligence hypothesis (Engh et al., 2005).

In accordance with the social intelligence hypothesis, spotted hyenas have demonstrated levels of *social* intelligence similar to those of cercopithicine primates. Hyenas recognize third party relationships (Engh et al., 2005), form coalitions (Smith et al., 2010), reconcile after aggressions (Wahaj et al., 2002) and cooperative to solve problems (Drea and Carter, 2009). Whereas hyenas excel cognitively in the social domain, no one has experimentally assessed their *technical* problem-solving skills, which are a key component of complex cognition (Reader and Laland, 2003). In this dissertation, I extend our current knowledge of the complex cognitive abilities of spotted hyenas by experimentally testing aspects of their numerical and technical intelligence. Additionally, I examine their social learning abilities, a critical, and yet previously untested, aspect of spotted hyena social intelligence.

An additional and powerful test of the social intelligence hypothesis involves comparing the cognitive abilities of closely related species that differ in their sociality. The social intelligence hypothesis predicts that the species with more complex social systems will exhibit more sophisticated cognitive abilities than their less social but closely related counterparts. Although this test is beyond the scope of the dissertation presented here, it is work that I plan to focus on in the future.

OVERVIEW OF CHAPTERS

Numerical Assessment

Spotted hyenas, like chimpanzees (*Pan troglodytes*), African lions (*Panthera leo*), spider monkeys (*Ateles geoffroyi*), elephants (*Loxodonta africana*) and many other gregarious carnivores, live in fission-fusion societies (Holekamp et al., 2007; Holekamp et al., 1997a). In fission-fusion societies, individuals occupy and defend a communal territory (Boydston et al., 2001; Harcourt and Waal, 1992). However, unlike in cohesive social groups, individuals in fission-fusion societies are rarely all found in the same place at the same time and instead they forage, rest, and travel in smaller subgroups, which change frequently in both size and composition. Fission-fusion societies are thought to be particularly cognitively demanding because they require that individuals quickly assess relationships among group members after periods of separation (de Waal and Tyack, 2003). Additionally, extreme numerical imbalances can occur during intergroup conflicts, which are potentially lethal. For example, if a larger subgroup from one clan encounters a smaller subgroup from another clan, the larger subgroup can attack at relatively low cost to themselves (Manson and Wrangham, 1991). Such conditions can therefore be expected to increase selection for the ability to assess numerical odds, or the ratio of number of territorial defenders to number of intruders, in order to gauge the costs of engaging in aggressive intergroup interactions.

Game theory predicts that individuals should assess numbers of potential opponents before engaging in aggressive interactions, particularly when numerical odds can determine outcomes of such interactions (Maynard Smith, 1982; Maynard Smith and Parker, 1976; Maynard Smith and Price, 1973). Thus, an ability to assess relative numbers of opponents should be highly advantageous in species living in fission-fusion societies (Hauser, 2001; Manson and Wrangham, 1991; Wrangham, 1999). In Chapter 1, I tested the following predictions of game theory: 1) that contest asymmetries can alter the cost/benefit ratio of entering into aggressive interactions (Maynard Smith, 1979), 2) that individuals should be most willing to engage in contests when they have the greatest numerical advantage (Wilson et al., 2001), and 3) that animals living in fission-fusion societies should be able to assess numerical odds (Hauser, 2001; Manson and Wrangham, 1991; Wrangham, 1999). In a playback experiment, I investigated the abilities of wild spotted hyenas to assess numerical advantage by presenting contact calls produced by one, two or three unknown hyenas, or ‘intruders’, to individuals in the study clans. I then compared the results of this study to similar studies on chimpanzees (Wilson et al., 2001) and African lions (McComb et al., 1994), both of which live in fission-fusion societies. If the social intelligence hypothesis is correct, then spotted hyenas should show abilities to assess numerical advantage that are comparable to those seen in chimpanzees and lions.

Hyenas conformed to predictions of game theory and the social intelligence hypothesis by increasing vigilance to playbacks of multiple unfamiliar intruders. Furthermore, hyenas distinguished not just between calls produced by one versus multiple intruders, but showed a fine-grained ability to assess numerical advantage, and they responded with increasing levels of vigilance to calls produced by one, two and three unknown intruders. Hyenas also took more risks by approaching the speaker when they outnumbered calling intruders. Lastly, this study provides experimental evidence that spotted hyenas can use contact calls to distinguish among individuals. These findings were published in *Animal Behaviour* (Benson-Amram et al. 2011).

Innovative Problem Solving

In Chapter 2, I turned my focus from numerical cognition to technical intelligence. Specifically, I investigated determinants of innovative problem solving in wild spotted hyenas. Innovation is a key characteristic that enables individuals to deal with novel social and ecological challenges (Hinde and Fisher, 1951; Kohler, 1925; Kummer and Goodall, 1985; Laland and Reader, 1999). However, our understanding of the importance of innovation for animals in their natural habitat is very limited because experimental investigations of innovation have been restricted to only a few taxa, and have focused on captive animals (Reader and Laland, 2003). Additionally, despite the important ecological and evolutionary consequences of innovation, we still know very little about the traits that vary among individuals within a species to make them more or less innovative.

I investigated the abilities of wild hyenas to solve a novel technical problem and I tested the hypothesis that individuals who engage in a greater range of initial behavioral strategies when confronted with a novel problem are more likely to solve that problem (Caruso, 1993; Skinner, 1981). I presented untrained wild hyenas with a puzzle box baited with meat. To access the meat hyenas moved a simple, laterally opening latch in one direction, allowing a door to open. I conducted 417 trials on 62 individuals, of which only 9 were able to solve the problem. The number of trials per individual ranged from 1–30, and the mean number of trials per individual was 6.71 ± 1.01 SE. Eighteen individuals participated in at least 8 trials during the 12-month study period. Successful individuals exhibited trial-and-error learning and decreased the amount of time required to open the puzzle box over successive trials. Exploration diversity, or the number of exploratory behaviors an individual exhibited when interacting with the puzzle box, and neophobia were the two major predictors of problem-solving success.

Domain-specific cognitive abilities?

Interestingly, the low overall success rate of hyenas on the novel technical problem suggests that, although wild spotted hyenas exhibit a remarkable ability to solve social problems, they show considerably less facility at solving the technical food-acquisition problem I presented to them. Wild cercopithicine primates appear to show the same discrepancy in their abilities to solve social vs. technical problems. The impressive social intelligence of wild baboons and vervet monkeys is well documented; however, experimental work on both species suggests relatively poor technical intelligence (Cheney and Seyfarth, 1985; Laidre, 2008; van de Waal and Bshary, 2010). One possible explanation for the poor technical problem-solving abilities exhibited by hyenas, baboons and vervet monkeys is that selection pressures associated with life in complex societies led to the evolution of domain-specific intelligence, such that these species are more socially than technically intelligent. In contrast, these species may not be less technically intelligent, but may be less successful at solving novel technical than social problems because they are more strongly affected by novelty in the technical problem-solving situation that we presented to them. Tests of social intelligence often investigate how well animals deal with novel configurations of familiar stimuli, such as conspecific vocalizations (Benson-Amram et al., 2011; Cheney and Seyfarth, 2007) and these familiar stimuli would not elicit the same neophobic responses as a puzzle box or other novel apparatus.

Comparing problem-solving abilities of captive and wild hyenas

In Chapter 3, I expand on the research described in Chapter 2 by investigating whether wild and captive spotted hyenas differ in their ability to solve the same novel technical problem. This work served two major goals: First, captive animals are typically less neophobic and more innovative than their wild counterparts (Reader and Laland, 2003; Visalberghi et al., 2003). If captive hyenas are significantly better than wild hyenas at solving the novel technical problem, then I can conclude that hyenas are not lacking the cognitive abilities necessary to solve this problem, and that wild hyenas are likely constrained by neophobia. Second, the vast majority of experimental work investigating innovative problem solving has been conducted on captive populations (Reader and Laland, 2003). There is some evidence that results from studies on captive animals cannot fully inform our understanding about how individuals in the wild will respond to novel challenges (Ramsey et al., 2007; Webster and Lefebvre, 2001). However, only three studies have compared problem-solving abilities in wild and captive populations of the same species using a single experimental paradigm and all three of these studies were conducted on birds (Bouchard et al., 2007; Gajdon et al., 2004; Webster and Lefebvre, 2001). Thus, it is unclear 1) how to apply the current literature on innovation to animals in their natural habitats, and 2) why captive and wild animals might differ in their problem-solving abilities and innovative tendencies. In Chapter 3, I presented the same novel technical problem to wild and captive spotted hyenas and then compared their problem-solving abilities. I then discuss whether these results support the various hypotheses that have been proposed to explain discrepancies in problem-solving abilities between wild and captive individuals.

I found that wild and captive populations show important differences in their abilities to solve the novel technical problem I presented to them. Captive hyenas were significantly more diverse in their initial exploratory behaviors and more successful at solving the novel problem than wild hyenas. I was able to rule out hypotheses suggesting that these differences result from excess energy and excess time of captive animals. I conclude that captive hyenas were more successful than wild hyenas at solving a novel technical problem because captive individuals are less neophobic and experience fewer distractions in their environment than their wild counterparts.

Social Learning

Social learning is a critical aspect of social intelligence that has received a lot of attention in studies of primate cognition (Bugnyar and Huber, 1997; Caldwell and Whiten, 2004; Call and Tomasello, 1995; Custance et al., 1999; Custance et al., 2001; Day et al., 2003; Whiten, 1998), but has not yet been examined in spotted hyenas. Social learning is a key component of complex cognition because it enables individuals to benefit from the expertise and knowledge of group members and is the basis for formations of traditions and culture (Day et al., 2003; Humphrey, 1976; Jolly, 1988; Russon, 1997; Whiten and Byrne, 1997; Whiten and Van Schaik, 2007). In Chapter 4, I further test the prediction of the social intelligence hypothesis that primate and non-primate mammals with similarly complex social systems will demonstrate comparable cognitive abilities by investigating the social learning abilities of spotted hyenas and comparing our results to those from studies on cercopithicine primates.

During the puzzle box experiments with the wild hyenas, described in Chapters 2 and 3, there were some indications that hyenas might be demonstrating social learning of the problem-solving task. I therefore set-up the experiment with the captive hyenas to specifically investigate whether or not hyenas show evidence of social learning when confronted with a novel technical problem. Eleven captive hyenas were ‘observers’ and had the opportunity to watch a conspecific, or ‘demonstrator,’ open the puzzle box just prior to each of their trials. Five hyenas served as ‘controls’ and did not have any opportunities to observe conspecifics interact with the puzzle box. Two hyenas served as demonstrators and consistently exhibited different patterns of exploratory behavior when interacting with the puzzle box. Thus, I also investigated the mechanism hyenas utilize when acquiring socially learned information. For example, I inquired whether observer hyenas showed evidence of imitation, by copying the actions of the demonstrator, or whether the actions of the demonstrators simply caused observers to become more attracted to a specific part of the puzzle box, a mechanism known as localized stimulus enhancement (Shettleworth, 2009).

I found no effect of social learning on problem-solving success or the diversity of initial exploratory behaviors in either the captive or the wild population. However, individuals in both populations were less neophobic after observing a conspecific interact with the puzzle box. Additionally, observing a conspecific solve the puzzle led both wild and captive hyenas to spend more time working on the latch side of the puzzle box. This demonstrates that hyenas likely acquire socially learned information via localized stimulus enhancement and not imitation. In other words, observers learned to focus more intensively on the functionally relevant aspect of the puzzle box, but did not show significant similarities to their demonstrator in the behavioral strategies they employed when interacting with the puzzle box. Thus, the social learning abilities of spotted hyenas appear to be based on relatively simple mechanisms. When I compare these results to equivalent studies done on cercopithicine primates I find that these results support the social intelligence hypothesis because cercopithicine primates appear to use the same, simple, but still powerful, social learning mechanisms as the hyenas (Ducoing and Thierry, 2005; Leca et al., 2010; van de Waal and Bshary, 2010, 2011; Zuberbuhler et al., 1996).

The research presented in this dissertation is the result of collaborative efforts and each chapter has been prepared as a manuscript with the input of co-authors. Thus, I use the term "we" instead of "I" throughout the remainder of this dissertation.

CHAPTER 1

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CHAPTER 1

NUMERICAL ASSESSMENT AND INDIVIDUAL CALL DISCRIMINATION BY WILD SPOTTED HYENAS (*CROCUTA CROCUTA*)

INTRODUCTION

Game theory predicts that animals should assess the strength and relative numbers of potential opponents before engaging in aggressive interactions (Maynard Smith, 1982; Maynard Smith and Parker, 1976; Maynard Smith and Price, 1973; Nash, 1951; Von Neumann and Morgenstern, 1944). The ability to assess numerical advantage should be prevalent in species with intergroup conflicts, particularly those living in fission–fusion societies (Hauser, 2001; Manson and Wrangham, 1991; Wrangham, 1999). Fission–fusion societies are stable social units in which individual group members are often found alone or in small subgroups and in which subgroup size and composition change frequently over time. Numerical imbalances may thus be more extreme in fission–fusion societies than in more cohesive social units. This variation in subgroup size may lead to higher intergroup aggression, involving potentially lethal attacks, because numerically superior subgroups can attack at relatively low cost to themselves (Manson and Wrangham, 1991). Such conditions can therefore be expected to increase selection for the ability to assess numerical odds, or the ratio of number of defenders to number of intruders, in order to gauge the costs of engaging in aggressive intergroup interactions.

Previous playback experiments showed that wild lions, *Panthera leo*, and chimpanzees, *Pan troglodytes*, both of which live in fission–fusion societies, spontaneously demonstrate rudimentary abilities to assess numerical advantage. Lions were able to distinguish between one and three foreign conspecifics, and they responded more aggressively when faced with fewer intruders and when their own group size was relatively large (McComb et al., 1994). Lone adult male lions were also slower to approach the sound source when hearing roars produced by three unknown males within their territory than when hearing roars produced by just one male (Grinnell et al., 1995). Similarly, chimpanzees varied their responses to calls produced by a single foreign male in their territory based on the number of male group members present in the listeners' party (Wilson et al., 2001); parties with three or more males consistently vocalized and approached the sound source whereas parties with fewer males stayed silent and rarely approached. Thus, both lions and chimpanzees adjust their responses to calls produced by foreign intruders based on numerical odds.

We conducted playback experiments to test the hypothesis that wild spotted hyenas can assess numerical advantage when hearing calls produced by one, two or three foreign intruders. Similar to lions and chimpanzees, spotted hyenas live in fission–fusion social groups, called clans, which contain up to 90 individuals that cooperate to defend a group territory (Boydston et al., 2001; Henschel and Skinner, 1991; Holekamp et al., 1997a; Holekamp et al., 1997b). In addition, spotted hyenas, lions and chimpanzees all have potentially lethal intergroup conflicts in which numerical advantage often determines outcomes (Kruuk, 1972; Kruuk and Macdonald, 1985; Packer et al., 1990; Wilson et al., 2002; Wrangham, 1999). Given the similarities among these species, we predicted that hyenas would demonstrate an ability to assess numerical advantage comparable to that demonstrated by lions and chimpanzees. Based on predictions of game theory that contest asymmetries can determine outcomes (Maynard Smith, 1979) and that individuals should be more willing to engage in contests when the benefits outweigh the costs (Wilson et al., 2001), we predicted that hyenas would take the greatest risks when they encountered the best numerical odds, and that they would be most cautious when confronting the worst numerical odds.

We used sound stimuli produced by one, two and three intruders to test whether hyenas can discriminate among various numbers of calling individuals. A variety of birds and mammals can discriminate among specific numbers of physical objects (Brannon and Terrace, 1998; Capaldi and Miller, 1988; Lyon, 2003; Pepperberg, 2006). However, we know little about the precision of animals' discrimination abilities when presented with variable numbers of acoustic stimuli. The ability of hyenas to distinguish precisely among one, two, or three different voices would indicate that they can discriminate among, and keep track of, calls produced by individual conspecifics. Individual discrimination based on vocalizations may be obligatory for arboreal species because group members are often out of sight of one another (Ghazanfar and Santos, 2004). The same logic may apply in species with fission–fusion societies, in which group members are often separated. We thus predicted that spotted hyenas would discriminate among individuals based on their calls.

We also tested whether hyenas show individual differences in their responses to calls produced by unknown intruders. If hyenas respond solely based on numerical odds, individuals should not vary significantly from other hyenas in how they respond to each treatment. However, hyenas may show significant variation among individuals if traits such as social rank also influence their responses. For example, the benefits of territorial defense and participation in intergroup contests may vary among individual group members, and individuals might modify their participation based on the benefits they are expected to receive (Kitchen, 2004, 2006; Kitchen and Beehner, 2007; Nunn, 2000). Earlier work with lions (Heinsohn and Packer, 1995) and black howler monkeys, *Alouatta pigra* (Kitchen, 2006), revealed marked variation among individuals in their responses to simulated intruders. Spotted hyena societies are rigidly structured by linear dominance hierarchies in which an individual's social rank determines its priority of access to food. Because food intake affects reproductive output among females, high-ranking females enjoy greater reproductive success and offspring survival than lower-ranking females (Hofer and East, 2003; Holekamp et al., 1996). If differential food access within the territory affects the value of the territory for adult female hyenas, high-ranking females should take more risks when hearing calls produced by territorial intruders, whereas low-ranking females should respond more cautiously and engage in fewer risky or aggressive behaviors. We tested whether individual adult females varied in their responses to calls produced by variable numbers of intruders, and whether responses could be predicted by social rank.

METHODS

Subjects and Study Site

We conducted playback experiments on members of two spotted hyena clans in the Masai Mara National Reserve (henceforth 'Mara') in southwestern Kenya. We collected data for this study from July 2007 to May 2008, and throughout this period we monitored the study clans daily during 0530–0900 and 1700–2000 hours. We determined territorial borders for the two study clans following methods from Boydston et al. (2001).

We identified individuals by their unique spots and other natural markings. We determined sex from the dimorphic shape of the glans of the erect phallus (Frank, 1990). We estimated age to ±7 days for all individuals born in both study clans, as described by Holekamp et al. (1996). We considered hyenas to be juveniles up to 24 months of age, and adults when they were older than 24 months. We used all-occurrence sampling (Altmann, 1974) to determine the social rank of each adult based on its position in a matrix of outcomes of dyadic, agonistic interactions, including unsolicited appeasements (Holekamp and Smale, 1990; Smale et al., 1993).

Acoustic Stimuli

We used spotted hyena whoop vocalizations as acoustic stimuli; each vocalization is a series of discrete calls that together form a whoop bout. Whoops are produced by both male and female hyenas of all ages, and function as long-distance contact calls (East and Hofer, 1991; Kruuk, 1972). To ensure that stimulus whoops were produced by individuals unknown to hyenas in our study clans, we obtained whoops recorded in Tanzania, Malawi and Senegal from the British Library. We obtained six different stimulus whoop bouts of high acoustic quality, all from the only extant subspecies of spotted hyenas. The British Library provided no information regarding the age, sex or identity of the hyenas that produced these whoop bouts. Therefore, it is possible that the same individual may have produced more than one of these calls. However, this seems highly unlikely, particularly because the whoop bouts recorded from single individuals in Tanzania and Malawi appear to be more similar to one another than the four whoop bouts recorded from individuals in Senegal (Fig. 1.1). In addition, previous research suggests that the structure and number of harmonics in whoops vary among individuals (East & Hofer 1991), and visual inspection of spectrograms of the whoop bouts from each caller revealed substantial variation (Fig. 1.1).

It is also possible that hyenas would respond to the playbacks based on the age or sex of the caller. Minimum fundamental frequency is a major acoustic characteristic distinguishing whoops of callers from different age and sex classes (Theis et al., 2007). Although minimum fundamental frequency varied among our stimulus whoops (Table 1.1), with the possible exception of whoop bout C, all whoops fell within the adult range (Theis et al., 2007). Juvenile whoops contain fewer and more widely spaced harmonics than adult whoops (East and Hofer, 1991), yet bout C has more harmonics than the other bouts, so it is likely that all the stimulus whoops were produced by adults. Nevertheless, we examined the acoustic properties of each whoop bout in detail (Table 1.1), and we incorporated variation in acoustic variables into our statistical analyses. We also included caller ID as a covariate in our analyses of behavioral responses to these stimuli (see Statistical Analyses).

Whoop vocalizations have acoustic properties that vary with call context and influence conspecific responses (Theis et al., 2007). To control for these effects, we constructed stimulus whoop bouts in which all interwhoop intervals were 2 s long. We also controlled for the number of calls per bout despite no evidence that this measure varies with call context or affects conspecific responses (Theis et al., 2007). The mean ± SE number of calls per bout was 9 ± 1.36 in the stimulus whoop bouts from the British Library, so we constructed bouts with nine calls to minimize manipulation of the sound stimuli. To do so, we removed or added calls as necessary, randomly using calls from the middle portion of the bout to avoid removing terminal calls, which often have a different structure (East and Hofer, 1991; Theis et al., 2007). We edited all stimulus whoop bouts using Raven (Charif et al., 2004) and Praat (Boersma and Weenink, 2004) software, and applied a filter function in Raven (Charif et al., 2004) to remove background noise.

Stimulus Configuration

The playback of whoops produced by foreign hyenas simulated intruders in the territories of our subject hyenas. To avoid confounding stimulus intensity with the number of callers

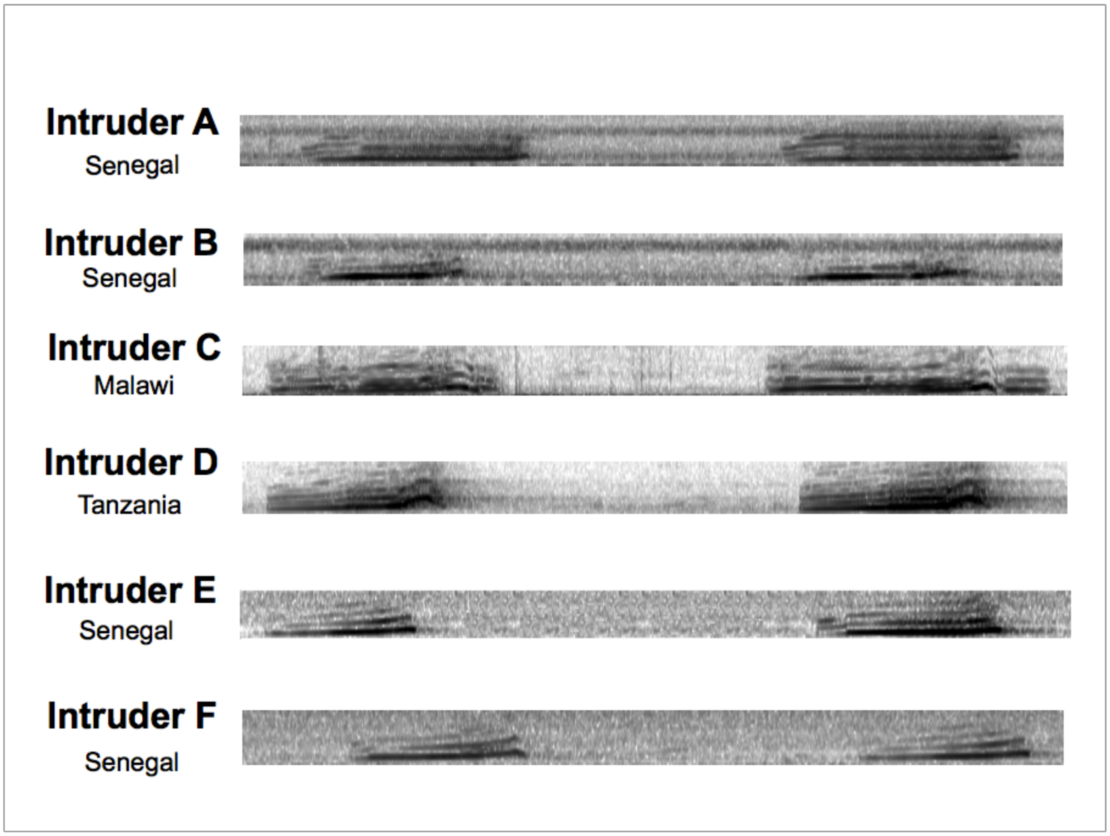

Figure 1.1. Spectrograms showing the structure of two whoop calls within a bout from each stimulus sound. For each caller, two individual whoops are shown, separated by an interwhoop interval. All spectrograms have the same frequency scale of 0–2 kHz

Table 1.1

Acoustic properties of stimulus whoops assessed in the present study

ID	Location	Min. fund. freq. (Hz)	Peak fund. freq. (Hz)	Whoop dur. (s)	Bout dur. (s)	RMS amp.*	Max amp.*	Max freq. (Hz)	Max power (dB)	Harmonics
A	SEN	264.5	443.3	2.01	36.8	2531.5	8158.1	354.1	117.4	4
		±4.9	±9.8	±0.16		±59.3	±254.8	±9.6	±0.3	
B	SEN	255.9	481.1	1.2	29.3	2078.8	6448.6	333.4	115.9	3.1
		±7.4	±25.1	±0.06		±156.7	±334.8	±11.1	±0.6	±0.2
C	MAL	320.6	509.9	1.86	34.8	1908.5	7860.2	448.7	115.8	5.4
		±10.4	±13.5	±0.07		±115.2	±491.6	±12.9	±0.8	±0.3
D	TZ	195.7	703.6	1.22	29.6	2623.6	11611±	373.2	121.0	3.4
		±4.4	±10.6	±0.03		±363.3	1374.8	±14.4	±0.9	±0.2
E	SEN	285.9	469.9	1.29	31.0	2959.3	8758.8	373.2	117.6	3.8
		±4.9	±15.9	±0.12		±459.4	±1175.9	±14.4	±1.5	±0.2
F	SEN	274.3	471.7	1.40	30.7	1474.2	5668.3	382.8	112.2	3.5
		±2.8	±25.7	±0.08		±159.5	±519.2	±15.1	±1.0	±0.2
GLM†		$F_{5, 48}$ = 43.1 P<0.01	$F_{5, 48}$= 28.4 P<0.01	$F_{5, 48}$ = 21.4 P<0.01		$F_{5, 48}$= 4.3 P<0.01	$F_{5, 48}$= 6.5 P<0.01	$F_{5, 48}$= 8.9 P<0.01	$F_{5, 48}$= 9.6 P<0.01	$F_{5, 48}$= 19.2 P<0.01

All measurements are means ± SE of all whoops within a bout, except for bout duration, which is the mean ± SE duration of a bout of nine whoops.

* RMS (root-mean-square) amplitude and maximum amplitude are measured in dimensionless sampling units, for more information see Charif et al. (2004).

† GLMs were conducted for each measure to compare overall variation among test stimuli.

(Hauser 2001), we conducted playback experiments using consecutive and nonoverlapping calls as test stimuli. To control stimulus duration, we played each focal hyena three consecutive whoop bouts, varying the identities of the callers but not the number of whoop bouts heard. There were three treatment conditions, each of which featured whoop bouts produced by one, two, or three different intruders. In the 1-intruder treatment we repeated a whoop bout produced by one individual three times. The 2-intruder treatment began with a whoop bout produced by one individual, followed by a whoop bout produced by a different individual, followed by a whoop bout produced by either the first or second individual. The 3-intruder treatment presented whoop bouts produced by three different individuals.

The order in which individuals were exposed to the three different treatments was randomized. The particular sound stimulus played was also essentially random, although we attempted to avoid playing the same calls to subjects multiple times. We used five stimulus configurations as sound stimuli for the 1-intruder treatment, six configurations for the 2-intruder treatment, and two configurations for the 3-intruder treatment. Stimulus configurations were used in an average ± SE of 3 ± 0.58 trials and individual hyenas heard each stimulus recording in an average ± SE of 1.19 ± 0.019 trials. Individual hyenas heard a specific recording no more than two times during the 11-month study period. Hyenas were involved, either as a focal subject or as an arriving individual during group trials, in an average ± SE of 1.94 ± 0.20 trials (range 1–5 trials). To reduce habituation to playback stimuli, we separated playbacks to any individual by at least 7 days, and the mean ± SE time between trials within individuals was 52.39 ± 9.17 days.

Playback Set-up

We conducted playbacks around dawn and dusk (0600–0900 and 1730–1900 hours) when wind was negligible, hyenas were active and ambient lighting conditions permitted high-quality data collection. We conducted playbacks near the center of the focal hyena's territory to increase the likelihood that the hyena would view the unfamiliar calls as coming from intruders. In addition, we conducted playbacks at least 250 m from active communal den sites.

Sex, age and social rank were known for each playback subject. We scored the body condition of each individual from 1 (thinnest) to 4 (fattest) using a previously established scale that reflects recent food consumption (Watts and Holekamp, 2008). To minimize variation in response due to motivation or hunger, we only conducted trials when individuals were in the two intermediate body conditions (normal or fat) and not when they were in the extreme body conditions (gaunt or obese).

We played whoop bouts from an iPod mounted in a concealed BOSE portable SoundDock; sound stimuli were broadcast from a research vehicle to which the hyenas were well habituated. Following methods used by Watts et al. (2010), we broadcast sounds 95.95 ± 1.60 m (mean ± SE) from the focal hyena(s). We measured distance from the focal individual(s) to the speaker at sound onset and again at sound offset using a Bushnell Yardage Pro Sport laser range finder. All sound stimuli were played at maximum volume, and at natural sound pressure levels (mean ± SE maximum pressure at 1 m = 109 ± 0.5 dB, measured with a Digital Sound Level Meter manufactured by Radio Shack set at a C-weighting). The playbacks sounded natural to our ears, and the hyenas responded to the broadcasts, as described below. Our methods follow those used in earlier playback experiments on hyenas and olive baboons, *Papio hamadryas anubis* (Lemasson et al., 2008; Watts et al., 2010).

Data Extraction from Videotaped Playbacks

We videotaped focal hyenas during the 3 min before sound onset and throughout the ‘response period’, which started at sound onset and lasted for at least 3 min after the sound stimulus ended. The duration of the sound stimulus (mean = 95.11 s, range 87–110 s) made it possible for the focal hyenas to assess the information presented to them by the callers while the sound was playing. We thus divided the response period into two intervals: (1) the ‘playback period’, during which the sound stimulus was playing, and (2) the remainder of the trial after sound offset.

We extracted the following behavioral measures from each videotaped playback trial: time orienting towards the speaker, response duration, latency to travel, direction of travel, distance moved and any instances of focal hyenas vocalizing. A hyena was orienting when its head was off the ground and facing the speaker, such that both ears were visible to the observer in the research vehicle. We defined response duration as the time from when a hyena first changed its behavior after sound onset until it ceased responding to the sound, or until the hyena went out of sight, whichever occurred first. A hyena that never altered its behavior during the playback trial was assigned a response duration of zero. We defined latency to travel as the time from sound onset until the focal hyena began moving. A hyena that failed to travel was assigned a latency of 3 min; failure to orient was handled in the same fashion. We recorded direction of travel as either approaching the speaker by moving towards it, or avoiding the speaker by moving away from it. Distance moved was the distance in meters that a focal hyena traveled from its starting position relative to the location of the speaker. In addition to the above measures, we also recorded the identity, age, sex and time of arrival for all hyenas that arrived at the playback location after sound onset. S.B.A., V.K.H. and S.L.D. extracted data, and interobserver reliability was $r = 0.98$ or higher.

