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Limited social learning of a novel technical problem by spotted hyenas

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ABSTRACT

Social learning can have profound evolutionary consequences because it drives the diffusion of novel behaviours among individuals and promotes the maintenance of traditions within populations. We inquired whether spotted hyenas (*Crocuta crocuta*), generalist carnivores living in complex, primate-like societies, acquire information from conspecifics about a novel problem-solving task. Previously, we presented wild hyenas with a food-access puzzle and found that social learning opportunities did not affect problem-solving success among observers, but did reduce observers' neophobia. However, we had little control over which individuals observed conspecifics solve the problem, and few wild hyenas were successful. Therefore, we conducted an experiment in captivity where we controlled observer access to two demonstration styles. Again, social learning opportunities did not affect problem-solving success, but tended to reduce neophobia among captive observers. Social learning opportunities also influenced problem-solving style. Captive hyenas showed limited evidence for directed social learning; low-ranking individuals paid closer attention to demonstrators than high-ranking individuals, although this greater attention did not result in greater success. We conclude that wild and captive hyenas exploit social learning opportunities similarly, and that the limited social learning shown by hyenas on this task is likely based on localized stimulus enhancement.

1. Introduction

Advantages of group living include exchange of information among group members and opportunities to learn adaptive behaviors from conspecifics (Lee, 1994; Giraldeau, 1997; Addessi & Visalberghi, 2001). Social learning enables individuals to benefit from the expertise and knowledge of other group members, and represents the basis for formation of traditions and culture (Humphrey, 1976; Jolly, 1988; Russon, 1997; Whiten & Byrne, 1997; Day et al., 2003; Whiten & Van Schaik, 2007). Social learning is hypothesized to be particularly adaptive for animals that forage opportunistically, use challenging techniques for food searching and handling, and are highly gregarious (Klopfer, 1959; Caldwell & Whiten, 2002). In this study, we examine the extent to which captive spotted hyenas use available social information when solving a novel food-access problem, and then compare the abilities of the captive hyenas to those previously found in wild hyenas confronting the same task. The results presented here are particularly valuable because they provide a direct comparison between the social learning abilities of wild and captive members of a single species.

Spotted hyenas offer a good model system for investigating the role of social learning in the acquisition of innovative behaviors for several reasons. First, spotted hyenas are generalist carnivores that hunt and scavenge a diverse array of prey (Cooper et al., 1999). Social learning may be particularly adaptive when these animals explore novel food sources (Huber et al., 2001; Moscovice & Snowdon, 2006), and naïve hyenas would likely benefit greatly from observing the foraging choices made by knowledgeable conspecifics. Second, spotted hyenas live in large, complex primate-like societies and exhibit patterns of competition and cooperation that are remarkably similar to those seen in cercopithicine primates (Frank, 1986; Holekamp, 1999; Holekamp et al., 2007; Holekamp, 2007). Although social learning has received a great deal of attention in studies of primate cognition (Call & Tomasello, 1995; Bugnyar & Huber, 1997; Whiten, 1998; Custance et al., 1999; Custance et al., 2001; Day et al., 2003; Caldwell & Whiten, 2004),

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and in studies outside of primates, such as fish (Brown & Laland, 2003), birds (Midford et al., 2000; Aplin et al., 2013; Boogert et al., 2008), rats (Galef, 2009), and bats (Wright et al., 2011), it has rarely been investigated in carnivores (Nel, 1999; but see Mersmann et al., 2011). However, given their primate-like social complexity, theoretically social learning should be no less adaptive for spotted hyenas than it is for many primates. Third, spotted hyenas are especially interesting with regard to directed social learning, which occurs when factors such as age, social rank, sex, relatedness, or patterns of association influence the likelihood of social learning, and the likelihood of attending to a demonstrator (Coussi-Korbel & Fragaszy, 1995). This is because spotted hyena societies, like those of cercopithicine primates, are structured by strict linear dominance hierarchies, in which an individual's social rank determines its priority of access to resources (Frank, 1986; East & Hofer, 2001). Most interestingly though, spotted hyenas are highly unusual among mammals in that adult females and their dependent offspring are socially dominant to adult males in the social group (Holekamp & Smale, 1991). This unique characteristic allows us to test whether spotted hyenas are biased towards learning from adult females when compared to mammals living in more typical male-dominated societies. Additionally, there may also be a sex difference among observers, where female hyenas pay more attention to female demonstrators, but males do not. For example, long-tailed macaques live in social groups with a dominant male, and there are some indications that male captive long-tailed macaques paid more attention to, and learned more from watching, the dominant male in the group demonstrate novel tool-using behavior than did females (Zuberbuhler et al., 1996). There is also evidence of directed social learning within social groups of female-dominated ringtail lemurs, *Lemur catta* (Kendal et al., 2010).

