PROBLEM SOLVING AND SOCIAL LEARNING IN SPOTTED HYENAS
(*CROCUTA CROCUTA*)

by

LINDSAY M. KUBINA

B.S., Kansas State University, 2002
M.S., Kansas State University, 2007

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Department of Psychological Sciences
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Abstract

Spotted hyenas (*Crocuta crocuta*) live in highly-complex, female-dominated groups called "clans." Due to their social arrangement, spotted hyenas were a logical species on which to test the social complexity hypothesis. In the present study, they were presented with a series of puzzle boxes designed to test problem-solving behavior. The five puzzles varied in difficulty. All spotted hyenas solved the puzzle with the lowest difficulty level, five out of six solved the medium puzzles at least once, and one out of six solved the high difficulty puzzle. Some decreases in behavior diversity and time working on the puzzles were observed over successful trials; however, the decreases were only significant for successful trials of one medium-level puzzle. Decreases in work time were observed for some unsuccessful trials and the decrease was statistically significant for the highest difficulty puzzle. Overall, spotted hyenas were proficient at problem solving in the present study.

Social learning is an important component of a lengthy juvenile period for spotted hyenas, and they have also been shown to influence one another's feeding behavior. Furthermore, spotted hyenas participate in scramble competition when feeding and forage for and hoard food. In light of these behaviors, social learning was examined using the social transmission of a flavor preference (STFP) procedure. STFP was not observed overall. The sex of the subjects did not significantly influence the results; however, subjects that interacted with each other longer were significantly more likely to show STFP. The STFP procedure may not be sensitive enough to detect social learning in spotted hyenas. Perhaps spotted hyenas have no need to learn STFP due to their digestive and/or immune systems.

The results of the current experiments make important contributions to existing knowledge. Data from other species like spotted hyenas are vital for evaluating the generality of

the social complexity hypothesis since support thus far has come from data on primates. This study was the first to investigate STFP in a species from the Feliformia suborder. Additionally, finding more evidence that spotted hyenas have advanced cognitive abilities is essential for researchers and zoo personnel who work with spotted hyenas in captivity.

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Dedication

To my family for their never-ending support.

Introduction

Spotted hyenas (*Crocuta crocuta*) are a highly social, carnivorous species that live in sub-Saharan Africa (Holekamp, Sakai, & Lundrigan, 2007a). The spotted hyena is the largest and most common type of hyena (Estes, 1991; Holekamp, 2006). The primary prey for spotted hyenas consists of vertebrates, mainly ungulates (Kruuk, 1972; Estes, 1991; Holekamp, 2006). Spotted hyenas live in matriarchal clans of varying sizes (anywhere from 6 to 90 animals), and their societies are extremely competitive (Estes, 1991; Holekamp, 2006; Holekamp et al., 2007a). However, despite the high level of competition observed in spotted hyena clans, cooperation is also present during certain activities like hunting large prey. In fact, spotted hyenas exhibit very efficient predatory behavior, and unlike other feliforms, are endurance hunters when necessary (Holekamp, 2006). Group hunts sometimes begin spontaneously, and at other times are deliberate journeys, usually led by a female. After a successful hunt, spotted hyenas have been observed caching parts of a kill underwater for later consumption (Kruuk, 1972; Estes, 1991). In addition to hunting prey, spotted hyenas also scavenge for food. Scavenging occurs both in groups and alone. When hunting or scavenging in groups, scramble competition is observed upon finding food (Estes, 1991). Scramble competition occurs when multiple members of a clan feed at the same time on a certain food source (Shettleworth, 2010).

Whether hunting or scavenging, hyenas are able to consume all parts of a kill due to their powerful jaws and teeth paired with a unique digestive system. In addition to the ability to digest all parts of a kill, spotted hyenas are also able to consume corpses that have been rotting for months (Estes, 1991). Spotted hyenas' senses of sight, smell, and hearing are all very acute, and although they are generally nocturnal, spotted hyenas are sometimes active during the day (Estes, 1991; Holekamp, 2006).

The complex social group of the spotted hyena is called a clan and is similar to that of old-world primates, for example baboons and macaques, where females are dominant. A clan can include multiple matrilineal kin groups along with multiple unrelated adult males. Matrilineal kin groups are comprised of related females and their young (Holekamp, 2006). The linear dominance hierarchies within each clan are important because rank affects access to resources. The rank of a female is determined by the social status of her mother, and the "inheritance" of rank requires much social learning during a long juvenile period (Holekamp, 2006; Holekamp et al., 2007a). Despite the often-fierce competition for food, spotted hyenas regularly cooperate when it comes to acquiring and maintaining social rank as well as when defending food and territory from neighboring clans (Holekamp, 2006). The fact that spotted hyenas sometimes compete fiercely with one another for food is one difference they have from the old-world primates (Holekamp et al., 2007a).

In addition to similarities in social structure, some researchers speculate that the social cognitive abilities of spotted hyenas are similar to those of primates. This claim is based on the fact that, like primates, spotted hyenas have complex social communication skills and use a wide variety of visual, acoustic, and olfactory signals when communicating with and discriminating among group members (Holekamp, 2006).

Despite all that is known about the ecology and social structure of the spotted hyena, the range of their cognitive abilities is still to be explored. The goal of this project was to learn more about the problem solving skills and social learning abilities of spotted hyenas. The reason for looking at both cognitive abilities is that existing research has shown that innovative problem-solving and social learning are related. Specifically, species that are innovative tend to be good at social learning (e.g. Reader and Laland, 2002; Bouchard, Goodyer, & Lefebvre, 2007). While the

advantages of being a successful problem-solver are obvious, if an animal can also learn effective strategies quickly from other group members, they can accrue additional benefits like greater access to food resources.

Learning more about spotted hyenas is important for several reasons. New knowledge about a relatively unstudied species is useful for expanding what is known about the social complexity hypothesis (discussed in the following section). Spotted hyenas are also valuable as research animals due to their unique immune systems and information about their cognitive abilities is helpful when creating an overall profile of the species. Additionally, zoos are increasingly adding spotted hyenas to their collections and in order to properly care for and enrich these animals, we must know about their cognitive capacity.

Chapter 1 - Assessing Problem-Solving Behavior in Spotted Hyenas: Puzzle Boxes

Introduction

Puzzle boxes were originally developed by Thorndike (1911) to study problem-solving behavior in animals. In Thorndike's experiments, domestic cats were placed inside of a puzzle box and food was available on the outside of the box. The cats had to figure out how to open the box and escape. After multiple trials, responses that led to escape, such as pulling a loop or pressing a button, began to occur more frequently than responses that did not lead to escape. The amount of time it took the cats to escape also decreased. Thorndike explained his results with the Law of Effect, which stated that behaviors associated with desirable outcomes will become more strongly connected to the situation and will therefore be more likely to occur when the situation is again presented. Conversely, behaviors associated with undesirable outcomes will have weakened connections with the situation and will be less likely to recur in that situation. Variations of puzzle boxes have been created that differ somewhat from the original task but have still proven useful in research on problem solving in animals.

Most puzzle boxes used currently require the subject to perform certain actions to extract food from the box. For example, a great ape may be required to undo a latch and open a hatch to retrieve a piece of candy inside a box (Dunbar, McAdam, & O'Connell, 2005) or a meerkat may have to rotate a lid in a certain direction to access a scorpion inside of a puzzle container (Thornton & Samson, 2012). However, despite the usefulness of many puzzle boxes found in current literature, a number of the puzzles cannot be used with spotted hyenas because the solutions require the use of forepaws that are similar to hands. Additionally, the size and incredible strength of spotted hyenas must be considered when designing apparatus for their use.

Puzzle boxes similar to those used in the present study were developed by Scott and Fuller (1965) and Frank and Frank (1985) in order to study problem solving behavior in quadrupeds. The puzzles required that the animals manipulate the box in a specific way to obtain a food dish that was inside of the puzzle box. Given a 2-minute time limit, the animals might, for example, have to pull a rope that was attached to the dish or push a plunger to force the dish out of the box. According to Frank and Frank (1985), when the time to solve each puzzle was limited, animals were required to plan actions in advance as well as conduct some of the trial-and-error internally since there was not enough time to physically use a trial-and-error method. Some of the more difficult puzzles could also be solved by utilizing actions that worked previously, so the ability to remember past solutions and generalize them to later puzzles was also tested. The animals further had to understand how to serially organize their behavior to solve some of the puzzles which required that they differentiate means from ends (Frank & Frank, 1985).

Scott and Fuller (1965) observed that the overall performance of puppies on puzzle boxes was quite variable and surprisingly poor. Basenjis had the highest percentages of successful trials (60-80% depending on the puzzle box), and cocker spaniels had the lowest (10-35%). In the study by Frank and Frank (1985), wolf pups succeeded in solving puzzles on 72.50% of trials and malamute puppies succeeded on only 18.75% of trials.

Researchers noted that the wolves were more persistent when faced with the puzzles and that when the puppies failed at the task, they returned to the start box and begged instead of continuing to work on the puzzle box (Frank and Frank, 1985; Scott and Fuller, 1965). The observed success and persistence of the wolves led to the prediction that spotted hyenas would solve the majority of the puzzle boxes with which they were presented.

Problem Solving in Spotted Hyenas and Their Relatives

The problem-solving abilities of species in the Feliformia suborder and Hyaenidae family remain largely unstudied. However, Thornton and Samson (2012) found evidence of innovative problem solving in wild meerkats. The meerkats were presented with three different puzzle containers, each requiring a different manipulation to access the scorpion (reward) inside. One container had a lid that could be rotated, one had a tab that could be pulled, and one had a tin foil lid that could be ripped, each action leading to the reward. Subordinate adults were particularly successful at solving the problems. The more persistent an individual was when working on the task, the more likely they were to solve it. However, the time spent working did not decrease over trials. Examination of the data revealed that the meerkats were solving the problems with trial and error; however, the meerkats were not learning to solve the problems more efficiently over time.

The ability to understand means-end connections can be useful when solving certain problems. Müller (2010) examined banded mongooses' capability for understanding means-end connections by presenting them with a food item in a plastic shell along with two anvils, one suitable for breaking open the shell. The mongooses picked the suitable and unsuitable anvils at equal rates and did not switch to the suitable anvil after an unsuccessful trial. These observations indicated that although mongooses were proficient at using anvils to gain food, they seemed to do so through trial and error learning rather than by an insightful understanding of the means-end connection.

The innovative problem-solving behavior of captive and wild spotted hyenas has been examined using a puzzle box that could be opened by sliding a latch to the side (Benson-Amram & Holekamp, 2012; Benson-Amram, Weldele, & Holekamp, 2013). Of the spotted hyenas tested,

73.7% of the captive animals and 14.5% of the wild animals were successful at solving the puzzle. Captive spotted hyenas were more persistent during their initial trial and showed greater diversity in their exploratory behaviors. Successful captive and wild spotted hyenas became faster at solving the puzzle over trials. Neophobia decreased success for both captive and wild spotted hyenas. Unsuccessful captive spotted hyenas showed a reduction in behavior over trials and were almost completely ignoring the box by the end of testing. This observation was in contrast to the wild spotted hyenas who continued to work on the puzzle throughout testing. The difference in success between captive and wild spotted hyenas was largely due to variations in the diversity of exploratory behavior and the effects of neophobia. Despite the disparities in the problem-solving behavior of captive and wild spotted hyenas, the animals were only tested on one puzzle task. The present study proposed the use of multiple puzzle tasks in an effort to clarify the nature of spotted hyenas' problem-solving abilities.

The Social Complexity Hypothesis

The social complexity hypothesis proposes that the advanced social and cognitive skills of some species evolved due to the selection pressure of group living and the need to be able to understand the dynamic behavior of conspecifics in the social group. Although this hypothesis has been supported by research using a variety of primates (Tomasello, Call, & Hare, 2003; Call et al., 2004; Hare, Call, & Tomasello, 2006), the predictions of the hypothesis have not been examined in other species. Since spotted hyenas live in clans similar to those of old-world primates (such as baboons and macaques), Holekamp (2006) and Holekamp et al. (2007a) suggested that they are an excellent species on which to test the social complexity hypothesis.

In fact, some research has shown that spotted hyenas have advanced social cognitive abilities similar to those of old-world primates (Holekamp, 2006). For example, spotted hyenas

are not only able to identify individuals within their clan (Kruuk, 1972), they can also recognize kin (Holekamp et al., 1999). Research has also shown that spotted hyenas are capable of learning about social ranks of other clan members and then later applying this knowledge in an advantageous way, such as during feeding (Holekamp, Sakai, & Lundrigan, 2007b).

The Current Study

Problem solving was assessed by presenting six spotted hyenas with a series of puzzle boxes. Based on the social complexity hypothesis and the performance of wolves on comparable puzzle boxes, I predicted that spotted hyenas could solve a series of puzzles to obtain food and that the success rates would depend on the difficulty of the puzzles. Furthermore, since spotted hyenas have been shown to solve a basic puzzle box and to have advanced social cognitive abilities, I also predicted that the time to solution (time working on puzzles) would decrease over the course of repeated testing with each puzzle. Demonstrating advanced cognitive skills in the form of problem solving would lend support to the social complexity hypothesis and contribute to existing knowledge about the cognitive abilities of spotted hyenas.

Method

Subjects

The subjects were six spotted hyenas (*Crocuta crocuta*). The subject information is summarized in Table 1.1. Charlie (male) and Smilla (female) were born August 17, 2008 and arrived at Sunset Zoo, Manhattan, KS, on January 26, 2009. They were tested from November 29, 2011 through December 24, 2011 and were 3 years and 3 months old at the start of testing. As of April 29, 2011, Charlie weighed 58 kg and Smilla weighed 61 kg.

Haji (female) was born on November 22, 2006 and arrived at the St. Louis Zoo, St. Louis, MO, on October 28, 2010. She weighed 64 kg at the time of testing. Tembo (male) was

born September 1, 2006 and arrived at the St. Louis Zoo with Haji. He weighed 62 kg at the time of testing. They were tested from July 17, 2013 through August 9, 2013. Haji was 6 years and 7 months old and Tembo was 6 years and 10 months old at the start of testing.

Askari (male) was born November 14, 2006 and weighed 55 kg at the time of testing. Grubbie (female) was born May 27, 1995 and weighed 54 kg at the time of testing. They both arrived at the Ft. Wayne Children's Zoo, Ft. Wayne, IN, on March 4, 2009. They were tested from February 3, 2014 through March 7, 2014. When testing began, Askari was 7 years and 2 months old and Grubbie was 18 years and 8 months old.

All of the subjects had similar body mass and had been at their respective zoos for about 3 years when they were tested. With the exception of Grubbie, all of the spotted hyenas were of similar age.

Table 1.1 Subject Information for Problem-Solving Study

Zoo	Name	Sex	Date of Birth	Date Arrived at Zoo	Dates of Testing	Age at Testing	Weight at Testing
Sunset	Charlie	male	08/07/08	01/26/09	11/29/11-12/24/11	3yr 3mo	58 kg
Sunset	Smilla	female	08/07/08	01/26/09	11/29/11-12/24/11	3yr 3mo	61 kg
St. Louis	Haji	female	11/22/06	10/28/10	07/17/13-08/09/13	6yr 7mo	64 kg
St. Louis	Tembo	male	09/01/06	10/28/10	07/17/13-08/09/13	6yr 10mo	62 kg
Ft. Wayne	Askari	male	11/14/06	03/04/09	02/03/14-03/07/14	7yr 2mo	55 kg
Ft. Wayne	Grubbie	female	05/27/95	03/04/09	02/03/14-03/07/14	18yr 8mo	54 kg

Materials

The Puzzle Box

Two puzzle boxes were constructed of Tamko EverGrain composite wood. The boxes were basically identical. Photographs and measurements of the puzzle boxes, puzzle apparatus and puzzle designs can be found in Appendix A, Figures A.1 through A.8. The sides had gaps between the boards that allowed the animals to see and smell the food reward (a 56 g piece of beef heart) but not reach it with their mouth or paws.

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The front side of the boxes had a door that could be raised to allow a food dish to slide in and out through an opening. The back of the boxes had a door that could be raised to make a second opening. The top of the boxes were removable (Appendix A, Figure A.1).

A metal pet-food bowl held the food reward for all trials (Appendix A, Figure A.2).

Preliminary Trial

A heavy-duty tension rod was used during Preliminary trials at Sunset and St. Louis to prevent the food bowl from sliding all the way to the back of the box and out of the animal's reach. A T-shaped piece made from the composite wood was made for this purpose and used in Ft. Wayne due to concerns about the safety of the spotted hyenas if the tension rod should be removed from the box. The tension rod and composite 'T' used for the Preliminary trials are shown in Appendix A, Figure A.3.