Sample Size

We conducted 39 playback trials: 35 to 12 lone adult female subjects and four to groups of adult hyenas. For nine adult females, we obtained matched samples in all three treatments when the subjects were alone. All trials to lone adult females started with an initial group size of one. In six of the 35 playbacks to lone adult females, conspecifics arrived at the playback location after sound onset and these trials had final group sizes greater than one. We therefore had 10 trials with final group sizes greater than one.

In our analyses of orienting behavior, our sample size was 34 trials. We excluded one trial on a lone hyena because several hyenas arrived while the sound stimulus was playing, which altered the focal hyena's orienting behavior. However, we included orienting data from the other five trials, in which conspecifics arrived at the playback location after sound stimulus offset. We could not extract orienting data for playbacks to groups due to inadequate video quality resulting from the wide angle needed to keep all group members on the screen at all times.

Statistical Analyses

Responses by lone hyenas to variable numbers of intruders

We compared the proportion of time lone hyenas spent orienting towards the speaker before sound onset and during the playback period when hearing the calls of one versus multiple intruders. We used generalized linear mixed models (GLMM) with proportion of time spent orienting as the continuous response variable and the following fixed predictor variables: period (either the 3 min preplayback period, or the playback period), intruder number (one versus multiple), and the interaction between period and intruder number. For response variables that only occurred in the period after sound onset (distance moved, response duration and latency to travel), intruder number was the only fixed predictor variable. To control for pseudoreplication, focal hyena identity (ID) was included as a random effect in all models.

We examined the abilities of hyenas to differentiate among calls produced by one, two and three intruders by comparing orienting behavior of lone hyenas across the three treatments. We only included orienting behavior in this analysis because very few lone hyenas moved after sound onset. For clarity, we refer to the 1-, 2- and 3-intruder treatments as T1, T2 and T3, respectively, and we refer to the first, second and third whoop bouts within each treatment with numerical subscripts. We compared orienting behavior during each round of whoop bouts across all three treatment conditions (e.g. $T1_1$ versus $T2_1$ versus $T3_1$) using a GLMM with proportion of time spent orienting during each whoop bout as a continuous response variable and with whoop bout duration and number of intruders as fixed predictor variables.

We next determined how the orienting behavior of lone hyenas within each treatment condition changed as they heard each successive whoop bout (e.g. $T1_1$ versus $T1_2$ versus $T1_3$). We used a GLMM with proportion of time spent orienting as the continuous response variable, and with whoop bout duration, whoop bout number and trial number as fixed predictor variables. Trial number was included as a predictor to determine whether hyenas were habituating to the playback stimuli in later trials. Our sample sizes for each treatment condition were 12 trials for T1, 12 trials for T2 and 10 trials for T3.

Individual differences in vigilance

To investigate individual variability in orienting responses across all trials, we used only the nine adult females for which we had matched samples across all three treatments. We used a likelihood ratio test to compare generalized linear models (GLM) with and without the ID of the focal hyena as a random effect. We also included social rank of the focal hyena as a covariate in the model.

Influence of intruder identity

We examined variation in the acoustic properties of the stimulus whoop bouts using GLM with the acoustic property of interest as the continuous response variable and intruder ID as a fixed predictor variable. The acoustic properties and their measurements are listed in Table 1. We then investigated whether the identity of the intruder influenced variation in orienting responses among lone hyenas. We examined responses to the first whoop bout across all treatment conditions, because these responses were expected to be the same. We used a likelihood ratio test to compare models with and without the ID of the intruder as a random effect. We then added each acoustic property as a fixed covariate to determine whether the magnitude of the random effect would decrease and would therefore show which acoustic properties were causing variation in orienting responses.

Effect of listener group size

We next examined the effects of listener group size and numerical odds on the probability that hyenas would approach the speaker. We focused on approach behavior in group trials because orienting behavior could not reliably be extracted for all individuals present in group trials. To avoid pseudoreplication, each group trial was assigned only one response value per analysis. We scored each group as ‘approaching the speaker’ when over 50% of the individuals present in a trial decreased their distance to the speaker. We performed a logistic regression with approach (Y/N) as the binomial response variable, arrivals (Y/N) as a binomial fixed effect, ID of the focal hyena as a random effect, and final group size, numerical odds at the end of the trial and rank of the focal hyena as continuous fixed effects. We separated highly correlated predictor variables into different models, and alternative models were compared using Akaike's Information Criterion (AICc) values corrected for low sample sizes. A smaller AICc value indicated a better-fitting model (Crawley, 2007).

We conducted all GLM, GLMM, logistic regressions and likelihood ratio tests in R 2.6.2 (R Development Core Team, 2006). Mean values are given ± SE. We considered results significant when $P < 0.05$.

RESULTS

Responses by Lone Hyenas to Variable Numbers of Intruders

In all treatments, lone females spent a greater proportion of time orienting towards the speaker after sound onset than during the 3 min prior to sound onset ($t_{53} = -10.35$, $P < 0.0001$; Fig. 1.2). Lone hyenas also spent significantly more time orienting towards the speaker when hearing the calls of multiple intruders than when hearing the call of a single intruder ($t_{53} = -3.04$, $P = 0.004$; Fig.1. 2). The interaction between playback period and intruder number was also significant ($F_{1, 53} = 5.53$, $P = 0.022$), showing that responses of focal hyenas to the playback depended upon the number of hyenas calling in the sound stimulus. Too few hyenas continued to orient during the 3 min period after sound offset to include those data in our analyses.

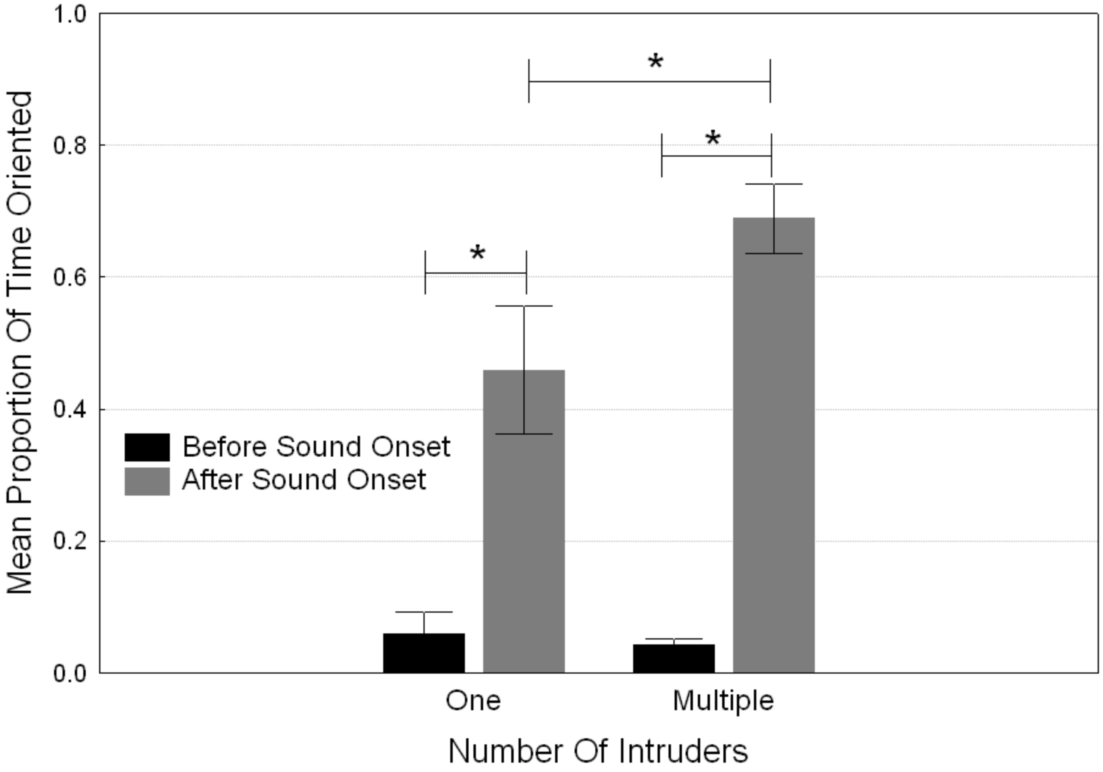

Figure 1.2. Mean ± SE proportion of time spent oriented towards the speaker in 34 trials with 12 lone hyenas during the 3 min before and after sound onset of playbacks of whoops from one intruder (*N* = 12 trials on 11 hyenas) or multiple intruders (*N* = 22 trials on 11 hyenas). $^*P < 0.05$

Lone hyenas varied in their orienting responses to calls produced by one, two and three intruders. We expected that hyenas in all three treatments would respond similarly to the first whoop bout because the first whoop bout of every trial was produced by a single unknown intruder. As expected, hyenas showed the same orienting response to the first whoop bout, regardless of treatment condition ($F_{2,20} = 1.87$, $P = 0.18$; Fig. 1.3). Focal hyenas then changed their orienting behavior after hearing the first whoop bout, depending on the sound stimuli they heard during the remainder of the playback trial. The grey bars in Fig. 1.3 show that hyenas in the 1- and 2-intruder treatments responded differently to the second whoop bout ($T1_2$ versus $T2_2$: $t_{19} = 2.59$, $P = 0.018$). Hyenas in the 2-intruder treatment oriented longer to the speaker than those in the 1-intruder treatment, most likely because they heard a whoop bout produced by an intruder they had not heard previously, whereas those in the 1-intruder treatment heard the same whoop bout as before. Likewise, the white bars in Fig. 1.3 show that hyenas in the 1-intruder treatment spent significantly less time oriented towards the speaker than hyenas in the 3-intruder treatment during the third whoop bout ($T1_3$ versus $T3_3$: $t_{19} = 2.27$, $P = 0.035$).

Hyenas' orienting responses demonstrated that they distinguished between whoops they had heard before and whoops to which they had not previously been exposed. Specifically, hyenas became less vigilant and spent less time oriented towards the speaker when they heard repeated whoop bouts produced by the same individual, even when whoops were not produced consecutively ($T1_1$ versus $T1_3$: $t_{22} = -2.49$, $P = 0.021$; $T2_2$ versus $T2_3$: $t_{21} = -2.27$, $P = 0.034$; Fig. 1.3); hyenas increased vigilance levels and time spent oriented only when they heard a new whoop bout that indicated an unfamiliar individual ($T3_1$ versus $T3_2$: $t_{17} = 2.17$, $P = 0.045$; $T3_1$

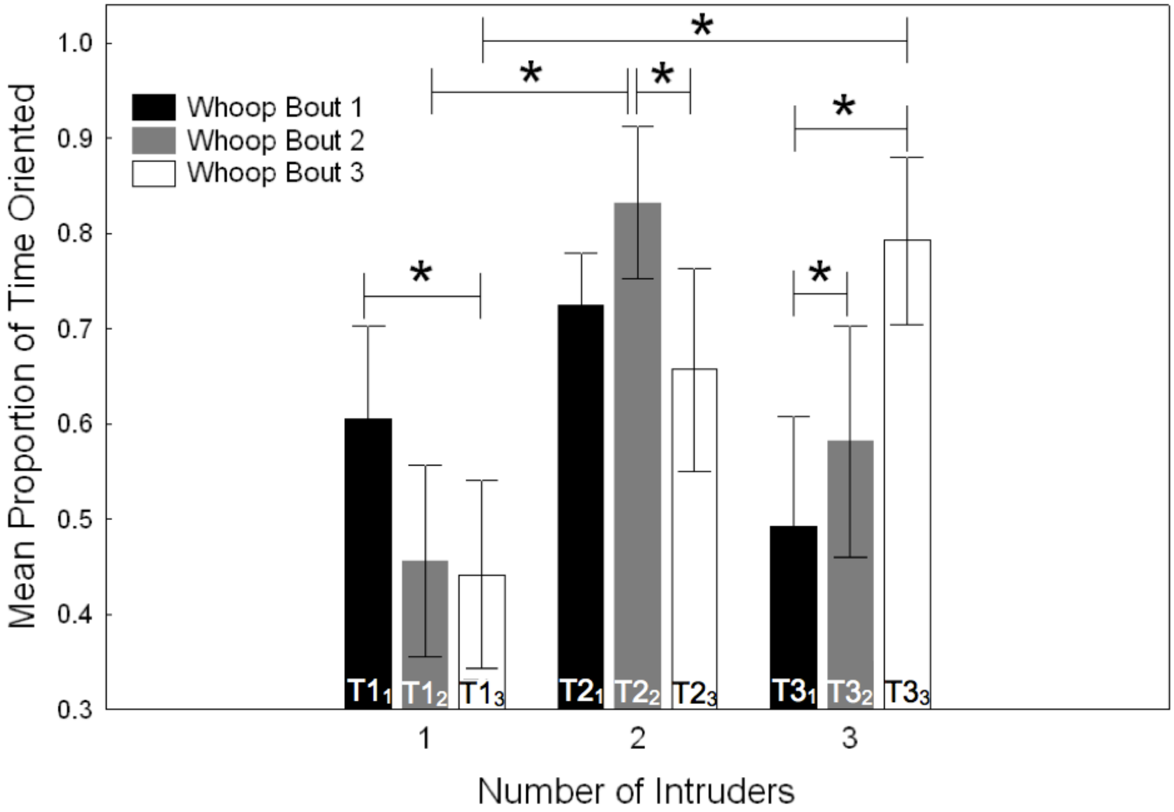

Figure 1.3. Mean ± SE proportion of time spent oriented towards the speaker in 34 trials with 12 lone hyenas during each whoop bout when hearing calls from one intruder (*N* = 12 trials on 11 hyenas), two intruders (*N* = 12 trials on 10 hyenas), or three intruders (*N* = 10 trials on 10 hyenas). T1, T2 and T3 refer to the 1-, 2- and 3-intruder treatments, respectively, and the numerical subscripts refer to the first, second and third whoop bouts within each treatment. $^*P < 0.05$

versus T3$_3$: $t_{17} = 3.29$, $P = 0.0043$).

Trial number was not a significant predictor of orienting behavior ($F_{3,7} = 0.16$, $P = 0.92$), demonstrating that hyenas did not habituate to the playback stimuli in later trials. Furthermore, hyenas did not show signs of habituation across whoop bouts within a trial because rather than diminishing responses in all our treatments, as would be expected during habituation, our subjects' responses intensified when they heard new voices in second or third bouts.

Focal hyenas vocalized in only three playback trials and, therefore, we were unable statistically to examine vocalizing as a response variable. However, the three instances of vocalizing occurred in response to three different stimulus configurations and were emitted by three different subjects. Thus, we saw no indication that a particular treatment or recording elicited vocalizations, or that any individual focal hyena vocalized more than others. We also saw no effect of treatment condition on response duration among lone hyenas ($F_{2,20} = 0.58$, $P = 0.57$). This finding is likely because significant orienting differences across treatments during the playback period were mitigated by a lack of orienting differences, and differences in other response variables included in this metric, across treatments once the playback period ended. We also found no effect of treatment condition on latency to travel ($F_{2,20} = 0.27$, $P = 0.77$) or distance moved ($F_{2,20} = 1.25$, $P = 0.31$) in trials involving lone hyenas. Hyenas that did approach the speaker usually waited until the sound stimulus ended, or until they heard a whoop bout repeated (in the 1- and 2-intruder treatments), before moving from their starting position (mean latency to travel = 146.89 ± 61.54 s).

Individual Differences in Vigilance

Individual hyenas varied in their orienting behavior across treatment conditions, with some individuals showing higher overall vigilance than others (likelihood ratio test: $\chi^2_1 = 50.55$, $P < 0.0001$; Fig. 1.4). Social rank was not a significant predictor of the mean proportion of time spent orienting ($F_{1,7} = 0.30$, $P = 0.60$). Some adult females showed high levels of variability in orienting behavior across all treatments (hyenas with large standard errors in Fig. 1.4), but we also found relatively low variance in roughly half of the adult females (hyenas with small standard errors in Fig. 1.4). Interestingly, females with low variance tended to be highly vigilant, on average.

Influence of Intruder Identity

Given that we found significant variation among intruders in the acoustic properties of their whoop calls (see Table 1.1), we inquired whether the identity of the intruder influenced orienting responses among lone hyenas. A likelihood ratio test revealed a significant difference in time spent orienting between linear mixed effect models with and without intruder ID as a random effect ($\chi^2_1 = 5.47$, $P = 0.019$). To determine which acoustic properties were responsible for this effect of intruder ID, we added each acoustic property to the model individually, and found that the addition of whoop duration, bout duration or RMS amplitude as a covariate eliminated the effect of intruder ID (whoop duration: $\chi^2_1 = 0.57$ $P = 0.45$; bout duration: $\chi^2_1 = 1.29$, $P = 0.26$; RMS amplitude: $\chi^2_1 = 0.28$, $P = 0.59$). RMS amplitude is defined as the root mean square, or 'effective' amplitude, which is calculated by taking the square-root of the mean of the square of all instantaneous amplitude values of the call (Charif et al., 2004). Bout duration is a consequence of differences in whoop duration when interwhoop intervals are equalized, so

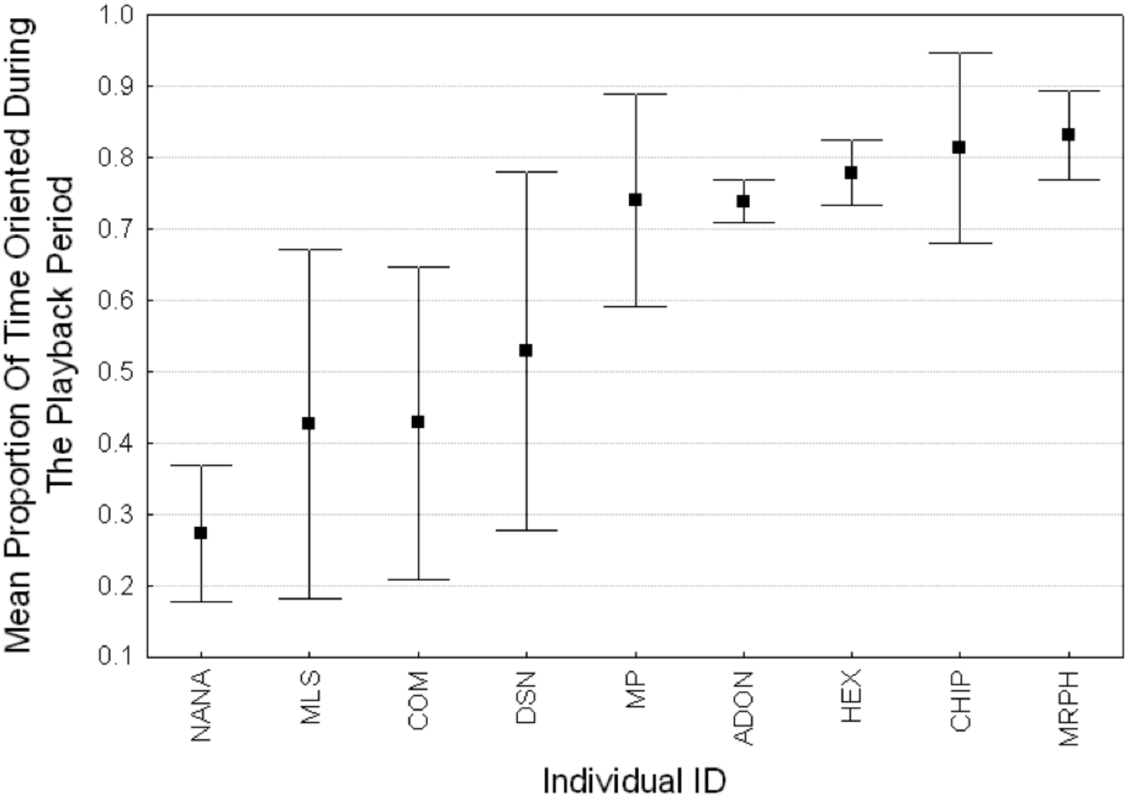

Figure 1.4. Mean ± SE proportion of time spent oriented during the playback period across all three treatment conditions for each individual hyena. Only adult females that experienced all three treatment conditions when alone (*N* = 9) were included.

these are effectively equivalent acoustic properties. Controlling for bout duration eliminated the significant effect of Intruder ID, demonstrating that hyenas oriented longer when hearing longer calls. Adding other acoustic properties had no effect on the significance of intruder ID as a random effect (minimum fundamental frequency: $\chi^2_1 = 4.27$, $P = 0.04$; peak frequency: $\chi^2_1 = 4.07$, $P = 0.04$; maximum frequency: $\chi^2_1 = 5.18$, $P = 0.02$; maximum amplitude: $\chi^2_1 = 3.95$, $P = 0.04$; power: $\chi^2_1 = 4.21$, $P = 0.04$; harmonics: $\chi^2_1 = 4.08$, $P = 0.04$). Thus, it appears that the effect of intruder ID on the orienting responses of lone hyenas can effectively be attributed to two acoustic properties of the whoop bouts: whoop duration and the RMS amplitude of the whoops.

Our use of calls recorded from outside of Kenya controlled for familiarity, but also introduced potential complications such as not knowing caller age or sex, and the use of calls from different locations. However, these variables did not appear to alter the responses of hyenas to the playbacks. For example, country of origin had no apparent effect on orienting responses by lone hyenas during the first whoop bout ($F_{2,20} = 1.65$, $P = 0.22$). Also, as noted above, we saw no indication that hyenas responded differently to any calls based on minimum fundamental frequency.

Effect of Listener Group Size

Overall, four hyenas, representing 33% of lone subjects, avoided the speaker, whereas no individuals in any group trial ever avoided the speaker. Across all three treatment conditions, final listener group size, defined as the number of clanmates present at the end of the trial, most strongly predicted whether hyenas approached the speaker during a playback trial (Table 1.2).

Specifically, lone individuals were significantly less likely to approach the speaker than were individuals in groups (*P* = 0.004; Table 2, Fig. 1.5a), and individuals in groups containing three or more hyenas were significantly more likely to approach the speaker than were individuals in groups containing fewer than three individuals (*P* = 0.006; Table 2, Fig. 1.5a). Final group size predicted approach behavior better than the presence of arriving individuals (AICc = 42.97 versus 45.93; Table 1.2), and the model with the lowest AICc value included only final group size as a predictor (Table 1.2). Neither rank of the focal hyena nor the number of different intruder calls heard was a significant predictor of approach behavior (Table 1.2).

Exact numerical odds did not significantly predict whether individuals would approach the speaker (*P* = 0.12; Table 1.2). However, individuals in groups with odds greater than 1:1 were significantly more likely to approach the speaker than individuals in groups with odds of less than or equal to 1:1 (*P* = 0.013; Table 2, Fig. 1.5b). With numerical odds greater than 1:1, hyenas approached the speaker more than twice as often as hyenas in groups with numerical odds less than or equal to 1:1 (Fig. 1.5b). This appeared to be caused by a nonlinear effect of numerical odds on the probability of approaching the speaker. Indeed, there appeared to be a threshold effect of numerical odds such that hyenas facing odds greater than one responded differently than hyenas confronting odds less than one.

DISCUSSION

Our results support the following predictions of game theory: contest asymmetries can alter the cost/benefit ratio of entering into aggressive interactions, individuals should be more willing to engage in contests when they have the numerical advantage, and animals living in

Table 1.2

Summary of model comparison results investigating approach behavior as a function of group size and numerical odds

Model	Predictor	Estimate	SE	*Z*	*P*	AICc
1	Final group size (continuous)	1.14	0.43	2.68	0.008	42.97
1b	Final group size group = 1 vs group > 1	2.42	0.85	2.85	0.004	45.57
1c	Final group size group < 3 vs group ≥ 3	2.53	0.93	2.7	0.006	46.15
2	Arriving individual	3.57	1.29	2.77	0.006	45.93
3	Final group size	0.98	0.50	1.97	0.048	43.4
	Arriving individual	2.25	1.48	1.52	0.13	
4	Numerical odds (continuous)	0.96	0.62	1.54	0.12	50.41
4b	Numerical odds, odds > 1 vs odds ≤ 1	2.92	1.17	2.48	0.013	46.2

Nonsignificant predictors	***Df***	**Log likelihood**	χ^2	***P***	**AICc**
Rank of focal hyena	3	-23.38	1.39	0.24	52.76
Number of intruders heard	4	-23.33	1.48	0.48	54.67

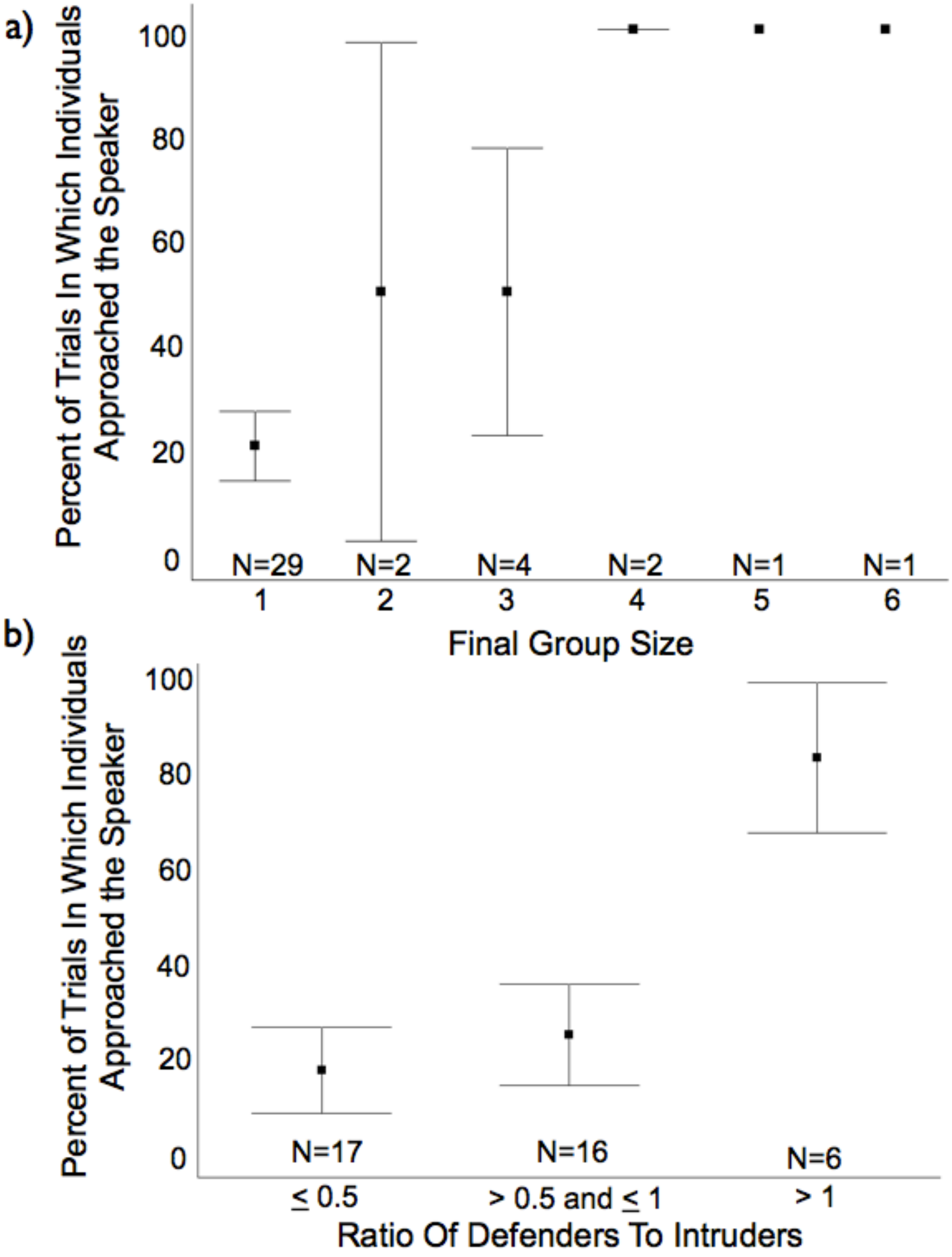

Figure 1.5. Mean ± SE percentage of trials in which at least 50% of individuals approached the speaker as a function of (a) final group size and (b) numerical odds (ratio of final playback subjects ('defenders') to the number of different intruder calls played) in all playbacks conducted (*N*=39). In (a), final group size included individuals that were not present at the start of the trial but that arrived during or immediately after the playback period. Focal hyena(s) were considered to have approached the speaker if their position at the end of the trial was closer to the speaker than it was at sound onset, as assessed using a range finder. In (b), a ratio less than one represents a situation in which the number of intruders played was greater than the number of defenders present at the end of the trial. A ratio equal to one means that the number of intruders played equaled the number of defenders present. A ratio greater than one represents a situation in which defenders outnumbered intruders.

fission–fusion societies should be able to assess numerical odds. Specifically, we have shown that wild spotted hyenas assess numerical advantage when exposed to calls from simulated intruders. The results support our prediction that wild hyenas show more caution when they are outnumbered, indicated here by enhanced vigilance, and take more risks when the numerical odds are in their favor, indicated here by approaching the speaker. Spotted hyenas thus show numerical assessment abilities comparable to those of lions, chimpanzees and howler monkeys (Kitchen, 2004; McComb et al., 1994; Wilson et al., 2001). Furthermore, spotted hyenas scale their vigilance based on the number of unique callers to which they are exposed, at least when there are three or fewer intruders calling. The results of this study thus provide the first experimental evidence that hyenas use acoustic information available in whoops to differentiate among individual callers, supporting our prediction that hyenas discriminate between individuals based on their calls.

Odds Ratios and Assessment of Numerical Advantage

Differences between trials involving lone hyenas and those involving groups suggest that hyenas have a fine-grained ability to assess numerical advantage. Lone hyenas assessed risk, but they rarely approached the speaker, which fits with previous research showing that animals often require a substantial numerical advantage before engaging in an aggressive interaction, especially when potential rewards are not particularly large (Wilson et al., 2002). The risk of injury may not be worth the reward of chasing an intruding individual out of the territory, especially when the hyena confronting intruders is not in the presence of a den, food, or vulnerable offspring. Although our sample size was small, we found that hyenas in larger groups and with better numerical odds appeared to be more proactive, by approaching more often, when hearing the calls of intruding individuals.

Further work is necessary to investigate the cognitive mechanisms or representations used by hyenas to assess numerical advantage. More research is also necessary to determine whether hyenas respond based on small differences in numerical advantage even when confronted with larger numbers of intruders. We do not know whether there is a point at which this ability breaks down. It would be interesting to study the degree to which numerical advantage predicts outcomes of interclan territorial disputes.

We believe that hyenas were responding to the number of unique callers because we controlled for other possible correlates of quantity, such as stimulus intensity and the number of whoops played. We reject the notion that hyenas were simply showing a habituation/dishabituation response to the calls of intruders because hyenas varied their approach behavior based on numerical odds and their own group size, which we would not expect from a habituation/dishabituation response. The ability to assess numbers of unique callers may be particularly important for spotted hyenas because hyenas are often found in small subgroups in their fission–fusion social system. In small subgroups, the presence of an additional group member or territorial intruder can significantly change the ratio of defenders to intruders, whereas in larger groups the presence or absence of a single individual will have less of an impact on numerical odds. Therefore, in small groups there is a substantial incentive to assess the precise number of individuals present before deciding to engage in an aggressive conflict.