Whiten and Mesoudi (2008) noted that the validity of the field of social learning is limited by the overwhelming focus on studies in captivity. Here, we compared social learning abilities of individuals from both wild and captive populations of spotted hyenas. By testing individuals in both populations using the same experimental apparatus, we were able to confirm our observations of social learning in a natural setting (Benson-Amram and Holekamp, 2012) with results from a controlled captive study. Our study shows that wild and captive hyenas acquire information through social learning in the same way, and joins only a handful of other studies in using the same experimental apparatus to investigate social learning in both wild and captive populations of a single species (Seferta et al., 2001; Webster & Lefebvre, 2001; Gajdon et al., 2004; Bouchard et al., 2007).

We previously reported that, among both wild and captive hyenas presented with a novel foraging task, those individuals that were less neophobic (i.e. less adverse to novel objects (Greenberg, 2003) and exhibited a greater diversity of initial exploratory behaviors were more successful problem solvers than more neophobic and less exploratory hyenas (Benson-Amram & Holekamp, 2012; Benson-Amram et al., 2013). Although social learning opportunities did not result in better problem-solving success in those studies, our findings led us to inquire whether hyenas acquired other beneficial information about the novel task by observing the behavior of conspecifics.

Social learning is mediated by a variety of different psychological mechanisms including social facilitation, stimulus enhancement, emulation, and imitation (Byrne, 1995). Studies of social learning in captive capuchin monkeys, *Cebus apella*, provide evidence for social facilitation (Visalberghi & Addessi, 2000), which occurs when individuals are more likely to perform a behavior in the presence of a conspecific performing the same behavior than when they are alone (Shettleworth, 2009). In contrast, domestic dogs, *Canis familiaris*, acquire socially transmitted information via stimulus enhancement (Mersmann et al., 2011), defined as an increased likelihood of an observer contacting or interacting with an object as a result of observing another individual interact with that object (Heyes, 1994; Shettleworth, 2009). More specifically, localized stimulus enhancement occurs when an observer is attracted to the specific part of an object seen being manipulated by a demonstrator (Huber et al., 2001). Unlike social facilitation, stimulus enhancement does not require the demonstrator to be present when the observer interacts with the object (Shettleworth, 2009). Captive keas, *Nestor notabilis*, emulate the actions of demonstrators when interacting with a novel food-access puzzle (Huber et al., 2001). Emulation occurs when an individual copies elements of a complex action, but does not fully imitate, or perform the same actions as, a demonstrator (Shettleworth, 2009). Finally, it appears that marmosets, *Callithrix jacchus*, (Voelkl and Huber, 2000), chimpanzees, *Pan troglodytes*, (Whiten et al., 1996; Whiten, 1998), gorillas, *Gorilla gorilla*, (Stoinksi et al., 2001), and banded mongoose, *Mungos mungo*, (Müller and Cant, 2010) may imitate a demonstrator's actions. Imitation, defined as "the copying of a novel or otherwise improbable act or utterance" (Thorpe, 1963), occurs when an observer becomes more likely than otherwise to exhibit the same novel action, action sequence, or combination of actions that it saw performed by a demonstrator (Hoppitt and Laland, 2008). Imitation is thought to be more cognitively demanding than other forms of social learning because it may require representations of another individual's intentions and perspective (Heyes and Galef Jr, 1996).

Here, we adopted an experimental approach to inquire which of these four social learning mechanisms are utilized by spotted hyenas. We predicted that, if hyenas learn via social facilitation, then individuals should show reduced neophobia toward, and increased interest in, the puzzle, but only when in the presence of a demonstrator. Social facilitation should not lead to a decrease in neophobia when hyenas view a demonstrator interact with the puzzle, but are then tested alone. In contrast, if hyenas learn via localized stimulus enhancement, then individuals observing a conspecific solve a novel food-access puzzle should spend more time working on relevant aspects of the puzzle than control individuals who had no access to a demonstrator. If hyenas learn socially through emulation, then observer hyenas should be more efficient problem-solvers and learn the solution faster than control hyenas. We also specifically tested whether observer hyenas showed evidence of imitation by using two different demonstrator individuals, each of which used a different behavioral strategy to solve the puzzle. If hyenas learn through imitation, then we expected that individuals would show behavior patterns similar to those of their demonstrator, and show patterns different from those of hyenas that observed a different demonstrator. Finally, we inquired whether hyenas show directed social learning. If so, given the matriarchal dominance hierarchy that structures spotted hyena society, we predicted that observer hyenas should attend more closely to a high-ranking female than to a low-ranking male demonstrator.

2. Methods

2.1. Subjects and study site

Experiments were conducted on members of a captive breeding colony of spotted hyenas maintained at the Field Station for Behavioral Research at the University of California, Berkeley. Data were collected from June to August 2008 when the colony housed 26 captive-born hyenas: 11 adult females, 11 adult males, and 4 juveniles (3 females and 1 male). Captive hyenas were considered adults once they reached two years of age. The hyenas were housed in outdoor or semi-outdoor enclosures, in groups of two or three individuals. Social rank was known within dyads and triads