The preliminary trial was simple enough that all animals could solve it. During the preliminary trial, about a third of the bowl stuck out from the front of the box, and the food was placed toward the back of the bowl. The tension rod or composite 'T' was placed behind the bowl. The animals were able to see and smell food through the top and sides of the puzzle box, and since the food bowl was sticking out of the box, they were able to use their nose or paw to get the bowl all the way out of the box to access food (Appendix A, Figure A.3).

Remove Bowl Puzzle

A heavy-duty tension rod was placed behind the food bowl to keep the bowl from sliding out of the animals' reach during the Remove Bowl Puzzle at Sunset and St. Louis. A T-shaped piece made from the composite wood was used for the same purpose in Ft. Wayne due to concerns about the safety of the spotted hyenas if they removed the tension rod from the box.

The tension rod and the composite 'T' used for the Remove Bowl Puzzle are shown in Appendix A, Figure A.4.

The Remove Bowl Puzzle was similar to the preliminary trial, except the food bowl was moved farther into the box such that the front of the bowl was even with the front of the box (Scott & Fuller, 1965; Frank & Frank, 1985). The tension rod or composite 'T' was placed behind the bowl (Appendix A, Figure A.4).

Cable Puzzle

For the Cable Puzzle, the bowl was moved to the back of the box, and a section of plastic-coated cable with a PVC handle (slightly curved elbow piece) at one end was attached to the bowl. The bowl could be removed by pulling on the handle or cable out from the front opening of the box (Scott & Fuller, 1965; Frank & Frank, 1985) (Appendix A, Figure A.5).

Lazy Susan Puzzle

The Lazy Susan Puzzle involved adding an L-shaped "revolving door" to the box that functioned similarly to a lazy Susan (Frank & Frank, 1985, p. 268). The lazy-Susan apparatus was constructed from Tamko EverGrain composite wood and was shaped like a right triangle. The food bowl sat in the middle of the triangle. The longest board of the lazy Susan covered the opening on the front of the box and stuck out farther than the front left side of the box. The animals had to push this board from behind (or pull it from the front) so that it caused a second (connected) board on the inside of the box to rotate and push the food bowl out of the gap in the front of the box (Appendix A, Figure A.6).

Remove Lid Puzzle

For the Remove Lid Puzzle, the front and rear doors of the box were closed, and two handles, fashioned from PVC pipe (slightly curved elbow pieces) and coated cable, were

attached to the lid. In order to access the food bowl, the animals were required to pull the lid off of the box (Scott & Fuller, 1965; Frank & Frank, 1985) (Appendix A, Figure A.7).

Plunger Puzzle

For the Plunger Puzzle, the food bowl was at the back of the box and attached to a plunger-type apparatus that stuck out of the back of the box (Frank & Frank, 1985). The plunger was made from PVC pipe. Instead of pulling the bowl out from the rear door or manipulating the bowl out through the front of the box, the animals had to push the plunger from the back of the box so that the plunger forced the bowl out through the front opening (Appendix A, Figure A.8).

Puzzle Difficulty

The puzzles varied in difficulty with the Remove Bowl Puzzle being the least difficult ("low difficulty") since the animals simply had to use their paw(s) or mouth to grab the bowl from the front opening. The Cable, Lazy Susan, and Remove Lid Puzzles all required that the animals pull on an item (cable/handle, board, lid handles, respectively) in order to be able to access the bowl. These three puzzles were of a comparable level of difficulty ("medium difficulty"). One puzzle, the Plunger Puzzle, was classified as "high difficulty" because the animals had to coordinate two behaviors: pushing the plunger into the box and then going to retrieve the bowl from the front opening. Additionally, this was the only puzzle where the solution required the animals to push the apparatus, and therefore the food bowl, away from themselves.

Additional Materials

Three digital video cameras were used to record all of the trials. Two cameras (a Canon Vixia HFR20, Canon Corporation, Ota, Tokyo, Japan and a Sony Handycam DCR-SX40, Sony Corporation, Konan Minato, Tokyo, Japan) were mounted to the inside of the test enclosure; one

recorded from the left and one from the right. A third camera (Flip video mini-camcorder, Cisco Systems, Inc., San Jose, CA) was used by the researcher to record all trials from the front (outside) of the enclosure. All trials were timed with a stopwatch. A second stopwatch was used on some trials to track inactivity or stereotypic behaviors. Stereotypic behavior, or a stereotypy, refers to a behavior or behavior pattern that is repeated over and over in the same way with no evident goal or function (Mason, 1991). An example of a sterotypy would be pacing along a wall or fence for an extended period of time.

Procedure

The spotted hyenas at Sunset and Ft. Wayne were food-deprived for 18 to 24 hours prior to each training and testing session. The spotted hyenas in St. Louis were partially fasted due to back-to-back test days. Instead of not receiving any food in the 18 to 24 hours prior to testing, they were given half of a normal ration. The 18 to 24 hour and partial fasts did not appear to cause the spotted hyenas any distress. No problems were anticipated with the fast periods since the Association of Zoos and Aquariums (AZA) guidelines for the care of hyenas (Shoemaker, Dulaney, & Noble, 2001) recommend fasting them one or two days per week due to the potential for obesity in captive spotted hyenas. Additionally, in the wild, hyenas may go for 2 to 5 days without a meal (Estes, 1991).

Reward training was conducted for 5 days prior to the start of test trials. During reward training, food was put in the bowl and the bowl was placed inside of the puzzle box with the lid removed. The animal was then released into the testing area and allowed to eat the food from the bowl. Similar to Scott and Fuller's (1965) study, the animal was given four trials over 3 days with the box facing forward. The box was then moved so that the left side was facing forward and two more days of training were conducted with four trials per day (Appendix A, Figure A.2).

This type of training allowed the animal to learn that food could be obtained from the metal bowl inside of the puzzle box.

Testing was conducted for 10 days. Each test day started with a preliminary trial (Frank & Frank, 1985). In order to keep the animal's attention, but not exhaust them, one preliminary trial was given per day followed by two puzzle trials. The puzzle trials consisted of two different puzzles. Table 1.2 contains the order of test trials for each test day. Each spotted hyena was presented with each puzzle four times by the end of testing, with a few exceptions. Since the design of the Remove Lid Puzzle was changed after the first time it was presented, Charlie and Smilla had three total trials with this puzzle instead of four. Smilla's first trial with the Plunger Puzzle was omitted since she was able to remove the lid from the box to access the plunger.

Table 1.2 Order of Test Trials for Each Test Day of the Problem-Solving Study

Test Day	Trial 1	Trial 2	Trial 3
1	Preliminary Trial	Remove Bowl Puzzle	Cable Puzzle
2	Preliminary Trial	Lazy Susan Puzzle	Plunger Puzzle
3	Preliminary Trial	Remove Lid Puzzle	Remove Bowl Puzzle
4	Preliminary Trial	Cable Puzzle	Lazy Susan Puzzle
5	Preliminary Trial	Plunger Puzzle	Remove Lid Puzzle
6	Preliminary Trial	Cable Puzzle	Remove Bowl Puzzle
7	Preliminary Trial	Plunger Puzzle	Lazy Susan Puzzle
8	Preliminary Trial	Remove Bowl Puzzle	Remove Lid Puzzle
9	Preliminary Trial	Lazy Susan Puzzle	Cable Puzzle
10	Preliminary Trial	Remove Lid Puzzle	Plunger Puzzle

The animals were given 30 to 40 minutes to solve each puzzle. This interval was much longer than the 2-minute interval used by Frank and Frank (1985) because tasks of this nature were novel to the spotted hyenas and some neophobia or fear was anticipated (A. Linde, personal communication, May 2, 2011).

Additionally, based on recommendations by A. Linde (personal communication, May 2, 2011) and the procedure of Frank and Frank (1985), the following protocol was used for administering each trial:

i.   The 30- to 40-minute interval began after the animal entered the test room.

ii. If the animal solved the puzzle during the allotted time, a "Success" was recorded.

iii. If the animal worked on the puzzle and then abandoned it for a full 10 minutes, the trial was recorded as a "Failure." In the interest of good animal welfare, if the animal performed a stereotypy for 8 minutes after working on the puzzle, the trial was ended, and a "Failure" was recorded.

iv. If the animal avoided or ignored the puzzle for the entire trial (or performed a stereotypy for 8 minutes without contacting the puzzle), the trial was scored as "No Participation" to differentiate it from a "Failure."

Behavior Definitions

The behavior diversity of each spotted hyena on each trial was calculated by recording the different types of behaviors the animals showed while working on the puzzles. The four behavior categories are described in Table 1.3.

Table 1.3 Behaviors Included in the Behavior Diversity Score of each Spotted Hyena in the Problem-Solving Study

Behavior	Description of Behavior
Dig/Paw box	The animal dug or pawed at the puzzle box or at the floor next to the puzzle box with one or both forepaws.
Bite box	The animal bit or chewed on the puzzle box or any part of the puzzle box (e.g. the bolts securing the lid).
Investigate	The animal visually examined or sniffed the puzzle box or puzzle apparatus.
Manipulate apparatus	The animal manipulated the apparatus with the mouth or paw(s) in some way such as chewing on or digging at the apparatus. "Apparatus" included the food bowl, the cable, handle(s), Lazy Susan, lid (for Remove Lid Puzzle), or plunger.

Each spotted hyena was given a 'behavior diversity' score of 1 through 4 based on how many of the aforementioned behaviors they performed. For example, if the animal dug at and investigated the puzzle box during the trial, they would be given a score of '2.' This procedure was similar to the 'exploration diversity' score used by Benson-Amram and Holekamp (2012) and Benson-Amram et al. (2013) who tracked spotted hyenas' biting, digging, investigating, pushing/pulling, and flipping of the puzzle box. The behaviors recorded in the current study varied from those used by Benson-Amram and Holekamp (2012) and Benson-Amram et al. (2013) due to the different puzzles used. The spotted hyenas tested in the present experiment were not able to push, pull, or flip the puzzle box since it was attached to a gate in their enclosure. Additionally, the puzzle box used by Benson-Amram and Holekamp (2012) and Benson-Amram et al. (2013) did not include any added apparatuses such as a cable or plunger.

Two measures of fearfulness were utilized when examining the behavior of the spotted hyenas in the current experiment and are listed in Table 1.4.

Table 1.4 Behaviors Used to Measure the Fearfulness of each Spotted Hyena in the Problem-Solving Study

Behavior	Description of Behavior
Latency to approach	This referred to the amount of time it took the animal to approach the puzzle box or puzzle apparatus after the trial began. (Benson-Amram and Holekamp (2012) and Benson-Amram et al. (2013) recorded the amount of time it took the spotted hyena to approach the puzzle box as a measure of neophobia.)
Jumping away	Jumping away occurred when an animal jumped away from the puzzle box or puzzle apparatus with two or more paws moving away from the puzzle box or apparatus. If the animal moved away from a falling apparatus like the lid in the Remove Lid Puzzle, a 'jump away' was not recorded since moving away from a heavy, falling object is safer than risking being hit.

The term 'fearfulness' was used in the present study rather than 'neophobia.' Neophobia refers to an individual's fear of a novel object or situation, and in the current study, some latency to approach and jumping away was observed in trials other than the initial (novel) trial. Therefore, fearfulness was a more accurate term because these behaviors persisted past the spotted hyenas' first (novel) experience with the puzzles.

Standard Operating Procedure (S.O.P.)

More information about the problem-solving experiment can be found in the S.O.P. (Appendix B).

Results

Percent of Successes

Each trial was recorded as a Success, Failure, or No Participation according to the criteria listed previously. The No Participation category was never used since all of the spotted hyenas contacted the puzzle box at least once during every trial. The percentage of successes was calculated for each animal on each puzzle. The percentages are shown in Table 1.3.

All of the spotted hyenas successfully completed the puzzle with the lowest level of difficulty, the Remove Bowl Puzzle. With regard to the medium level puzzles, the success-rate of the spotted hyenas became more variable on the Cable Puzzle. Although three of the spotted hyenas solved it every time, Askari only solved it the first and last times he saw it and Tembo only solved it the first time. The Lazy Susan Puzzle was solved by all the spotted hyenas with little difficulty. Four of the spotted hyenas solved the Remove Lid Puzzle each time it was presented. Tembo solved it three out of four times. Charlie was the only spotted hyena to solve the Plunger Puzzle, the puzzle with the highest level of difficulty.

Photos of the spotted hyenas interacting with each puzzle can be found in Appendix C.

Table 1.5 Percent of Successes for Each Spotted Hyena on Each Puzzle in the Problem-Solving Study

(Each puzzle was presented to each animal a total of four times*)

	Charlie	Smilla	Haji	Tembo	Askari	Grubbie
Sex	Male	Female	Female	Male	Male	Female
Age at Testing	3yr 3mo	3yr 3mo	6yr 7mo	6yr 10mo	7yr 2mo	18yr 8mo
Location	Sunset	Sunset	St. Louis	St. Louis	Ft. Wayne	Ft. Wayne
Remove Bowl Puzzle	100%	100%	100%	100%	100%	100%
Cable Puzzle	100%	100%	100%	25%	50%	0%
Lazy Susan Puzzle	100%	100%	100%	100%	100%	0%
Remove Lid Puzzle	100%	100%	100%	75%	100%	0%
Plunger Puzzle	75%	0%	0%	0%	0%	0%

*Charlie and Smilla were presented with the Remove Lid Puzzle three times since the design was changed after the first trial with it. Smilla's first trial with the Plunger Puzzle was omitted because she removed the lid from the box to access the plunger.

Time Working

For every trial, the total amount of time spent working on the puzzle was recorded along with total trial time. The complete timed data are in Appendix D.

Successful Trials

Figures 1.1 through 1.5 illustrate the change in time working successfully on each puzzle over test days. Overall, the spotted hyenas solved the Remove Bowl Puzzle quickly starting with the first trial. The time spent working did not change significantly over trials. Askari did show some variability in working time but no significant decrease. He tended to take slightly longer

(not significant) than the other spotted hyenas to solve this puzzle, most likely due to his fear of the bowl. All of the spotted hyenas that solved the Cable Puzzle 100% of the time showed a decrease in working time over the test period, however this decrease was not significant. The spotted hyenas overall showed a significant decrease in time working across successful trials of the Lazy Susan Puzzle, $F(3, 12)=13.25$, $p<0.05$ (Figure 1.3). The only spotted hyena that showed a decrease in working time over the test days on the Remove Lid was Haji and this decrease was not significant. The rest of the spotted hyenas did not show any consistent changes in working time on the Remove Lid Puzzle. Charlie's working times on the Plunger Puzzle did not change significantly over test days.
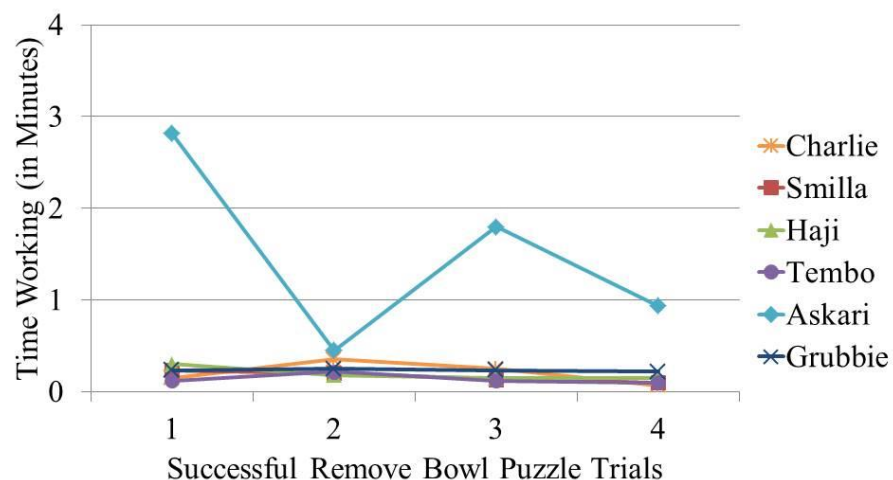
Figure 1.1 Change in time spent working successfully on Remove Bowl Puzzle.
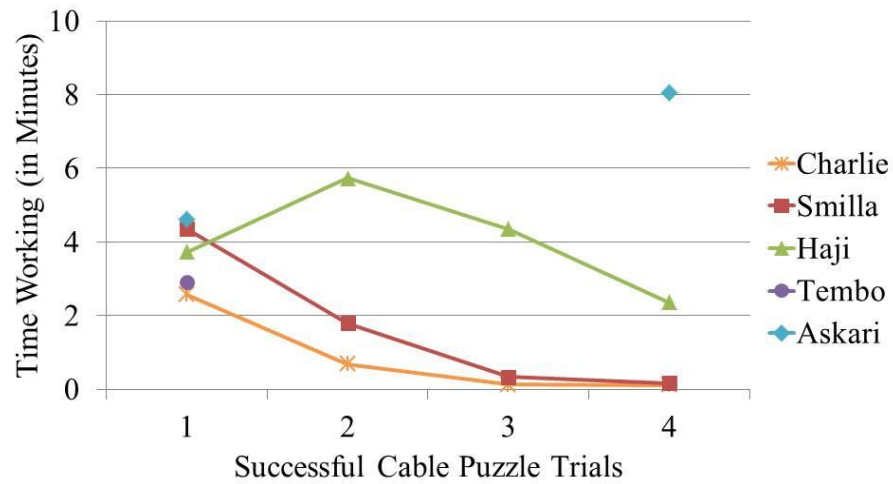
Figure 1.2 Change in time spent working successfully on Cable Puzzle.
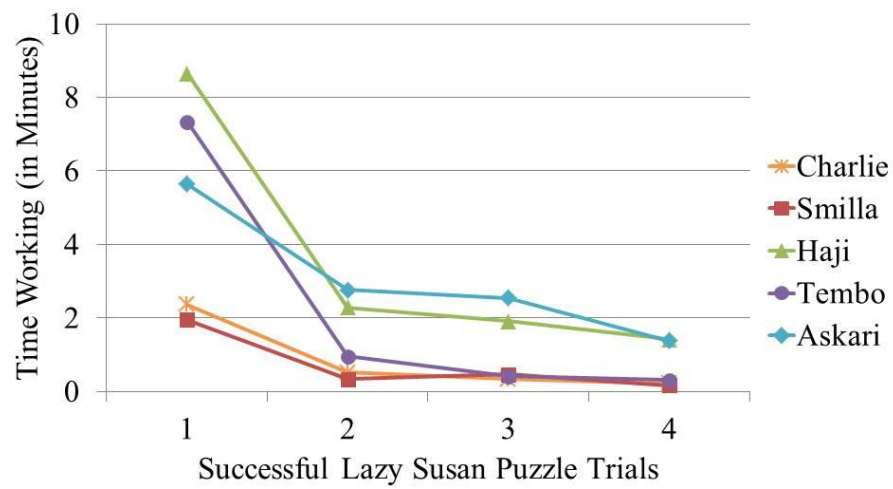
Figure 1.3 Change in time spent working successfully on Lazy Susan Puzzle.