It is interesting to consider what factors other than inter-group conflict with unpredictable group size could promote the evolution of numerical representation abilities. Previous experimental work has found that American coots count the number of eggs in their nest as a defense against brood parasitism (Lyon, 2003). However, we would not necessarily expect that birds without a history of extreme brood parasitism would show the same ability to count their offspring. Additionally, while numerical assessment can be highly advantageous for group-living species, we would not expect solitary animals to have evolved this particular skill, unless numerical assessment is advantageous in another domain, such as a mother needing to keep track of multiple, highly mobile, offspring.

Individual Differences in Vigilance

We expected hyenas to follow predictions of game theory and respond differently to different numbers of intruders. Although a few females did react as expected and increase vigilance when there were more intruders, some females showed little variation in their responses to the three treatment conditions, which mostly involved a constant, high level of vigilance. Consistent differences in how individuals respond to the calls of territorial intruders has also been found in lions (Heinsohn and Packer, 1995); some female lions consistently approached the speaker first, while other females consistently lagged behind their groupmates. Heinshohn & Packer (1995) could not attribute these differences in approach behavior to any measure of fighting ability in lions, such as age or body size. We found no effect of rank on the responses of focal hyenas to calls of conspecific intruders in the clan’s territory, which matches a previous study showing that hyenas of all social ranks participate in territorial advertisement and defense (Boydston et al., 2001).

Individual variation in vigilance responses might result from differences in what each individual has experienced in the recent past. Although possible, we think it is unlikely that one of our study animals heard an unknown intruder in the day preceding a playback experiment. We drive the home range of the focal hyena(s) for several hours every morning and evening to record all sightings of unknown individuals within the home ranges of our study clans. We sighted unknown individuals on four separate occasions during the 11-month study period, and the shortest interval between sighting an unknown hyena and conducting a playback experiment was 3 days. Given the low probability that our subjects had interacted with unknown hyenas immediately before playbacks, the individual variation in vigilance responses observed here suggest personality differences, as does earlier work from our laboratory (Pangle and Holekamp, 2010; Watts et al., 2010), but further research is needed to investigate this possibility.

Individual-based Vocal Discrimination

Hyenas' responses to the playbacks seemed based on the numerical odds they faced, and not on the specific identity of the callers. However, we found evidence that hyenas can distinguish among calls to assess numerical odds. Two vocalizations produced by spotted hyenas, the whoop (East and Hofer, 1991) and the giggle (Mathevon et al., 2010), have structural variation that might allow hyenas to identify conspecifics as unique individuals. However, we cannot assume that animals can discriminate individuals by exploiting such individually variable acoustic signals (Schibler and Manser, 2007). Individual variation in acoustic structure of vocalizations may have no adaptive function, and may simply be a by-product of morphological variation in callers. It is therefore important to test experimentally for individual discrimination in a wide variety of taxa, given how fundamental such discrimination abilities appear to be in the evolution of complex social cognition (de Waal and Tyack, 2003).

Individual variation in the acoustic structure of vocalizations and the ability to discriminate individuals based on acoustic signals appear to be widespread among mammals (Blumstein and Daniel, 2004; Cheney and Seyfarth, 1988; Cheney et al., 1995; Wich and de

Vries, 2006). For example, male Thomas langur monkeys, *Presbytis thomasi*, distinguish, keep track of, and remember group members (Wich and de Vries, 2006), vervet monkeys, *Cercopithecus aethiops*, discriminate between individual callers (Cheney and Seyfarth, 1988), and baboons, *Papio cynocephalus ursinus* (Cheney et al., 1995) recognize calls of specific female group members. Several studies have also used playback experiments to demonstrate recognition of groups of individuals, such as groupmates versus individuals from neighboring groups or kin versus nonkin (Frommolt et al., 2003; McComb et al., 1993; Reby et al., 2001; Sayigh et al., 1999).

Prior to the current study, no experiments had been done asking whether hyenas actually use the information in whoop or giggle vocalizations to distinguish among individuals. Our use of consecutive and nonoverlapping calls as sound stimuli required hyenas to distinguish among individuals based on their vocalizations in order to determine the number of unique callers. In addition, because the stimulus calls were not played simultaneously, focal hyenas had to remember which calls they had heard earlier to identify novel calls. Had hyenas simply been counting calls without distinguishing among them, the responses observed in all three playback treatments should have been statistically indistinguishable, but that was not the case.

This result is consistent with previous findings on the cognitive abilities of spotted hyenas. For example, previous playback experiments indicated that hyenas recognize certain classes of individuals, such as maternal kin and offspring, from their whoop vocalizations (Holekamp et al., 1999). In addition, hyenas demonstrate complex social cognitive abilities that appear to require individual recognition, including recognition of third-party relationships among group members (Engh et al., 2005), and individual assessment of potential social partners based on their relative value (Smith et al., 2007). Interestingly, spotted hyenas also show individual discrimination in chemical signals; Drea et al. (2002a) performed a habituation–dishabituation experiment to show that males discriminate between novel and familiar scents of females in a single reproductive state. Thus, hyenas can discriminate individuals using multiple sensory modalities.

Conclusion

Spotted hyenas conform to predictions of game theory and show comparable abilities to assess numerical advantage to those seen in lions, chimpanzees and howler monkeys. Hyenas also assess the number of unique callers, thereby demonstrating an ability to discriminate among individuals based on their vocalizations. Spotted hyenas live in complex societies, and social complexity is thought to be a major driving force in the evolution of complex cognitive abilities in mammals. Our findings support this idea by providing evidence that primates and carnivores with similarly complex social systems have evolved similarly complex abilities to assess numerical advantage.

CHAPTER 2

DIVERSITY OF INITIAL EXPLORATORY BEHAVIORS IS A KEY DETERMINANT, AND NEOPHOBIA IS A CRITICAL INHIBITOR, OF INNOVATIVE PROBLEM-SOLVING SUCCESS IN WILD SPOTTED HYENAS

INTRODUCTION

Innovation, solving a novel problem or finding a new solution to an existing problem, allows animals to exploit novel resources or to use familiar resources more efficiently (Kummer and Goodall, 1985; Morand-Ferron and Quinn, 2011; Reader and Laland, 2003). Innovation thus improves the ability of animals to survive in complex, changing environments and to explore and create new niches (Sol et al., 2005). Despite the evolutionary consequences of innovation (Nicolakakis et al., 2003; Reader and Laland, 2003), within-species variation in innovative tendencies remains poorly understood (Laland and Reader, 1999). Although a few studies have demonstrated individual variation in problem-solving abilities (Cole et al., 2011; Laland and Reader, 1999; Morand-Ferron et al., 2011; Morand-Ferron and Quinn, 2011; Pfeffer et al., 2002), we know very little about the characteristics that vary among individual conspecifics to make them more or less innovative (Overington et al., 2011).

Here we test a hypothesis suggesting that individuals who initially confront a novel problem with a greater range of behavioral strategies are more likely to eventually solve that problem (Caruso, 1993; Parker, 1974; Skinner, 1981). Although this has been shown in human infants (Caruso, 1993; Siegler, 1995), it has, to our knowledge, never been experimentally confirmed in non-human animals. To do so, we presented hyenas with a novel food-access puzzle, measured the diversity of exploratory behaviors each individual employed when interacting with the novel problem, and related this diversity to whether or not the individual ever managed to solve the problem.

Along with initial exploratory diversity, we also examined the relative contributions of persistence and neophobia to problem-solving success. Persistence has been shown to influence problem-solving success in woodpecker finches (Tebbich et al., 2010). In addition, individuals must approach novel objects and enter novel feeding situations to successfully solve foraging problems and utilize new food resources (Tebbich et al., 2009). Neophobia is defined as fear of novel stimuli (Bergman and Kitchen, 2009; Greenberg, 1983, 1990), and several studies have found that neophobic individuals are less likely than others to participate in novel problem solving tasks, and are thus unlikely to innovate or solve problems (Bouchard et al., 2007; Cole et al., 2011; Greenberg, 2003; Seferta et al., 2001; Webster and Lefebvre, 2001). Additionally, because learning is necessary for a one-time innovation to become a successful problem-solving strategy, we examined patterns of response acquisition among individuals who were successful at solving the problem, and who were tested in multiple trials.

Previous studies have examined whether exploratory tendency is positively correlated with innovativeness among species (Webster and Lefebvre, 2001) and among individuals within a species (Biondi et al., 2010; Cole et al., 2011; Overington et al., 2011), though the results of these studies are mixed. Several studies found that variation in exploration of a novel environment was unrelated to variation in problem-solving success (Biondi et al., 2010; Cole et al., 2011), whereas others have found a positive correlation between exploration and innovation (Overington et al., 2011; Webster and Lefebvre, 2001). Exploration is typically measured by quantifying the extent to which an individual investigates a novel area, including both the time spent in the novel area and the amount of space the individual covers (Biondi et al., 2010; Cole et al., 2011; Overington et al., 2011; Webster and Lefebvre, 2001). In this study we focused on the behaviors that wild hyenas exhibited when interacting with the novel problem-solving apparatus, and thus we did not investigate general exploratory behavior. Additionally, while exploratory behavior is often regarded as a necessary precursor to innovation (Kendal et al., 2005; Reader and Laland, 2003), it is not sufficient for the emergence of an innovation (Biondi et al., 2010). For an innovation to occur, it is likely that innovators must also exhibit some mental abilities, such as creativity (Reader, 2003). Measures of an individual's ability to think flexibly about the possible functions of objects are major components of tests of human creativity (Bonk, 2003; Christensen et al., 1960; Wallach and Kogan, 1965). Likewise, we argue that the diversity of behavioral responses an animal exhibits when first confronted with a novel problem-solving task is indicative of its ability to think flexibly about the problem (Parker, 1974).

Lastly, it is unclear whether variation in innovation stems in part from temperament differences and should be considered a personality trait, such that some individuals are more innovative than others regardless of their social rank, age, or sex (Cole et al., 2011; Laland and Reader, 1999; Verbeek et al., 1994), whether developmental or social environmental factors such as age and social rank drive innovation rate, or whether state-dependent variables such as motivation drive innovation rate, in which case we would expect body condition (i.e. fatness) to be correlated with the diversity of initial exploratory behaviors and the frequency of problem-solving success (Bouchard et al., 2007; Box, 2003; Cole et al., 2011; Laland and Reader, 1999; Lefebvre, 2000; Reader and Laland, 2001, 2003; Russon, 2003). To address these possibilities, we tested effects of individual identity, social rank, age, sex, and body condition on initial exploratory diversity, neophobia, and problem-solving success.

We chose to study innovation in hyenas because they exhibit species characteristics that are postulated to be closely associated with innovation (Lefebvre and Bolhuis, 2003; Reader and Laland, 2003). For instance, innovation is thought to be vital for generalist and opportunistic species (Lefebvre and Bolhuis, 2003). Spotted hyenas are generalist carnivores that use a variety of tactics to hunt a diverse array of prey, including at least 30 different species (Cooper et al., 1999). Furthermore innovation rates among invasive species are generally positively correlated with colonization success (Lefebvre and Bolhuis, 2003; Sol and Lefebvre, 2000; Sol et al., 2002); spotted hyenas are the most abundant large carnivore in sub-Saharan Africa, with a wide distribution that suggests great invasion success (Holekamp and Dloniak, 2010). Lastly, spotted hyenas have demonstrated complex social cognitive abilities. For example, hyenas recognize third party relationships (Engh et al., 2005), form coalitions (Smith et al., 2010), reconcile after fights (Wahaj et al., 2002) and demonstrate cooperative problem solving (Drea and Carter, 2009). However, although hyenas excel cognitively in the social domain, no one has previously assessed their technical problem-solving skills.

METHODS

Subjects and study site

The subjects were individuals from two neighbouring clans of spotted hyenas in the Masai Mara National Reserve, Kenya. Individuals were identified by unique spot patterns and other natural markings such as ear notches. Observations were conducted daily, from 0530-0900 and from 1700-2000, on an average of 23.5 days per month between May 2007 and May 2008. Hyenas were considered juveniles prior to reproductive maturity or dispersal; adults were post-dispersal males and breeding females (Holekamp et al., 1996). Sex was determined from the dimorphic shape of the glans of the erect phallus (Frank, 1990). In the Talek West clan, age was known for all individuals born in the study clan to ±7 days as described by Holekamp et al. (1996). In the Fig Tree clan, the same method was used to age (to ±7 days) all individuals born after 2006. Age of older individuals was determined (to +/- 6 months) based on tooth wear using methods described by Van Horn et al (2003). Throughout this study we conducted all occurrence sampling (Altmann, 1974) of all agonistic behavior, and used these data to generate a matrix of outcomes of dyadic agonistic interactions, from which we assigned each individual a social rank, as described previously (Holekamp and Smale, 1990; Smale et al., 1993). The highest-ranking adult in each clan was assigned a rank of 1 (Szykman et al., 2001). Juvenile rank is maternally inherited so juveniles were assigned ranks immediately below those of their mothers.

During the study period the Talek West clan contained 46-48 members, including 12-13 adult females with their juvenile offspring and 10 adult males, and the Fig Tree clan contained 36-38 members, including 10 adult females with their juvenile offspring and 7-8 adult immigrant males. The hyenas in our study clans were never exposed to a puzzle box or any manipulative problem-solving tasks prior to this study.

Apparatus

We designed a 60×31×37 cm puzzle box, essentially a cage of welded 10.5 cm rebar. It had a single 34-cm door on one long side and rebar handles in the centre of each short side (Fig. 2.1 insets). When it was baited with about 2 kg of raw meat, the box weighed more than 35 kg. The spacing between the bars of the box was sufficient to allow hyenas to both see and smell the meat inside. To obtain access to the meat, the hyena had to slide a 12 cm bolt latch laterally and swing open the door. The hyenas could also see and touch the entire latch mechanism, which could be opened using either the mouth or the forepaws. The end handles allowed the animals to drag the apparatus, to upend it, and in some cases even to throw it as part of their exploratory behavior. The puzzle box was designed so that hyenas would have to use behaviors in their existing repertoire in a novel fashion. Hyenas often pull carcasses, or pull limbs off of carcasses when faced with inter- or intra-specific competition. Therefore, moving the bolt latch laterally to open the door of the puzzle box represents a novel application of an existing behavior in the hyena repertoire.

Procedure

Puzzle box trials were conducted as part of a long-term research project, so researchers were already closely monitoring the hyenas in our study clans when the current experiment began. The hyenas in our study clans are habituated to our research vehicle and regularly tolerate the close proximity of our vehicle while we are collecting behavioral observations via video and voice recorders or while collecting faecal samples.

When an appropriate subject animal was sighted in an accessible location, we parked our research vehicle approximately 100 m upwind of the hyena. The box was placed onto the ground on the opposite side of the vehicle and set-up in a location that provided good visual access, both for the subject and for the observer. The box was oriented with the door toward the hyena, and the latch handle was left protruding at 90° from the box, parallel to the ground. We then pulled the vehicle back approximately 50 m from the box and initiated observations. A trial began when a hyena approached to within a 5-m radius of the box (thereby becoming a “focal hyena”); the trial ended when the hyena left the 5-m radius and remained outside of it for 5 min, or when it moved to at least 200 m from the box. All trials were conducted by SBA and were videotaped in their entirety from inside the research vehicle.

To assess hyena body condition at the time of testing, we used a fatness index, a previously established method of evaluating body condition (Watts and Holekamp, 2008). The body condition of each hyena present during a puzzle box trial was recorded as gaunt, normal, fat or obese.

Sampling

Because we were working with a wild population, subjects for these experiments were chosen opportunistically, based on which animals were available in at the time. However, every attempt was made to conduct equal numbers of trials with all the individuals in each of the clans, and to balance the number of participants in each age, sex, and rank category. All trials with the same individual were separated by at least 12 h, with the exception of three pairs of trials that occurred during the same morning or evening observation session. The mean time between consecutive trials was 37.9 ± 6.4 d for all individuals with multiple trials. We accounted for this variation by including time between trials as a covariate in our analyses. Within the constraints of balanced sampling, successful individuals continued to be offered trial opportunities until they had achieved proficiency in the task, defined as opening the box in less than 60 s on three consecutive trials. We attempted to conduct 8 trials with each unsuccessful individual, and we continued to present the puzzle box to unsuccessful individuals until we reached this goal or until the study period ended.

Lone hyenas were preferentially selected for experimental study, but conspecifics sometimes also approached and participated in the trial. If multiple hyenas were present within a

20 m radius of the puzzle box at any point during a trial, it was defined as a 'group trial,' and behavioral data were extracted for each focal individual who approached within 5 m of the puzzle box. For all focal hyenas in a group trial we noted the total number of conspecifics present within 20 m of the puzzle box (group size) and whether any of the conspecifics present were higher-ranking than the focal hyena. For all individuals present in a group trial but who failed to approach to within 5 m of the puzzle box, we recorded their lack of participation and minimum distance from the puzzle box.

In total, we conducted 417 trials on 62 individuals. The number of trials per individual ranged from 1–30, and the mean number of trials per individual was 6.71 ± 1.01 SE. Eighteen individuals participated in at least 8 trials during the 12-month study period. We conducted trials with 34 females, 26 males, and 2 individuals who died before we were able to sex them. Of these, 28 were adults and 34 were juveniles, including 25 high-ranking, 19 mid-ranking, 14 low-ranking individuals, and 4 individuals whose rank was uncertain at the time of testing.

Data Extraction

A trial was defined as a deployment of the puzzle box during which the hyena approached to within a 5-m radius. The puzzle box was initially a wholly novel stimulus for the hyenas, so we estimated neophobia by examining the latency of each focal hyena to contact the box once it entered the 5-m radius during its initial trial.

Successful trials were those in which the puzzle box was opened. Unsuccessful trials included those in which the hyena contacted the box, but failed to open it, as well as those in which the hyena did not actually interact with the box, despite spending time within the 5-m radius. To investigate determinants of problem solving, we categorised each individual's overall success based on whether it was ever able to open the box during any of its trials in the course of the study.

We calculated the number of different exploratory behaviors hyenas exhibited when interacting with the puzzle box, and we used this number as the individual's 'exploration diversity'. Focal hyenas exhibited a range of exploratory behavior patterns when interacting with the puzzle box. The five most consistent patterns were catalogued as: biting, digging, flipping the box, investigating, and pushing or pulling the box. 'Biting' was defined as clamping down on the box with the teeth without displacement of the puzzle box in any direction. 'Digging' involved moving dirt or grass with the forepaws at the base of the puzzle box. 'Pushing or Pulling' involved using the mouth to move the box laterally. 'Flipping' involved using the mouth to toss the box into the air, resulting in a new side of the box touching the ground. 'Sniffing' involved using the nose to investigate the box while oriented toward it: this did not include contact with the box, and generally occurred with the mouth closed. We determined exploration diversity for the focal individual in each trial as the number of different exploratory patterns shown, an integer between 0 and 5.

From the videotaped record, we extracted the amount of "work time" for each subject, which was the time it spent with its head down working on the puzzle box, until it either opened the box and retrieved the meat or stopped working and ended the trial. If a conspecific other than the focal hyena opened the puzzle box or interfered with the focal animal's interaction with the box, work time was not scored. We used work time as our measure of persistence in this study.

Statistical analyses

To investigate learning, we used generalized linear mixed models (GLMM) to examine how work time changed over successive trials for successful and unsuccessful individuals. Sample size varied among trials because work time could not be calculated for all successful or unsuccessful individuals in every trial. To control for pseudoreplication, focal hyena ID was included as a random effect in all generalized linear mixed models where individuals were represented multiple times. The effects of time between trials and body condition on work time were also investigated by including these measures as fixed predictor variables in relevant models.

To investigate determinants of success in problem solving, we used logistic regression with overall success (Y/N) as the binomial response variable, and with predictor variables of: 1) work time, exploration diversity, and latency to approach the puzzle box from the initial trial, 2) the age, rank, and sex of the focal hyena, and 3) all two- and three-way interactions terms between work time, exploration diversity, and latency to approach. To ensure that individuals were not simply more exploratory because they spent longer working on the puzzle box, work time was included as the first covariate in all analyses that included exploration diversity. We also used GLMM to examine how age, rank, and sex affected exploration, neophobia, and persistence. Exploration diversity, work time, and latency to approach the puzzle box were each log transformed to achieve a normal distribution. Alternative models were compared using Akaike's Information Criterion (AIC) values. A smaller AIC value indicates a better-fitting model (Crawley, 2007) and the results from the model with the lowest AIC value are reported here.

To investigate whether variation in innovation stems from temperament differences, we inquired whether there were consistent individual differences in exploration diversity for all individuals who participated in multiple trials. We used a likelihood ratio test to compare generalized linear models with and without the ID of the focal hyena as a random effect.

To account for the influence of social factors on analyses of individual performance, we also included whether the trial was a group trial, and whether or not a higher-ranking conspecific was present during the trial, as predictor variables in relevant models. Mean values are given ± standard error. Differences between groups were considered significant when $P \leq 0.05$.

All data extraction from videotapes was done by SBA. All statistical tests were conducted in R 2.6.2 (R Development Core Team, 2006).

RESULTS

Problem-solving success and individual learning

Of the 62 individuals who interacted with the puzzle box, nine (or 14.5% of subjects) opened the puzzle box at least once, and seven opened the puzzle box multiple times. Fig. 2.1 presents a learning curve by showing the average work time for all individuals who were successful in a given trial. Trial number was a significant predictor of work time ($F_{18, 63} = 2.31$, $P = 0.0076$; Fig. 2.1) and exploration diversity ($F_{21, 101} = 2.72$, $P < 0.0001$) demonstrating that successful hyenas improved their performance with experience. Specifically, successful hyenas became significantly faster at opening the puzzle box and exhibited significantly fewer exploratory behaviors as they learned how to solve the problem. In contrast, unsuccessful individuals did not show a reduction of effort across trials ($F_{13, 122} = 0.55$, $P = 0.89$) nor alter their exploratory behavior with experience ($F_{13, 120} = 0.82$, $P = 0.63$).

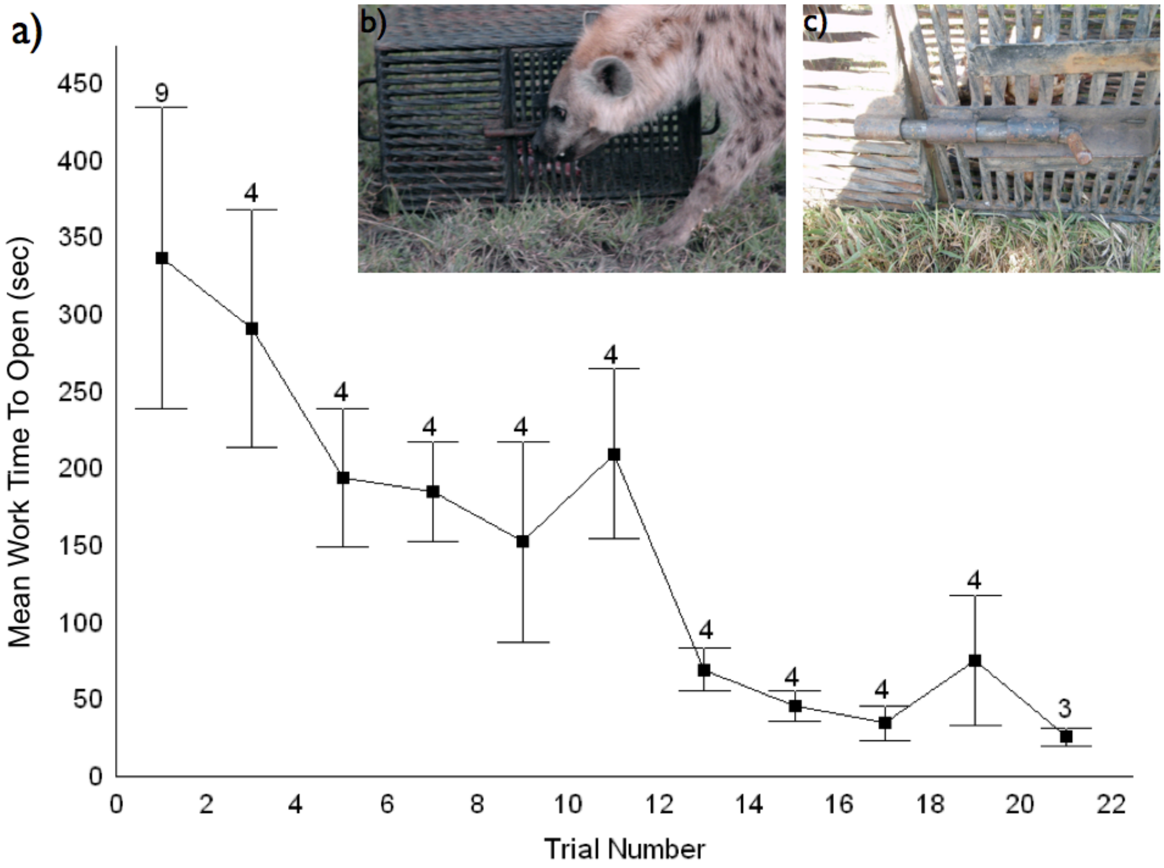

Figure 2.1. For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this dissertation. a) represents an average learning curve for successful wild hyenas when interacting with the puzzle box. The learning curve represents the mean ± SE work time for all individuals who were successful in a given trial. Trial 1 represents the trial in which an individual was initially successful, and may not be the first time an individual interacted with the puzzle box. Sample sizes in trials 2 through 22 varied because not all seven hyenas that opened the puzzle box multiple times were successful in every trial. b) represents an image of the puzzle box apparatus used in the experiment. c) represents a close-up image of the latch mechanism that hyenas had to move laterally in order to access the meat inside the puzzle box.

Characteristics associated with problem-solving success

Only exploration diversity, persistence, and neophobia were retained in the best-fitting model to explain variation in problem-solving success (Table 2.1). Individuals who exhibited a greater diversity of exploratory behaviors during their first trial were significantly more successful than individuals with lower exploration diversity ($X^2_1 = 4.67$, $P = 0.031$; Fig. 2.2a). More persistent hyenas, those who spent more time working on the box during their first trial before giving up, tended to be somewhat more successful than less persistent hyenas ($X^2_1 = 1.99$, $P = 0.16$; Fig. 2.2b). Individuals who were eventually successful in opening the puzzle box also had lower latencies to approach the puzzle box, so were less neophobic, than individuals who were never successful ($X^2_1 = 4.14$, $P = 0.042$; Fig. 2.2c). All two- and three-way interaction terms involving work time, exploration diversity, and latency to approach were non-significant (see Table 2.1), indicating that all three of these measures independently influenced variation in problem-solving success and that exploration diversity did not depend on work time. Neither sex, rank, nor age of the focal hyena significantly predicted variation in success, and were not included in the best-fitting model (Table 2.1). Time between trials and body condition did not significantly explain variation in any response variable.

Time between trials and body condition did not significantly explain variation in work time or exploration diversity for either successful (Time between trials on work time: $F_{1,\ 169} = 0.11$, $P = 0.74$; Time between trials on exploration diversity: $F_{1,\ 169} = 0.28$, $P = 0.60$; Body condition on work time: $F_{1,\ 169} = 2.062$, $P = 0.15$; Body condition on exploration diversity:

Table 2.1. Summary of model comparison results investigating problem-solving success

Predictor	χ^2	Df	*P*	AIC
Best model				35.41
Work Time	1.99	1	0.16	
Exploration Diversity	4.66	1	0.031	
Latency to Approach	4.14	1	0.042	
Not retained in best model				
Age	0.058	1	0.81	37.35
Rank	0.77	1	0.38	36.69
Sex	0.59	1	0.44	36.32
Work Time * Exploration Diversity	0.13	1	0.72	40.92
Work Time * Latency to Approach	0.36	1	0.55	40.92
Exploration Diversity * Latency to Approach	0.0066	1	0.94	40.92
Work Time * Exploration Diversity * Latency to Approach	0.26	1	0.61	42.66

The inclusion of the following factors as predictors of problem-solving success failed to further improve the fit of our best model: age, sex, and rank of the focal hyena as well as all 2- and 3-way interactions involving work time, exploration diversity and latency to approach the puzzle box. The model was based on data from the initial trial on all 62 hyenas that participated in the experiment.

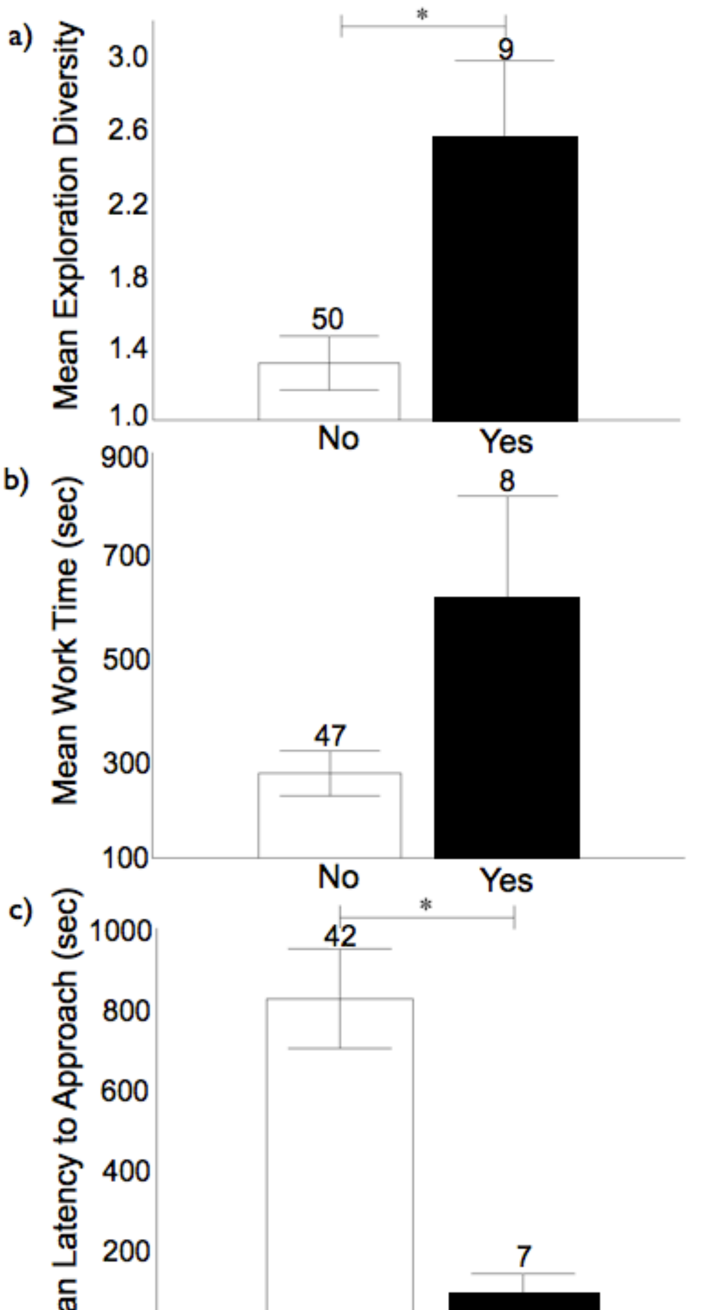

Figure 2.2. Mean ± SE a) exploration diversity, b) work time, and c) latency to approach in the initial trial with the puzzle box for all individuals for whom these measures could be scored. Bars indicate whether an individual was ever successful in opening the puzzle box. Asterisks represent significant differences where * = $p < 0.05$.