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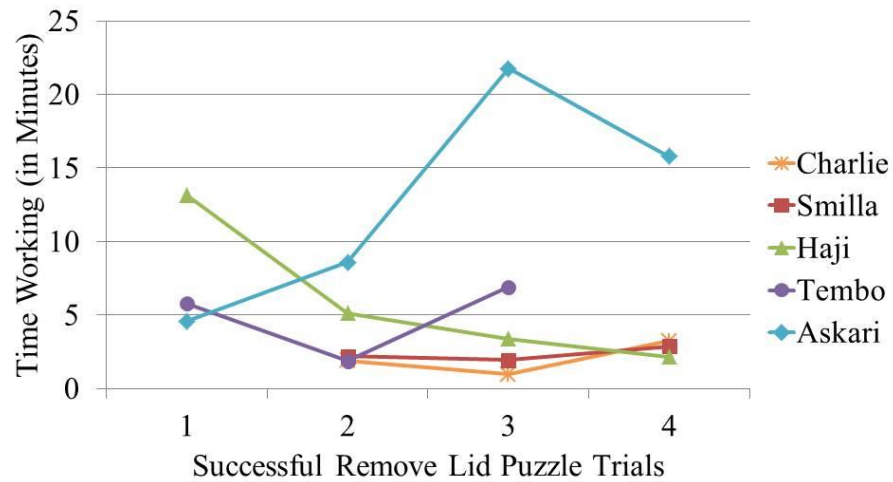
Figure 1.4 Change in time spent working successfully on Remove Lid Puzzle.

Note: Charlie and Smilla were presented with the Remove Lid Puzzle three times since the design was changed after the first trial with it.
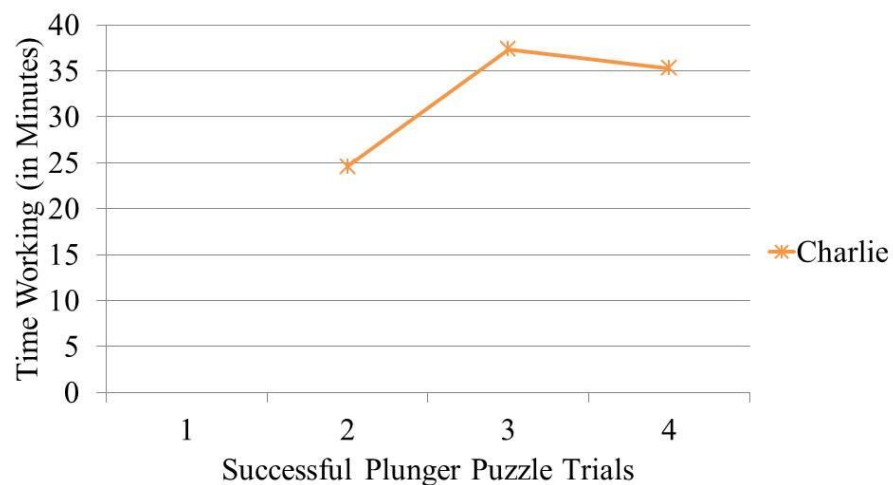
Figure 1.5 Change in time spent working successfully on Plunger Puzzle.

Unsuccessful Trials

Figures 1.6 through 1.9 illustrates the time spent working on unsuccessful trials. None of

the spotted hyenas showed a significant decrease in time working over unsuccessful Cable

Puzzle trials. Grubbie was the only spotted hyena to fail all trials of the Lazy Susan Puzzle and

the Remove Lid Puzzle. Grubbie's time working over trials did not decrease significantly for

either the Lazy Susan or the Remove Lid Puzzle. With the exception of Charlie, all of the spotted

hyenas were unsuccessful at every Plunger Puzzle trial, and the time working decreased

significantly from the first to the last trial, $F(2, 11)=8.76$, $p<0.05$. The average decrease in work

time was 8.33 min (SD=2.33 min) (Figure 1.9).
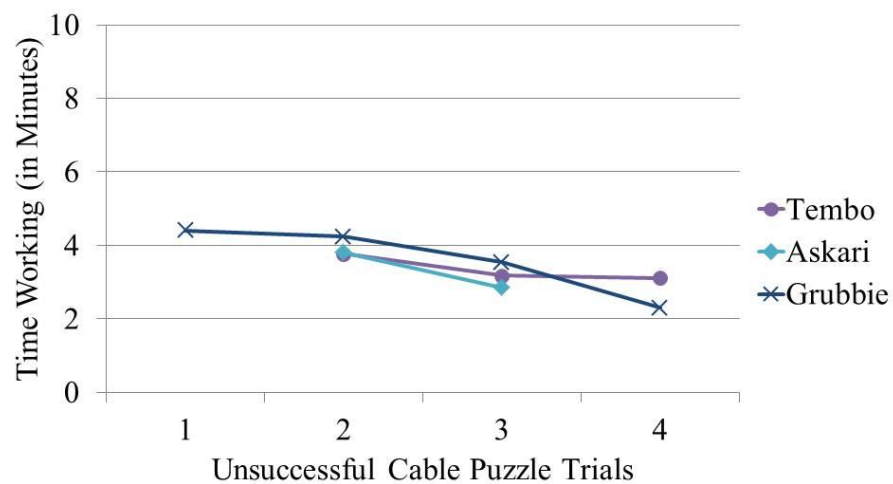
Figure 1.6 Change in time spent working unsuccessfully on Cable Puzzle.
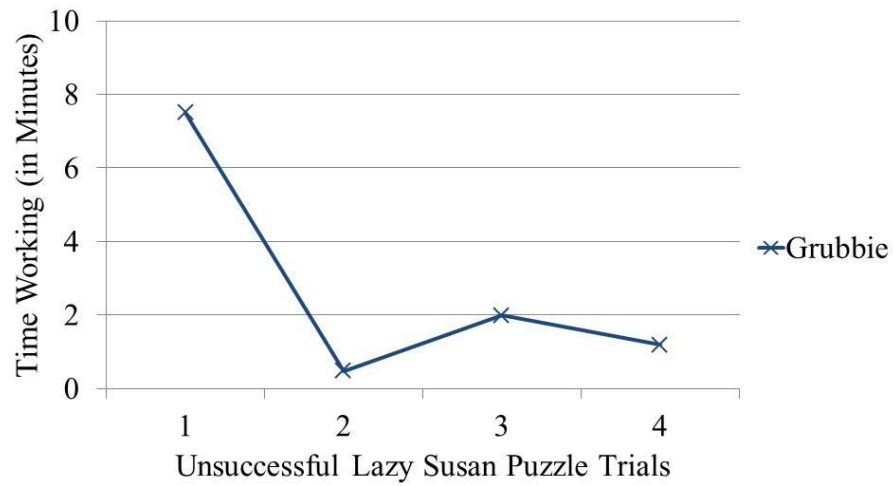
Figure 1.7 Change in time spent working unsuccessfully on Lazy Susan Puzzle.
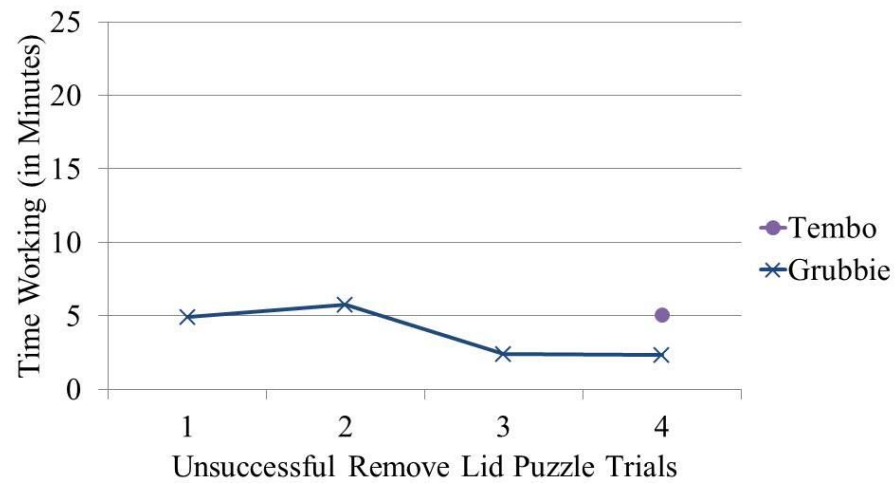
Figure 1.8 Change in time spent working unsuccessfully on Remove Lid Puzzle.
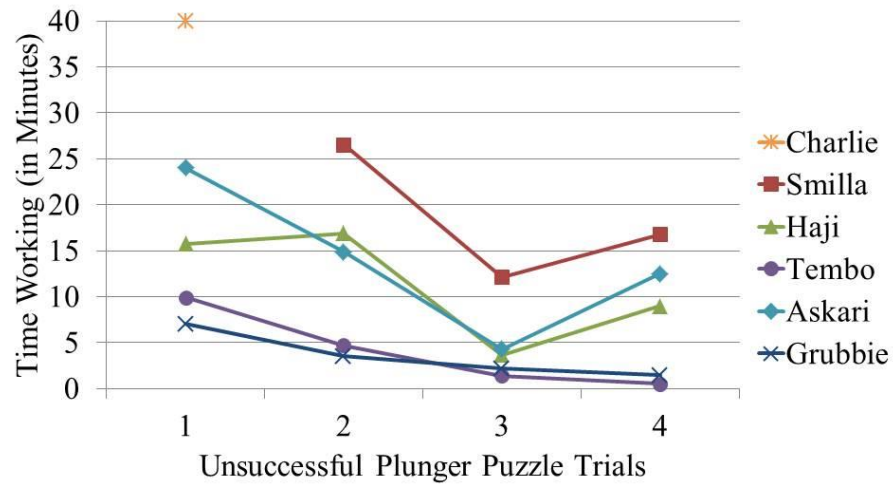
Figure 1.9 Change in time spent working unsuccessfully on Plunger Puzzle.

Note: Charlie actually worked on the Plunger Puzzle for 54 min on the first trial, however to keep figures consistent, that number was rounded down to an even 40 min.