$F_{1,\,169} = 0.077$, $P = 0.78$) or unsuccessful (Time between trials on work time: $F_{1,\,134} = 0.56$, $P = 0.45$; Time between trials on exploration diversity: $F_{1,\,134} = 0.097$, $P = 0.76$; Body condition on work time: $F_{1,\,123} = 0.16$, $P = 0.69$; Body condition on exploration diversity: $F_{1,\,123} = 0.68$ $P = 0.41$) individuals. Additionally, neither time between trials nor body condition significantly predicted whether or not a successful individual was able to open the puzzle box in a given trial (Time between trials: $X^2_1 = 0.72$, $P = 0.40$; Body condition: $X^2_1 = 0.092$, $P = 0.76$).

Juveniles had significantly greater exploration diversity ($F_{1,\,50} = 8.026$, $P = 0.0066$; Fig. 2.3a) and were more persistent ($F_{1,\,51} = 7.65$, $P = 0.0079$; Fig. 2.3b) and less neophobic ($\mathrm{F}_{1,\,44} = 23.11$, $P < 0.0001$; Fig. 2.3c) than adults during initial trials. However, neither sex nor rank of the focal hyena significantly affected exploration diversity (Sex: $F_{1,\,54} = 1.75$, $P = 0.19$; Rank: $F_{1,\,54} = 0.64$, $P = 0.43$), persistence (Sex: $F_{1,\,49} = 0.18$, $P = 0.68$; Rank: $F_{1,\,47} = 2.38$, $P = 0.13$), or neophobia (Sex: $F_{1,\,46} = 0.69$, $P = 0.41$; Rank: $F_{1,\,34} = 1.79$, $P = 0.19$).

Individual Variation in Exploration Diversity

We found consistent variation in exploration diversity among individuals ($X^2_1 = 88.18$, $P < 0.0001$; Fig. 2.4). As Fig. 2.4 shows, exploration diversity ranged from individuals who exhibited no exploratory behaviors in any trial to an individual who averaged over three exploratory behavior types per trial. Successful individuals were concentrated on the more diverse end of the range (Fig. 2.4).

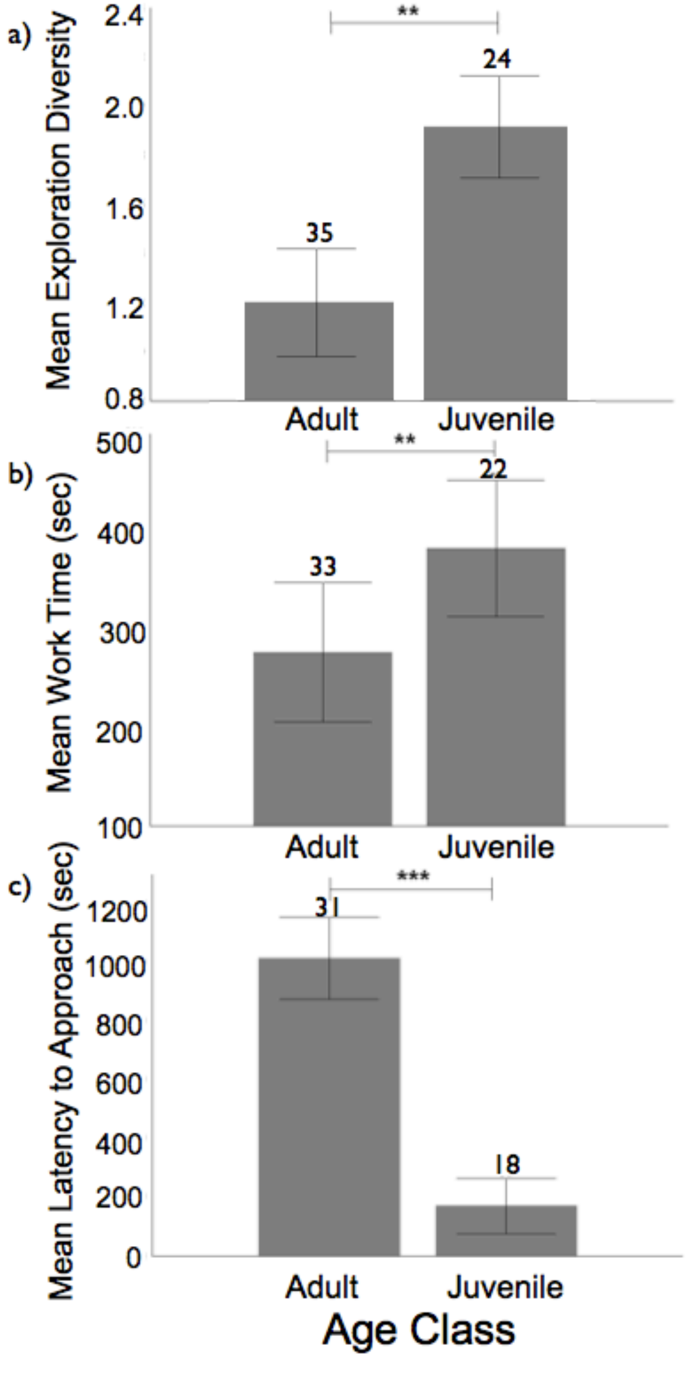

Figure 2.3. Mean ± SE a) exploration diversity, b) work time and c) latency to approach the puzzle box during the initial trial for each focal hyena divided by age class. Asterisks represent significant differences where ** = $p < 0.01$ and *** = $p < 0.001$.

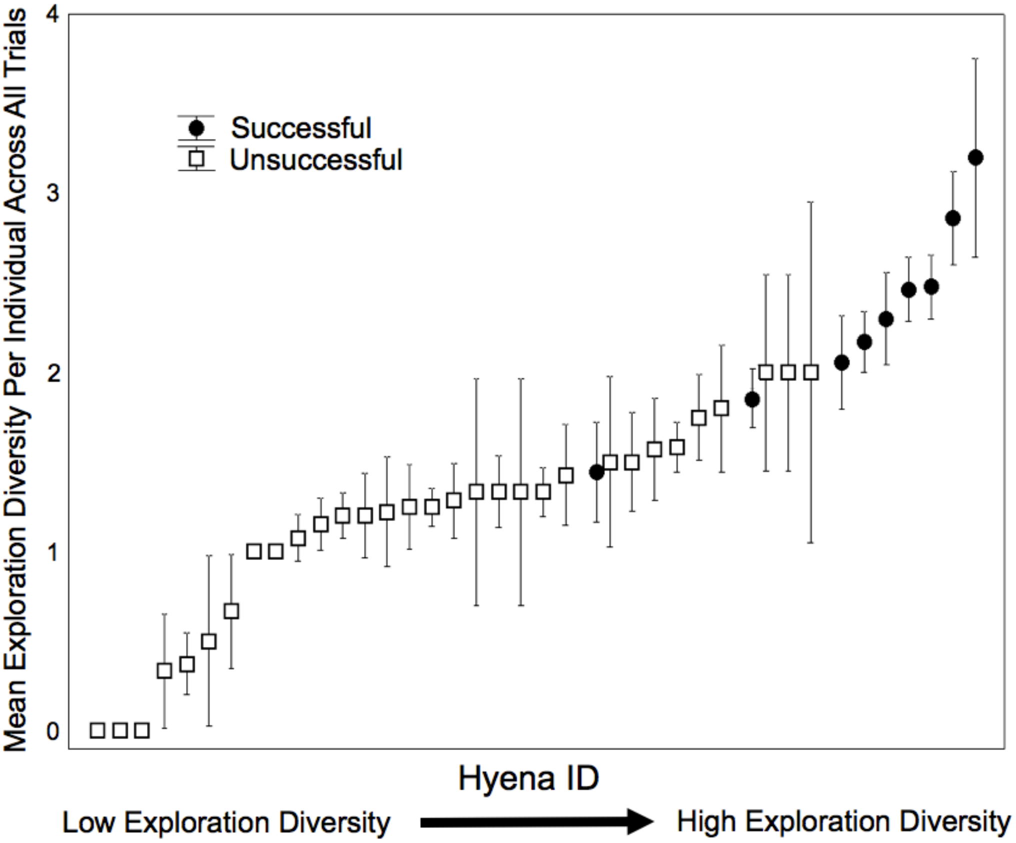

Figure 2.4. Mean ± SE exploration diversity across all trials for each individual hyena that participated in multiple puzzle box trials (N=40). Individual hyenas are listed along the x-axis. Box color indicates whether the individual ever opened the puzzle box.

Social effects

The presence of a conspecific at the puzzle box during a hyena's initial exposure to the novel object significantly decreased its latency to approach to the puzzle box ($F_{1, 35} = 4.51$, $P = 0.041$). However, the social environment during a trial may also have had inhibitory influences on persistence and access to the latch side of the puzzle box for lower-ranking hyenas. The presence of higher-ranking conspecifics during a trial tended to decrease the amount of time lower-ranking focal hyenas worked on the puzzle box before giving up ($F_{1, 180} = 3.08$, $P = 0.081$), and also tended to decrease the percent of time successful hyenas spent on the latch side of the puzzle box before opening it ($F_{1, 75} = 2.99$, $P = 0.088$). There was no difference in success (Fisher Exact Probability Test, $P = 0.40$), exploration diversity ($T_{38} = -1.38$, $P = 0.18$) or persistence ($T_{38} = -0.76$, $P = 0.45$) between hyenas that had or had not seen the puzzle box opened.

DISCUSSION

Our results support the hypothesis that the diversity of initial exploratory behaviors plays a vital role in innovative problem solving by animals in their natural habitat. However, exploration diversity was not the only significant predictor of problem-solving success. Instead, the combination of high exploration diversity and low neophobia was most likely to result in successful problem solving of the novel puzzle box task. Our data are consistent with those from previous studies on other taxa showing that neophobia can have an inhibitory effect on innovation (Greenberg, 2003), and that adults are more neophobic than juveniles in the wild (Reader and Laland, 2003). Interestingly, although hyenas show an impressive ability to solve social problems (Holekamp et al., 2007), only a small percentage of individuals tested solved this novel technical problem, even after multiple opportunities to do so.

Characteristics associated with problem-solving success

Although individuals who give up quickly are likely to be less successful than more persistent individuals, persistence alone will not necessarily lead to greater problem-solving success. Perseverative errors occur when individuals repeat the same behavioral response over and over, despite the absence of any stimulus or reward, and are thought to inhibit problem solving and learning (Hauser, 1999). To solve problems reliably, individuals must avoid such errors and instead seek out alternative solutions to the problem. Thus, it appears that individuals who are both creative and persistent will be more successful at solving novel problems than individuals who possess only one, or neither, of these characteristics. Our results support this idea. Exploration diversity and persistence were major behavioral attributes of successful hyenas. Surprisingly, our statistical models showed that exploration diversity and persistence had independent influences on problem-solving success. Thus it seems that successful individuals both cycle through different exploratory behaviors more quickly, and spend more time interacting with the puzzle box, than less-successful individuals.

Additionally, in order to successfully solve novel problems, individuals must be willing to engage with unfamiliar objects or situations. Although there are certainly costs associated with reduced neophobia, such as increased predation risk and disease transmission (Day et al., 2003), our results clearly show the benefits by demonstrating that less neophobic individuals are significantly more successful problem solvers than more cautious individuals.

As expected, once the successful hyenas learned the solution to the problem, they became very efficient and reliable problem-solvers. Successful hyenas became significantly faster and exhibited significantly fewer exploratory behaviors across trials as they became proficient in solving the puzzle box task. Thus, it appears that once a hyena learns that a particular strategy works, that individual then becomes less exploratory and focuses on the particular behaviors associated with problem-solving success.

Influences on exploration diversity, persistence and neophobia

Four major factors thought to influence innovation are age, sex, rank and individual temperament differences (Bergman and Kitchen, 2009; Boogert et al., 2006; Bunnell and Perkins, 1980; Fragaszy et al., 1997; Katzir, 1982, 1983; Reader and Laland, 2001, 2003; Sigg, 1980). Our results indicate that both state-dependent variables, such as age, and individual differences in temperament influence variation in innovation among spotted hyenas. As has been shown in primates (Hauser, 1988; Kendal et al., 2005; Kummer and Goodall, 1985; Reader and Laland, 2003), we found that juvenile hyenas exhibited significantly greater exploratory diversity and were more persistent and less neophobic than adults. The increased exploratory behavior of juveniles may be due to juveniles receiving more protection and having more spare time to devote to exploration, social play and problem solving than adults (Kummer and Goodall, 1985; Reader and Laland, 2003). Another possible explanation is that juvenile hyenas are likely to be highly motivated to acquire food resources given that they are not fully competent at acquiring their own food. Highly motivated individuals may be more willing to incur the potential costs of approaching and exploring novel objects or novel foods than individuals with reliable access to resources (Reader and Laland, 2003). Spotted hyenas do not achieve full competency as hunters until 5-6 years of age, which is well past the age of reproductive maturity (Holekamp et al., 1997a). Young hyenas are not only less competent at capturing prey, but they are also less effective at feeding during scramble competition at carcasses where there is intense feeding competition (Holekamp et al., 1997a). Juvenile spotted hyenas are therefore at a distinct disadvantage compared to adults when it comes to acquiring resources.

In contrast, innovation may be more common in adults if the innovation builds upon skills or expertise that adults acquire through experience (Reader and Laland, 2003). Innovation may also require a degree of strength or level of physical ability or coordination that juveniles may not yet possess (Box, 2003; Reader and Laland, 2003; Russon, 2003). It is possible that the large size and weight of the puzzle box favored adults over juveniles. This might explain why there was no effect of age on success despite the greater exploration diversity and persistence of younger hyenas.

We observed significant variation among individuals in their exploration diversity across all trials, and their relative rankings on this trait could not be attributed to such factors as age, rank or sex. Successful individuals clustered at the most exploratory end of the range, supporting the idea that variation in innovation can stem, in part, from temperament differences. Similar results have been found in fish and birds, where studies have shown that personality may play a role in innovative problem solving (Laland and Reader, 1999; Reader and Laland, 2003; Verbeek et al., 1994).

Surprisingly, we did not see any rank effect or sex differences in exploration diversity, persistence, neophobia or problem-solving success. Laland and Reader (1999) found that female guppies are more likely to innovate than males and reasoned that this sex difference might be due to the greater metabolic demands imposed on females by growth and reproduction. This same reasoning might also apply to mammals in which maternal investment in reproduction far outweighs male investment (Reader and Laland, 2003). However, male chimpanzees show higher rates of innovation than females in contexts associated with acquiring access to mates (Reader and Laland, 2001). Although female hyenas do bear most costs of reproduction, they are also highly unusual among mammals in being socially dominant to adult males. Their social dominance and priority of access to resources may mitigate some of the energetic demands on female spotted hyenas. Additionally, unlike male chimpanzees, male hyenas do not physically compete with other males for access to females, which suggests a greater role of female mate choice than male-male contest competition in sexual selection in spotted hyenas (Engh et al., 2002). Thus, the lack of rank effects and sex differences in innovative problem solving may be a consequence of unique aspects of spotted hyena biology.

Problem-solving success and individual learning

Although spotted hyenas are extremely adept at solving social problems, only 15% of them managed to solve a technical food-acquisition problem in the wild, even when many of them had multiple opportunities to solve the problem. Those hyenas that were able to solve the problem became significantly faster at opening the puzzle box over successive trials. The shape of the learning curve (Fig. 2.2) also demonstrated that hyenas learned via trial-and-error. If the curve was steep and smooth, this might suggest insight or a spontaneous solution; however, the jagged and shallow shape of the learning curve is more strongly indicative of trial-and-error (Thorndike, 1911; Werdenich and Huber, 2006).

Interestingly, the success rate that we found in this study is similar to that documented in wild vervet monkeys (*Cercopithicus aethiops*) that were tested on a comparable novel problem-solving task in which they were asked to access out-of-reach food (van de Waal and Bshary, 2010). Vervet monkeys were able to open a baited box in order to access a fruit reward: 17 out of 53, or 32%, of individuals tested were able to solve the problem. However, only 2 out of 30, or 7%, of individuals in groups without frequent access to human facilities were successful (van de Waal and Bshary, 2010). Hyenas and vervet monkeys both show remarkable social dexterity (Cheney and Seyfarth, 2007; Holekamp et al., 2007) so their similarly low success rates when encountering a novel food acquisition problem suggest that these species may be much better at solving novel social than technical problems. These species have been tested with only one, or a few, technical problems to date and we cannot, therefore, generalize the results of these studies to draw conclusions about overall non-social intelligence. However, given that these species are generalists with broad distributions, we found their poor performance in the novel technical tasks they confronted surprising. One possible explanation for the low success rates observed in these studies is that wild animals may be more strongly negatively affected by novelty, and thus more constrained by neophobia, than we anticipated. If this is true, then wild animals are likely to be less successful at solving novel technical than social problems, which often test how well animals deal with novel configurations of familiar stimuli, such as conspecific vocalizations (Benson-Amram et al., 2011; Cheney and Seyfarth, 2007). These familiar stimuli would not elicit the same neophobic responses as a puzzle box or other novel test apparatus.

It would be an interesting test of the social intelligence hypothesis to compare our results to similar studies done on non-social species. Unfortunately, to our knowledge, there are no comparable tests of problem-solving success in a wild, non-social species. Although it is outside the scope of this dissertation, we are planning a comparative study to test problem-solving abilities of several carnivore species that vary along a continuum of sociality.

Conclusion

In sum, our study demonstrates that the diversity of initial exploratory behaviors is a critical determinant of innovative problem solving in non-human animals. A likely benefit of complex brains is the ability to respond flexibly to novel situations and to innovate solutions to novel problems. One behavioral mechanism that individuals might employ to increase the likelihood of discovering solutions to novel problems is to increase the variety of behavioral responses they exhibit when confronted with a novel object. In fact, measures of an individual's ability to think flexibly about the possible functions of objects are a major component of tests of human creativity (Bonk, 2003; Christensen et al., 1960; Wallach and Kogan, 1965). Just as large groups of animals appear to experience increased innovative output due to the greater diversity and skill sets of group members (Liker and Bókony, 2009; Morand-Ferron and Quinn, 2011), our work demonstrates that individual animals also benefit from diverse exploratory responses.

CHAPTER 3

A COMPARISON OF PROBLEM-SOLVING ABILITIES BETWEEN WILD AND CAPTIVE SPOTTED HYENAS

INTRODUCTION

Animals often face novel ecological and social problems that they must solve in order to survive and reproduce. Innovation is defined as solving a novel problem or finding a new solution to an existing problem (Hinde and Fisher, 1951; Kohler, 1925; Kummer and Goodall, 1985; Laland and Reader, 1999; Reader and Laland, 2003) and it enables animals to exploit novel resources or utilize familiar resources in a more efficient manner (Lefebvre et al., 1997; Reader and Laland, 2003). Innovation thus improves the ability of animals to survive in complex, changing environments (Sol et al., 2005).

Despite the important evolutionary consequences of innovation (Nicolakakis et al., 2003; Reader and Laland, 2003), research on this subject has been limited in scope. The two most common approaches have been either analyzing anecdotal accounts of innovation from the literature (Lefebvre et al., 1997; Reader and Laland, 2001) or presenting novel technical problems to captive individuals (Bond et al., 2007; de Mendonca-Furtado and Ottoni, 2008; Heinrich and Bugnyar, 2005; Kohler, 1925; Povinelli, 2000; Santos et al., 2006; Tebbich et al., 2007; Visalberghi et al., 1995). Only a few studies have experimentally investigated innovation in wild animals confronting novel challenges (Biro et al., 2003; Bouchard et al., 2007; Morand-Ferron et al., 2011; Morand-Ferron and Quinn, 2011; Webster and Lefebvre, 2001).

There is some evidence that data from studies on captive animals cannot fully inform our understanding about how individuals in the wild can be expected to respond to novel challenges

(Ramsey et al., 2007; Webster and Lefebvre, 2001). Captive primates demonstrated less neophobia to novel objects than did their wild counterparts (Visalberghi et al., 2003), and in studies comparing anecdotal accounts from the literature, higher rates of innovation (Reader and Laland, 2003) than wild primates. Similarly, wild marmosets performed poorly on a manipulative problem-solving task that other primate species successfully solved in captivity (Halsey et al., 2006). Likewise, wild baboons demonstrated very low success rates on three novel problem-solving tasks, which were similar, but not identical, to problems that captive baboons successfully solved (Laidre, 2008). Thus, it appears that studies of innovation in captive animals may suffer from low external validity (Ramsey et al., 2007; Webster and Lefebvre, 2001), possibly because captive animals may be forced to spend time near a novel object or respond to a test situation that they would choose to avoid in the wild (Seferta et al., 2001). Previous research has found that increased persistence can positively impact problem-solving success (Tebbich et al., 2010). In addition, individuals must approach novel objects and enter novel feeding situations to successfully solve foraging problems and utilize new food resources (Tebbich et al., 2009). Neophobia is defined as fear of novel stimuli (Bergman and Kitchen, 2009; Greenberg, 1983, 1990), and several studies have found that neophobic individuals are less likely than others to participate in novel problem solving tasks, and are thus unlikely to innovate and solve problems (Bouchard et al., 2007; Cole et al., 2011; Greenberg, 2003; Seferta et al., 2001; Webster and Lefebvre, 2001). Thus, if captivity influences either the amount of time that individuals interact with a novel problem or their likelihood of responding to a test situation by approaching a novel apparatus, then it is likely that captive animals will be more successful than individuals in their natural habitat.

Experimental investigations of innovation in both wild and captive populations of the same species should be useful for connecting results from the majority of previous studies that were conducted with captive populations to a broader understanding of the importance of innovation for individuals in their natural habitats. If by-products of a captive lifestyle, such as reduced neophobia to man-made objects, bias the abilities of captive individuals such that they consistently perform better on novel technical problems than their wild counterparts, then we should incorporate this bias into our interpretation of studies from captive populations. However, in order to assess whether captive animals are reliably more innovative than their wild counterparts, we need more studies that directly test this question across a range of taxa. To date, only three studies have compared innovative problem-solving abilities in wild and captive populations of the same species using a single experimental paradigm, and all three of these studies were conducted on birds (Bouchard et al., 2007; Gajdon et al., 2004; Webster and Lefebvre, 2001). Interestingly, these studies all found that captive individuals exhibited better technical problem-solving skills than their wild counterparts (Bouchard et al., 2007; Gajdon et al., 2004; Webster and Lefebvre, 2001).

Here, we compared the performance of wild and captive spotted hyenas in solving a novel technical problem. We previously reported the results of an experimental study on wild hyenas, which found that only 15% of wild individuals were able to solve a novel problem-solving task, even when many of them had multiple opportunities to do so (See Chapter 2: Benson-Amram and Holekamp, *in prep*). This study also investigated determinants of problem-solving success in wild hyenas and found that individuals that exhibited a greater diversity of exploratory behaviors in their initial encounter with the problem were eventually more successful than individuals with a lower diversity of exploratory behaviors (See Chapter 2: Benson-Amram and Holekamp, *in prep*). There was also a strong trend for more persistent individuals to be more successful than less persistent individuals. Additionally, neophobia was a major inhibitor of innovative problem-solving success among the wild hyenas. Specifically, more neophobic individuals, those that took longer to approach the problem in their initial trial, were significantly less successful than less-neophobic individuals, those that approached the apparatus more quickly. Here, we tested whether captive hyenas differ from the wild hyenas in their overall ability to solve the same novel technical problem, and whether the diversity of initial exploratory behaviors, persistence and neophobia had the same influences on technical problem solving among captive hyenas.

Based on findings from previous studies comparing problem-solving abilities between individuals in captivity and in the wild (Bouchard et al., 2007; Gajdon et al., 2004; Webster and Lefebvre, 2001), we predicted that captive hyenas would be more successful at solving a novel technical problem, and thus more innovative, than wild hyenas. In a captive environment, individuals are confined to a space within close proximity of the novel object for the entire duration of a trial, whereas wild hyenas can choose to leave the vicinity of the novel object at any time. We therefore predicted that all captive hyenas would spend a relatively longer period of time working on the problem-solving task, and thus be more persistent, than wild hyenas. Additionally, animals with a history of interacting with man-made objects have been shown to be less neophobic than individuals with less access to human facilities (van de Waal and Bshary, 2010) and we therefore predicted that captive hyenas would be less neophobic, and thus approach the problem-solving apparatus faster, than wild hyenas. It is also possible that captive animals have better learned the affordances of man-made objects and are therefore more adept at manipulating them in novel situations (Call and Tomasello, 1996). We predicted that captive hyenas would be more diverse in their exploratory behavior than wild hyenas. Despite these predicted differences, we expected that captive hyenas would learn the solution to the novel technical problem via trial-and-error learning, which is the same method of learning demonstrated by wild hyenas (See Chapter 2: Benson-Amram and Holekamp, *in prep*).

Lastly, wild hyenas show a strong effect of age on exploration diversity, persistence, and neophobia (See Chapter 2; Benson-Amram and Holekamp, *in prep*). Juvenile primates are thought to be more innovative and less neophobic than adults because they have more spare time to devote to exploration and problem solving (Kummer and Goodall, 1985; Reader and Laland, 2003). We predicted that captive juvenile hyenas would exhibit similar exploratory tendencies as the wild juveniles and would exhibit greater exploration diversity and less neophobia than adults.

METHODS

Subjects and study site - Wild

Experiments were conducted from May 2007 – May 2008 on members of two neighboring study groups in the Masai Mara National Reserve, Kenya. Hyenas were observed daily, from 0530-0900 and from 1700-2000, and all experimental trials were conducted during these observation hours. Age, sex, social rank, and identity of each individual member of both groups were known (Benson-Amram and Holekamp, *in prep;* Frank, 1990; Holekamp et al., 1996; Van Horn et al., 2003). Hyenas were considered juveniles up until reproductive maturity (approximately 2 years of age), and adults included only post-dispersal males and breeding females (Holekamp et al., 1996). We never exposed these wild hyenas to a manipulative problem-solving task prior to this study.

Subjects and study site – Captive

Experiments were conducted on members of a captive breeding colony at the Field Station for Behavioral Research at the University of California, Berkeley. Data were collected from June - August 2008 when the colony housed 26 hyenas: 11 adult females, 11 adult males, and 4 juveniles under 2 years of age (3 female and 1 male). The captive hyenas were housed in outdoor or semi-outdoor enclosures, in groups of two or three individuals. Social rank was known within dyads and triads of individuals housed together, but social ranks were not determined for each individual in relation to all other hyenas in the colony. Social ranks within dyads and triads were assessed independently by caretakers, and were determined through observations of submissive and aggressive behavior and through observations of displacement in competitive feeding situations (Drea et al., 2002b; Frank et al., 1989; Mathevon et al., 2010). All hyenas at the field station were born in captivity. The founders of the colony were originally collected in 1984 and 1985 from the same district in Kenya in which the wild study animals reside.

Five captive individuals participated in 1995 in a study of cooperative problem solving that involved pulling ropes (Drea and Carter, 2009). None of the other hyenas in the colony had been exposed to any manipulative problem-solving task prior to the current experiments. The captive hyenas have also been subjects of studies focused on the endocrine basis of genital masculinization and social dominance among female spotted hyenas (Drea et al., 1998; Glickman et al., 1987; Glickman et al., 1992). As such, many of these hyenas were treated *in utero* with anti-androgens or aromatase inhibitors. Previous studies found no effect of these treatments on communication, cognition or social behavior (Drea and Carter, 2009; Drea et al., 2002b). Nevertheless, to account for the potential influence of these variables on problem-solving success here, we included the following covariates in our statistical analyses: whether or not each hyena had previous experience as subject in a problem-solving experiment and its hormone treatment group.

Experimental apparatus

The experimental apparatus was a rebar puzzle box, inspired by Thorndike's (1911) dissertation work, baited with raw meat; it had a simple bolt latch that the hyenas needed to slide laterally for the door to swing open (Fig. 3.1), thereby allowing the hyena access to the meat inside. The box was designed such that subjects could both see and smell the meat inside the box. The hyenas could also see and touch the entire latch mechanism, which could be opened using either the mouth or the forepaws. The puzzle box was designed so that hyenas would have to use behaviors in their existing repertoire in a novel fashion. Hyenas often pull carcasses, or pull limbs off of carcasses. Therefore, moving the bolt latch laterally to open the door of the puzzle box represents a novel application of an existing behavior in the hyena repertoire.
Due to logistical constraints, we used slightly different puzzle boxes for the wild and captive hyenas. Both puzzle boxes had 2 rebar handles, one located centrally on each short side and a single door on one long side. The puzzle boxes for the two groups were nearly the same size (dimensions of L: 60cm × H: 31cm × W: 37cm with a 34 cm long door for the wild and L: 63.5cm × H: 33cm × W: 33cm with a 39cm long door for the captive hyenas). However, due to the different materials available in Kenya and the U.S., the captive puzzle box weighed 45kg whereas the wild puzzle box weighed 35kg. Despite the weight of these boxes, both captive and wild hyenas were able to lift, flip and drag them around.

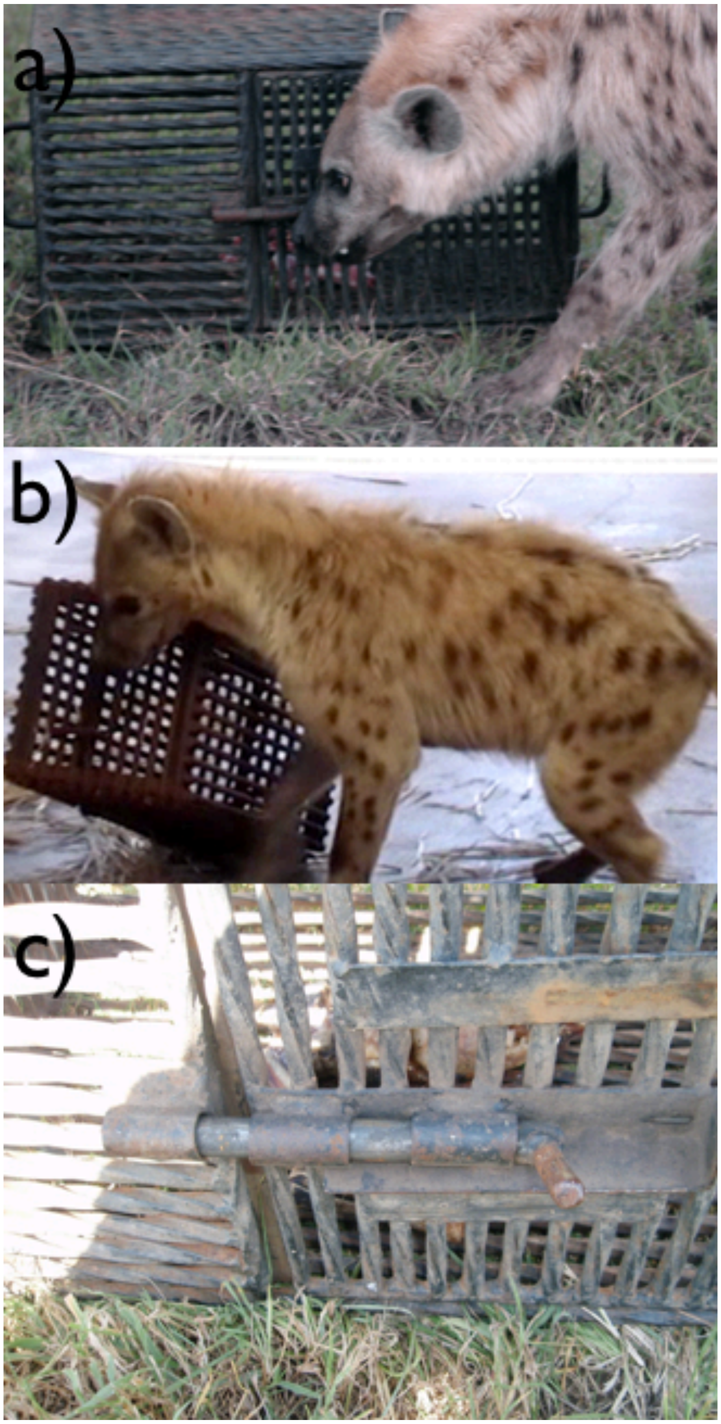

Figure 3.1. Images of the puzzle boxes used in the experiments on the a) wild and b) captive populations. In a) a wild hyena is biting the latch of a puzzle box while in b) a captive hyena is flipping a puzzle box. In c) the image is a close-up of the latch bolt that hyenas needed to move laterally to access the meat inside the puzzle box.

Experimental procedure - Wild

When a potential subject was seen in an accessible location we drove approximately 100m upwind of the hyena, and set the baited box on the ground there. The box was baited with approximately 2kg of raw meat. We left the latch handle protruding at 90° from the box, parallel to the ground. A trial began when a hyena approached to within 5m of the box, and ended when the hyena left the 5m-radius around the box and remained beyond this radius for 5 min, or when it moved to at least 200m from the box.

Subjects for these experiments were opportunistic and self-selected in that individuals chose whether or not to approach the puzzle box. However, every attempt was made to conduct trials with all the hyenas in each group, and to balance the number of participants in each age, sex, and rank category. We targeted successful individuals until they reached a level of proficiency, defined as opening the box three consecutive times in less than 60 s. We attempted to conduct eight trials with each unsuccessful wild individual, and we continued to present the puzzle box to unsuccessful individuals until we reached this goal or until the study period ended.

We assessed motivation by recording hyena body condition at the time of testing using a fatness index (Watts and Holekamp, 2008). However, body condition was found to have no effect on problem-solving success, persistence or the diversity of initial exploratory behaviors for wild hyenas (See Chapter 2: Benson-Amram and Holekamp, *in prep*). So, we did not include body condition as a covariate in our analyses here. Additionally, although the mean ± SE time between trials varied (37.87 ± 6.36 days), previous analyses found no significant effect of time between trials on problem-solving success, persistence or the diversity of initial exploratory behaviors in the wild hyenas (See Chapter 2: Benson-Amram and Holekamp, *in prep*); we therefore did not include this factor in our analyses here.

Experimental procedure - Captive

Captive hyenas sometimes have neophobic responses to novel situations (Drea and Carter, 2009) so we gave each captive individual a ten min habituation period in the 39m^2 test enclosure just prior to its first trial of the day. This allowed hyenas to investigate the test enclosure in the absence of the puzzle box, and minimized the amount of time hyenas spent investigating the enclosure during the experimental trial. After the habituation period, captive hyenas were moved back into a holding pen while we set-up the puzzle box. Hyenas at the field station were trained in advance of testing to move from one enclosure to another (Drea and Carter, 2009). As had been done with the wild hyenas, the puzzle box was baited with raw meat (approximately 1kg of beef ribs) and the latch handle was left protruding at 90° from the box.

Trials began when the hyena left the holding pen and entered the enclosure containing the puzzle box. Trials either ended when the hyena opened the box and removed the meat, or after 30 min had passed. Hyenas were moved back into the holding pen at the end of each trial. All hyenas were food deprived for 24 h prior to experiments to bring all individuals to the same moderately high level of motivation. All captive trials were conducted between 1100 and 1630 h. We attempted to conduct at least 6 trials with each individual, usually 3 trials per day on 2 consecutive days.

Sample size

We conducted 417 trials on 62 wild hyenas and 170 trials on 19 captive hyenas. The number of trials per individual ranged from 1–39. In total, 22 wild and 15 captive hyenas participated in at least 6 trials and the mean number of trials per individual was 7.23 ± 0.96 SE. Eighteen individuals participated in at least 8 trials during the 12-month study period.

Using wild hyenas, we conducted trials with 19 adult females, 9 adult males, 15 juvenile females, 17 juvenile males, and 2 juveniles of unknown sex. Using captive hyenas, we conducted trials with 9 adult males, 7 adult females, and 3 juvenile females.

Data extraction from videotaped trials

All puzzle box trials involving both wild and captive hyenas were videotaped in their entirety, and behavioral data were extracted from the videotaped trials. A trial was defined as a deployment of the puzzle box during which the hyena approached to within a 5-m radius. The puzzle box was initially a wholly novel stimulus for the hyenas, so we estimated neophobia by examining the latency of each focal hyena to contact the box once it entered the 5-m radius during its initial trial, or for the captive hyenas, once they entered the enclosure with the baited puzzle box. Individuals who participated in trials but never contacted the box were assigned a contact latency of 1800 s (30 min). Our neophobia measure did not allow us to include individuals who decided not to participate in a trial by remaining outside of the 5 m radius around the box.

Successful trials were those in which the puzzle box was opened. Unsuccessful trials included those in which the hyena contacted the box, but failed to open it, as well as those in which the hyena did not actually interact with the box, despite spending time within the 5-m radius. To investigate determinants of problem solving, we categorised each individual's overall success based on whether it was ever able to open the box during any of its trials in the course of the study.

We calculated the number of different exploratory behaviors hyenas exhibited when interacting with the puzzle box, and we used this number as the individual's 'exploration diversity'. Wild focal hyenas exhibited a range of exploratory behavior patterns when interacting with the puzzle box. The five most consistent patterns were catalogued as: biting, digging, flipping the box, investigating, and pushing or pulling the box. 'Biting' was defined as clamping down on the box with the teeth without displacement of the puzzle box in any direction. 'Digging' involved moving dirt or grass with the forepaws at the base of the puzzle box. 'Pushing or Pulling' involved using the mouth to move the box laterally. 'Flipping' involved using the mouth to toss the box into the air, resulting in a new side of the box touching the ground. 'Investigating' was scored when a focal animal was within 1m of the box and orienting toward the box: this did not include contact with the box, and generally occurred with the mouth closed. In order to have a direct comparison of the exploratory behavior exhibited by wild and captive hyenas, we examined the same set of five exploratory behaviors in the captive hyenas as well. If a hyena demonstrated all 5 of these behaviors at least once during a trial it received the maximum exploration diversity score of 5. If a hyena demonstrated none of these behaviors, it received an exploration diversity score of 0.

From the videotaped record, we extracted the amount of "work time" for each subject, which was the time it spent with its head down working on the puzzle box, until it either opened the box and retrieved the meat or stopped working and ended the trial. Among wild hyenas, if a conspecific other than the focal hyena opened the puzzle box or interfered with the focal animal's interaction with the box, work time was not scored. We used work time as our measure of persistence in this study.

Social influences

Among wild hyenas, lone individuals were preferentially selected for participation in trials. However, conspecifics sometimes also approached and participated in the trial. If multiple hyenas were present within a 20m-radius of the puzzle box at any point during a trial then this was defined as a ‘group trial’ and behavioral data were extracted for each individual, or ‘focal hyena’, who approached within 5m of the puzzle box. Previous analyses of these data, which controlled for pseudoreplication, revealed no effect of social context on problem-solving success (See Chapter 2: Benson-Amram and Holekamp *in prep*). However, we did find that the presence of conspecifics by the box decreased neophobia among naïve wild hyenas (See Chapter 2: Benson-Amram and Holekamp, *in prep*). Therefore, we considered social context for the wild hyenas in our analyses of neophobia, but not in our analyses of problem-solving success.

The social context experienced by the captive hyenas during their puzzle box trials was different from that experienced by the wild hyenas. In captivity, only the focal hyena was present in the test enclosure during a puzzle box trial. However, we did initially set-up the captive study to investigate social learning in spotted hyenas. Thus, 11 captive hyenas were ‘observers’ and had the opportunity to watch a conspecific, or ‘demonstrator,’ open the puzzle box just prior to each of their trials. Five hyenas served as ‘controls’ and did not have any opportunities to observe conspecifics interact with the puzzle box. Two hyenas served as demonstrators. The demonstrators were not trained to open the puzzle box, but were consistently successful in all of their trials. We therefore included social treatment group (demonstrator, observer, and control) in our analyses of captive hyenas.

Statistical analyses

We used generalized linear models (GLM; R 2.13.0) to test effects of social influences, captivity, age, social rank, and sex on problem-solving success, exploration diversity, persistence, and neophobia. Following analyses previously conducted with data from wild hyenas (See Chapter 2: Benson-Amram and Holekamp, *in prep*), we used GLM to examine the influence of exploration diversity, persistence, and neophobia on problem-solving success among the captive hyenas. Work time and latency to approach the puzzle box were log-transformed to achieve normal distributions. To ensure that individuals were not simply more diverse in their exploratory behavior because they spent more time working on the puzzle box, work time was included as the first covariate in all analyses that included exploration diversity. One outlier was excluded from our analyses on neophobia among captive hyenas because this individual did not receive a 10-min habituation period prior to the start of its first trial. However, we ran all tests on neophobia with and without this outlier, and found that the relative significance of the results and the effect direction were the same in all cases.

We determined how wild and captive individuals ranked in their exploration diversity across all trials with the puzzle box using a likelihood ratio test that compared GLMs with and without the ID of the focal hyena as a random effect. Captivity was included as a fixed covariate to determine if captive hyenas had higher mean exploration diversity scores than wild hyenas. To assess learning, we used generalized linear mixed models (GLMM; R 2.13.0) to examine how work time changed over successive trials among successful individuals. We included population (wild vs. captivity) as a fixed covariate to determine whether wild and captive hyenas differ in the rate at which they learn the puzzle box task. Focal hyena ID was included as a random effect.

Mean values are given ± standard error. Differences between groups were considered significant when $P \leq 0.05$.

RESULTS

We found no difference in success ($X^2_1 = 2.52$, $P = 0.11$), exploration diversity ($F_{1,16} = 0.060$, $P = 0.81$) or persistence ($F_{1,17} = 2.82$, $P = 0.11$) between captive hyenas who observed a conspecific open the box and those who did not. There was also no effect of previous experience in a cooperative problem-solving experiment or hormone treatment group on success (Experience: $X^2_1 = 1.63$, $P = 0.20$; Hormone: $X^2_2 = 1.77$, $P = 0.41$), exploration diversity (Experience: $F_{1,13} = 0.12$, $P = 0.73$; Hormone: $F_{2,14} = 0.54$, $P = 0.59$), persistence (Experience: $F_{1,14} = 2.59$, $P = 0.13$; Hormone: $F_{2,15} = 1.14$, $P = 0.35$), or neophobia (Experience: $F_{1,13} = 0.22$, $P = 0.65$; Hormone: $F_{2,14} = 0.38$, $P = 0.69$) among the captive hyenas. We therefore did not consider social influences, previous experience in cognition experiments, or hormone treatment group any further here.

Comparison of problem solving and exploration diversity between captive and wild hyenas

As predicted, captive hyenas were significantly more successful than wild hyenas ($X^2_1 = 23.39$, $P < 0.0001$). Only 14.5% of wild hyenas (9 of 62) ever succeeding in opening the puzzle box: whereas 73.7% of captive hyenas (14 of 19) were successful. Captive hyenas were also more persistent during their initial trial than wild hyenas ($t_{72} = -2.67$, $P = 0.0094$). On average, unsuccessful captive hyenas spent 14.9 ± 2.8 min working on the puzzle box during their first trial: whereas the average work time for wild hyenas in their first trial was only 5.3 ± 0.9 min.

We compared the percent of captive and wild hyenas that opened the puzzle box during only the first five minutes of the initial trial, and found that captive hyenas were still significantly more successful than their wild counterparts ($X^2_1 = 20.41$, $P < 0.0001$). Interestingly, all successful captive hyenas were able to open the puzzle box in their initial trial, whereas only two of the nine successful wild hyenas succeeded in their first trial.

There was significant variation among individuals in how diverse they were in their exploratory behaviors. Some individuals exhibited higher mean exploration diversity scores than others across all trials with the puzzle box (likelihood ratio test: $X^2_1 = 218.83$, $p < 0.0001$; Fig. 3.2). As Figure 3.2 shows, captive hyenas cluster at the most diverse end of the spectrum and subject population, either captive or wild, was a significant predictor of mean exploration diversity score ($F_{1, 55} = 40.74$, $P < 0.0001$; Fig. 3.2). Successful hyenas from both subject populations also cluster at the most diverse end of the spectrum (Fig. 3.2).

Characteristics associated with problem-solving success among captive hyenas

Similar to what was found in the wild (See Chapter 2: Benson-Amram and Holekamp, *in prep*), exploration diversity was a strong predictor of success among captive hyenas. Successful captive individuals were significantly more diverse in their exploratory behaviors than unsuccessful individuals in their initial trial with the puzzle box ($X^2_1 = 17.25$, $P < 0.0001$; Fig. 3.3). Interestingly, successful captive hyenas actually spent less time working on the puzzle box in their initial trial than their unsuccessful counterparts ($X^2_1 = 4.65$, $P = 0.031$). However, because all successful captive hyenas opened the puzzle box during their initial trial, successful hyenas exhibited more exploratory behaviors in a

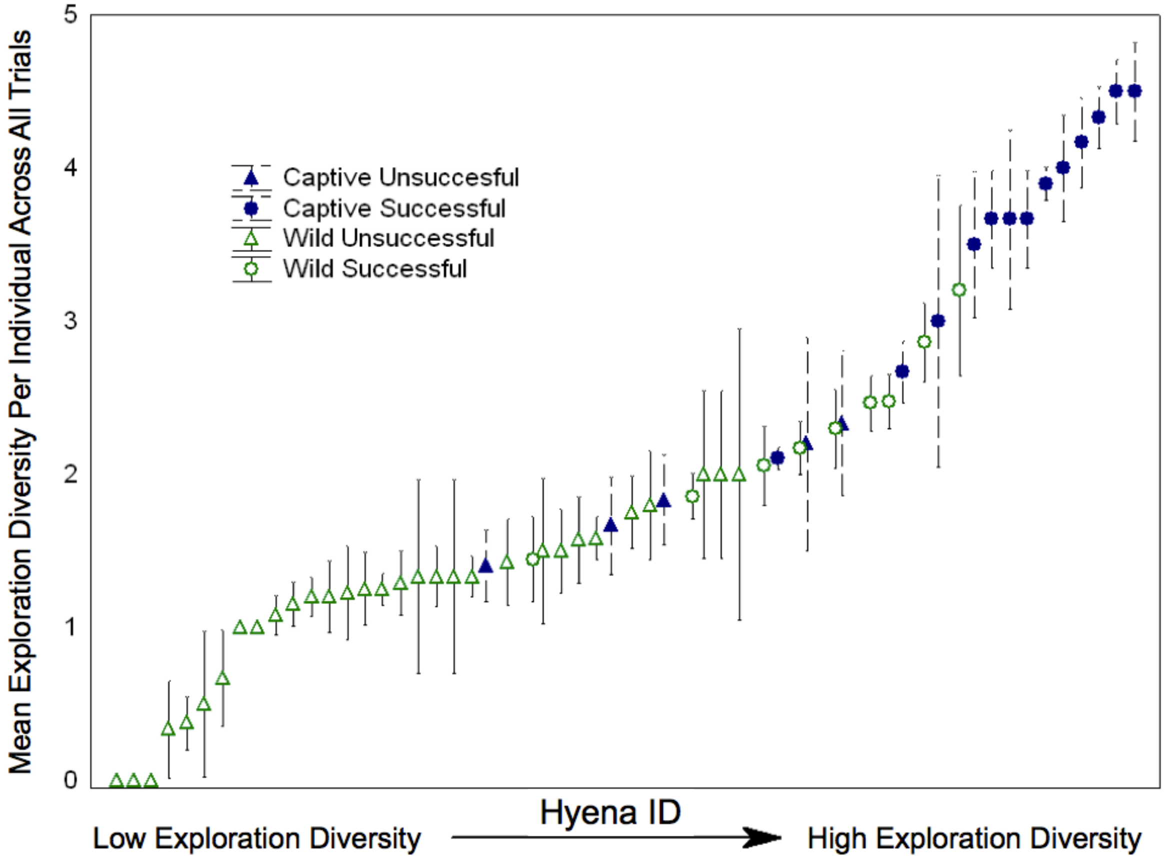

Figure 3.2. Mean ± SE exploration diversity across all trials for each individual hyena that participated in multiple puzzle box trials (*N* = 58). Individual hyenas are ranked in order of their mean exploration diversity along the x-axis. Symbol shape indicates whether the individual was captive or wild. Symbol shading indicates whether or not the individual was ever successful in opening the puzzle box.

shorter period of time than did unsuccessful individuals (Fig 3.3). Neophobia also had a significant negative effect on success among the captive hyenas ($X^2_1 = 5.05$, $P = 0.025$), with successful individuals exhibiting less neophobia in their initial trial than did unsuccessful individuals. The wild hyenas showed a similar trend (See Chapter 2: Benson-Amram and Holekamp, *in prep*).

Individual learning

We found no difference in the rate at which successful captive and wild hyenas learned the problem-solving task ($F_{1, 21} = 0.34$, $P = 0.57$; Fig. 3.4). Fig. 3.4 presents the learning curves from the first six successful trials for both wild and captive hyenas by showing the average work time to open the box for all individuals who were successful during a given trial. Trial number was a significant predictor of work time to open among captive hyenas ($F_{5, 52} = 6.083$, $P < 0.0001$; Fig. 3.4), which matches the findings previously reported in the wild hyenas (See Chapter 2: Benson-Amram and Holekamp, *in prep*). Thus, successful wild and captive hyenas improved their performance with experience and became significantly faster at opening the box over time (Fig. 3.4). Unsuccessful captive hyenas showed a steady decline in their box-oriented behavior across successive trials and showed a near extinction of any box-oriented behavior by their sixth trial ($F_{5, 18} = 9.20$, $P < 0.001$). Interestingly, this result differs from what we found in the wild population, where unsuccessful hyenas showed no reduction in effort over time (See Chapter 2: Benson-Amram and Holekamp, *in prep*).

The effect of age and sex on problem solving, exploration diversity and neophobia

We found interesting differences between wild and captive populations with respect to the influence of age on problem solving, exploration diversity and neophobia. Although we

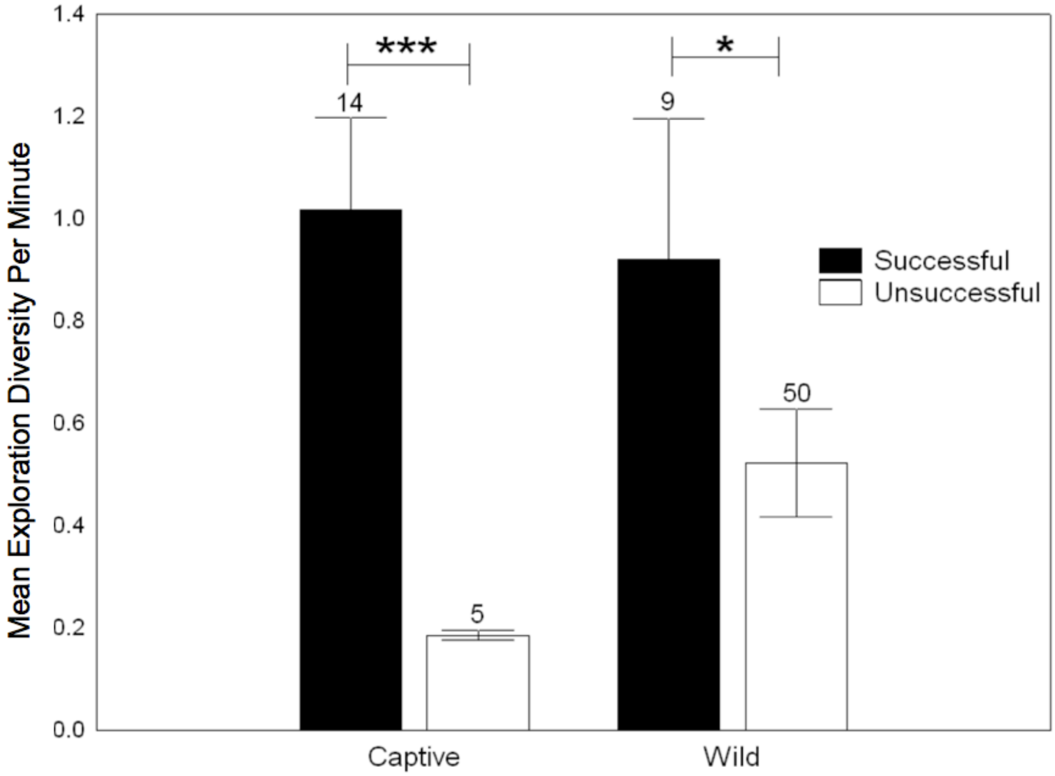

Figure 3.3. Mean ± SE exploration diversity per min for each captive and wild focal hyena during the initial trial for all individuals for whom this measure could be calculated ($N = 78$). Exploration diversity per min is calculated by dividing the number of different box-oriented exploratory behaviors by work time and is given in the number of behaviors per min. Bar shading indicates whether or not an individual was ever successful in opening the puzzle box. Asterisks represent significant differences where * = $P < 0.05$ and *** = $P < 0.001$

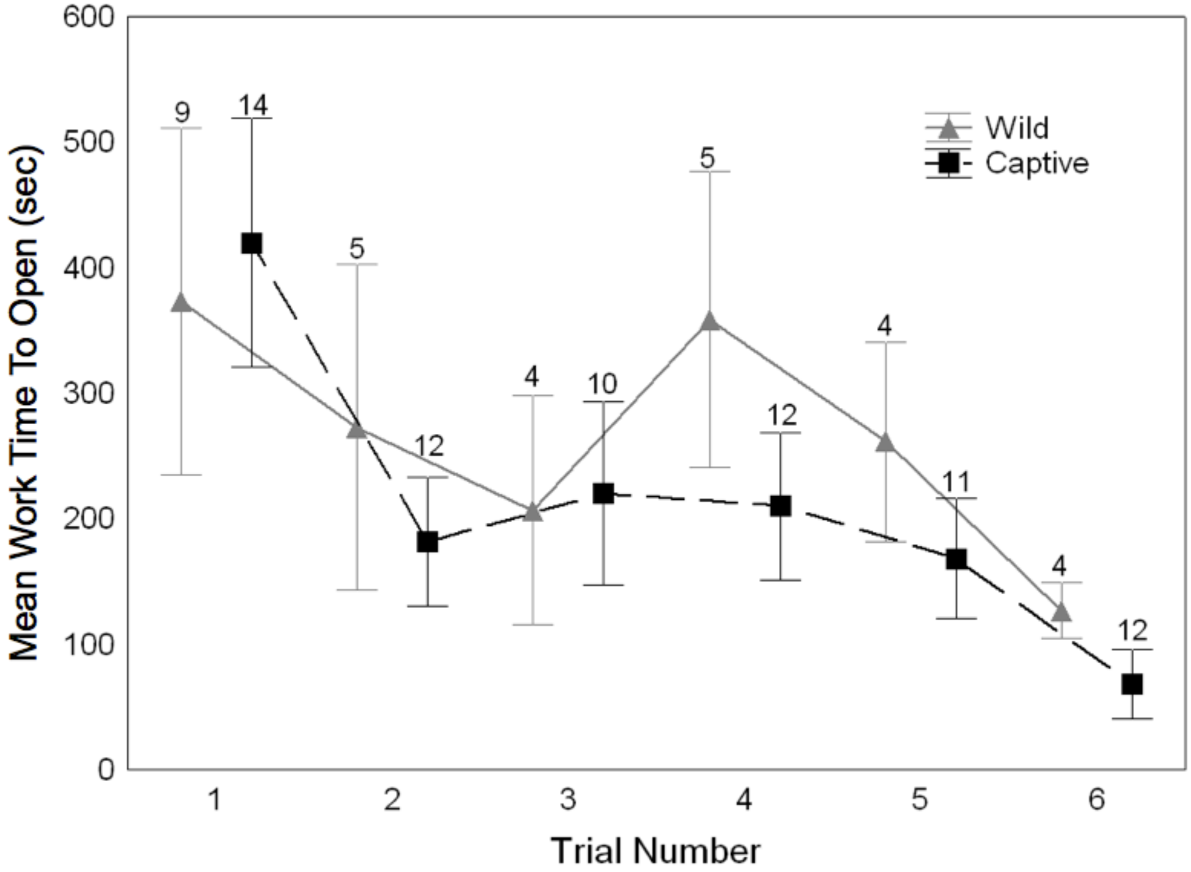

Figure 3.4. Average learning curve for successful wild and captive hyenas when interacting with the puzzle box. The learning curve represents the mean ± SE work time for all individuals who were successful in a given trial. Trial 1 represents the trial in which an individual was initially successful, and may not be the first time an individual interacted with the puzzle box. Sample sizes varied because not all hyenas that opened the puzzle box multiple times were successful in every trial.

found no age affect on success in the wild population (See Chapter 2: Benson-Amram and Holekamp, *in prep*; Fig. 3.5a), here we found that captive adults were significantly more successful than captive juveniles ($X^2_1 = 9.84$, $P = 0.0017$; Fig. 3.5a). In fact, although over 80% of captive adults were able to open the puzzle box, no captive juveniles were successful. Captive juveniles also had significantly lower exploration diversity scores ($F_{1,\ 16} = 11.13$, $P = 0.0042$; Fig. 3.5b) and were more neophobic ($F_{1,\ 16} = 20.22$, $P = 0.00037$; Fig. 3.5c) than adults, which is the opposite of what we found in the wild population (See Chapter 2: Benson-Amram and Holekamp, *in prep*; Fig. 3.5b-c). Because of this strong effect of age and because all of the captive juveniles we tested were female, we only used data from adults when examining the effect of sex on success, exploration diversity, and neophobia among captive hyenas. Sex did not significantly affect exploration diversity ($F_{1,\ 13} = 0.46$, $P = 0.51$) or neophobia ($F_{1,\ 13} = 0.65$, $P = 0.43$) among captive adults, which matches results from the wild population (See Chapter 2: Benson-Amram and Holekamp, *in prep*). However, we did find a trend for captive adult females to be less successful than captive adult males ($X^2_1 = 3.68$, $P = 0.055$). Two of the 16 captive adults tested failed to open the puzzle box and both were female. As in the wild populations, there was no effect of social rank on success ($X^2_1 = 0.01$, $P = 0.91$), exploration diversity ($F_{1,\ 16} = 0.09$, $P = 0.77$), persistence ($F_{1,\ 17} = 1.55$, $P = 0.23$), or neophobia ($F_{1,\ 16} = 0.60$, $P = 0.45$) among captive hyenas. However, it should be noted that social ranks among captive hyenas could achieve values of only one or two, which is quite different from the situation in the wild.

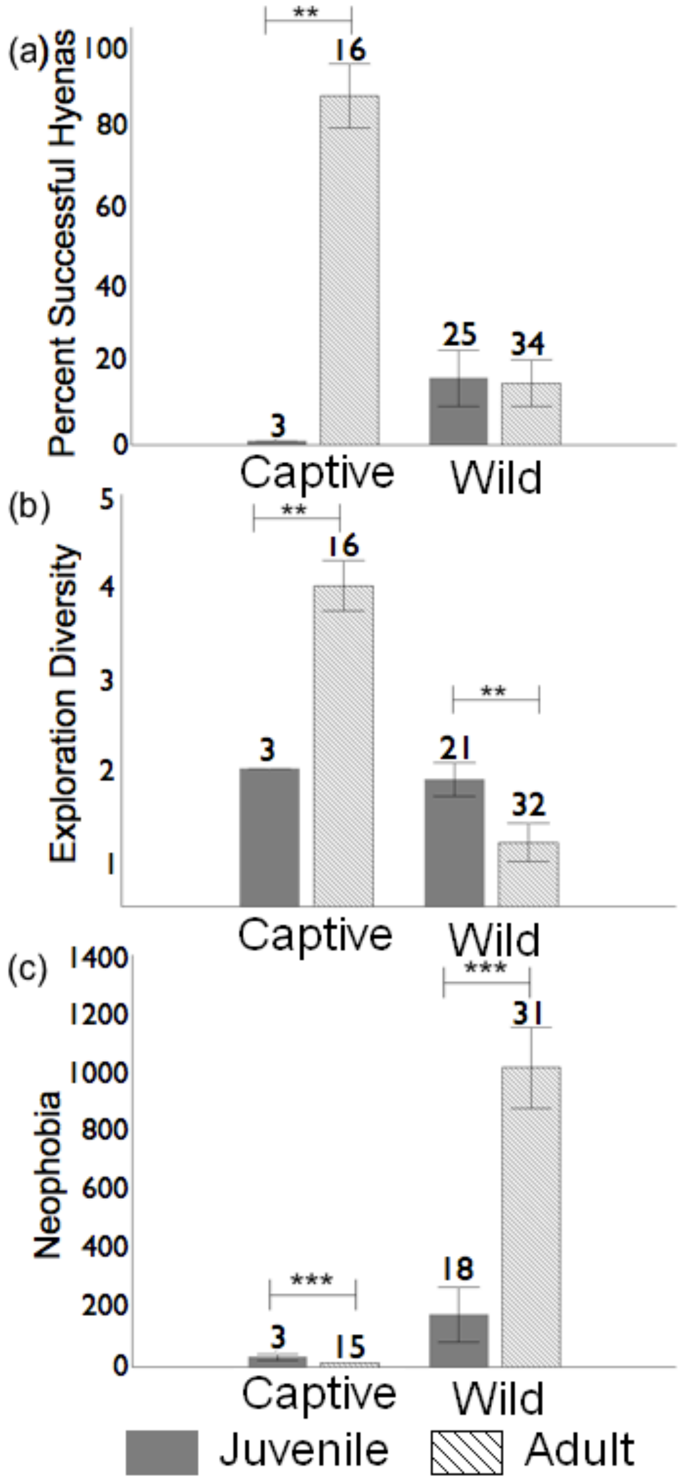

Figure 3.5. A comparison of a) the percent of individuals that were ever successful in opening the puzzle box, b) mean ± SE exploration diversity during the initial trial, and c) mean ± SE latency to approach the puzzle box during the initial trial, between captive and wild individuals divided by age class. Asterisks represent significant differences where ** = $P < 0.01$ and *** = $P < 0.001$.

DISCUSSION

As predicted, we found a striking difference in the percent of captive and wild hyenas that were able to solve a novel technical problem, even when members of both populations were allowed multiple opportunities to do so. These results match previous findings indicating that captive animals outperform their wild counterparts on novel problem-solving tasks (Bouchard et al., 2007; Gajdon et al., 2004; Webster and Lefebvre, 2001). Our data also support our prediction that captive hyenas would be more diverse in their exploratory behaviors than wild hyenas in their interactions with the puzzle box. A similar finding has been reported for hamadryas baboons, in which captives invented several behaviors that had never been seen in the wild (Kummer and Kurt, 1965). Not surprisingly, here captives were also more persistent than wild hyenas, which was likely because captive individuals were in a confined space with the puzzle box for up to 30 min, whereas wild hyenas could choose to leave the puzzle box at any time. Additionally, captive hyenas were significantly less neophobic than the wild hyenas. In fact, on average, captives approached the novel puzzle box nearly 100 times faster than the wild hyenas.