Behavior diversity

Behavior diversity decreased significantly over successful trials for the spotted hyenas that solved the Lazy Susan Puzzle, $F(3, 12)=9.45$, $p<0.05$ (Figure 1.12). Behavior diversity did not decrease significantly for any of the puzzles over unsuccessful trials. Figures 1.10 through 1.18 display the change in behavior diversity for each animal on each puzzle on successful and unsuccessful trials. For detailed data on behavior diversity during testing, refer to Appendix E, Table E.1.
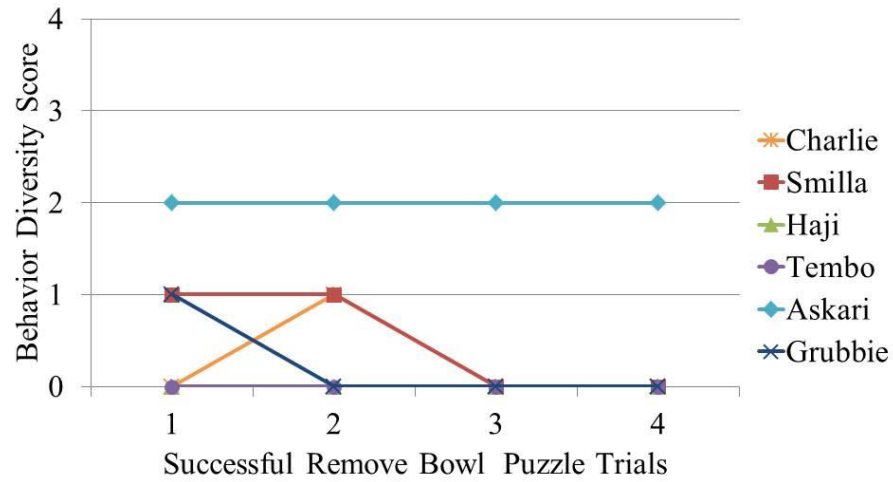
Figure 1.10 Change in behavior diversity over successful Remove Bowl Puzzle trials.
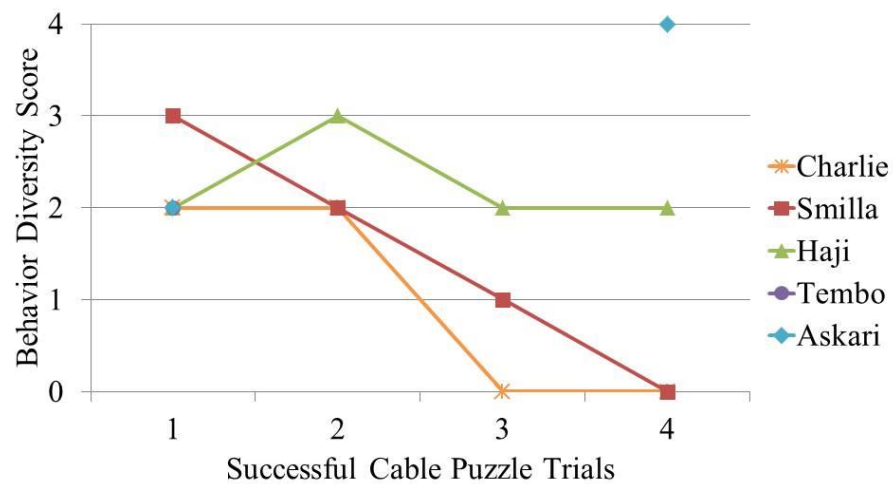
Figure 1.11 Change in behavior diversity over successful Cable Puzzle trials.
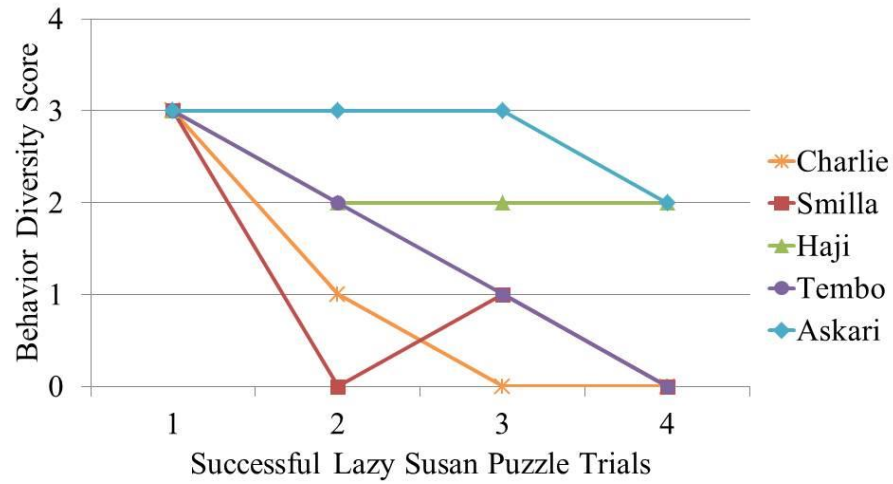
Figure 1.12 Change in behavior diversity over successful Lazy Susan Puzzle trials.
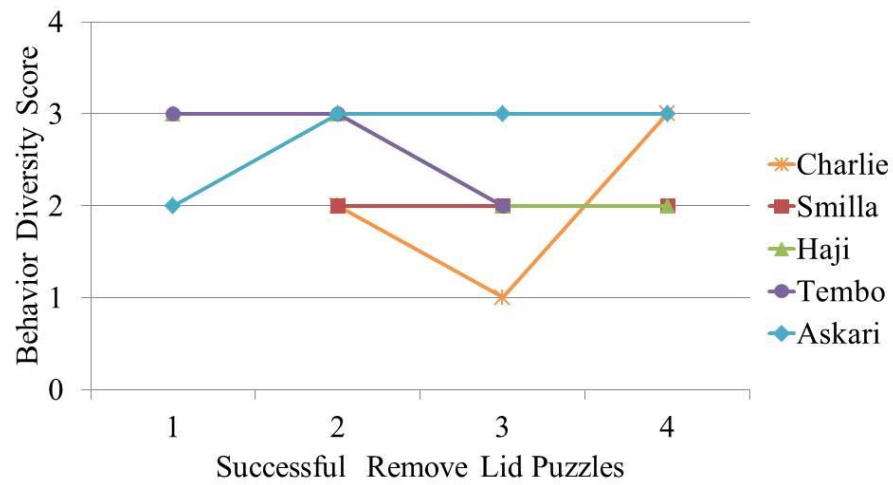
Figure 1.13 Change in behavior diversity over successful Remove Lid Puzzle trials.
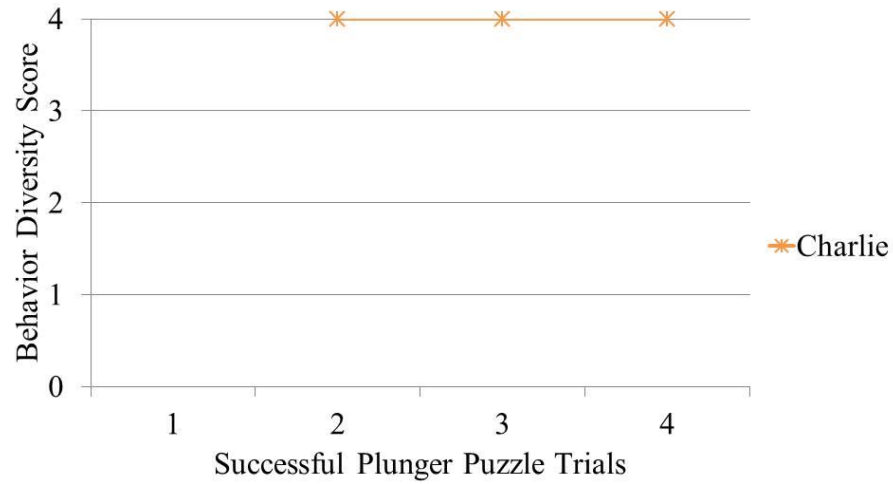
Figure 1.14 Change in behavior diversity over successful Plunger Puzzle trials.
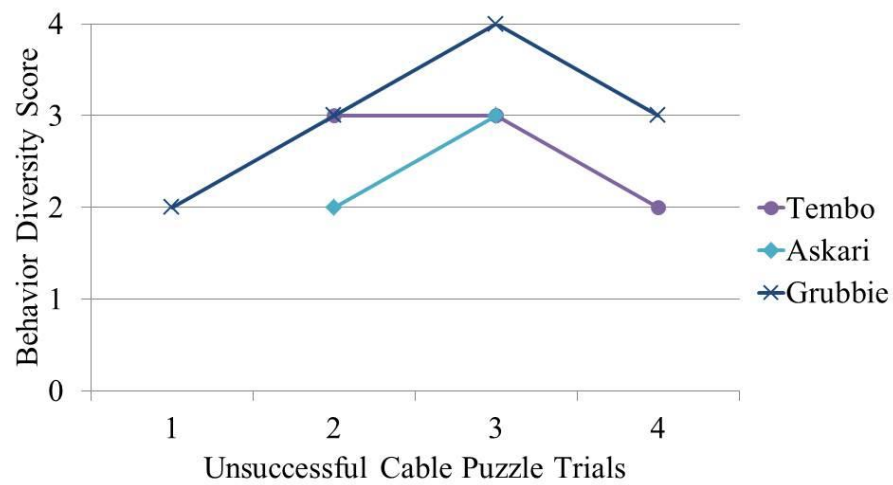
Figure 1.15 Change in behavior diversity over unsuccessful Cable Puzzle trials.
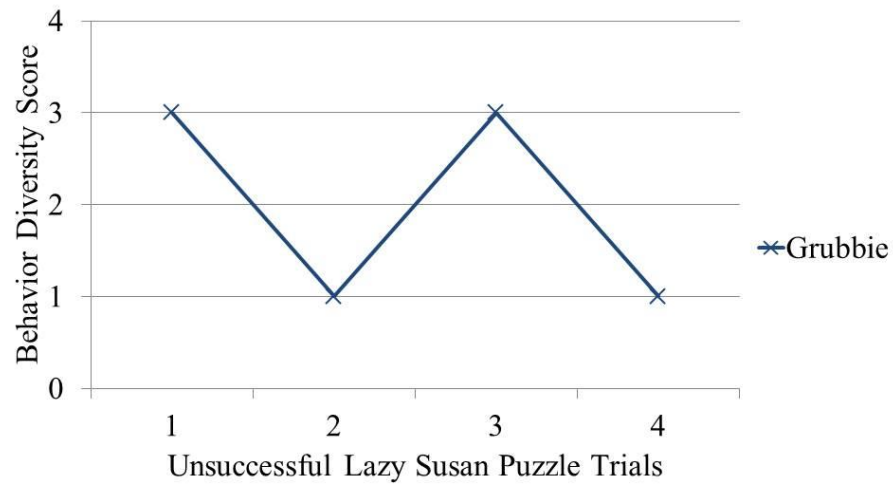
Figure 1.16 Change in behavior diversity over unsuccessful Lazy Susan Puzzle trials.
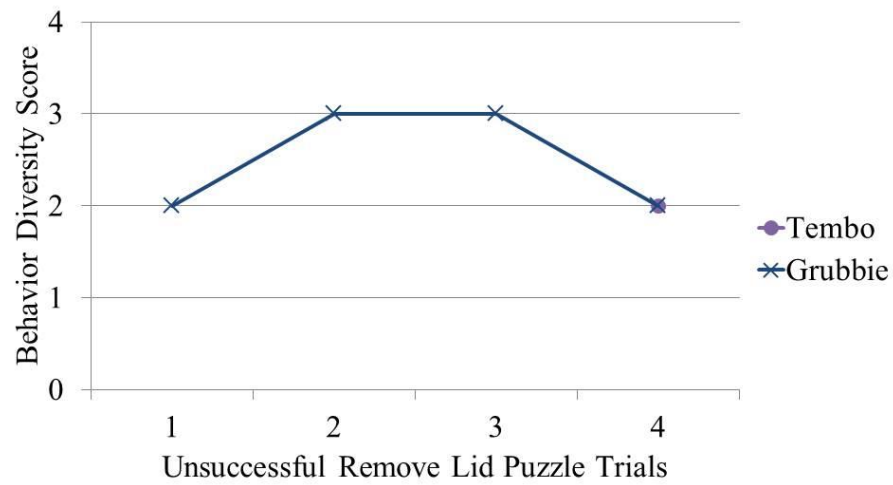
Figure 1.17 Change in behavior diversity over unsuccessful Remove Lid Puzzle trials.
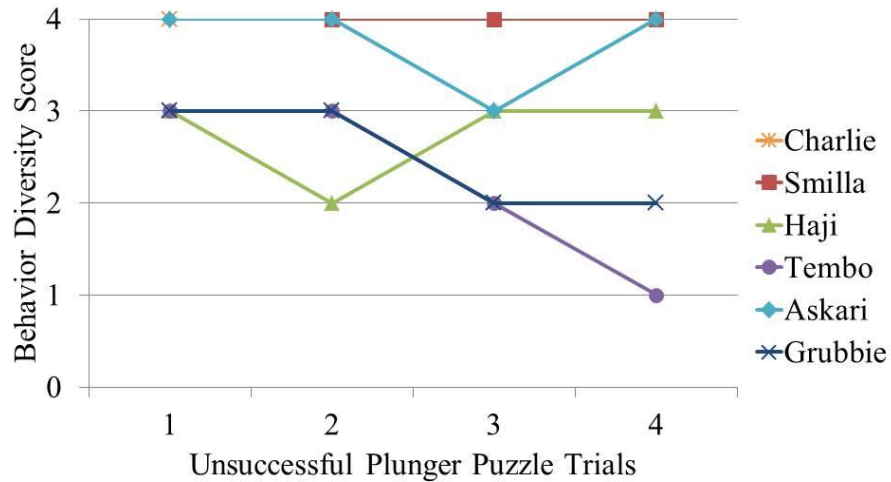
Figure 1.18 Change in behavior diversity over unsuccessful Plunger Puzzle trials.

Fearfulness

No significant effects were found for latency to approach the puzzle box. All of the

spotted hyenas approached the puzzle box in less than 6 seconds, with few exceptions. Askari

had a latency to approach the box of 7 seconds or more on ten of his twenty total puzzle trials.

Four out of six spotted hyenas took 11 to 20 seconds to approach the Lazy Susan Puzzle when it

was the first puzzle they experienced after the Cable Puzzle the day before. Detailed data on

latency to approach the puzzle box is presented in Appendix F, Table F.1.

Jumping away from the box or the apparatuses was rare overall, and no significant effects

across trials were found. However, all of the spotted hyenas jumped away from the Cable Puzzle

1 to 14 times the first time it was presented. For Charlie, this was the only time he jumped away

from any puzzle. Askari jumped away from all of the puzzles on every trial 1 to 40 times. The

two times that Askari solved the Cable Puzzle, trials 1 and 4, he jumped away 14 and 15 times,

respectively. The two times that Askari did not solve the Cable Puzzle, trials 2 and 3, he only

jumped away 4 times each trial and worked less on the puzzle overall. The more Askari

interacted with the Cable Puzzle, the more he startled himself, but the interaction also made it

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more likely he would solve the puzzle. Almost every time Askari jumped away from a puzzle, he would go right back to working on it. Appendix G, Table G.1 contains detailed data for jumping away.

Discussion

The data from the problem-solving study support the prediction that overall these spotted hyenas were capable of solving the majority of the puzzle boxes they experienced. All of the spotted hyenas easily solved the Remove Bowl Puzzle which had a low level of difficulty; they simply had to pull the bowl out of the front of the box with their paw or mouth. Successful performance among the spotted hyenas was more variable on the medium difficulty puzzles (Cable, Lazy Susan, and Remove Lid Puzzles), all of which had a solution that required manipulation of an apparatus to move the bowl to where it could be accessed. The manipulation for the medium difficulty puzzles was usually a type of pulling motion either with the mouth or paw(s). The spotted hyenas were generally unsuccessful at solving the high difficulty puzzle (Plunger Puzzle) that required the food to be pushed away from them in order to be accessed.

On successful trials for the Cable, Lazy Susan, and Remove Lid Puzzles, the time working decreased over test days for most of the spotted hyenas indicating that they were learning to solve the puzzles more efficiently. A variety of behaviors were observed when the animals worked on the puzzles: visually examining and sniffing the puzzle box and apparatuses, digging at the box or the floor by the box, biting or chewing on the box, and manipulation of the various apparatuses by chewing, pulling, or pawing. When the spotted hyenas were not working on the puzzle, they sometimes would lie down or stood by the door, but more often they exhibited a stereotypy such as pacing.

Patterns Associated with Different Types of Learning

With respect to the data on time working to solution, the patterns on the graphs for successful trials indicated that trial and error, not insight, learning was occurring. If insight learning had occurred, the curves would be steep and smooth or would show no improvement followed by a steep decline. However, the curves were shallow and jagged, which is associated with trial and error learning. Similar patterns were observed by other researchers examining problem-solving behavior in spotted hyenas (Benson-Amram & Holekamp, 2012; Benson-Amram et al., 2013). Research conducted with wild mongooses and meerkats also showed that they used trial-and-error learning when solving problems (Müller, 2010; Thornton & Samson, 2012).

Learning Differences Between Spotted Hyenas in the Current Study

Askari was observed by the researcher to be the most fearful and skittish of the spotted hyenas tested. On the first trial with the Plunger Puzzle, he jumped away from the plunger 40 times. During the Remove Bowl Puzzle trials, any time the bowl made a noise, he would jump away which led to longer times working on the puzzle. For the Cable Puzzle, Askari was the only spotted hyena who solved the puzzle on two non-sequential trials and during his interactions with this puzzle, he was quite fearful of the apparatus. The Remove Lid Puzzle also took him longer to work on because when one of the handles or the lid made a noise, he would jump back or run to the back of the test area. Oddly, although he was easily startled by the puzzle box and apparatuses, he typically resumed work right after jumping or running away.

Individual Puzzles

With the exception of the Remove Bowl Puzzle, Grubbie would only work on the puzzles for a few minutes before going to sleep or starting a stereotypy. Note that she is much older than the other spotted hyenas.

Remove Bowl, Lazy Susan, and Remove Lid Puzzles

All of the spotted hyenas successfully and quickly completed the Remove Bowl Puzzle. The success of the subjects was not surprising given the simplicity of this task. All of the spotted hyenas solved the Lazy Susan Puzzle every time it was presented with the exception of Grubbie who never solved it. The Remove Lid Puzzle was solved on every trial by all of the spotted hyenas, except for Tembo who solved the puzzle three out of four times and Grubbie who never solved it. Interestingly, although Tembo solved this puzzle three times, he would not retrieve the food bowl or eat the food when it was within reach. Tembo seemed nervous about putting his head in the box to access the food, which was also the case during training trials. Haji did not eat the food the second time she solved the Remove Lid Puzzle, most likely because she gagged and startled herself by stretching her neck too far over the edge of the box when trying to retrieve the bowl.

Cable Puzzle and Means-End Connections

The success rates of the spotted hyenas who solved the Cable Puzzle were more variable than the success rates on the other puzzles. This may be partly due to the distance between the apparatus and the bowl being greater than in the Remove Bowl, Remove Lid and Lazy Susan Puzzles. Perhaps the distance and the set-up of the Cable Puzzle made it similar to tasks used to test for the ability to detect means-end connections and demonstrate insight learning. In a basic string task, two strings are present and one is attached to a treat. The subject can see the link and

if they are capable of making a means-end connection and insight learning, they will immediately pull the string attached to the treat. Dogs have trouble with means-end tasks as measured by performance on a string task and show trial and error learning (Osthaus, Lea, & Slater, 2005). Similarly, the spotted hyenas in the experiment showed trial and error learning.

Cable Puzzle and Fear

The limited success on the Cable Puzzle for Tembo and Askari may have been due to their fear of the cable and PVC handle. All of the spotted hyenas seemed cautious when first approaching this apparatus, but Tembo and Askari in particular appeared nervous about the cable and handle. Tembo was exceptionally stressed the second time he saw the Cable Puzzle and did not solve it that day or over the next two trials. Frank and Frank (1985) similarly noticed that when the bowl "clattered" out of the box during this puzzle that the puppies were quite startled and then failed the puzzle on later trials. The wolf pups, on the other hand, did not seem fazed by the sound. Other researchers have also found that neophobia or fearfulness can interfere with problem solving (Bouchard, Goodyer, & Lefebvre, 2007; Benson-Amram et al., 2013).

Plunger Puzzle

Charlie was the only spotted hyena to solve the Plunger Puzzle. He first chewed, pulled, and bounced the plunger enough to inch the bowl toward the front opening of the box. Then he would go to the front opening and paw the bowl the rest of the way out, usually while lying on his side. Although this was not the "predicted" way to solve the Plunger Puzzle, the strategy was effective for him. Charlie's time working on the Plunger Puzzle did not change over trials indicating that he was not learning to solve the puzzle more efficiently.

The poor performance of the spotted hyenas on the Plunger Puzzle is primarily attributed to the complexity of the task: pushing something away from oneself is not a typical way to

obtain a goal. Adding to the complexity of this task was that to solve it, the animals had to serially organize their behavior. They first had to push the plunger into the box and then move around to the other side of the box and pull the bowl out. The spotted hyenas would sometimes manipulate the plunger such that the bowl would be near the opening, but they did not go to check the opening before further manipulating the plunger and moving it back, or they checked the front opening before trying the plunger. Either way, the behavior of most of the spotted hyenas during these trials never appeared organized.

Studies have shown variability in the capacity of other species to learn tasks similar to the Plunger Puzzle. Garber, Gomes, and Bicca-Marques (2012) presented wild capuchins with a puzzle box where they could either push or pull a dowel rod to obtain a treat. The capuchins could not learn to push the dowel to access the treat. They were able to learn to pull the dowel through trial-and-error learning. On the other hand, four species of great apes (24 out of 25 subjects) were able to learn to push a stick farther into a tube to force a treat out the other end of the tube (Volter & Call, 2012). The problem could not be solved by pulling the stick, similar to the plunger in the Plunger Puzzle used in the current experiment. These results combined with data from the present study suggest that a higher level of intelligence is required to solve problems like the Plunger Puzzle.

Perhaps the memories of solving the Remove Bowl, Cable, Lazy Susan, and Remove Lid Puzzles interfered with successful performance on the Plunger Puzzle. For the Remove Bowl, Cable, Lazy Susan, and Remove Lid Puzzles, the spotted hyenas had to pull something toward them (a bowl, cable/handle, board, or lid/handle, respectively) in order to solve the problem. For the Plunger Puzzle, the solution required a different behavior of pushing something away; therefore, generalizing past solutions was not effective.

The inability to inhibit unproductive behavior (such as pulling behavior) negatively impacts problem-solving behavior. Santos, Ericson, and Hauser (1999) found that captive cotton-top tamarins performed poorly at retrieving a treat from a transparent box when the opening was on the side. The tamarins had difficulty inhibiting the behavior of reaching straight forward for the treat. After operant training on the task, the tamarins were able to solve it. Perhaps spotted hyenas could learn to solve the plunger task with an operant training procedure designed to inhibit pulling on the plunger.

Problem-Solving Behavior of Puppies and Wolf Pups Compared to Adult Spotted Hyenas

The puzzles used to measure problem-solving behavior in the current study were similar to puzzles employed by Scott and Fuller (1965) and Frank and Frank (1985) for the same purpose. The behavior of the puppies in Scott and Fuller's (1965) study was quite variable and depended on the breed being tested. The puppies in Frank and Frank's (1985) study were generally unsuccessful at solving the problems, while the wolf pups performed well on most of the puzzles. Researchers attributed this finding to the observations that wolves immediately began working on the puzzle boxes when released into the test area and were more persistent when working on the puzzles. The puppies briefly investigated the box, and once they figured out that the food was not accessible, they returned to the start-area to beg, sit, or lie down. It is worth noting that persistence alone does not lead to successful problem-solving if the animal perseverates on unsuccessful behaviors (Benson-Amram & Holekamp, 2012). In the current study, Grubbie tended to perseverate on digging behavior even though she did not make any progress toward a solution with the digging strategy.

Adult spotted hyenas were more consistently successful than puppies at the Remove Bowl and Remove Lid Puzzles; spotted hyenas' performance was similar to that of the wolf pups (Scott & Fuller, 1965; Frank & Frank, 1985). The spotted hyenas were more successful at the Lazy Susan Puzzle than puppies and wolves (Frank & Frank, 1985). Like the puppies and wolves, spotted hyenas had mixed success on the Cable Puzzle and performed poorly on the Plunger Puzzle (Scott & Fuller, 1965; Frank & Frank, 1985). Compared to puppies and wolf pups, adult spotted hyenas appear to have better problem-solving abilities. An interesting follow-up study could examine whether spotted hyena cubs' performance on the puzzles was more similar to that of puppies, wolf pups, or adult spotted hyenas.

Problem-Solving Behavior of Other Captive and Wild Spotted Hyenas Compared to Spotted Hyenas in Current Study

Benson-Amram et al. (2013) compared the problem-solving performance of wild and captive spotted hyenas using a puzzle box that opened with a sliding latch. They labeled animals as successful if they solved at least one of six trials. Of the captive spotted hyenas, 73.7% were successful at opening the box, while only 14.5% of wild spotted hyenas were successful. The success rates observed in the current study were similar to what Benson-Amram et al. (2013) observed in captive spotted hyenas. All of the spotted hyenas in the current experiment solved at least one puzzle. Specifically, with the exception of Grubbie, who only solved the Remove Bowl Puzzle, all of the spotted hyenas solved the Remove Bowl, Cable, Lazy Susan and Remove Lid Puzzles at least once. Charlie solved the Plunger Puzzle three times.

Benson-Amram and Holekamp (2012) and Benson-Amram et al. (2013) observed that successful wild and captive spotted hyenas had lower levels of neophobia, and after multiple successful trials became faster at solving the puzzles as well as decreased their behavior

diversity. In the current experiment, no significant effects of neophobia or fear on problem-solving skills were observed. Interestingly, in the present study, Askari was overall successful at problem solving, yet he showed the most fearful behavior. Conversely, Grubbie showed very little fear but also was largely unsuccessful at problem solving. Although decreases in time working and behavior diversity over successful trials were observed on most of the puzzles, only the data for the Lazy Susan Puzzle were significant. These patterns indicate that the spotted hyenas in the current study were generally becoming more efficient at solving the puzzles over time, similar to the spotted hyenas in other studies (Benson-Amram & Holekamp, 2012; Benson-Amram et al., 2013).

Over unsuccessful trials, other researchers have observed that wild spotted hyenas do not change exploratory behavior or decrease effort. Unsuccessful captive spotted hyenas, on the other hand, decrease effort over time almost to the point of extinction (Benson-Amram & Holekamp, 2012; Benson-Amram et al., 2013). There were not a large number of unsuccessful trials in the present experiment, and no significant changes in behavior diversity were found over unsuccessful puzzle trials, similar to what other researchers observed with wild spotted hyenas (Benson-Amram & Holekamp, 2012; Benson-Amram et al., 2013). With regard to time spent working on unsuccessful puzzle trials, no significant changes were found for the Cable and Remove Lid Puzzles. The time working on unsuccessful Lazy Susan trials appeared to be decreasing, but was not significant. On the Plunger Puzzle, the time working on unsuccessful trials decreased significantly over time indicating that repeated failures led to a decrease in effort. Benson-Amram et al. (2013) likewise observed that unsuccessful captive spotted hyenas decreased effort over trials.

Variables that Potentially Influence Problem Solving

Animals' relationships with humans may be a source of interference for problem-solving abilities. When puppies could not easily solve the puzzles in Frank and Frank's (1985) study, they would return to the start area and look at or beg from the researcher instead of continuing to attempt a solution. Pepperberg (2004) found that language training hindered grey parrots' ability to learn to obtain a treat suspended from a string. The parrots without language training could easily learn to solve the puzzle. The parrots with language training did not learn to solve the task and just asked the researcher to hand them the treat instead of attempting a solution. Captive spotted hyenas are not typically faced with unsolvable problems unless the problems are artificially arranged by their keepers. Generally, keepers do everything for animals in captivity. The researcher and keepers anecdotally observed in the current study that when a spotted hyena was unable to solve a puzzle, they would walk over to or look at the researcher or keeper. Sometimes the spotted hyena would roll over, paw at the researcher or keeper behind the gate, or act "cute" (similar to when they were soliciting treats outside of the testing situation).

Problem-solving skills may also be influenced by the dominant or subordinate status of an animal. Subordinate animals generally have to be more innovative problem solvers because they have to work harder to gain access to resources. Reader and Laland (2001) reported that low-ranking chimps are more innovative and Thornton and Samson (2012) showed that subordinate meerkats were the most successful problem solvers. Dominance hierarchies are important in spotted hyena society (e.g. Holekamp, 2006) and the effect of dominant or subordinate status on problem-solving behavior in spotted hyenas would be an interesting direction for future research.

Conclusion

The current data support the social complexity hypothesis in that these animals live in highly organized social groups and are proficient at solving a variety of puzzles to obtain food. This finding combined with previous research demonstrating the various cognitive abilities of spotted hyenas reinforces the idea that they have advanced cognitive abilities. To further investigate this hypothesis, these puzzles should be presented to brown hyenas, striped hyenas, and aardwolves (a member of the Hyaenidae family). One would expect the performance of brown hyenas to be less successful than spotted hyenas because while they are still social, they live in smaller, less complex groups and forage alone. Aardwolves would likely perform the worst because they are almost completely solitary, especially when foraging (Estes, 1991). The performance of striped hyenas might fall somewhere in-between brown hyenas and aardwolves because striped hyenas are largely solitary but sometimes associate with family groups made up of offspring of varying ages. No evidence of social rank-order is observed in striped hyena groups (Estes, 1991).

Given the differences in problem-solving success found by Benson-Amram et al. (2013) in captive versus wild spotted hyenas, comparing and contrasting the performance of captive and wild hyenas on the puzzles could be a source of valuable information. Testing the performance of captive spotted hyenas housed in groups of three of more animals would be interesting because the captive spotted hyenas in the present study were housed in pairs and typically spotted hyenas would live in large groups. If wild and captive aardwolves performed poorly compared to wild and captive spotted hyenas, strong support would be provided for the social complexity hypothesis in a non-primate species.

Chapter 2 - Evaluating Social Learning in Spotted Hyenas: Social Transmission of a Flavor Preference

Introduction

The social transmission of a flavor preference (STFP) is a social learning phenomenon that was first described by Galef and Wigmore (1983). The basic procedure involves first feeding a novel food to a demonstrator animal and then allowing the demonstrator animal and an observer of the same species to interact. Finally, the observer animal is given a choice between the food consumed by the demonstrator (the target flavor) and a different novel food (the distractor flavor).

Social, omnivorous, opportunistic foragers, like rats, dwarf hamsters, and dogs, readily learn flavor preferences from each other and will consume significantly more of the food consumed by the demonstrator (Galef & Wigmore, 1983; Lupfer, Frieman, & Coonfield, 2003; Lupfer-Johnson & Ross, 2007). STFP is also a unique learning phenomenon in that the outcome is affected by whether or not the species being tested is social. In social species, such as dwarf hamsters, STFP is easily demonstrated; on the other hand, non-social species like golden hamsters do not show STFP (Lupfer, Frieman, & Coonfield, 2003).

Spotted hyenas are highly social, forage for food, and sometimes cache (hoard) food underwater (Kruuk, 1972; Estes, 1991). These characteristics led to the prediction that spotted hyenas would learn a flavor preference from a conspecific. Additionally, when spotted hyenas are feeding, scramble competition is observed (Estes, 1991). Scramble competition does not mean that animals will eat anything; rather, once food is found, all of the animals will rush in and eat as much as possible as quickly and efficiently as they know how. According to Shettleworth (2010), species that participate in scramble competition and are also highly social, opportunistic

foragers tend to be excellent at social learning. Social learning is highly beneficial when participating in scramble competition because the fastest, most efficient animals consume the greatest quantity food, and being able to learn the techniques of those animals is important (Lefebvre & Giraldeau, 1996).

Further, although STFP had not been studied in spotted hyenas, Yoerg (1991) studied social influences on flavor aversion in spotted hyenas. Yoerg (1991) began the experiment by creating a flavor aversion. Illness was induced in spotted hyenas by giving them a novel food containing lithium chloride. Following this experience, the spotted hyenas would no longer eat the novel food. After establishing the flavor aversion, Yoerg (1991) put the subjects in a social (group) feeding situation and presented the novel food to which they had been averted. Despite previously refusing the averted, novel food, three of the four spotted hyenas ate the food during the group feeding. All four ate the averted, novel food when presented with it the day after the group feeding. The attenuation of a flavor aversion by social feeding suggests that spotted hyenas influence one another's feeding behavior and supports the prediction that they would show STFP.

One function of socially acquiring a flavor preference is to learn what foods are safe to eat thereby allowing animals to avoid foods that might lead to gastrointestinal distress or other illness. However, spotted hyenas are known for their ability to consume almost anything without becoming ill, so there may be no need to learn about what is safe to eat. Estes (1991) observed that spotted hyenas are able to consume corpses that have been rotting in the sun for months without ill-effects. Whether this ability is a result of immune or digestive system qualities is unknown; however, some data indicate that the immune system of spotted hyenas may be uniquely resilient. Harrison et al. (2004) found that despite spotted hyenas' having antibodies to

several feline and canine diseases such as feline panleukopenia virus/canine parvovirus, obvious clinical disease was not present. Furthermore, one group of researchers found that being seropositive for rabies did not affect survival or longevity in spotted hyenas and also did not lead to development of behavioral symptoms (East et al., 2001).

The information-centre hypothesis is often invoked as an explanation for STFP. This hypothesis posits that when social animals live in environments where the presence of food is unpredictable or randomly distributed, it would be advantageous to be able to communicate information about food between conspecifics. Additionally, the dissemination of information typically occurs at a common site such as a den or nest (Ward & Zahavi, 1973). The den or nest would be the "information-centre," and this is where STFP would occur in the wild.

In the present study, STFP was used to assess social learning in spotted hyenas. The overall hypothesis was that spotted hyenas would show a flavor preference. STFP was expected because spotted hyenas share characteristics with other species that show STFP. These characteristics include a high level of social behavior between conspecifics, and displaying foraging and hoarding as part of their feeding system. Furthermore, the following observations support the prediction that spotted hyenas would exhibit STFP. First, social learning in spotted hyenas is an important part of their ecology for many interactions including feeding. Next, spotted hyenas exhibit scramble competition when feeding and animals improve at this behavior through social learning. Finally, previous research has shown that spotted hyenas socially influence one another's feeding behavior (Yoerg, 1991).

Method

Subjects

The subjects were eight spotted hyenas (*Crocuta crocuta*). All of the subjects were housed in pairs at their facility and had similar body mass. Complete subject information can be found in Table 2.1.

Charlie (male) and Smilla (female) were born August 17, 2008 and arrived at Sunset Zoo, Manhattan, KS, on January 26, 2009. They were tested from November 10, 2011 through November 15, 2011 and were 3 years and 2 months old at the start of testing. As of April 29, 2011, Charlie weighed 58 kg and Smilla weighed 61 kg.

Kibo's (male) date of birth was October 29, 1998. At the time of testing from March 25, 2013 through March 30, 2013, he weighed 58 kg and was 14 years and 4 months old. Ngozi (female) was born on May 2, 1999. She weighed 64 kg and was 13 years and 10 months old at the time of testing. They arrived at the Denver Zoo on May 3, 2004.

Haji (female) was born on November 22, 2006 and arrived at the St. Louis Zoo, St. Louis, MO, on October 28, 2010. She weighed 64 kg at the time of testing. Tembo (male) was born September 1, 2006 and arrived at the St. Louis Zoo with Haji. He weighed 62 kg at the time of testing. They were tested from June 23, 2013 through June 28, 2013. Haji was 6 years and 7 months old and Tembo was 6 years and 9 months old at the start of testing.

Askari (male) was born November 14, 2006 and weighed 55 kg at the time of testing. Grubbie (female) was born May 27, 1995 and weighed 54 kg at the time of testing. They both arrived at the Ft. Wayne Children's Zoo, Ft. Wayne, IN, on March 4, 2009. They were tested from March 10, 2014 through March 14, 2014. When testing began, Askari was 7 years and 3 months old and Grubbie was 18 years and 9 months old.