Interestingly, all of the successful captive hyenas solved the problem in their initial trial. While this result could appear to indicate insight in the captive hyenas, we argue that the captive hyenas are in fact demonstrating trial-and-error learning. The captive hyenas approached the experimental apparatus very quickly and then immediately proceeded to investigate and manipulate the apparatus. We saw no indication that any hyena exhibited behavioral indications of insightful problem solving (Beck, 1967; Kohler, 1925; Yerkes, 1927), including “hesitation, pause, or attitude of quiet concentration,” the “appearance of a critical point at which the organism suddenly, directly and definitely performs the required act,” or “ready repetition of adaptive response after once performed" (Yerkes, 1927 p. 156). Additionally, when we examine the individual learning curves of each successful captive hyena, we see that only two individuals, Scooter and Zawadi, show near mastery of the solution after their initial trial. All other successful captive hyenas learn the solution more slowly and show patterns that clearly indicate trial-and-error learning.

Several hypotheses have been put forward to explain the greater innovative tendencies among captive than wild animals (Kummer and Goodall, 1985; Reader and Laland, 2003); here we examined the extent to which our data conformed to predictions of each of these hypotheses.

H1: Excess energy

Excess energy may enable captive animals to innovate solutions to problems in their environment (Kummer and Goodall, 1985). If this hypothesis is correct, then success rates should differ between hyenas with high-food intake and those that are more food-deprived. However, when we examine success rates among only the wild hyenas, we see no evidence that individuals with better access to resources are more successful than those with low priority of access to resources. Spotted hyena societies are rigidly structured by linear dominance hierarchies in which an individual's social rank determines its priority of access to food. If differential food access influenced problem-solving ability, then social rank should have a significant effect on problem-solving success, but that was not the case. Thus, our results from the wild hyenas do not support this prediction. Additionally, the excess energy hypothesis predicts that there should be no difference in success between individuals with equivalent food intake. Here we turn to our results from the captive population where we found significant differences in success between juveniles and adults despite the fact that food intake for individuals in both age groups was equivalent. Thus, neither the captive nor the wild data support the hypothesis that excess energy enabled captive individuals to be more successful than the wild hyenas.

H2: More frequent exposure to the novel problem

Captive hyenas may have been more successful because they participated in six trials in a two-day period, compared to the wild hyenas that, on average, had significantly longer intervals between trials. The shorter time between trials among the captive individuals may have led to a more rapid learning of the problem and it's solution. If more frequent exposure to the novel problem leads to higher success rates in captive animals, then there should be no difference in the success of captive and wild individuals in their initial trial. However, 73.7% of captive individuals opened the puzzle box in their initial trial compared to only 3.2% of wild individuals. Additionally, we saw no difference in the rate at which captive and wild individuals learned the novel problem-solving task (Fig. 3.4). Thus, our data suggest that the greater success of captive hyenas was not simply a result of the frequency with which they interacted with the box.

H3: More experience with man-made objects

Captive individuals have had far more exposure to metallic man-made objects than wild individuals, which may result in less neophobia among captive than wild animals when exposed to a novel apparatus like the one used here (Huber and Gajdon, 2006; van de Waal and Bshary, 2010). Previous work has shown that neophobia negatively affects problem-solving success (Bouchard et al., 2007; Cole et al., 2011; Greenberg, 2003; Seferta et al., 2001; Webster and Lefebvre, 2001). For example, 33% of vervet monkeys with frequent access to human facilities and man-made objects solved a novel food-access puzzle whereas only 7% of vervet monkeys in more isolated areas were able to solve the same problem (van de Waal and Bshary, 2010).

We see evidence for neophobia inhibiting problem-solving success in both the captive and wild hyenas. First, captive hyenas were both significantly less neophobic and more successful than the wild hyenas. Second, if neophobia has a negative impact on problem-solving success, then captive individuals having less experience with metal man-made objects should be less successful than more experienced individuals. We found that captive juvenile hyenas were significantly more neophobic, less diverse in their exploratory behavior, and less successful than captive adults. In contrast, wild adults were more neophobic and less diverse in their exploratory behaviors than juveniles. This interesting result that age had a significant, but opposite, impact on determinants of innovative problem-solving in both populations may be due to a natural tendency for younger hyenas to be more exploratory and less neophobic than adults, but in captivity, the experience that adults have with man-made objects becomes relatively more important in terms of reducing neophobia towards a novel man-made apparatus.

An interesting prediction of this hypothesis that we were not able to test in this study is that wild hyenas should exhibit less neophobia and higher success rates if they were presented with a natural food-access puzzle, such as meat entrapped in a termite mound or in an antelope skeleton. It would be difficult to create a natural food-access puzzle that still presents a challenge for the hyenas, but the results of that study would greatly clarify the validity of this hypothesis.

H4: More undisturbed time with the novel problem

Captive individuals may be more successful because they have more time to spend working on a novel problem than do wild individuals (Kummer and Goodall, 1985). If this were true, then we would expect that, if we limited the amount of time available to captive hyenas to work on the problem, the difference in success rates between the two populations would disappear. Wild hyenas spent an average of five min working on the puzzle box in their initial trial, so we limited our analyses to only examine the percent of captive hyenas that successfully opened the puzzle box during the first five min of their initial trial. However, even during this limited time period, captive hyenas were still significantly more successful than their wild counterparts. Thus, it does not appear that the actual amount of time spent working caused the stark difference in success between the two populations.

We cannot rule out the possibility that the time captive individuals spent working on the problem was of higher quality. Wild hyenas have many other distractions to which the captive hyenas are not exposed, such as conspecific interactions, sexual interests, potential predators and limited time in which to forage. In both wild and captive populations, exploration diversity played an important role in problem-solving success. This suggests that individuals who are less distracted by their surroundings and more focused on the problem-solving task are likely to try more exploratory behaviors and be more successful than less focused individuals.

Conclusion

It appears that the significant difference in problem-solving success between the wild and captive populations is likely due to two factors. First, captive hyenas have fewer distractions and fewer conflicting motivations than wild hyenas, which likely leads to a more focused and higher quality work time for the captive individuals. Second, captive hyenas have more experience with, and exposure to, man-made objects and therefore are likely to be less neophobic and thus more innovative than wild hyenas. It also remains possible that captivity has had an ‘enculturation effect’ whereby captive hyenas have developed greater cognitive capacities due to their interaction with humans and their experience with man-made objects (Tomasello and Call, 2004; van de Waal and Bshary, 2010; Whiten and Van Schaik, 2007), or that captive hyenas have better learned the affordances of man-made objects and are therefore more adept at manipulating them in novel situations (Call and Tomasello, 1996). Further experimental work is needed to elucidate the relative contributions of these factors to the superior problem-solving abilities and exploration diversity observed among captive animals.

CHAPTER 4

LIMITED SOCIAL LEARNING OF A NOVEL TECHNICAL PROBLEM BY WILD AND CAPTIVE SPOTTED HYENAS

INTRODUCTION

Two major groups of hypotheses have been put forward to explain the evolution of complex intelligence. The first group of hypotheses focuses on ecological explanations for the evolution of intelligence and suggests that sophisticated cognitive abilities evolved due to complex physical environments, such as the need to remember when and where food will be available, known as the 'cognitive mapping hypothesis' (Milton, 1981), or the need to use tools to extract food from nuts or shells, known as the 'extractive foraging hypothesis' (Parker and Gibson, 1977). The second group of hypotheses, most notably the 'social intelligence hypothesis', posits that sophisticated cognitive abilities evolved due to life in complex societies, such as the need to recognize, respond appropriately to, and manipulate the actions of conspecifics (Byrne and Whiten, 1988; Humphrey, 1976; Jolly, 1966).

The social intelligence hypothesis has gained favor through comparative primate research, which suggests that the evolution of complex intelligence has been more strongly driven by social than physical aspects of the environment (Amici et al., 2008; Byrne, 1994; Cheney et al., 1986; Cheney and Seyfarth, 1985, 1990; Dunbar, 1992, 1995). However, if the social intelligence hypothesis is correct, then many of the cognitive abilities observed in primates should also occur in non-primate mammals that live in primate-like societies (de Waal and Tyack, 2003; Schultz and Dunbar, 2006; Tomasello and Call, 1997). Fewer studies have focused on testing cognitive abilities in other animal taxa and the lack of data from non-primates limits our understanding of the generality of the social intelligence hypothesis (Engh et al., 2005; Harcourt and Waal, 1992; Kamil, 1987).

Spotted hyena societies are similar to those of cercopithicine primates with respect to group size, hierarchical structure, and patterns of competition and cooperation (Frank, 1986; Holekamp et al., 2007; Holekamp, 1999, 2007). Specifically, hyenas and cercopithicine primates live in stable social groups in which group members recognize each other individually (Benson-Amram et al., 2011; Holekamp, 1999) and cooperate to defend group territory (Boydston et al., 2001; Harcourt and Waal, 1992). In both taxa, females are philopatric whereas males disperse (Cheney and Seyfarth, 1983; Henschel and Skinner, 1987; Pusey and Packer, 1987; Smale et al., 1997). Social groups contain multiple adult males as well as several matrilines of adult female relatives and their offspring. Additionally, societies in both taxa are characterized by strict linear dominance hierarchies, in which individuals' social ranks determine their priority of access to resources (East and Hofer, 2001; Frank, 1986; Tilson and Hamilton, 1984; Wrangham and Waterman, 1981). Juveniles inherit ranks directly below those of their mothers (Holekamp and Smale, 1991), and individuals in both taxa acquire their rank via the same mechanisms, such as maternal support in agonistic interactions and coalition formation (Engh et al., 2000; Horrocks and Hunte, 1983).

Given their remarkably similar social systems, similarities in cognitive abilities between spotted hyenas and cercopithicine primates could reasonably be attributed to convergent evolution, and such similarities would support the social intelligence hypothesis (Engh et al., 2005). Indeed, in accordance with the social intelligence hypothesis, spotted hyenas have demonstrated abilities in the domain of social cognition that are similar to those of cercopithicine primates in the few areas that have been examined to date. Hyenas recognize third party relationships (Engh et al., 2005), form coalitions (Smith et al., 2010), reconcile after fights (Wahaj et al., 2002) and cooperate to solve problems (Drea and Carter, 2009).

Social learning is an important aspect of social cognition that has received a great deal of attention in studies of primate cognition (Bugnyar and Huber, 1997; Caldwell and Whiten, 2004; Call and Tomasello, 1995; Custance et al., 1999; Custance et al., 2001; Day et al., 2003; Whiten, 1998), but has not yet been examined in spotted hyenas. Social learning is a key component of complex cognition because it enables individuals to benefit from the expertise and knowledge of other group members, and represents the basis for formation of traditions and culture (Day et al., 2003; Humphrey, 1976; Jolly, 1988; Russon, 1997; Whiten and Byrne, 1997; Whiten and Van Schaik, 2007). Here we further test the social intelligence hypothesis by examining its prediction that primate and non-primate mammals with similarly complex social systems should demonstrate comparable social learning abilities. Specifically, we test social learning in spotted hyenas and compare our results to those from studies on cercopithicine primates.

The complexity of social learning varies among gregarious species, with some animals acquiring information via the cognitively less-demanding mechanisms of social facilitation or stimulus enhancement, whereas other animals use more complex and cognitively demanding mechanisms, such as emulation or imitation (Byrne, 1995). Imitation is thought to be more cognitively demanding than other forms of social learning because it may require representations of another individual's intentions and perspective (Heyes and Galef Jr, 1996). Social facilitation occurs when individuals are more likely to perform a behavior when in the presence of a conspecific performing the same behavior than when they are alone (Shettleworth, 2009). Stimulus enhancement is defined as an increased likelihood of an observer contacting or interacting with an object as a result of observing another individual interact with that object

(Heyes, 1994; Shettleworth, 2009). Localized stimulus enhancement occurs when an observer is attracted to a specific part of the object that they saw the demonstrator manipulate (Huber et al., 2001). Unlike social facilitation, stimulus enhancement does not require the demonstrator to be present when the observer interacts with the object (Shettleworth, 2009). Emulation occurs when an individual copies elements of a complex action, but does not fully imitate, or perform the same actions, as a demonstrator (Shettleworth, 2009). Imitation, defined as “the copying of a novel or otherwise improbable act or utterance, or some act for which there is clearly no instinctive tendency” (Thorpe, 1963), occurs when an observer becomes more likely to exhibit the same novel action, action sequence, or combination of actions that they observed a demonstrator perform (Hoppitt and Laland, 2008).

Animals across a wide range of taxa have been shown to utilize the various mechanisms of social learning. For example, domestic dogs, *Canis familiaris*, acquire socially transmitted information via stimulus enhancement (Mersmann et al., 2011). Studies of social learning in captive capuchin monkeys, *Cebus apella*, show evidence for social facilitation (Visalberghi and Addessi, 2000). Captive keas, *Nestor notabilis*, emulate the actions of demonstrators when interacting with a novel food-access puzzle (Huber et al., 2001) and it appears that chimpanzees, *Pan troglodytes*, and gorillas, *Gorilla gorilla*, may imitate a demonstrator’s actions (Stoinksi et al., 2001; Whiten, 1998; Whiten et al., 1996).

Surprisingly, only a few studies have examined social learning in cercopithicine primates and the results of these studies suggest that social learning abilities of these animals are based on cognitively less-demanding mechanisms. Wild vervet monkeys, *Cercopithecus aethiops*, appear to acquire socially learned information via localized stimulus enhancement (van de Waal and Bshary, 2010, 2011). Specifically, vervet monkeys increased participation in a novel problem-solving task when they observed a female conspecific solve the novel problem and they contacted the same part of the apparatus as that contacted by the demonstrator (van de Waal and Bshary, 2010). Wild vervet monkeys did not show any evidence of emulation or imitation (van de Waal and Bshary, 2011). Additionally, watching a demonstrator did not increase problem-solving success in observers (van de Waal and Bshary, 2011). Stimulus enhancement also appears to be the main mechanism maintaining stone-handling traditions in free-ranging Japanese macaques, *Macaca fuscata* (Leca et al., 2010) and driving the social transmission of spontaneous tool use in long-tailed macaques, *Macaca fascicularis* (Zuberbuhler et al., 1996). Additionally, in a study of tool-use learning, Ducoing and Thierry (2005) found that Tonkean macaques, *Macaca tonkeana*, failed to learn to use objects as tools through social observation, despite being able to learn to use the same tools through individual learning.

Here, we experimentally investigated social learning abilities of captive and wild spotted hyenas. Given that spotted hyenas societies are most similar to those of cercopithicine primates, we predicted that, if the social intelligence hypothesis is correct, hyenas should use the same cognitively less-demanding social learning mechanisms that were observed in cercopithicine primates, such as localized stimulus enhancement. Specifically, we predicted that if hyenas learn via localized stimulus enhancement, then individuals observing a conspecific solve a novel food-access puzzle should spend more time working on relevant aspects of the puzzle than control individuals, that did not have access to a demonstrator. In contrast, if hyenas learn via social facilitation, then individuals should show reduced neophobia and increased interest toward the puzzle, but only when in the presence of a demonstrator. If hyenas learn socially through emulation, then observer hyenas should be more efficient problem-solvers and learn the solution faster than control hyenas. We also specifically inquired whether observer hyenas showed evidence of imitation by using “demonstrator” individuals with different methods of solving the puzzle. If hyenas learn through imitation, then we expected that individuals would show patterns of exploratory behavior similar to those of their demonstrator, and show different patterns from hyenas that observed a different demonstrator.

We previously reported results from a study on wild hyenas where we presented individuals with a novel food-access puzzle to investigate determinants of technical problem-solving success (See Chapter 2: Benson-Amram and Holekamp, *in prep*). The behavior of the wild hyenas during that study led us to inquire whether they were acquiring information through social observation. Here we present data confirming our observations of social learning of a novel technical problem in wild hyenas. However, since the majority of social learning studies are conducted in captivity (Whiten and Mesoudi, 2008), we conducted a follow-up study with captive hyenas in order to investigate mechanisms of social learning in a more controlled setting. The results presented here are particularly valuable because they enable a direct comparison between the social learning abilities of wild and captive populations of the same species. Experimental demonstrations of social learning in wild mammals are very rare (Muller and Cant; van de Waal and Bshary, 2011). Experiments on captive animals can provide convincing evidence of the social learning capabilities of a species, but the extension of those findings to social learning among animals in their natural habitats is controversial (Galef, 2004; Van Schaik et al., 2003). For example, although captive keas, *Nestor notabilis*, showed evidence of learning about a novel food access puzzle via emulation, a follow-up study failed to find evidence of social learning in wild keas confronting a similar task (Gajdon et al., 2004). Captive animals are usually in closer proximity to the demonstrator, and experience fewer distractions, than wild animals, and thus may exhibit more complex social learning abilities than we see in the wild (van de Waal and Bshary, 2011). Thus, demonstrating that captive animals use more complex social learning mechanisms does not necessarily mean that wild conspecifics regularly use social learning to solve problems, or that they acquire socially learned information in the same way (van de Waal and Bshary, 2011).

Lastly, Van de Waal and Bshary (2010) showed that wild vervet monkeys paid more attention to a dominant female than to a dominant male demonstrator. We inquired whether captive hyenas showed the same directed social learning as vervet monkeys; this occurs when factors such as the age, social rank, sex, relatedness or patterns of association influence the likelihood of social learning, and the likelihood of attending to a demonstrator (Coussi-Korbel and Fragaszy, 1995). Spotted hyenas are highly unusual among mammals in that adult females and their dependent offspring are socially dominant to all adult males in the social group. Given the matriarchal dominance hierarchy of spotted hyena societies, we predicted that, if hyenas show directed social learning, they should pay more attention to female than to male demonstrators.

EXPERIMENT IN CAPTIVITY

METHODS

Subjects and study site

Experiments were conducted on members of a captive breeding colony at the Field Station for Behavioral Research at the University of California, Berkeley. Data were collected from June - August 2008 when the colony housed 26 hyenas: 11 adult females, 11 adult males, and 4 juveniles under 2 years of age (3 female and 1 male). The captive hyenas are housed in outdoor or semi-outdoor enclosures, in groups of two or three individuals. Social rank is known within dyads and triads of individuals housed together, but social ranks have not been determined for each individual relative to all other hyenas in the colony. Social ranks within dyads and triads are assessed independently by caretakers and are determined through observations of submissive and aggressive behavior and through observations of displacement in competitive feeding situations (Drea et al., 2002b; Frank et al., 1989; Mathevon et al., 2010). All hyenas in the colony were born in captivity; colony founders were originally collected in 1984 and 1985 from the same district in Kenya in which the wild study animals reside.

Five captive individuals participated in a study of cooperative problem solving in 1995 (Drea and Carter, 2009). None of the other hyenas in the colony had been exposed to a manipulative problem-solving task prior to these experiments. These hyenas have also been subjects of studies focused on the endocrine basis of genital masculinization and dominance of female spotted hyenas (Drea et al., 1998; Glickman et al., 1987; Glickman et al., 1992). As such, many of these hyenas were treated *in utero* with anti-androgens or aromatase inhibitors. Previous studies found no effects of these treatments on communication, cognition or social behavior (Drea and Carter, 2009; Drea et al., 2002b). Additionally, as described in Chapter 3, we found no effect of previous experience in a cognition experiment or hormone treatment group on the abilities of hyenas to solve the same food-access puzzle that we are examining here (Benson-Amram et al., *in prep.*).

Experimental apparatus

The experimental apparatus was a rebar puzzle box inspired by Thorndike's (1911) dissertation work. The box was baited with raw meat; it had a simple bolt latch that the hyenas needed to slide laterally for the door to swing open (Fig. 4.1), thereby allowing the hyena access to the meat inside. The box was designed such that subjects could both see and smell the meat inside. The hyenas could also see and touch the entire latch mechanism, which could be opened using either the mouth or the forepaws. The puzzle box was designed so that hyenas would have to use behaviors in their existing repertoire in a novel fashion to successfully solve the problem. Hyenas often pull carcasses, or pull limbs off of carcasses. Therefore, moving the bolt latch laterally to open the door of the puzzle box represents a novel application of an existing behavior in the hyena repertoire.

The puzzle box had 2 rebar handles, one located centrally on each short side and a single door on one long side. The puzzle box for the captive hyenas had the following dimensions: L: 63.5cm × H: 33cm × W: 33cm with a 39cm long door, and weighed 45kg. Despite the weight of the box, hyenas were able to move the box by pulling and pushing it.

Experimental procedure

Eleven captive hyenas were 'observers' and had the opportunity to watch a conspecific, or 'demonstrator,' open the puzzle box just prior to each of their own trials. Six hyenas served as 'controls' and did not have any opportunities to observe conspecifics interact with the puzzle box. Two hyenas, one adult male and one adult female, served as demonstrators. The demonstrators were not trained to open the puzzle box, but were nevertheless consistently successful in all of their trials. The experimental protocol for the initial trial for each demonstrator hyena was identical to the protocol for the control hyenas. For this reason, we

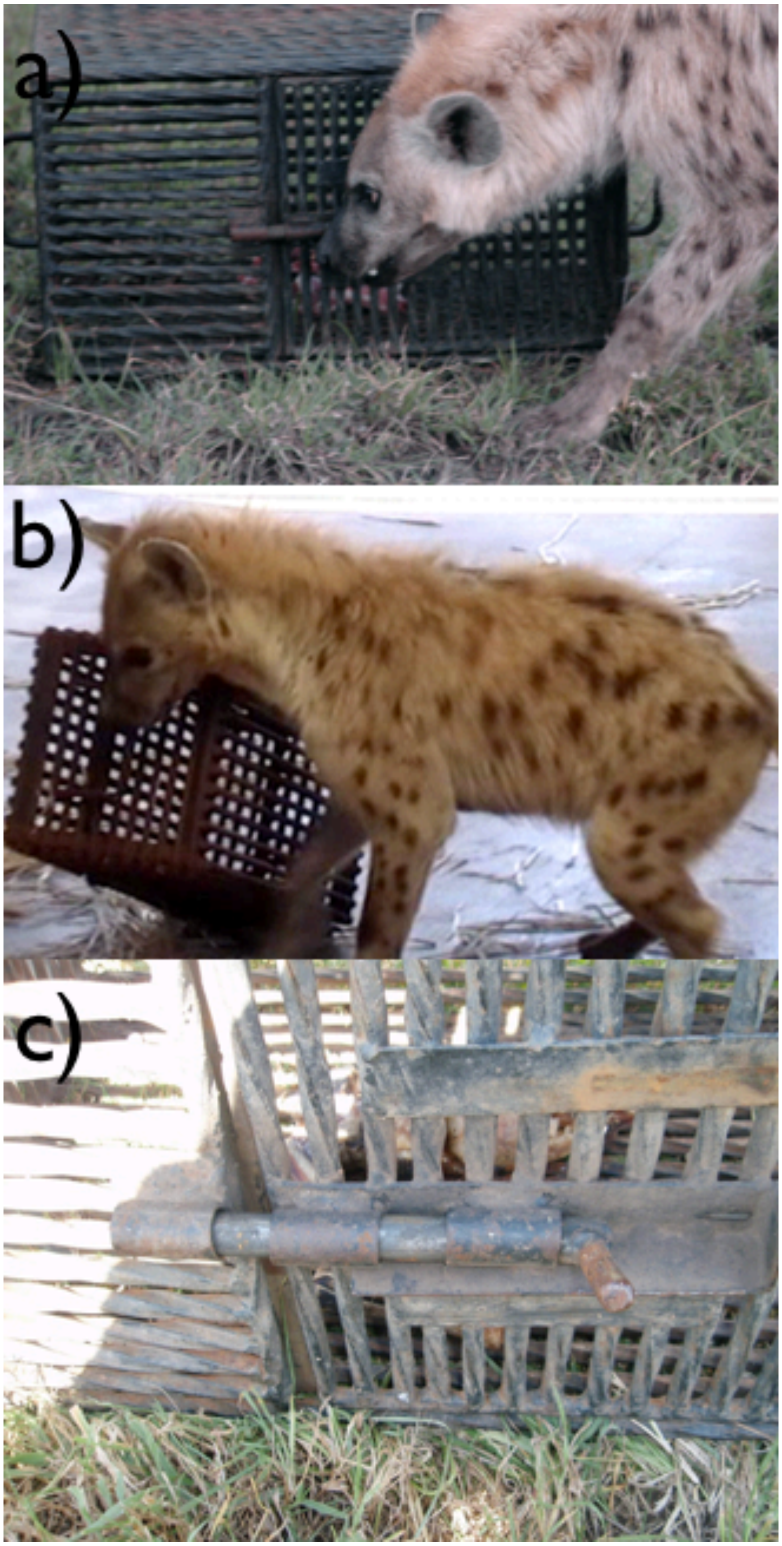

Figure 4.1. Images of the puzzle boxes used in the experiments on the a) wild and b) captive populations. In a) a wild hyena is biting the latch of a puzzle box while in b) a captive hyena is flipping a puzzle box. In c) the image is a close-up of the latch bolt that hyenas needed to move laterally to access the meat inside the puzzle box

Table 4.1. Details of the captive hyenas used in the experiments

ID	Treatment Group[1]	Sex	Age Class[2]	Social Rank[3]	Hormonal Treatment	Prior Exp.	Success
Scooter	Demonstrator	F	A	Dominant	Control	No	Y
Cass	Observer – S	F	A	Dominant	Control	No	Y
Kombo	Observer – S	F	A	Dominant	Control	No	N
Nakuru	Observer – S	F	A	Subordinate	Anti-androgen	Yes	Y
Robie	Observer – S	M	A	Subordinate	Anti-androgen	No	Y
Rocco	Observer – S	M	A	Subordinate	Control	No	Y
Zawadi	Observer – S	M	A	Dominant	Anti-androgen	No	Y
Bramble	Demonstrator	M	A	Subordinate	Control	No	Y
Gremlin	Observer – B	M	A	Subordinate	Anti-androgen	Yes	Y
Haji	Observer – B	F	J	Subordinate	Anti-androgen	No	N
Harley	Observer – B	F	J	Dominant	Control	No	N
Ursa	Observer – B	F	A	Subordinate	Control	No	N
Winnie	Observer – B	M	A	Subordinate	Anti-androgen	Yes	Y
BJ	Control	F	A	Dominant	Gonadectomized	No	Y
Denali	Control	M	A	Subordinate	Control	No	Y
Dusty	Control	M	A	Dominant	Gonadectomized	No	Y
Gulliver	Control	M	A	Subordinate	Anti-androgen	Yes	Y
Jambo	Control	F	J	Subordinate	Anti-androgen	No	N
Nairobi	Control	F	A	Dominant	Anti-androgen	Yes	Y

Each captive subject is listed along with its treatment group, sex, age, social rank, previous hormone treatment, whether or not it had previously participated in a study of cooperative problem solving conducted in 1995, and whether it was ever successful in opening the puzzle box.

[1] Treatment group refers to whether the subject was a demonstrator, an observer of the female demonstrator, Scooter (Observer-S), an observer of the male demonstrator, Bramble (Observer-B), or in the control group that did not have access to a demonstrator.

[2] Hyenas were considered adults (A) when they were over 24-months and juveniles (J) when they were under 24-months of age.

[3] Social rank refers to the rank of the subject relative to the one or two other hyenas with whom they are housed.

included the two demonstrator hyenas as members of the control group in analyses of behavior during the initial trial with the puzzle box and the sample size for the control group for these analyses was 8 hyenas. Five observer hyenas watched the adult male and six observers watched the adult female. Hyenas were assigned to observer and control groups before the experiments began. Hyenas were assigned to treatment groups to balance sex, age, rank and hormone treatment group (Table 4.1).

All hyenas were food deprived for 24 h prior to experiments to bring all individuals to a moderate motivation level. All captive trials were conducted between 1100 and 1630 h. Captive hyenas sometimes have neophobic responses to novel situations (Drea and Carter, 2009) so we gave individuals a ten min habituation period in the $39m^2$ test enclosure just prior to their first trial of the day. This allowed hyenas to investigate the test enclosure in the absence of the puzzle box, and minimized the amount of time hyenas spent investigating the enclosure during the experimental trial. After the habituation period, hyenas were moved back into the holding pen while we set-up the puzzle box. Hyenas at the field station were trained in advance of testing to move from one enclosure to another (Drea and Carter, 2009).

For the social learning trials, an observer hyena was moved into the enclosure adjacent to the test enclosure. The two enclosures were separated by a chain-link fence through which the hyenas could both see and smell the adjacent enclosure (Fig. 4.2). The puzzle box was set-up in the test enclosure such that the box was approximately 2 m from the chain-link fence. Additionally, the door and latch of the puzzle box faced the fence and adjacent enclosure. The puzzle box was baited with raw meat (approximately 1kg of beef ribs) and the latch handle was left protruding at 90° from the box.

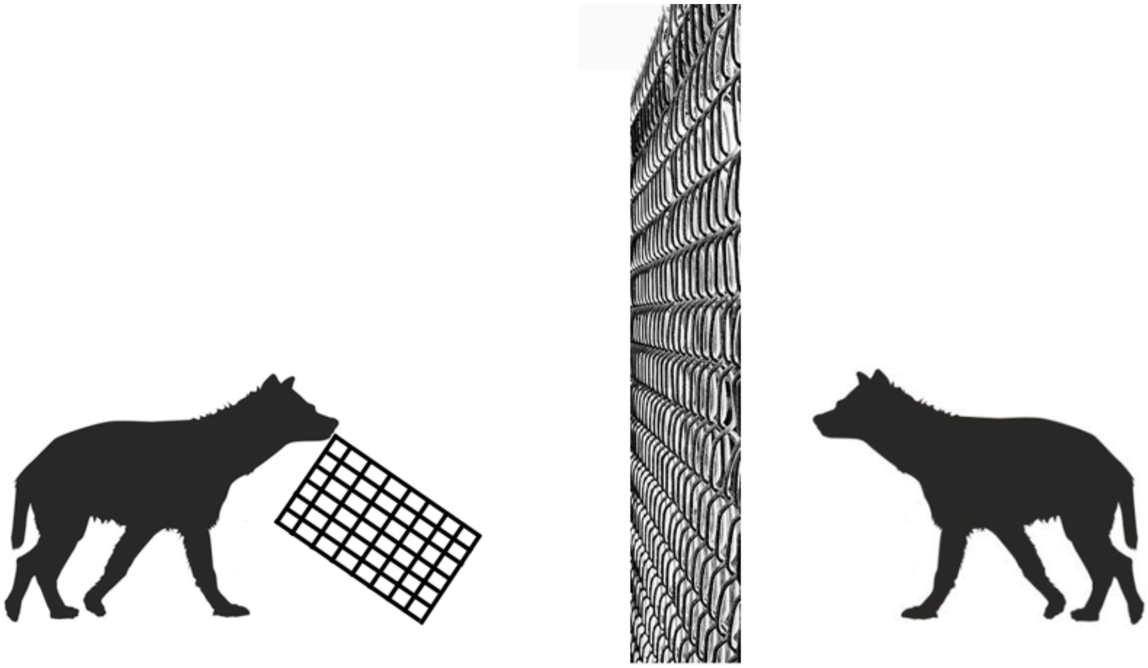

Figure 4.2. A representation of the experimental set-up for the social learning trials in the captive population. The demonstrator and observer are separated by a chain-link fence. The demonstrator is on the left side of the figure and is lifting the puzzle box. The observer is on the right side of the figure and is oriented toward the demonstrator. Prior to the start of each trial the baited puzzle box is placed 2 m from the fence with the latch side of the puzzle box facing the fence and the observer's enclosure. The hyena images are taken with permission from Van Meter (2010).