Table 2.1 Subject Information for Social Learning Experiment

Zoo	Name	Sex	Date of Birth	Date Arrived at Zoo	Dates of Testing	Age at Testing	Weight at Testing
Sunset	Charlie	male	08/07/08	01/26/09	11/10/11-11/15/11	3yr 2mo	58 kg
Sunset	Smilla	female	08/07/08	01/26/09	11/10/11-11/15/11	3yr 2mo	61 kg
Denver	Kibo	male	10/29/98	05/03/04	03/25/13-03/30/13	14yr 4mo	58 kg
Denver	Ngozi	female	05/02/99	05/03/04	03/25/13-03/30/13	13yr 10mo	64 kg
St. Louis	Haji	female	11/22/06	10/28/10	06/23/13-06/28/13	6yr 7mo	64 kg
St. Louis	Tembo	male	09/01/06	10/28/10	06/23/13-06/28/13	6yr 9mo	62 kg
Ft. Wayne	Askari	male	11/14/06	03/04/09	03/10/14-03/14/14	7yr 3mo	55 kg
Ft. Wayne	Grubbie	female	05/27/95	03/04/09	03/10/14-03/14/14	18yr 9mo	54 kg

Procedure

Following the procedures of Galef and Wigmore (1983) and Lupfer-Johnson and Ross (2007), one animal was the demonstrator and a second was the observer. The animals at Sunset and Denver were food-deprived for 18 to 24 hours prior to testing. However, after the spotted hyenas in Denver ate all of both food choices, the spotted hyenas at St. Louis and Ft. Wayne

were only deprived of half of their total diet in the 24 hours prior to testing. Additionally, the amount of pork offered for the Choice Phase was increased so that any potential preference for one flavor over the other could be measured. Both trials at Sunset and the first trial at Denver used 1200 g pork/240 g sauce mix for each observer choice. The second trial at Denver and both trials at St. Louis and Ft. Wayne used 2300 g pork/460 g sauce mix.

The demonstrator was isolated for 30 minutes and fed 720 g of flavored, ground pork (Demonstrator-Alone Phase). After 30 minutes, the food was weighed to make sure that 20% of it was eaten by the demonstrator. Then, the demonstrator and the observer were allowed to interact for 10 minutes (Interaction Phase). Next, the observer was isolated for 30 minutes and offered a choice between the pork consumed by the demonstrator (target) and a second flavor of ground pork (distractor) (Choice Phase). At the end of the 30-minute period, the amount of each flavor of pork remaining was measured. Two different pairs of flavors were used and each animal was a demonstrator once and an observer once (see Table 2.2). The two trials were separated by 4 days.

Table 2.2 Design for Social Learning Experiment

Zoo	Trial	Demonstrator Name	Sex	Observer Name	Sex	Target Flavor*	Distractor Flavor*
Sunset	1	Smilla	F	Charlie	M	CH	ST
Sunset	2	Charlie	M	Smilla	F	GB	CC
Denver	1	Ngozi	F	Kibo	M	CC	GB
Denver	2	Kibo	M	Ngozi	F	ST	CH
St. Louis	1	Tembo	M	Haji	F	CH	ST
St. Louis	2	Haji	F	Tembo	M	GB	CC
Ft. Wayne	1	Askari	M	Grubbie	F	CC	GB
Ft. Wayne	2	Grubbie	F	Askari	M	ST	CH

*CH = HealthPro Vita Gravy Hip and Joint Savory Roast Chicken, ST = HealthPro Vita Gravy Skin and Coat Savory Sirloin Steak, CC = Variety Pet Foods Mixables Cape Cod Picnic, GB = Variety Pet Foods Mixables Greek Banquet

The Interaction Phase was video-recorded in order to track the total amount of time the observer and demonstrator spent interacting. The total time interacting was then broken down into time spent on individual types of interactive behaviors and was logged according to the criteria listed in Table 2.3.

Table 2.3 Behaviors Used to Measure the Interaction between the Observer and the Demonstrator in the Interaction Phase of the Social Learning Study

Behavior	Description of Behavior
Sniff head/mouth/nose	The observer directed sniffing behavior at the head, mouth, or nose of the demonstrator.
Sniff body	The observer sniffed any part of the demonstrator's body excluding the head, mouth, or nose.
Playing	The observer played, roughhoused, or rolled around with the demonstrator.

Standard Operating Procedure (S.O.P.)

More information about the social learning experiment can be found in the S.O.P. (Appendix H).

Materials

One metal pet-food bowl (28.58 cm diameter, 10.16 cm deep, 3.6 liter) was used to hold the target flavor during the Demonstrator-Only Phase at Sunset and was placed in the center of their enclosure. The spotted hyenas in Denver and St. Louis were not accustomed to metal bowls, so the food for the demonstrators was placed directly on the ground in the center of the test area. The demonstrators in Ft. Wayne were fed through the food chute in the front side of their enclosure.

Two concrete food bowls (pictured in Appendix I) were used to present the animals with different flavor choices (the "target" flavor and a second novel flavor called the "distractor") during the Choice Phase. The concrete bowls were placed approximately 91.44 cm apart in the testing area during the Choice Phase (Appendix I). Flavored sauces were added to ground pork to

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create two different novel pairs of flavors. The amount of sauce added to each portion was equal to 20% of the total weight of the meat. For example, 600 g of pork would have 120 g of sauce added. The two pairs of flavors follow:

Pair 1: HealthPro Vita Gravy Hip and Joint Savory Roast Chicken
HealthPro Vita Gravy Skin and Coat Savory Sirloin Steak
(by HealthPro Nutrition, El Monte, CA)

Pair 2: Variety Pet Foods Mixables Cape Cod Picnic
Variety Pet Foods Mixables Greek Banquet
(by Variety Pet Foods, Englewood, CO)

A digital video camera (Flip video mini-camcorder, Cisco Systems, Inc., San Jose, CA) was used to record the Interaction and Choice Phases. A stopwatch was used to keep track of the different phases of the procedure, and a digital scale (Taylor Cal-Max 3847 Digital Food Scale, Taylor Precision Products, Oak Brook, IL) was used to measure food portions.

Results

Choice Phase

If STFP occurred, then the observers would have eaten more of the target flavor than the distractor flavor during the Choice Phase. However, no significant preference for the demonstrator's diet was found. Out of the eight trials, three of the observers ate more of the target flavor, three ate more of the distractor flavor and two ate all of both flavors. Figure 2.1 shows the percent of the target flavor eaten out of the total amount eaten by each observer during the Choice Phase. Table 2.3 gives more detailed information about the results of the Choice Phase.

The flavor (target versus distractor) first approached and consumed by the observer and amount of time spent with the target bowl and the distractor bowl during the Choice Phase did not affect the results.
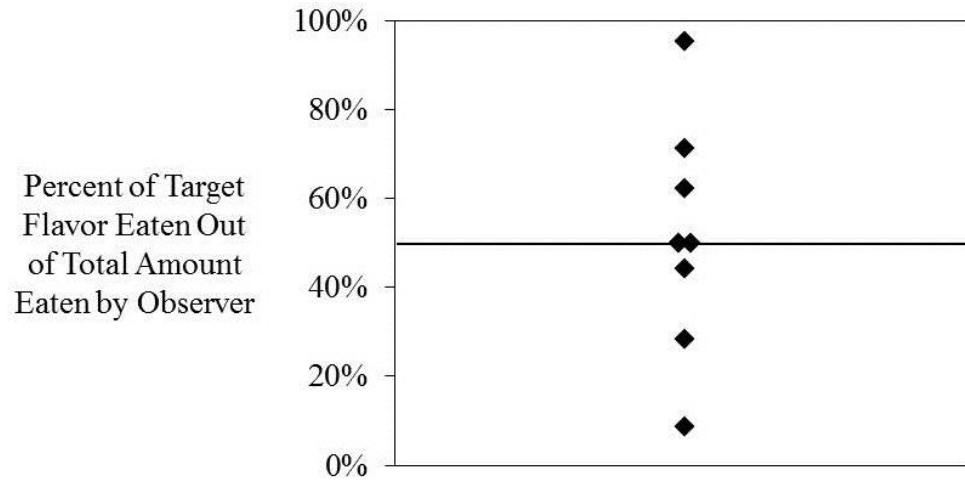
Figure 2.1 Percent of target flavor consumed out of total amount consumed for each observer during the Choice Phase (8 total trials) of the social learning experiment.
*Note The horizontal line marks 50% (no preference).

Table 2.4 Detailed Results of the Choice Phase of the Social Learning Experiment

Zoo	Trial	Demonstrator Name	Sex	Observer Name	Sex	Target*	Distractor*	Starting Weight Target	Starting Weight Distractor	Amount Consumed Target	Amount Consumed Distractor	Percent Target Consumed Out of Total Amount Consumed by Observer
Ft. Wayne	2	Grubbie	F	Askari	M	ST	CH	2748 g	2750 g	973 g	48 g	95.30%
Ft. Wayne	1	Askari	M	Grubbie	F	CC	GB	2750 g	2748 g	1568 g	632 g	71.27%
St. Louis	2	Haji	F	Tembo	M	GB	CC	2734 g	2734 g	1055 g	642 g	62.17%
Denver	1	Ngozi	F	Kibo	M	CC	GB	1440 g	1440 g	1440 g	1440 g	50.00%
Denver	2	Kibo	M	Ngozi	F	ST	CH	2760 g	2760 g	2760 g	2760 g	50.00%
Sunset	2	Charlie	M	Smilla	F	GB	CC	1428 g	1439 g	641 g	810 g	44.18%
Sunset	1	Smilla	F	Charlie	M	CH	ST	1440 g	1440 g	116 g	292 g	28.43%
St. Louis	1	Tembo	M	Haji	F	CH	ST	2736 g	2719 g	129 g	1345 g	8.75%

*CH = HealthPro Vita Gravy Hip and Joint Savory Roast Chicken, ST = HealthPro Vita Gravy Skin and Coat Savory Sirloin Steak, CC = Variety Pet Foods Mixables Cape Cod Picnic, GB = Variety Pet Foods Mixables Greek Banquet

Since spotted hyenas live in a matriarchal society, the sex of the demonstrator might be expected to influence the results; however, this was not the case. When the demonstrator was female, 58.97% ($SD=24\%$) of the total food consumed by the observer was the Target flavor. When the demonstrator was male, 43.55% ($SD=22\%$) of the total food consumed by the observer was the Target flavor. This difference was not significant, $t(6)=.80$, $p>0.05$.

A preference for the ST flavor overall was observed whether it was the target or the distractor. Any time ST was the target or distractor during the Choice Phase, 77.07% ($SD=18\%$) of the total eaten was ST. In contrast, when CH was a choice, 23.05% ($SD=18\%$) of the total eaten was CH. No preference for CC or GB was observed in the Choice Phase. When CC was available, 53.82% ($SD=12\%$) of the total consumed during the Choice Phase was CC. When GB was presented as a choice, 46.34% ($SD=12\%$) of the total consumed was GB.

Interaction Phase

Although the effect did not quite reach significance, the observers that interacted for longer amounts of times with their demonstrators were the most likely to show STFP, $t(6)=2.40$, $p=0.0531$. Detailed data for the Interaction Phases is shown in Table 2.4.

Table 2.5 Time Spent Interacting and Time Spent on Specific Behaviors During the Interaction Phase of the Social Learning Experiment

Zoo	Trial	Observer Name	Observer Sex	Target*	Percent Target Consumed Out of Total Amount Consumed by Observer	Total Time Interacting	Time Sniffing Head/ Mouth/Nose	Time Sniffing Body	Time Playing	Total Trial Time**
Ft. Wayne	2	Askari	M	ST	95.30%	1 min 4 s	13 s	20 s	31 s	10 min 11 s
Ft. Wayne	1	Grubbie	F	CC	71.27%	2 min 9 s	48 s	44 s	37 s	10 min 13 s
St. Louis	2	Tembo	M	GB	62.17%	26 s	14 s	12 s	0 s	9 min 11 s
Denver***	1	Kibo	M	CC	50.00%	11 s	---	---	---	5 min 47 s
Denver***	2	Ngozi	F	ST	50.00%	4 s	---	---	---	5 min 40 s
Sunset	2	Smilla	F	GB	44.18%	3 s	1 s	2 s	0 s	10 min 32 s
Sunset	1	Charlie	M	CH	28.43%	37 s	2 s	34 s	0 s	10 min 43 s
St. Louis	1	Haji	F	CH	8.75%	25 s	16 s	9 s	0 s	5 min 1 s

*CH = HealthPro Vita Gravy Hip and Joint Savory Roast Chicken, ST = HealthPro Vita Gravy Skin and Coat Savory Sirloin Steak, CC = Variety Pet Foods Mixables Cape Cod Picnic, GB = Variety Pet Foods Mixables Greek Banquet

**Some of the Interaction Phases were shortened due to the animals appearing stressed and/or pacing.

***The male spotted hyena in Denver (Kibo) would only approach the female (Ngozi) through the gate. The total time interacting at the gate was recorded, but it was not possible for the animals to display the specific behavior categories. Thus no times are recorded for Sniff Head/Mouth/Nose, Sniff Body, and Playing.

Qualitative Descriptions of Behaviors Observed During the Interaction Phase

The behaviors observed during the Interaction Phase differed slightly at each zoo. At Sunset, each Interaction Phase began with a "greeting ceremony" where the spotted hyenas simultaneously sniffed each other's genitals while standing parallel to one another with the inside rear leg lifted (Estes, 1991). These spotted hyenas spent most of the interaction sniffing around the stall, pacing, and staring at the researchers. Although very little obvious sniffing of the head and mouth region of the demonstrator was noted, the spotted hyenas had a brief, minor "tussle" while pacing by the front gate area and some mouth and head contact was observed then.

The situation at Denver was unique in that the female was so dominant that the male would not approach her. Whenever she was present in the same stall, he would lay down on an elevated platform and remain still. Therefore the Interaction Phase was conducted with each spotted hyena in an adjoining stall with a heavy-gauge wire mesh gate in-between them. Previous research by Galef and Wigmore (1983) demonstrated that rats would show STFP even when separated by a wire mesh divider. Once the spotted hyenas in Denver were separated, they would sniff each other's head, face, and mouth area through the mesh. When they were not sitting by each other on either side of the mesh, the spotted hyenas would pace or lay down.

Two stalls were used in St. Louis to allow the spotted hyenas enough space to interact without fighting (the gate between the two stalls was open). These spotted hyenas showed brief greeting ceremonies and a few short bouts of head/mouth sniffing. Overall, they interacted minimally with each other and spent most of the Interaction Phase pacing, standing at the door, and eventually lying down.

The spotted hyenas at Ft. Wayne interacted with each other more than any of the other pairs of spotted hyenas. They started each Interaction Phase with several obvious head and mouth sniffs that lasted a few seconds each time. They spent some of the time playing with each other or lightly "roughhousing." Pacing was also observed.

Discussion

The spotted hyenas in this study did not show STFP despite previous research showing that spotted hyenas influence one another's feeding behavior and the observation that juvenile spotted hyenas go through extensive social learning periods during development. STFP was also anticipated because spotted hyenas are highly social, forage, hoard, and participate in scramble competition when feeding, all of which predict good social learning abilities.

Although other highly social species like rats, dwarf hamsters, and dogs readily show STFP, the finding that spotted hyenas do not show it is not entirely surprising given that spotted hyenas can eat almost anything due to their digestive and/or immune systems. The ability to eat almost anything may have abolished the need to learn STFP. Additionally, captive spotted hyenas have no need to learn about what is safe to eat since they live at a facility that feeds them regularly.

Perhaps not enough interaction occurred between the observers and the demonstrators for STFP. The amount of interaction between the two animals seemed to be an important factor in the current experiment. Despite all of the spotted hyena pairs showing some interaction with one another, STFP was not observed in the majority of trials. Typically, when social interaction happens during the Interaction Phase, a flavor preference is demonstrated (Galef & Wigmore, 1983; Lupfer-Johnson & Ross, 2007). However, previous researchers did not quantify the interactions between observers and demonstrators, so it is not known if the amount or type of

interaction affects STFP. The present data suggest that the time spent interacting during the Interaction Phase may influence STFP. A variable other than social interaction may lead to STFP. The presence of carbon disulfide on rats' breath mediates social influence on flavor selection in rats (Galef et al., 1988) and Lupfer-Johnson and Ross (2007) proposed investigating this possibility in dogs.

The fact that the spotted hyenas tested in this study live in captivity in pairs could have influenced the results. The captive arrangement is dramatically different from their natural living situation which includes living in a clan of up to 100 animals. Perhaps captivity has disrupted this particular social learning ability. If tested, wild spotted hyenas might show a flavor-preference since they have to hunt or forage for food and flavor information could be helpful in these endeavors. And since female spotted hyenas are dominant and do not allow subordinates to feed, knowing what the dominant female has been eating and actually avoiding that food (and a potential conflict) could be adaptive to wild spotted hyenas living in a clan. Although the sex of the demonstrator did not affect the results of the current study, replicating the procedure with wild spotted hyenas might reveal influences of sex STFP.

The lack of social learning in this case could also be a function of the selected task. Perhaps social learning would occur in a different situation. Drea and Carter (2009) showed that pairs of spotted hyenas can solve a cooperative task to obtain food and in some cases one of the animals was naïve to the task so some social learning had to happen in order for the spotted hyenas to coordinate their behavior. However, Benson-Amram et al. (2013) investigated the influence of watching another spotted hyena solve a puzzle-box and found no effect of problem-solving performance, indicating that social learning did not occur for that task. Research on social learning in spotted hyenas would clearly benefit from utilizing other social learning

paradigms. For example, Pongracz, Miklosi, Kubinyi, Topal, and Csanyi (2003) found that social learning influenced performance on a detour task in dogs. Typically, dogs have difficulty with this type of task and observing another dog solve the task facilitated performance for those dogs that had not solved the detour problem on their own. Replicating this study with spotted hyenas could yield interesting information about the social learning abilities of spotted hyenas in a context not directly related to feeding

Perhaps STFP was not observed due to the flavors used. Previous studies have made use of cocoa- and cinnamon-flavored diets (Galef & Wigmore, 1983) or basil- and thyme-flavored diets (Lupfer-Johnson & Ross, 2007). These flavors could not be used in the current study as the safety of cocoa powder, ground cinnamon, dried basil and dried thyme have not been tested in spotted hyenas. The sauces selected for the current study may not have been distinctive enough.

If spotted hyenas are capable of social learning as some research suggests (e.g. Drea & Carter, 2009), the STFP procedure might not be a sensitive enough test of spotted hyenas' capacity for social learning. In the present experiment, three of the observers preferred the target, three preferred the distractor, and two ate all of both flavors; therefore, adding data from more subjects might create a clearer picture of whether or not spotted hyenas show STFP. Testing captive spotted hyenas housed in larger groups or wild spotted hyenas living in a clan would allow researchers to examine any potential effects of dominant or subordinate status on STFP. Given the importance of rank in spotted hyena society, the effects of social status on social learning must be considered.

General Discussion

Although spotted hyenas did not show social learning in the form of social transmission of a flavor preference (STFP) in the present study, they were able to solve the majority of the puzzles with which they were presented indicating that spotted hyenas have advanced problem-solving skills. The results of the current problem-solving study combined with previous research showing that spotted hyenas have excellent social cognitive abilities leads to the conclusion that spotted hyenas have a high level of intelligence.

The results of the present study raise interesting possibilities for future research. Other studies have shown that problem solving and social learning are related. To investigate the effects of social learning on problem solving, spotted hyenas that were unsuccessful at solving puzzles could be allowed to watch successful spotted hyenas solve the puzzles. Perhaps viewing successful problem-solving strategies would lead to successful performance. Benson-Amram et al. (2013) did not find any effects of an unsuccessful spotted hyena watching a successful performance; however, they made use of only one puzzle. The puzzle designs used in the current experiment would allow the effects of social learning on performance to be compared across puzzles of varying difficulty. Pongracz et al. (2003) found that social learning facilitated performance on a detour problem-solving task in dogs, and replicating the work of Pongracz et al. (2003) in spotted hyenas would contribute to knowledge of the interaction between social learning and problem solving.

The goal of the present study was to learn more about the problem solving skills and social learning abilities of spotted hyenas. The results of the current experiments make important contributions to existing knowledge about problem solving, social learning, and spotted hyenas in general. First, data supporting the social complexity hypothesis has been gathered largely from

primates; therefore, collecting data from other species like hyenas is vital for evaluating the generality of that hypothesis. Additionally, STFP has never been investigated in a species from the Feliformia suborder. Further, finding additional evidence that spotted hyenas have advanced cognitive abilities is essential for researchers and zoo personnel who work with spotted hyenas in captivity. The level of intelligence possessed by spotted hyenas may make them more prone to boredom and developing negative behaviors such as stereotypies.

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Appendix A - Photos and Measurements for Puzzle Box, Apparatuses, and Set-Up for Problem-Solving Study

Front view of puzzle box with lid on. Bottom board is a door (57.15 cm wide, 13.65 cm tall) that can be raised.

Rear view of puzzle box with lid on. Bottom board has a door (28.89 cm wide, 13.65 cm tall) in the middle that can be raised.

Side view of puzzle box with lid on.

Inside of puzzle box (without lid).

The puzzle box was 51.60 cm tall, 63.50 cm wide, and 92.71 cm deep. The gaps between the boards were 3.02 cm wide. The box with the lid weighed about 79.4 kg.

Figure A.1 The puzzle box.

Front view of puzzle box without lid.

Metal food bowl (28.58 cm diameter, 10.16 cm deep, 3.6 liter capacity).

Side view of puzzle box without lid.

Set-up for training trials.

During training trial days (conducted prior to beginning testing), the lid is removed from the box.

Figure A.2 Training trial set-up.

'T' made of composite wood (57.47 cm wide, 75.25 cm long) used to stop food bowl from sliding back out of the animal's reach.

Tension rod (59.37 cm long, 1.59 cm wide, 0.95 cm thick) used to stop food bowl from sliding back out of the animal's reach.

Front corner view of preliminary trial set-up.
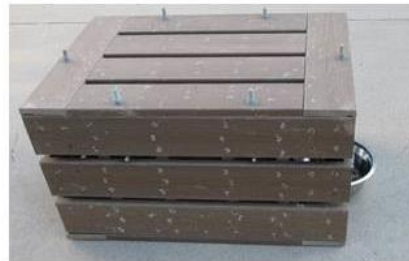
Side view of preliminary trial set-up.

Inside view of preliminary trial set-up.

Preliminary trial for the start of each test day. The opening in the front of the box measured 59.37 cm wide and 15.88 cm tall.

Figure A.3 Preliminary trial.

'T' made of composite wood (57.47 cm wide, 63.82 cm long) used to stop food bowl from sliding back out of the animal's reach.

Tension rod (59.37 cm long, 1.59 cm wide, 0.95 cm thick) used to stop food bowl from sliding back out of the animal's reach.

Front view of Remove Bowl Puzzle set-up.

Side view of Remove Bowl Puzzle set-up.

Inside view of Remove Bowl Puzzle set-up.

The opening in the front of the box measured 59.37 cm wide and 15.88 cm tall.

Figure A.4 Remove Bowl Puzzle.

Food bowl attached to cable/PVC handle used for Cable Puzzle. Section of cable was 1.22 m long, .95 cm diameter. Handle was 18.42 cm long, 3.81 cm diameter.

Inside view of Cable Puzzle set-up.

Side view of Cable Puzzle set-up.

Front view of Cable Puzzle set-up.

Front view of solved Cable Puzzle.

Figure A.5 Cable Puzzle.
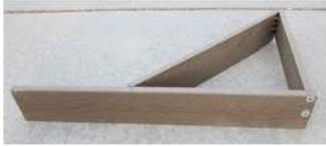
Lazy Susan apparatus used for Lazy Susan Puzzle (weighed 7.2 kg). Longest board (remained outside of box) was 93.03 cm long, board perpendicular to longest board was 50.48 cm long, angled board was 70.80 cm long.

Front view of Lazy Susan Puzzle set-up.

Front view of solved Lazy Susan Puzzle.

Inside view of Lazy Susan Puzzle set-up.

Inside view of solved Lazy Susan Puzzle.

Figure A.6 Lazy Susan Puzzle.

PVC/cable handles used for Remove Lid Puzzle. PVC pieces were 18.42 cm long, 3.81 cm diameter. Cable pieces were 71.12 cm long, .48 cm diameter.

Front view of Remove Lid Puzzle set-up.

Front corner view of Remove Lid Puzzle set-up.

Side view of solved Remove Lid Puzzle (animal could reach food bowl so this counted as a solution).

Front corner view of solved Remove Lid Puzzle (animal could reach food bowl so this counted as a solution).

Side view of solved Remove Lid Puzzle.

Front view of solved Remove Lid Puzzle.

Figure A.7 Remove Lid Puzzle.

Plunger apparatus used for Plunger Puzzle. PVC was 5.08 cm diameter. Plunger was 1.26 m from handle end to outside edge of bowl and two cross-pieces were .52 m across.

Rear view of solved Plunger Puzzle.
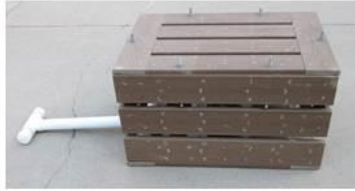
Side view of Plunger Puzzle set-up.

Front view of solved Plunger Puzzle.

Inside view of Plunger Puzzle set-up.
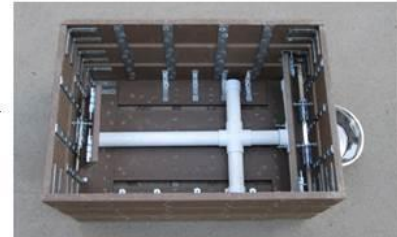
Inside view of solved Plunger Puzzle.

Rear door was raised to create an opening (29.53 cm wide and 16.19 cm tall).

Figure A.8 Plunger Puzzle.

Appendix B - S.O.P. for Problem-Solving (Puzzle Box) Study

Materials Checklist:

▪ 5.67 kg of beef heart
▪ Knife
▪ 10 metal pet-food bowls
▪ Digital scale
▪ Tarp
▪ Stopwatch
▪ Three digital camcorders with memory cards, power cords, extra batteries, and chargers
▪ Extension cords

Puzzle box accessories:

▪ Tension rod or composite T (Preliminary trial and Remove Bowl Puzzle)
▪ Coated cable and handle (bowl attached) (Cable with Handle Puzzle)
▪ "Lazy-Susan" apparatus (Lazy Susan Puzzle)
▪ "Plunger" apparatus (bowl attached) (Plunger Puzzle)
▪ Two PVC/coated cable handles with clips (Remove Lid Puzzle)
▪ Square U-bolts
▪ Wrench, pliers, hammer, awl

Procedure

▪ The animals will be food-deprived for 24 hr prior to each test session.
▪ All items will be removed from the test area.
▪ The animals will be kept out of the building while the test area is being set-up.

▪ **TRAINING PHASE**
   ▪ The top of the box will be removed.
   ▪ A bowl, containing one 56 g piece of beef heart, will be placed inside of the puzzle box.
   ▪ The animal will be released into the test area and allowed to eat the food from the bowl.
   ▪ *Training Days 1-3*
      ▪ 4 trials per day with box facing forward
   ▪ *Training Days 4-5*
      ▪ 4 trials per day with left side of box facing forward

▪ **TESTING PHASE**
During the Testing Phase, the animal will not be allowed to view puzzle box set-up.

   ▪ The animal will be given a minimum of 30-40 min to solve each puzzle.
   ▪ The following protocol will be used for administering each trial:
      ▪ The 30-40-min interval will begin after the animal enters the test room.
      ▪ If the animal solves the puzzle during the allotted time, a "Success" will be recorded.
      ▪ If the animal works on the puzzle and then abandons it for a full 10 min, the trial will be recorded as a "Failure." In the interest of good animal welfare, if the animal performs a stereotypy for 8 min after working on the puzzle, the trial will be ended, and a "Failure" will be recorded.
      ▪ If the animal avoids or ignores the puzzle for the entire trial (or performs a stereotypy for 8 min without contacting the puzzle), the trial will be scored as "No Participation" to differentiate it from a "Failure."

- To set-up the **<u>Preliminary Trial</u>**, remove the lid of the box. The front door of the box should be opened and secured with the hooks inside the front of the box. Place the longer composite 'T' behind the bowl with the top of the 'T' against the bowl to keep it from sliding back. Slide the bowl, containing 56 g of beef heart, in through the front door of the box until it reaches the 'T' (about one-third of the bowl will stick out from the opening). Secure the lid of the box. For this puzzle, the box will face forward. The braces on the rear of the box will be attached to the gate with square U-bolts to prevent the animal from dragging the box around the test area.
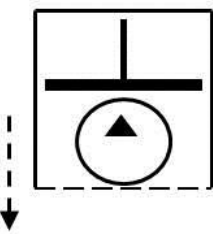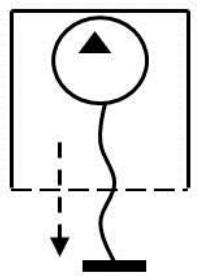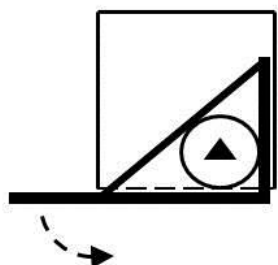
- For the **<u>Remove Bowl Puzzle</u>**, remove the lid of the box and open the front door of it, securing the door with the hooks inside the front of the box. Place the shorter composite 'T' behind the bowl with the top of the 'T' against the bowl to keep it from sliding back. Slide the bowl, containing 56 g of beef heart, in through the front door of the box until it reaches the 'T' (the front of the bowl should be even with the front opening and not stick out of the box at all). Secure the lid of the box. For this puzzle, the box will face forward. The braces on the rear of the box will be attached to the gate with square U-bolts to prevent the animal from dragging the box around the test area.
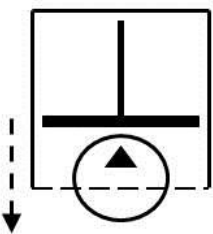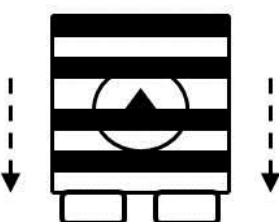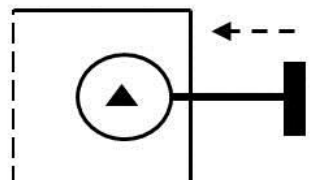
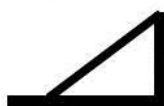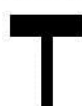- For the **<u>Cable Puzzle</u>**, remove the lid of the box and open the front door of it, securing the door with the hooks inside the front of the box. The bowl with the plastic-coated cable attached to it will be used. Put 56 g of beef heart in the bowl and push it to the back of the box with the coated cable and handle stretched out through the front door. Secure the lid of the box. For this puzzle, the box will face forward. The braces on the rear of the box will be attached to the gate with square U-bolts to prevent the animal from dragging the box around the test area.

- For the **<u>Lazy Susan Puzzle</u>**, remove the lid of the box and open the front door of it, securing the door with the hooks inside the front of the box. The lazy Susan apparatus will be attached to the front of the box by inserting the bolt into the hinge on the right edge of the front-door opening. The bowl, containing 56 g of beef heart, will be set in the triangle-shaped part of the lazy Susan. Close the lazy Susan and secure the lid of the box. For this puzzle, the box will face forward. The braces on the rear of the box will be attached to the gate with square U-bolts to prevent the animal from dragging the box around the test area.

- For the **<u>Remove Lid Puzzle</u>**, remove the L-shaped bolts from the lid of the box. Remove the lid to close and secure both the front and rear doors. Put the bowl with 56 g of beef heart inside the box. Attach the two PVC/coated cable handles to the lid and set it on top of the box. For this puzzle, the front of the box will be turned to face left. The braces on the side of the box will be attached to the gate with square U-bolts to prevent the animal from dragging the box around the test area.

- For the **<u>Plunger Puzzle</u>**, remove the lid of the box and open the front door of it, securing the door with the hooks inside of the box. Open the rear door of the box and secure it with the hook inside the back of the box. Put 56 g of beef heart in the bowl that is attached to the plunger apparatus. Insert the long end of the plunger through the rear door from the inside of the box. Be sure the plunger is pulled out as far as it will go through the rear door. Secure the lid of the box. For this puzzle, the front of the box will be turned to face left. The braces on the side of the box will be attached to the gate with square U-bolts to prevent the animal from dragging the box around the test area.

▪ PUZZLE SCHEMATICS

▪ ORDER OF TRIALS FOR EACH TEST DAY

Test Day	Trial 1	Trial 2	Trial 3
1	Preliminary Trial	Remove Bowl Puzzle	Cable Puzzle
2	Preliminary Trial	Lazy Susan Puzzle	Plunger Puzzle
3	Preliminary Trial	Remove Lid Puzzle	Remove Bowl Puzzle
4	Preliminary Trial	Cable Puzzle	Lazy Susan Puzzle
5	Preliminary Trial	Plunger Puzzle	Remove Lid Puzzle
6	Preliminary Trial	Cable Puzzle	Remove Bowl Puzzle
7	Preliminary Trial	Plunger Puzzle	Lazy Susan Puzzle
8	Preliminary Trial	Remove Bowl Puzzle	Remove Lid Puzzle
9	Preliminary Trial	Lazy Susan Puzzle	Cable Puzzle
10	Preliminary Trial	Remove Lid Puzzle	Plunger Puzzle

Appendix C - Spotted Hyenas Interacting with Each Puzzle in the Problem-Solving Study

Tembo working on (left) and solving (right) the Remove Bowl Puzzle.

Smilla working on (left) and solving (right) the Cable Puzzle.