Demonstrator trials began when the demonstrator hyena left the holding pen and entered the test enclosure containing the puzzle box. Demonstrators were only allowed out of the holding pen when the observer hyena was positioned within 2 m of the fence. Demonstrator trials ended when the demonstrator opened the box and removed the meat, at which point demonstrators were moved back into the holding pen. Following each demonstrator trial we would re-bait the puzzle box and set it back in the starting position. An observer hyena was then let into the test enclosure to begin a trial. Observer trials ended when the subject opened the box and removed the meat, or when 30 min had passed, whichever came first. We would then repeat this sequence so that observer trials were always preceded by a demonstrator trial. For the control hyenas, we followed the same protocol except that control hyenas did not observe a demonstrator prior to their trials. We attempted to conduct at least three trials per day for two consecutive days, such that each observer and control hyena had 6 trials.

In total, we conducted 170 trials on 19 captive hyenas. All observer and control hyenas had 6 trials each with the exception of four individuals: two hyenas observing the adult male only had 5 trials, one control hyena had 4 trials, and one hyena observing the adult female had only one trial. One demonstrator hyena had 38 total trials and the other had 39 total trials. We conducted trials with 9 adult males, 7 adult females, and 3 juvenile females (Table 4.1).

Data extraction from videotaped trials

All puzzle box trials were videotaped in their entirety, and behavioral data were extracted from the videotaped records using the program JWatcher (Blumstein et al., 2006). We extracted detailed behavioral data from the initial trial of each observer and control hyena, and from all demonstrator trials. The JWatcher data were extracted by SBA and two research assistants;

interobserver reliability was high across all behavioral measures used (R = 0.98, range = 0.90 – 0.99). A full ethogram of the behaviors emitted by captive hyenas when interacting with the puzzle box appears in Appendix 1. JWatcher automatically recorded both the duration and number of occurrences of each behavior observed in a trial.

A ‘successful’ individual was defined as one that opened the puzzle box during its trial. An ‘unsuccessful’ individual was defined as a hyena that was present within 5m of the box during a trial, but failed to open the puzzle box. The puzzle box was a novel stimulus for the hyenas, so we measured ‘neophobia’ by examining the latency of each focal hyena to contact the puzzle box in its initial trial once it entered the enclosure with the baited puzzle box.

We calculated both the number and frequency of exploratory behaviors each focal hyena exhibited when interacting with the puzzle box. Ten different exploratory behaviors were included in this measure (push, pull, dig, foot contact, mouth contact on latch, mouth contact on handles, lift, flip, rub, and lower) and these are defined in Appendix B. We limited our analysis to these ten behaviors because these were the behaviors that had high interobserver reliability scores across all data extractors. We used the number of different exploratory behaviors hyenas exhibited when interacting with the puzzle box as a measure of ‘exploration diversity’. If a hyena demonstrated all 10 of these behaviors at least once during a trial it received the maximum exploration diversity score of 10. If a hyena demonstrated none of these behaviors, it received an exploration diversity score of 0.

Finally, we recorded the duration of time a hyena spent with it’s head down working on the puzzle box, ‘work time’, until it either opened the puzzle box and retrieved the meat, or until it stopped working on the unopened puzzle box and ended the trial. Along with total work time, we recorded both the amount of work time a hyena spent on the side of the puzzle box with the latch and on the sides of the box with the handles. We also extracted the percent of the demonstrator's work time that each observer hyena spent oriented toward the puzzle box, in order to examine how attentive each observer hyena was to the actions of their demonstrator.

Statistical analyses

In order to examine the effects of social learning in the absence of individual trial-and-error learning we limited our analyses with the captive hyenas to the initial trial with the puzzle box. The only exception was the analysis on learning across all trials for all subjects (Fig. 4.3). Additionally, previous analyses showed that captive juveniles were significantly more neophobic and less successful than captive adults on this task (See Chapter 3: Benson-Amram et al. *in prep*). In fact, all of the captive juveniles were unsuccessful in solving this novel food-access puzzle (See Chapter 3: Benson-Amram et al. *in prep*). Thus, in order to get the clearest picture of social learning in this species we only included trials on adults in our analyses, unless we were specifically testing the effect of age.

We used generalized linear models (GLM; R 2.13.0) to test the effect of social learning on problem-solving success, exploration diversity and neophobia. We did not examine the effect of social learning on persistence because all of the captive adults that ever opened the puzzle box did so during their first trial. Latency to approach the puzzle box was log-transformed to achieve a normal distribution. One outlier was excluded from our analyses on neophobia in the captive hyenas because this individual did not receive a 10-min habituation period prior to the start of their first trial. However, we ran all tests on neophobia with and without this outlier, and the relative significance and direction of the results were the same in all cases.

We used generalized linear mixed models to examine how work time changed over successive trials for observer versus control hyenas. We included whether or not the subject was in the control or observer treatment group as a fixed covariate to determine whether hyenas in these two treatments differed in the rate at which they learned the puzzle box task. Focal hyena ID was included as a random effect.

In order to examine whether observer hyenas showed similar box-oriented behavior to the demonstrator they observed, we first needed to ensure that the two demonstrator hyenas differed from one another in their box-oriented behavior. To do this, we examined each response variable using generalized linear models with demonstrator ID as the predictor variable. For these analyses, we only used data from the initial demonstration trial for each observer hyena. For the response variables that differed significantly between the two demonstrators, we then tested whether the observer and control hyenas differed in their exploratory behavior and whether the observer hyenas matched the behavior of the particular demonstrator they watched. All of the response variables used in these analyses are listed in Table 4.2. To control for work time we used residuals from a generalized linear model that included work time as the sole predictor variable as our response variable when examining the differences between demonstrators and treatment groups. We used a quasipoisson distribution for analyses of count data.

To examine the factors affecting the amount of attention observers paid to the demonstrators, assessed as the total time an observer hyena spent oriented toward its demonstrator while the demonstrator was working on the puzzle box, we used generalized linear models with residuals corrected for the demonstrators work time as the response variable and with the following predictor variables: the sex, age, and social rank of the focal hyena and the ID of the demonstrator. Alternative models were compared using Akaike’s Information Criterion

(AIC) values. A smaller AIC value indicates a better-fitting model (Crawley, 2007) and the results from the model with the lowest AIC value are reported here.

Mean values are given ± standard error. Differences between groups were considered significant when $P \leq 0.05$.

RESULTS

Effect of social learning opportunity on problem-solving success

The likelihood of success in opening the puzzle box did not differ between observer and control hyenas ($\chi^2_1 = 2.52$, $P = 0.11$). In fact, there was a trend for control hyenas to be more successful than observer hyenas. Only two captive adults failed to solve the problem, and both of these individuals were in the observer treatment group. Interestingly, all of the captive hyenas that solved the problem were successful in their initial trial. There was also no difference in exploration diversity or persistence between captive hyenas that observed a conspecific open the box and those that did not (exploration diversity: $F_{1, 16} = 0.060$, $P = 0.81$; persistence: $F_{1, 17} = 2.82$, $P = 0.11$; See Chapter 3). Likewise, the percent of time observers spent oriented toward their demonstrator had no effect on problem-solving success ($F_{1, 7} = 3.034$, $P = 0.13$). In fact, unsuccessful hyenas actually tended to spend a greater percent of work time oriented toward their demonstrator than successful hyenas.

However, we did find that observer hyenas showed a trend toward being less neophobic than control hyenas ($F_{1, 17} = 4.0$, $P < 0.062$; Fig. 4.3a). Specifically, hyenas that observed a conspecific open the puzzle box approached the box more quickly in their initial trial than

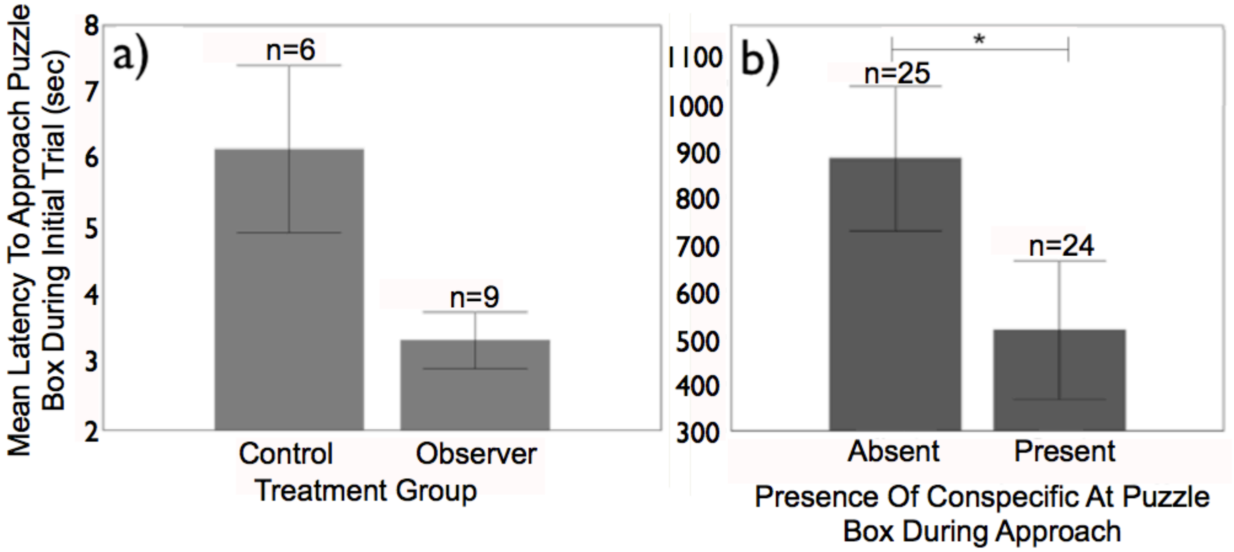

Figure 4.3. Mean ± SE latency to approach the puzzle box during the initial trial, in captive adults (N = 15) and wild individuals (N = 49) sorted on the basis of social learning context. One captive hyena was excluded from this analysis because this individual did not receive a 10-min habituation period in the test enclosure prior to the start of their first trial. Asterisks represent significant differences where * = *P* < 0.05.

control hyenas without access to a demonstrator. This is similar to a result previously reported in the wild hyenas (See Chapter 3: Benson-Amram and Holekamp, *in prep*), where we found that the presence of a conspecific at the puzzle box during a hyena's initial exposure to the novel object significantly decreased the hyena's neophobia to that object ($F_{1,35} = 4.51$, $P < 0.041$; Fig 4.3b).

Despite reducing neophobia, opportunities for social learning did not improve the speed at which observers learned the problem-solving task. As Figure 4.4 shows, individuals in both groups become significantly faster at opening the puzzle box over successive trials ($F_{1,56} = 17.52$, $P = 0.0001$; Fig. 4.4). The learning curves for the control and observer hyenas were nearly identical and observers and controls did not differ in their work time across all trials with the puzzle box ($F_{1,12} = 2.26$, $P = 0.16$; Fig. 4.4). If anything, the controls learned faster than the observers. If we limit our analysis to the initial trial, we similarly see no significant difference in work time to open the puzzle box between the observer and control hyenas, although controls tended to succeed faster ($F_{1,14} = 2.80$, $P = 0.12$; Fig. 4.4).

Factors influencing attention paid to demonstrators:

Both subordinate hyenas and juveniles paid significantly more attention to their demonstrator than did dominant hyenas or adults (Rank: $F_{1,8} = 6.55$, $P = 0.038$; Fig. 4.5a; Age: $F_{1,9} = 6.76$, $P = 0.035$; Fig. 4.5b). In contrast, male and female observers paid equal attention to the demonstrators ($F_{1,7} = 2.09$, $P = 0.20$). Furthermore, there was no evidence that observers paid more attention to a female than to a male demonstrator ($F_{1,6} = 0.078$, $P = 0.79$).

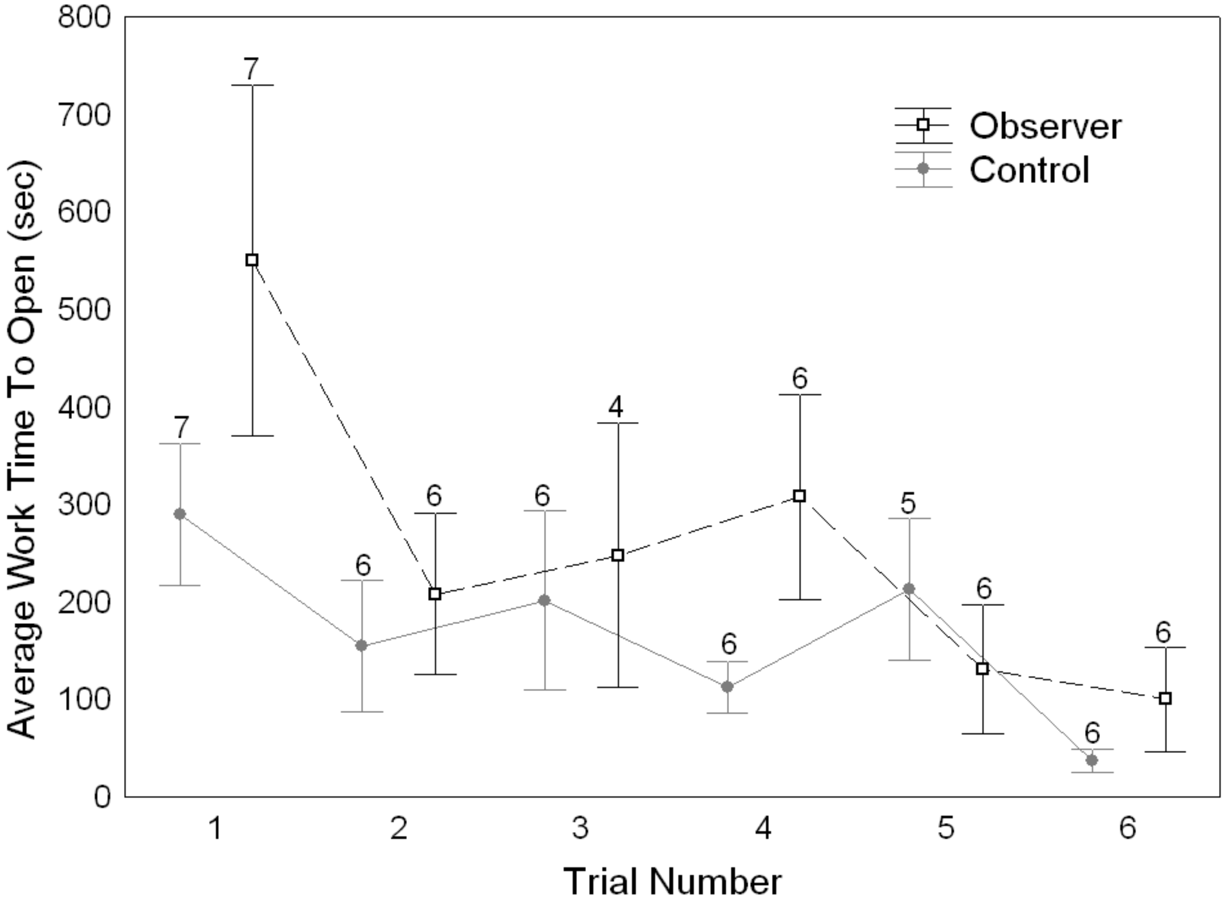

Figure 4.4. Average learning curves for successful observer (N = 7) and control (N = 5) captive hyenas when interacting with the puzzle box. The learning curves represent the mean ± SE work time for all individuals who were successful in a given trial. Sample sizes varied because not all hyenas were successful in every trial.

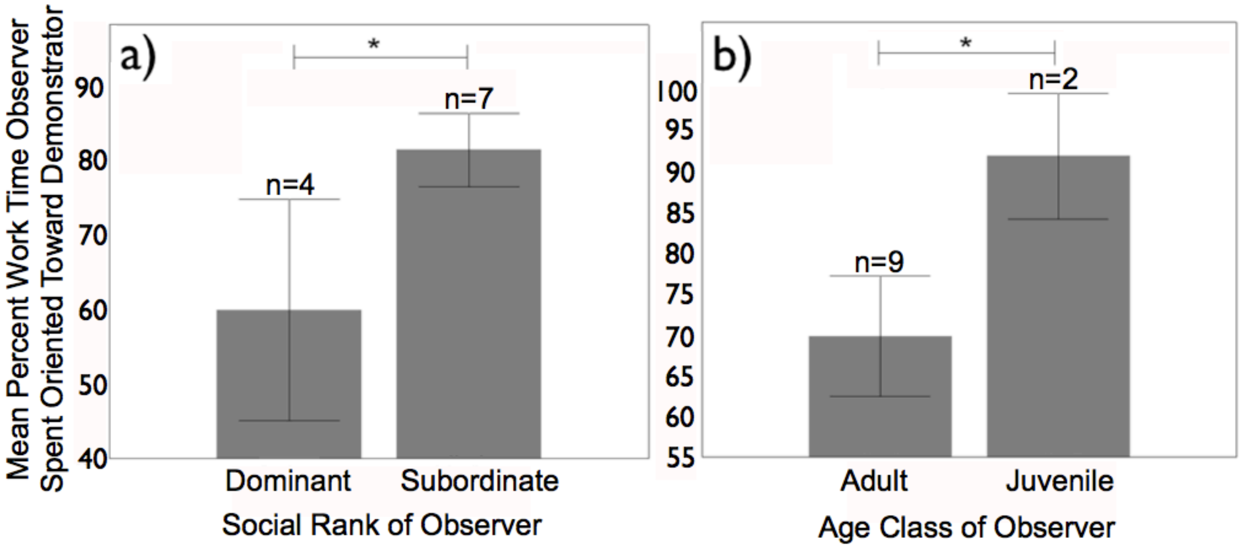

Figure 4.5. Mean ± SE percent of work time spent the observer spent oriented toward the demonstrator during the demonstrator's initial trial in front of the observer sorted on the basis of a) social rank and b) age class of the observer. All captive individuals that were in the observer treatment group are included here (N = 11).

Effect of demonstrators on exploratory behavior

The two demonstrators showed significant differences in many aspects of their box-oriented behavior (Table 4.2). In general, the female demonstrator spent more time focused on the latch (Latch Duration: $t_9 = 2.028$, $P = 0.073$; Fig. 4.6a) and generally did not move the box; whereas the male demonstrator frequently used the handles to pull (Pull Duration: $t_9 = -2.23$, $P = 0.053$), lift (Lift Number: $t_9 = -2.40$, $P = 0.040$), and flip (Flip Number: $t_9 = -2.22$, $P = 0.054$) the puzzle box (Handle Number: $t_9 = -4.13$, $P = 0.0026$; Table 4.2). Overall, the male demonstrator exhibited significantly more exploratory behaviors when interacting with the puzzle box than did the female demonstrator (Exploration diversity: $t_9 = -3.84$, $P = 0.0040$; Table 4.2). The demonstrators did not differ in their latency to contact either the latch ($F_{2,\ 13} = 0.15$, $P = 0.86$) or the handles ($F_{2,\ 13} = 1.33$, $P = 0.30$) of the puzzle box.

Despite the consistently different behavioral strategies employed by the demonstrators, observers only differed significantly in the amount of time they spent working on the latch side of the puzzle box (Fig 4.6a; Table 4.2). Observers of the female demonstrator spent significantly more time working on the latch than either observers of male demonstrator ($t_{13} = 2.76$, $P = 0.016$) or individuals in the control group ($t_{13} = 2.34$, $P = 0.036$). Observers of the female demonstrator also showed a trend toward contacting the latch more frequently than hyenas in other treatment groups (vs. Observers of the male demonstrator: $t_{13} = 2.012$, $P = 0.066$; vs. Control: $t_{13} = 1.96$, $P = 0.071$; Fig. 4.6b; Table 4.2). Surprisingly, there was no correlation between the proportion of time an observer spent watching the demonstrator and the degree of

Table 4.2. Results of generalized linear models examining the effect of Demonstrator ID and treatment group on box-oriented behavior.

Behavior	**Demonstrator S vs. Demonstrator B** [1]	**Observer S vs. Observer B** [2]	**Observer S vs. Control** [2]	**Observer B vs. Control** [2]
Latch Duration [3]	*P* = 0.073	***P* = 0.016**	***P* = 0.036**	NS
Latch Number [4]	NS	*P* = 0.066	P = 0.071	NS
Handle Duration [3]	NS	NS	NS	NS
Handle Number [4]	***P* = 0.0026**	NS	NS	NS
Dig Duration [5]	NS	NS	*P* = 0.080	NS
Dig Number [6]	NS	NS	*P* = 0.089	NS
Exploration Diversity [7]	***P* = 0.0040**	NS	NS	NS
Pull Duration [5]	***P* = 0.053**	NS	NS	NS
Pull Number [6]	NS	NS	NS	NS
Lift Number [6]	***P* = 0.040**	NS	NS	NS
Flip Number [6]	***P* = 0.054**	NS	NS	NS

All response variables were corrected for work time in the statistical model.

[1] Demonstrator data were taken from the first trial each demonstrator had with each observer. Demonstrator S is Scooter, the female demonstrator, and had n=6 first trials in front of adult observers. Demonstrator B is Bramble, the male demonstrator, and had n=3 trials first trials in front of adult observers.

[2] Observer and control data were taken from each focal hyena's initial trial with the puzzle box. Observer S refers to hyenas that watched Scooter open the puzzle box (n=6 adults). Observer B refers to hyenas that watched Bramble open the puzzle box (n=3 adults). The sample size for control hyenas was 5 adults.

[3] Latch and handle duration are measures that combine the time spent biting and licking the sides of the puzzle box with either the latch or handles, respectively.

[4] Latch and handle number denote all instances when a focal hyena initiated mouth contact with either the latch or handle sides of the puzzle box, including licking and biting the box.

[5] Dig and pull duration refer to the total time spent digging around the base of the puzzle box or pulling the box (see Appendix 1).

[6] Dig, pull, lift, and flip number refer to the total number of times the focal hyena initiated these behaviors during a trial (see Appendix 1).

[7] Exploration diversity is the total number of different exploratory behaviors that a focal hyena exhibited during a puzzle-box trial.

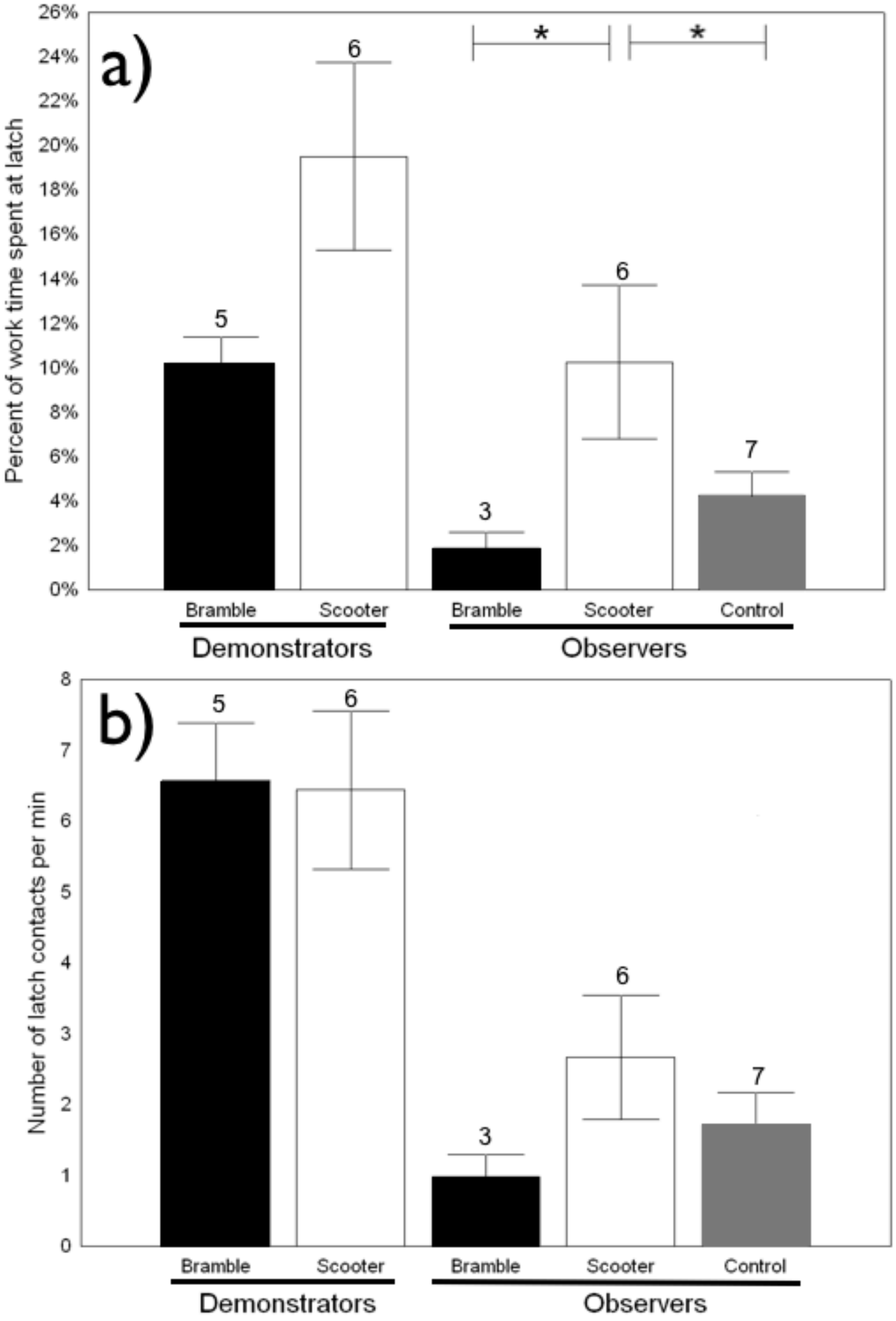

Figure 4.6. Mean ± SE a) percent of work time spent at the latch and b) number of times per min the focal hyena contacted the latch for both demonstrators and observers. Bar color represents social treatment group. The black and white bars on the left side of the figure represent the male and female demonstrator respectively. The black and white bars on the right side of the figure represent observers of either the male or the female demonstrator and the grey bar represents the control group without access to a demonstrator. All captive adults that were tested in the experiment are included here (N = 16). Asterisks represent significant differences where * = $P < 0.05$.

copying of the demonstrators actions for any behavior that we examined (Work Time: r = -0.095, N = 11, *P* = 0.78; Latch Duration: r = 0.19, N = 11, *P* = 0.58; Latch Number: r = 0.35, N = 11, *P* = 0.28; Flip Number: r = 0.44, N = 11, *P* = 0.18; Push Number: r = 0.033, N = 11, *P* = 0.93; Lift Number: r = 0.42, N = 11, *P* = 0.20; Pull Number: r = 0.30, N = 11, *P* = 0.38; Handle Duration: r = 0.14, N = 11, *P* = 0.69; Handle Number: r = 0.36, N = 11, *P* = 0.28).

EXPERIMENT IN THE WILD

Subjects and study site

Experiments were conducted from May 2007 – May 2008 on members of two neighboring study groups in the Masai Mara National Reserve, Kenya. Hyenas were observed daily, from 0530-0900 and from 1700-2000, and all experimental trials were conducted during these observation hours. Age, sex, social rank, and identity of each individual member of both groups were known (Benson-Amram and Holekamp, *in prep;* Frank, 1990; Holekamp et al., 1996; Van Horn et al., 2003). Hyenas were considered juveniles up until reproductive maturity (approximately 2 years of age), and adults included only post-dispersal males and breeding females (Holekamp et al., 1996). We never exposed these wild hyenas to a manipulative problem-solving task prior to this study.

Experimental apparatus

We presented wild hyenas with the same novel food-access puzzle that we presented to the captive hyenas (Fig. 4.1). However, due to logistical constraints, we used slightly different puzzle boxes for the wild and captive hyenas. The puzzle boxes for the two groups had the same design, 2 rebar handles, one located centrally on each short side and a single door on one long side, and were nearly the same size (dimensions of L: 60cm × H: 31cm × W: 37cm with a 34 cm long door for the wild). However, due to the different materials available in Kenya and the U.S., the wild puzzle box weighed 35kg, which is 10kg less than the box we used in the captive study. Despite the weight of the puzzle box, both wild hyenas were able to lift, flip and drag the box.

Experimental procedure

When a potential subject was seen in an accessible location we drove approximately 100m upwind of the hyena, and set the baited box on the ground there. The box was baited with approximately 2kg of raw meat. We left the latch handle protruding at 90° from the box, parallel to the ground. A trial began when a hyena approached to within 5m of the box, and ended when the hyena left the 5m-radius around the box and remained beyond this radius for 5 min, or when it moved to at least 200m from the box.

Subjects for these experiments were opportunistic and self-selected in that individuals chose whether or not to approach the puzzle box. However, every attempt was made to conduct trials with all the hyenas in each group, and to balance the number of participants in each age, sex, and rank category. We targeted successful individuals until they reached a level of proficiency, defined as opening the box three consecutive times in less than 60 s. We attempted to conduct eight trials with each unsuccessful wild individual, and we continued to present the puzzle box to unsuccessful individuals until we reached this goal or until the study period ended.

We assessed motivation by recording hyena body condition at the time of testing using a fatness index (Watts and Holekamp, 2008). However, body condition was previously found to have no effect on problem-solving success, persistence or the diversity of initial exploratory behaviors for wild hyenas (See Chapter 2: Benson-Amram and Holekamp, *in prep*). So, we did not include body condition as a covariate in our analyses here. Additionally, although the mean ± SE time between trials varied (37.87 ± 6.36 days), previous analyses found no significant effect of time between trials on problem-solving success, persistence or the diversity of initial exploratory behaviors in the wild hyenas (See Chapter 2: Benson-Amram and Holekamp, *in prep*); we therefore did not include this factor in our analyses here.

Among wild hyenas, lone individuals were preferentially selected for participation in trials. However, conspecifics approached and participated in approximately half of the trials. If multiple hyenas were present within a 20m-radius of the puzzle box at any point during a trial then this was defined as a 'group trial' and behavioral data were extracted for each individual, or 'focal hyena', who approached within 5m of the puzzle box. Previous analyses of these data, which controlled for pseudoreplication, revealed no effect of social context on problem-solving success (See Chapter 2: Benson-Amram and Holekamp, *in prep*). However, we did find that the presence of conspecifics by the box decreased neophobia among naïve wild hyenas (See Chapter 2: Benson-Amram and Holekamp, *in prep*). Here, we conducted additional analyses on more detailed behavioral data to determine whether wild hyenas that had seen the puzzle box opened displayed exploratory behavior consistent with a particular mechanism of social learning, such as localized stimulus enhancement or production imitation.

Sample size

We conducted 417 trials on 62 wild hyenas. The number of trials per individual ranged from 1–39. In total, we conducted trials with 19 adult females, 9 adult males, 15 juvenile females, 17 juvenile males, and 2 juveniles of unknown sex. 22 wild hyenas participated in at least 6 trials and the mean number of trials per individual was 7.23 ± 0.96 SE. 13 wild hyenas observed a conspecific successfully open the puzzle box before they had any opportunities for individual learning.

Data extraction from videotaped trials

Behavioral data were extracted from videotaped trials. A trial was defined as a deployment of the puzzle box during which the hyena approached to within a 5-m radius. As in the captive study, we recorded whether the focal hyena successfully opened the puzzle box, its latency to contact the box once it entered the 5-m radius during its initial trial, its work time, and the time spent on the latch side of the puzzle box. Individuals who participated in trials but never contacted the box were assigned a contact latency of 1800 s (30 min). Among wild hyenas, if a conspecific other than the focal hyena opened the puzzle box or interfered with the focal animal's interaction with the box, work time was not scored. We used work time as our measure of persistence in this study.

We calculated the number of different exploratory behaviors hyenas exhibited when interacting with the puzzle box, and we used this number as the individual's 'exploration diversity'. Wild focal hyenas exhibited a range of exploratory behavior patterns when interacting with the puzzle box. The five most consistent patterns were catalogued as: biting, digging, flipping the box, investigating, and pushing or pulling the box. 'Biting' was defined as clamping down on the box with the teeth without displacement of the puzzle box in any direction. 'Digging' involved moving dirt or grass with the forepaws at the base of the puzzle box. 'Pushing or Pulling' involved using the mouth to move the box laterally. 'Flipping' involved using the mouth to toss the box into the air, resulting in a new side of the box touching the ground. 'Investigating' was scored when a focal animal was within 1m of the box and orienting toward the box: this did not include contact with the box, and generally occurred with the mouth closed. If a hyena demonstrated all 5 of these behaviors at least once during a trial it received the maximum exploration diversity score of 5. If a hyena demonstrated none of these behaviors, it received an exploration diversity score of 0.

Statistical analyses

Social learning in the wild hyenas was examined using generalized linear models (GLM; R 2.13.0) to test effects of social influences on problem-solving success, exploration diversity, neophobia, persistence and the percent of work time spent on the latch side of the puzzle box. We included the following predictor variables in our models: 1) whether or not the focal hyena had been present when a conspecific previously opened the puzzle box, and 2) whether or not a conspecific was already interacting with the puzzle box when the focal hyena initially approached the puzzle box. Additionally, to ensure that individuals were not simply more diverse in their exploratory behavior because they spent longer working on the puzzle box, work time was included as the first covariate in all analyses that included exploration diversity. Work time and latency to approach were log-transformed to achieve normal distributions.

Mean values are given ± standard error. Differences between groups were considered significant when $P \leq 0.05$.

RESULTS

We previously reported that watching a conspecific open the puzzle box did not significantly increase problem-solving success in the wild hyenas (Fisher Exact Probability Test, $P = 0.40$; See Chapter 2). Likewise, there was no difference in either exploration diversity or persistence between hyenas that had or had not seen the puzzle box opened (Exploration Diversity: $T_{38} = -1.38$, $P = 0.18$; Persistence: $T_{38} = -0.76$, $P = 0.45$). Successful individuals were more diverse in their exploratory behaviors and more persistent in the trial following their initial success than were hyenas that had seen a conspecific open the puzzle box in the preceding trial (Exploration Diversity: $T_{38} = -5.99$, $P < 0.0001$; Persistence: $T_{38} = -2.63$, $P = 0.013$). In contrast, the percent of work time spent at the latch appeared to be influenced more by social observation than personal experience ($F_{2,\ 36} = 5.94$, $P = 0.0059$; Fig. 4.7). Hyenas that were present during a trial in which another hyena opened the puzzle box spent a significantly greater percent of their work time during the following trial on the latch side of the puzzle box than either hyenas that had experience opening the puzzle box ($T_{38} = 2.21$, $P = 0.034$; Fig. 4.7) or hyenas that had neither seen the box opened nor opened it themselves ($T_{38} = 3.37$, $P = 0.0018$; Fig. 4.7). Surprisingly, hyenas that had successfully opened the puzzle box did not spend significantly more time at the latch than hyenas that had neither seen the box opened nor opened it themselves ($T_{38} = 0.55$, $P = 0.58$). Thus it appears that observing a conspecific open the puzzle box led wild hyenas to focus their attention on the latch side of the puzzle box. However, this increased focus on the functionally relevant part of the puzzle box did not increase the likelihood of success in observers, which suggests that wild hyenas do not gain an understanding of the solution through observing it.

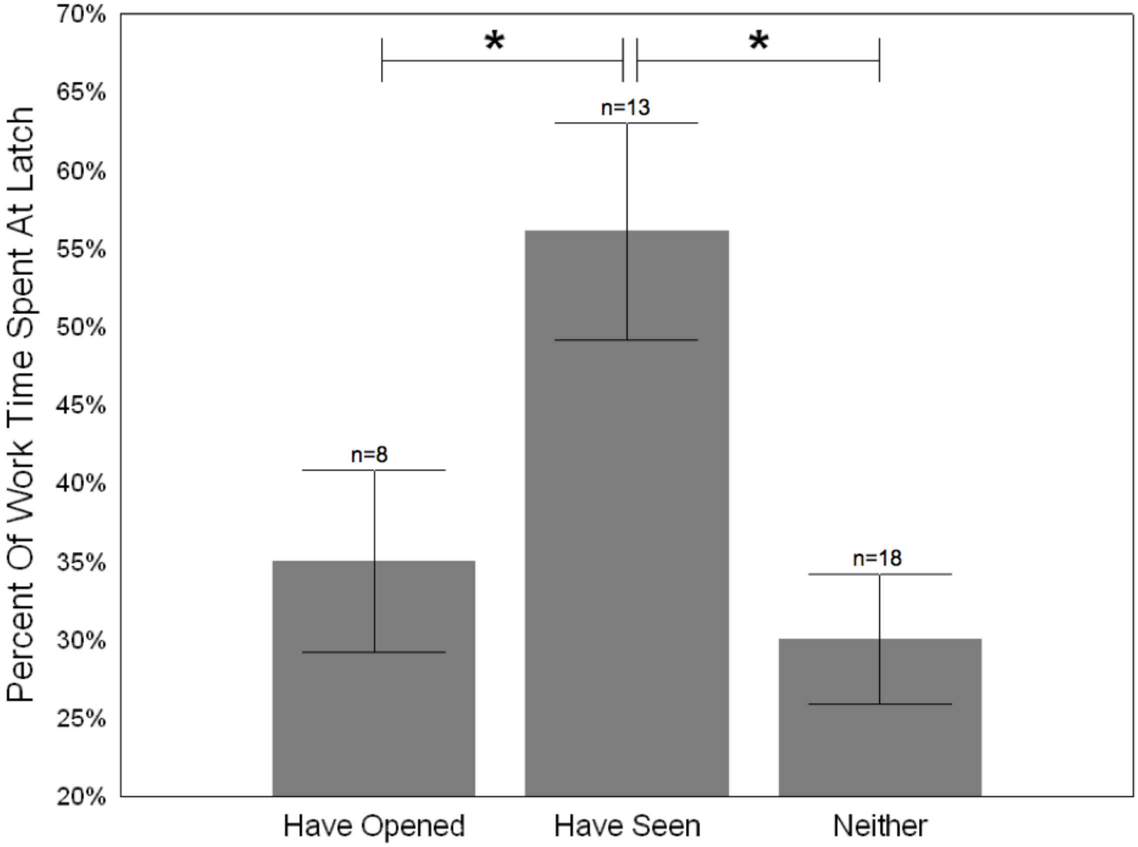

Figure 4.7. Mean ± SE percent of work time spent on the side of the puzzle box with the latch exhibited by wild individuals in the following 3 categories: 1) successful hyenas in the trial after they first open the puzzle box (N = 8), 2) unsuccessful hyenas in the trial following one where they were present when a conspecific open the puzzle box (N = 13), or 3) unsuccessful hyenas who have not been present while a conspecific opened the puzzle box in their first trial with the puzzle box (N = 18). Asterisks represent significant differences where * = $p < 0.05$.

GENERAL DISCUSSION

Whiten and Mesoudi (2008) noted that the validity of the field of social learning is limited by the overwhelming focus on studies in captivity. Here, we investigated social learning in both a wild and captive population of spotted hyenas. By testing individuals in both populations using the same experimental apparatus, we were able to confirm our observations of social learning in a natural setting with results from a controlled captive study. Our study shows that wild and captive hyenas acquire socially learned information in the same way and joins only a handful of others in using the same experimental apparatus to investigate social learning in both wild and captive populations of any single species (Bouchard et al., 2007; Gajdon et al., 2004; Seferta et al., 2001; Webster and Lefebvre, 2001).

Mechanisms of social learning

Our results provide evidence for social influences on object exploration in both wild and captive spotted hyenas. Specifically, observing a conspecific open the puzzle box led observers to focus more attention on the latch side of the box, which shows that hyenas are likely learning to focus on the functionally relevant aspect of the problem via localized stimulus enhancement (Caldwell and Whiten, 2004; Huber et al., 2001). As Caldwell and Whiten (2004) point out, localized stimulus enhancement can serve as a powerful force in social learning, even in the absence of imitation. By focusing the attention of observers on the functionally important part of the object, individuals can learn about the object and find the solution via trial-and-error learning faster than they would without this focus.

Observing a conspecific open the puzzle box also tended to decreased neophobia of both wild and captive hyenas. Neophobia can be a strong inhibitor of problem-solving success and behavioral flexibility because individuals that fail to engage with a novel problem or food resource cannot possibly succeed in solving the problem or utilizing new resources in their environment (Bouchard et al., 2007; Cole et al., 2011; Greenberg, 2003; Seferta et al., 2001; Webster and Lefebvre, 2001). Captive control and observer hyenas were tested individually, such that no other hyena was present in either the test enclosure or an adjacent enclosure during the focal hyena's trial. Our results in the captive hyenas, therefore, cannot be attributed to social facilitation, which requires the presence of the demonstrator. However, social facilitation may have played a role in the reduced neophobia of wild hyenas. Previous work has shown that observer hyenas are more likely to eat, drink, scent mark, greet conspecifics, investigate olfactory stimuli, and play in the presence of a conspecific demonstrating the same behavior (Glickman et al., 1997). Social facilitation may also play a role in the acquisition of cooperative problem-solving behavior (Drea and Carter, 2009). It would be interesting to investigate further whether social facilitation improves the abilities of spotted hyenas to solve novel food-access puzzles by also testing captive hyenas in groups.

The results from our study indicate that the social learning abilities of spotted hyenas may be relatively limited. Our results imply that hyenas are not gaining an understanding of the problem, or its solution, through social learning. Observing a conspecific open the puzzle box did not lead to an increase in problem-solving success, persistence, or innovation in observers in either the wild or captive population. These results are similar to those obtained in keas (Huber et al., 2001) and common marmosets (Caldwell and Whiten, 2004), where subjects also learned via localized stimulus enhancement without an increase in success rates. Opportunities for social learning also did not improve the rate at which hyenas became proficient at opening the puzzle box, nor did they decrease the time it took observers to solve the problem in their first trial. In fact, we actually found a trend in the opposite direction from what was expected, where, on average, successful control hyenas took less time to open the puzzle box in their initial trial than did the successful observer hyenas. Additionally, the attentiveness of the observer during the demonstrator's trial did not affect the extent to which an observer's actions matched those of the demonstrator. Observer hyenas saw the demonstrator consume the meat reward, and we, therefore, cannot discern if observing eating is necessary for social learning, and whether hyenas learn the goal of the problem and thus show goal-directed behaviors, though this appears unlikely (Hoppitt and Laland, 2008; Palameta and Lefebvre, 1985; Whiten and Ham, 1992).

Comparing social learning in the wild and captive populations

Wild hyenas appear to acquire socially learned information using the same basic mechanism as the captive hyenas. Unlike previous findings in keas (Gajdon et al., 2004) and marmosets (Halsey et al., 2006), we saw no evidence that captive individuals have more advanced cognitive abilities, or use more complex mechanisms of social learning, than their wild counterparts. This result is particularly interesting because captive hyenas are significantly more successful than wild hyenas at solving this novel problem-solving task (Benson-Amram et al., *in prep.*). The results of this study confirm that the increased success rate in the captive hyenas cannot be attributed to more cognitively-advanced social learning abilities and, instead, is likely due to factors such as reduced neophobia to man-made metallic objects and higher-quality work time due to fewer distractions and competing interests in the captive environment (Benson-Amram et al., *in prep.*).

Directed social learning

We found limited evidence for directed social learning (Coussi-Korbel and Fragaszy, 1995) in captive spotted hyenas. Directed social learning occurs when factors such as the age, social rank, sex, relatedness or patterns of association influence the likelihood of social learning, and the likelihood of attending to a demonstrator (Coussi-Korbel and Fragaszy, 1995). Vervet monkeys exhibit directed social learning and pay more attention to a female versus male demonstrator (Van de Waal and Bshary, 2010). Here, captive juvenile and subordinate hyenas spent a significantly greater proportion of the demonstrator's trial oriented toward the demonstrator than did adults and dominant hyenas. However, this increased attentiveness did not lead to an increase in problem-solving success. Male and female observers did not differ in their attentiveness to the demonstrator and, with our limited sample size, the identity of the demonstrator did not affect attentiveness in observers. In captivity, juvenile hyenas were significantly more neophobic, less innovative and less successful at solving the novel problem-solving task than adults. If social learning enables individuals to benefit from the expertise of more experienced group members (Russon, 1997), then juveniles would likely benefit more from attending to conspecifics than adults would. Additionally, lower-ranking individuals likely need to monitor the actions of dominant group members in order to avoid aggressive interactions and to capitalize on opportunities to scrounge resources. Dominant individuals can usually control access to resources and thus may not need to be as attentive to the behavior of subordinates. Dominant individuals may also have been frustrated by their inability to access the test enclosure while the demonstrator was interacting with the puzzle box, and this may have led to more stereotyped pacing behavior, which would have led to a decrease in overall attentiveness to the demonstrator.

Comparing social learning abilities of spotted hyenas and cercopithicine primates

Overall, our results support the prediction of the social intelligence hypothesis that non-primates and primates with similarly complex social systems will exhibit comparable cognitive abilities. Three separate studies of social learning in cercopithicine primates provide evidence that stimulus enhancement is the main mechanism of social learning in wild vervet monkeys (van de Waal & Bshary 2010, 2011), free-ranging Japanese macaques (Leca et al. 2010) and captive long-tailed macaques (Zuberbuhler et al. 1996). Likewise, stimulus enhancement is the mechanism of social learning with the most support in this study. Additionally, as in the hyenas, social learning opportunities did not increase problem-solving success in vervet monkeys (van de Waal & Bshary 2011) or Tonkean macaques (Ducoing and Thierry, 2005).

Conclusion

Living in a socially complex society requires that individuals recognize, interact with, and monitor the states of other group members. If intelligence evolved in response to these selection pressures, then it is probable that natural selection also favored the ability to observe and learn from the actions of conspecifics (Bugnyar and Huber, 1997). Social learning is likely an important influence, along with associative learning, in the development of various skills and cognitive abilities in spotted hyenas. For example, hyenas probably rely heavily on social learning when acquiring hunting skills, when learning about predators and when learning their social rank. Our results support this view by demonstrating that spotted hyenas learn from observing conspecifics and that they rely on the same social learning mechanism as cercopithicine primates with similarly complex social systems. However, the social learning abilities of these species appear rather limited when compared to some other primates and birds (Bugnyar and Huber, 1997; Huber et al., 2001; Stoinksi et al., 2001; Whiten et al., 1996). Vervet monkeys, baboons and spotted hyenas all appear to have less aptitude for solving technical than social problems (Benson-Amram and Holekamp, *in prep;* Cheney and Seyfarth, 1985; Laidre, 2008) and it is possible that these species have evolved domain-specific cognitive abilities. To investigate this possibility, we plan to examine the role of social learning, and the mechanisms used, when hyenas are confronted with novel social problems rather than the novel technical problem used here.

APPENDICES

APPENDIX A

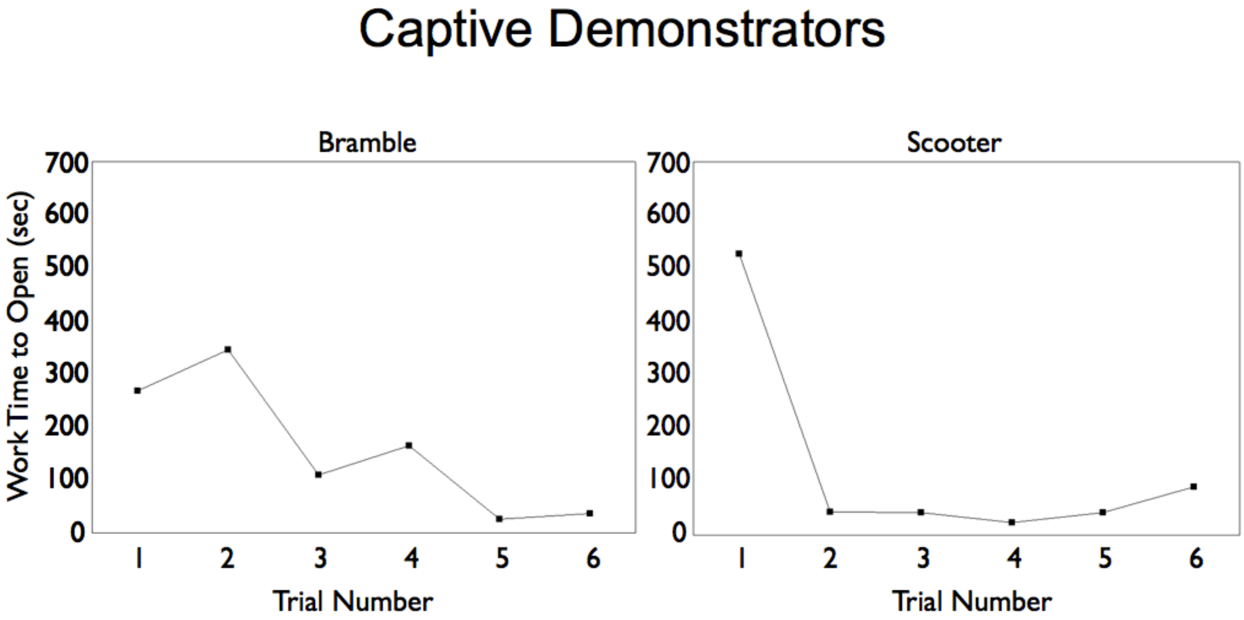

Figure A.1. Individual learning curves from the two demonstrators used in the captive study

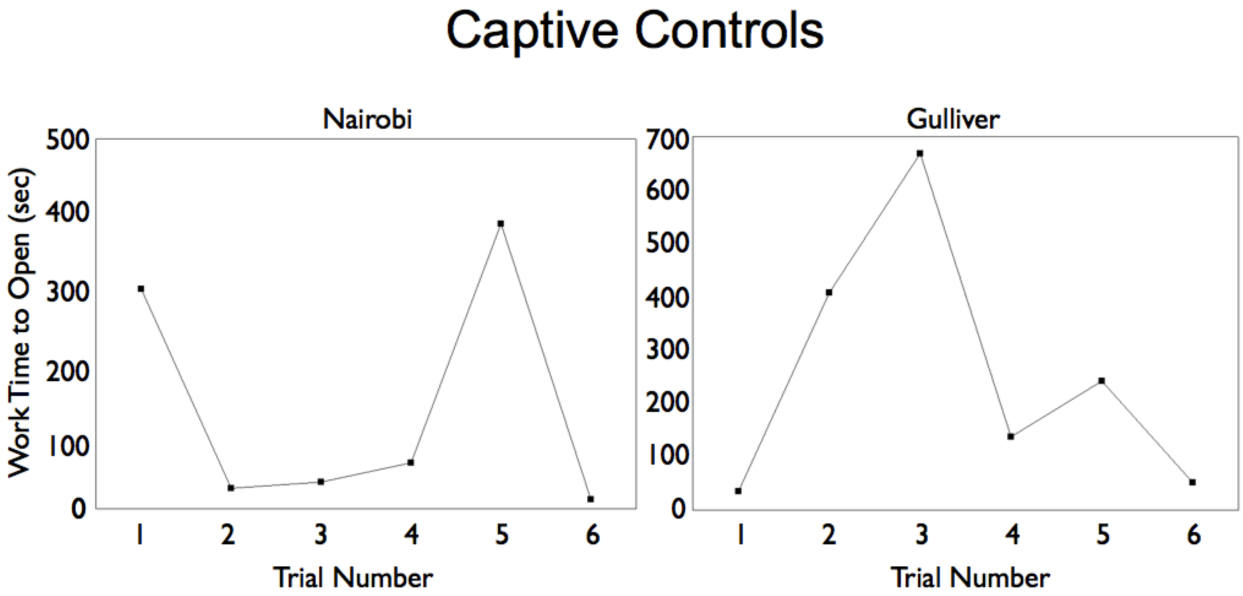

Figure A.2. Individual learning curves from a representative sample of hyenas in the control treatment group from the captive study

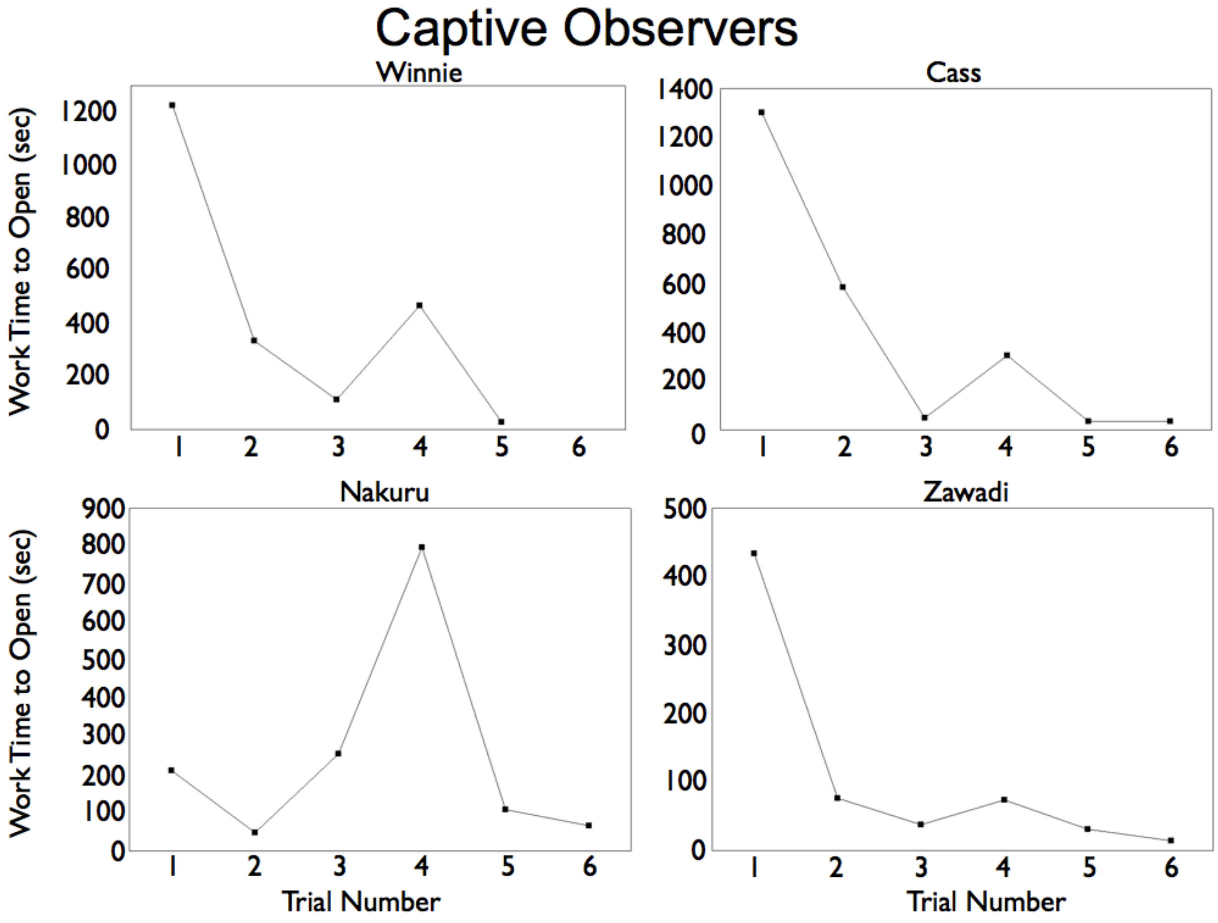

Figure A.3. Individual learning curves from a representative sample of individuals in the observer treatment group from the captive study

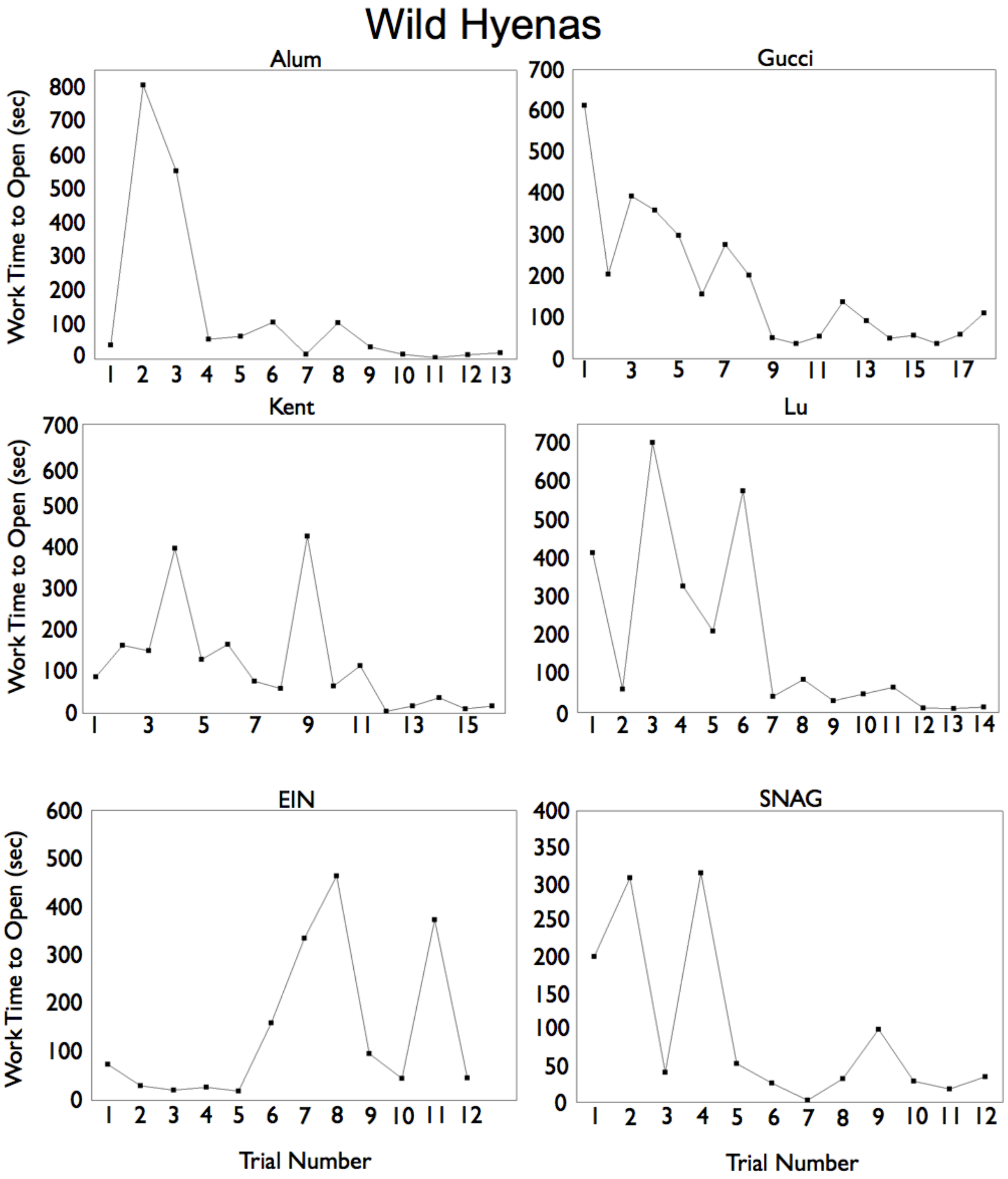

Figure A.4. Individual learning curves from successful wild hyenas

APPENDIX B

Table B.1. A behavioral ethogram of box-oriented behaviors recorded in the captive population.

Behaviors	**Definition**
Approach	subject comes within 1m of box
Back Off	subject increases distance from itself to the box or a conspecific, still orienting to box or conspecific
Bite	subject clamps down on box with teeth, does not include any movement of box with mouth
Circle	subject moves from one side of the box to another while sniffing and orienting toward box
Dig	subject moves straw (or makes motion on concrete) with front paw on ground by the side of the box
Explore Area	sniffing, walking through, looking at enclosure 1m away from box
Flip	subject uses mouth to move box into air or onto its side
Foot on Box	subject places foot on box, usually this entails subject placing foot on the top of the box
Head Bob	head wagging up and down or sideways
Head In Box	subject puts head into box
Leave	subject starts within 5m of box and increases distance from box until it is greater than 5m to box. Subject is walking away from box. Only applies when subject is leaving of its own accord, not due to displacement by a conspecific or due to other distractions or competing stimuli
Lick	subject places and moves tongue along box
Lift	subject moves box upward into the air, not enough to flip
Look	subject has gaze directed toward box, conspecific
Lower	to put face and/or body low to ground on one or both forelegs without lying down, level with meat
Open with Mouth	subject moves latch laterally with its mouth such that the door swings open or is free to swing open
Open With Body	subject moves latch laterally with it's body (not mouth or foot), often an accidental by-product of rubbing against the box
Open with Foot	subject moves latch laterally with its foot such that the door swings open or is free to swing open
Pull	subject uses mouth on handle or main box or latch to move box in the direction of the subject. Often the subject will also move backwards while it is moving the box
Pull Open Door	subject pulls open door further open, pulls unlatched door toward self
Push	subject uses mouth or body to move box away from the subject (can also be used in latch push where subject puts mouth on latch and tries to move it laterally in the opposite direction to open the box
Recline Against	lying in contact with box or conspecific with head down and gaze undirected
Recline Proximity	lying within 5 m of box or conspecific with head down and gaze undirected

Table B.1 (continued)

Behaviors	**Definition**
Retrieve Meat	subject removes meat from box with mouth
Return	after leaving, subject then comes back to within 5m of box within 5 minutes of walking away from the box
Rub	subject rubs body against that of box
Release	mouth goes from bite contact with the box to not contacting the box. Used to end a bite.
Scan	a movement of the subject's face of at least 90 degrees from the midsagittal plane
Sniff	hyena uses nose to smell. Sniffing does not include contact with the box and while the individual is sniffing the mouth is generally closed.
Stand	all four feet on the ground, head can be up looking or down sniffing
Start Session	subject comes within 5m of box
Unintentional Open	the puzzle box door opens as an accidental by-product of the box banging the ground after a flip or lift. Can also happen if subject is pulling the box along the ground and the latch gets pulled open by friction or by getting caught on a fence, etc.

Modifiers	**Definition**
Air	not the ground or the box or a conspecific, but the air
Conspecific	another hyena
Enclosure	when looking around the pen, not looking specifically at a human or at the box
Ground by box	area of soil or concrete in 1m radius surrounding box
Handle	2 sides of the box with a handle on it, or the handle itself
Human Experimenter	when looking at a person who is present while the puzzle box trial is taking place
Latch	side of the box with the latch and door on it, or the latch itself
Main	the 3 sides of the box with no latch or handle
Open Box	the box with the latch in the open position and with the door swinging free
?	Unknown

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LITERATURE CITED

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