Askari working on (left) and solving (right) the Lazy Susan Puzzle.

Haji working on (left) and solving (right) the Remove Lid Puzzle.

Charlie working on (left) and solving (right) the Plunger Puzzle.

Appendix D - Complete Data on Working Time and Trial Time for Problem-Solving Study

The tables in this section list the amount of time (in minutes) that spotted hyenas spent working on each puzzle along with the total length of the trial. Over the 10 test days, the spotted hyenas were presented with each puzzle a total of four times. The shaded cells are successful trials.

	Remove Bowl Puzzle											
	Trial 1			Trial 2			Trial 3			Trial 4		
	Working Time	Trial Time	% Trial Working	Working Time	Trial Time	% Trial Working	Working Time	Trial Time	% Trial Working	Working Time	Trial Time	% Trial Working
Charlie	0.15	0.15	100.00%	0.35	0.55	63.64%	0.25	0.25	100.00%	0.07	0.07	100.00%
Smilla	0.23	0.23	100.00%	0.20	0.70	28.57%	0.13	0.15	88.89%	0.10	0.12	85.71%
Haji	0.30	0.32	94.74%	0.18	0.20	91.67%	0.15	0.15	100.00%	0.15	0.15	100.00%
Tembo	0.12	0.13	87.50%	0.22	0.23	92.86%	0.12	0.12	100.00%	0.10	0.12	85.71%
Askari	2.82	3.65	77.17%	0.45	0.63	71.05%	1.80	2.13	84.38%	0.93	0.97	96.55%
Grubbie	0.23	0.25	93.33%	0.25	0.25	100.00%	0.23	0.25	93.33%	0.22	0.25	86.67%

	Cable Puzzle											
	Trial 1			Trial 2			Trial 3			Trial 4		
	Working Time	Trial Time	% Trial Working	Working Time	Trial Time	% Trial Working	Working Time	Trial Time	% Trial Working	Working Time	Trial Time	% Trial Working
Charlie	2.57	2.60	98.72%	0.68	0.70	97.62%	0.13	0.15	88.89%	0.12	0.13	87.50%
Smilla	4.35	4.45	97.75%	1.80	1.92	93.91%	0.33	0.52	64.52%	0.17	0.17	100.00%
Haji	3.73	4.27	87.50%	5.73	20.15	28.45%	4.35	5.22	83.39%	2.37	2.97	79.78%
Tembo	2.92	2.93	99.43%	3.77	25.73	14.64%	3.18	18.48	17.22%	3.12	10.40	29.97%
Askari	4.62	10.78	42.81%	3.82	18.92	20.18%	2.85	22.40	12.72%	8.05	9.50	84.74%
Grubbie	4.40	23.80	18.49%	4.23	25.17	16.82%	3.53	16.13	21.90%	2.30	14.88	15.45%

	Lazy Susan Puzzle											
	Trial 1			Trial 2			Trial 3			Trial 4		
	Working Time	Trial Time	% Trial Working	Working Time	Trial Time	% Trial Working	Working Time	Trial Time	% Trial Working	Working Time	Trial Time	% Trial Working
Charlie	2.37	2.45	96.60%	0.52	0.52	100.00%	0.33	0.35	95.24%	0.22	0.23	92.86%
Smilla	1.95	1.97	99.15%	0.33	0.35	95.24%	0.47	0.58	80.00%	0.17	0.18	90.91%
Haji	8.65	9.93	87.08%	2.28	3.55	64.32%	1.92	2.03	94.26%	1.42	1.58	89.47%
Tembo	7.33	11.92	61.54%	0.95	1.72	55.34%	0.42	0.43	96.15%	0.32	0.33	95.00%
Askari	5.65	9.62	58.75%	2.77	3.57	77.57%	2.55	2.82	90.53%	1.38	1.47	94.32%
Grubbie	7.50	29.25	25.64%	0.48	12.10	3.99%	1.98	14.92	13.30%	1.18	12.50	9.47%

	Remove Lid Puzzle											
	Trial 1			Trial 2			Trial 3			Trial 4		
	Working Time	Trial Time	% Trial Working	Working Time	Trial Time	% Trial Working	Working Time	Trial Time	% Trial Working	Working Time	Trial Time	% Trial Working
Charlie	---	---	---	1.90	1.92	99.13%	0.97	0.97	100.00%	3.23	3.32	97.49%
Smilla	---	---	---	2.18	2.28	95.62%	1.95	2.02	96.69%	2.88	2.92	98.86%
Haji	13.13	23.27	56.45%	5.15	6.33	81.32%	3.40	3.60	94.44%	2.17	3.33	65.00%
Tembo	5.77	10.25	56.26%	1.88	2.07	91.13%	6.92	22.33	30.97%	5.12	15.48	33.05%
Askari	4.58	5.33	85.94%	8.58	8.85	96.99%	21.77	24.30	89.57%	15.80	19.32	81.79%
Grubbie	4.90	16.60	29.52%	5.73	16.77	34.19%	2.38	14.08	16.92%	2.33	12.87	18.13%

	Plunger Puzzle											
	Trial 1			Trial 2			Trial 3			Trial 4		
	Working Time	Trial Time	% Trial Working	Working Time	Trial Time	% Trial Working	Working Time	Trial Time	% Trial Working	Working Time	Trial Time	% Trial Working
Charlie	54.33	68.37	79.47%	24.62	26.53	92.78%	37.37	39.93	93.57%	35.28	36.65	96.27%
Smilla	---	---	---	26.53	50.25	52.80%	12.17	31.15	39.06%	16.78	40.97	40.97%
Haji	15.75	31.60	49.84%	16.92	34.47	49.08%	3.68	16.73	22.01%	9.00	24.72	36.41%
Tembo	9.93	18.17	54.68%	4.70	21.10	22.27%	1.38	13.08	10.57%	0.50	6.57	7.61%
Askari	24.05	41.75	57.60%	14.88	29.05	51.23%	4.28	18.03	23.75%	12.48	23.65	52.78%
Grubbie	7.05	27.98	25.19%	3.53	12.48	28.30%	2.17	9.03	23.99%	1.47	8.72	16.83%

Appendix E - Complete Behavior Diversity Data for Problem-Solving Study

Table E.1 Behavior Diversity Scores for the Problem-Solving Study

		Subject: Charlie					Subject: Smilla					Subject: Haji					Subject: Tembo					Subject: Askari					Subject: Grubbie			
		Puzzle*					Puzzle*					Puzzle*					Puzzle*					Puzzle*					Puzzle*			
		RB	CA	LS	RL	PL	RB	CA	LS	RL	PL	RB	CA	LS	RL	PL	RB	CA	LS	RL	PL	RB	CA	LS	RL	PL	RB	CA	LS	RL	PL
Trial 1	Bite Box	0	0	1	--	1	0	1	1	--	--	0	0	1	1	1	0	0	1	1	1	0	0	1	0	1	0	0	1	0	0
	Dig/Paw Box	0	0	0	--	1	0	0	0	--	--	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
	Investigate Box or Apparatus	0	1	1	--	1	1	1	1	--	--	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	Manipulate Apparatus	0	1	1	--	1	0	1	1	--	--	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1
	Behavior Diversity Score	0	2	3	--	4	1	3	3	--	--	0	2	3	3	3	0	2	3	3	3	2	2	3	2	4	1	2	3	2	3

*Puzzle abbreviations are as follows: RB=Remove Bowl, CA=Cable, LS=Lazy Susan, RL=Remove Lid, and PL=Plunger

Note: Shaded cells indicate successful trials.

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Trial 2		Subject: Charlie					Subject: Smilla					Subject: Haji					Subject: Tembo					Subject: Askari					Subject: Grubbie				
		Puzzle*					Puzzle*					Puzzle*					Puzzle*					Puzzle*					Puzzle*				
		RB	CA	LS	RL	PL	RB	CA	LS	RL	PL	RB	CA	LS	RL	PL	RB	CA	LS	RL	PL	RB	CA	LS	RL	PL	RB	CA	LS	RL	PL
	Bite Box	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	1	0	1	1	0	0	0	1	1	0	0	0	0	1
	Dig/Paw Box	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	1
	Investigate Box or Apparatus	1	1	0	1	1	1	1	0	1	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1
	Manipulate Apparatus	0	1	1	1	1	0	1	0	1	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0	1	0	1	0
	Behavior Diversity Score	1	2	1	2	4	1	2	0	2	4	0	3	2	3	2	0	3	2	3	3	2	2	3	3	4	0	3	1	3	3

*Puzzle abbreviations are as follows: RB=Remove Bowl, CA=Cable, LS=Lazy Susan, RL=Remove Lid, and PL=Plunger

Note: Shaded cells indicate successful trials.

		Subject: Charlie					Subject: Smilla					Subject: Haji					Subject: Tembo					Subject: Askari					Subject: Grubbie				
		Puzzle*					Puzzle*					Puzzle*					Puzzle*					Puzzle*					Puzzle*				
		RB	CA	LS	RL	PL	RB	CA	LS	RL	PL	RB	CA	LS	RL	PL	RB	CA	LS	RL	PL	RB	CA	LS	RL	PL	RB	CA	LS	RL	PL
Trial 3	Bite Box	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1	0	1	1	1	1	0	1	0	0	0
	Dig/Paw Box	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
	Investigate Box or Apparatus	0	0	0	0	1	0	1	0	1	1	0	1	1	1	1	0	1	0	1	1	1	1	1	1	1	0	1	1	1	1
	Manipulate Apparatus	0	0	0	1	1	0	0	1	1	1	0	1	1	1	1	0	1	1	1	0	1	1	1	1	1	0	1	1	1	0
	Behavior Diversity Score	0	0	0	1	4	0	1	1	2	4	0	2	2	2	3	0	3	1	2	2	2	3	3	3	3	0	4	3	3	2

*Puzzle abbreviations are as follows: RB=Remove Bowl, CA=Cable, LS=Lazy Susan, RL=Remove Lid, and PL=Plunger

Note: Shaded cells indicate successful trials.

Trial 4	Subject: Charlie Puzzle*					Subject: Smilla Puzzle*					Subject: Haji Puzzle*					Subject: Tembo Puzzle*					Subject: Askari Puzzle*					Subject: Grubbie Puzzle*				
	RB	CA	LS	RL	PL	RB	CA	LS	RL	PL	RB	CA	LS	RL	PL	RB	CA	LS	RL	PL	RB	CA	LS	RL	PL	RB	CA	LS	RL	PL
Bite Box	0	0	0	1	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0
Dig/Paw Box	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1
Investigate Box or Apparatus	0	0	0	1	1	0	0	0	1	1	0	1	1	1	1	0	1	0	1	1	1	1	1	1	1	0	1	1	1	1
Manipulate Apparatus	0	0	0	1	1	0	0	0	1	1	0	1	1	1	1	0	0	0	1	0	1	1	1	1	1	0	1	0	1	0
Behavior Diversity Score	0	0	0	3	4	0	0	0	2	4	0	2	2	2	3	0	2	0	2	1	2	4	2	3	4	0	3	1	2	2

*Puzzle abbreviations are as follows: RB=Remove Bowl, CA=Cable, LS=Lazy Susan, RL=Remove Lid, and PL=Plunger

Note: Shaded cells indicate successful trials.

Appendix F - Complete Latency to Approach the Puzzle Box Data for Problem-Solving Study

Table F.1 Latency to Approach the Puzzle Box or Puzzle Apparatus in the Problem-Solving Study (in Seconds*)

	Subject: Charlie Puzzle **					Subject: Smilla Puzzle **					Subject: Haji Puzzle **					Subject: Tembo Puzzle **					Subject: Askari Puzzle **					Subject: Grubbie Puzzle **				
Trial	RB	CA	LS	RL	PL	RB	CA	LS	RL	PL	RB	CA	LS	RL	PL	RB	CA	LS	RL	PL	RB	CA	LS	RL	PL	RB	CA	LS	RL	PL
1	1	1	1	--	1	1	1	1	--	--	1	2	12	2	6	1	1	16	3	1	1	5	20	3	11	2	5	11	2	2
2	1	1	1	1	1	1	1	1	5	1	1	2	2	1	1	2	1	2	2	1	8	13	6	2	5	2	2	2	1	2
3	1	1	1	1	1	1	2	1	1	2	1	1	1	1	2	1	2	1	2	2	3	15	3	3	5	1	2	2	3	1
4	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	2	2	2	3	11	4	2	2	1	2	2	1	1

*All latency to approach times less than one second were rounded to one second.

**Puzzle abbreviations are as follows: RB=Remove Bowl, CA=Cable, LS=Lazy Susan, RL=Remove Lid, and PL=Plunger

Appendix G - Complete Jumping Away Data for Problem-Solving Study

Table G.1 Number of Times Spotted Hyenas Jumped Away from Puzzle Box or Puzzle Apparatus During the Problem-Solving Study

Trial	Subject: Charlie Puzzle *					Subject: Smilla Puzzle *					Subject: Haji Puzzle *					Subject: Tembo Puzzle *					Subject: Askari Puzzle *					Subject: Grubbie Puzzle *				
	RB	CA	LS	RL	PL	RB	CA	LS	RL	PL	RB	CA	LS	RL	PL	RB	CA	LS	RL	PL	RB	CA	LS	RL	PL	RB	CA	LS	RL	PL
1	0	1	0	--	0	0	5	0	--	--	0	5	0	0	0	0	5	0	5	0	10	14	9	7	40	0	3	0	0	2
2	0	0	0	0	0	0	0	0	2	0	0	1	1	0	0	0	0	0	0	2	2	4	4	5	3	0	3	0	5	0
3	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	2	0	7	4	1	10	2	0	1	0	1	0
4	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	3	15	4	9	7	0	0	0	1	0

*Puzzle abbreviations are as follows: RB=Remove Bowl, CA=Cable, LS=Lazy Susan, RL=Remove Lid, and PL=Plunger

Appendix H - S.O.P. for Social Learning (STFP) Experiment

Materials Checklist
- 7.5 kg ground pork
- 2 concrete bowls
- 3 metal bowls
- 2 mixing spoons
- 2 mixing bowls
- Digital scale
- Digital video camera
- Stopwatch

Flavor Pair 1
- HealthPro Vita Gravy Hip and Joint Savory Roast Chicken
- HealthPro Vita Gravy Skin and Coat Savory Sirloin Steak

Flavor Pair 2
- Variety Pet Foods Mixables Cape Cod Picnic
- Variety Pet Foods Mixables Greek Banquet

Note: Order of flavor pairs and which flavor is the target or distractor will be counterbalanced.

Procedure
- The animals will be food-deprived for 24 hr prior to the experiment.
- The animals will be kept outside while the experimental area is being set-up.
- The pork and flavors will be mixed in the commissary and covered in order to keep the scent of the non-target flavor out of the building until it is presented.
- To prepare the two flavors of ground pork:
  - For the demonstrator:
    - 600 g of ground pork will be mixed with 120 g of the target flavor in a mixing bowl using a mixing spoon. The mixture will be placed into a metal food bowl.
  - For the observer:
    - First, 2300 g of ground pork will be mixed with 460 g of the target flavor in the same mixing bowl using the same spoon. The mixture will be placed into a second metal bowl and will remain outside of the building until it is placed into one of the concrete bowls (when the Choice Phase begins).
    - Next, 2300 g of ground pork will be mixed with 460 g the distractor flavor in the second mixing bowl using the second mixing spoon. This mixture will be placed into the third metal bowl and will be covered. The mixture will also remain outside of the building until it is placed into the other concrete bowl (when the Choice Phase begins).
- Demonstrator-Alone Phase
  - The food for the demonstrator will be placed in the test room.
  - The demonstrator will be allowed into the test room given 30 min to eat the food.
- Interaction Phase
  - The demonstrator and observer will be given 10 min to interact (without food present).
  - The Interaction Phase will be video-recorded.
- Choice Phase
  - The two choices for the observer will be placed in the concrete bowls in the test room (approx. 91.44 cm apart), and the observer will get 30 min with the two flavor choices.
  - The amount of each flavor remaining will be weighed and recorded.
  - The Choice Phase will be video-recorded.

Appendix I - Concrete Bowls and Set-Up for Social Learning (STFP) Experiment

The concrete bowls (left photograph) were 20.48 cm tall and had a total diameter of 27.31 cm. The area between the outside and inside edges of the bowls was 5.72 cm and the bowls were 11.43 cm deep. The bowls weighed 18.14 kg. Square U-bolts were set in the concrete for use as handles since the bowls were quite heavy. Experimental set-ups from two of the zoos are pictured in the middle and right photographs.

Concrete bowls used for flavor-preference study

Set-up of flavor-preference study in Denver

Set-up of flavor-preference study in St. Louis