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A comparison of innovative problem-solving abilities between wild and captive spotted hyaenas, *Crocuta crocuta*

Sarah Benson-Amram [a,*], Mary L. Weldele [b], Kay E. Holekamp [a]

[a] *Department of Zoology, Michigan State University, East Lansing, MI, U.S.A.*
[b] *Department of Psychology, University of California, Berkeley, CA, U.S.A.*

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Innovative problem solving enables individuals to deal with novel social and ecological challenges. However, our understanding of the importance of innovation for animals in their natural habitat is limited because experimental investigations of innovation have historically focused on captive animals. To determine how captivity affects innovation, and whether captive studies of animal innovation suffer from low external validity, we need experimental investigations of innovation in both wild and captive populations of the same species in diverse taxa. Here we inquired whether wild and captive spotted hyaenas differ in their ability to solve the same novel technical problem, and in the diversity of exploratory behaviours they exhibit when first interacting with the problem. Our results suggest that wild and captive populations show important differences in their innovative problem-solving abilities. Captive hyaenas were significantly more successful at solving the novel problem, and significantly more diverse in their initial exploratory behaviour, than were wild hyaenas. We were able to rule out hypotheses suggesting that these differences result from excess energy or time available to captive animals. We conclude that captive hyaenas were more successful because captive individuals were less neophobic and more exploratory than their wild counterparts. These results have important implications for our interpretation of studies on innovative problem solving in captive animals and aid our attempts to gain a broader understanding of the importance of innovation for animals in their natural habitat.

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

Despite the potentially important ecological and evolutionary consequences of innovation (Nicolakakis et al. 2003; Reader & Laland 2003), research on this subject has been limited in scope. A common approach has been analysing anecdotal accounts of innovation from the literature (Lefebvre et al. 1997; Reader & Laland 2001). Unfortunately, innovations are rarely observed in the field, both because innovations are rare and unpredictable, and also because thousands of hours of behavioural observations are necessary to gain a comprehensive knowledge of the behaviour of the study species, which is a prerequisite for recognizing an act as an innovation (van Schaik et al. 2006). Thus, researchers have adopted the strategy of inducing innovation by presenting captive individuals with a novel problem-solving task (Köhler 1925; Visalberghi et al. 1995; Povinelli 2000; Heinrich & Bugnyar 2005; Santos et al. 2006; Bond et al. 2007; Tebbich et al. 2007; Boogert et al. 2008; de Mendonca-Furtado & Ottoni 2008; Liker & Bókony 2009; Overington et al. 2011). To date, only a few studies have implemented this experimental approach with wild animals in their natural habitat (Webster & Lefebvre 2001; Biro et al. 2003; Bouchard et al. 2007; Morand-Ferron & Quinn 2011; Morand-Ferron et al. 2011; Benson-Amram & Holekamp 2012; Thornton & Samson 2012).

There is some evidence that data from studies on captive animals cannot fully inform our understanding about how individuals in the wild should be expected to respond to novel challenges (Webster & Lefebvre 2001; Ramsey et al. 2007). For example, captive primates demonstrated less neophobia, defined as an aversion to novel stimuli (Greenberg 1983, 2003; Bergman & Kitchen 2009), to novel objects than did their wild counterparts

* Correspondence and present address: S. Benson-Amram, School of Biology, University of St Andrews, St Andrews, Fife KY16 9TF, U.K.
E-mail address: sba2@st-andrews.ac.uk (S. Benson-Amram).

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(Visalberghi et al. 2003). Furthermore, in studies comparing anecdotal accounts from the literature, captive primates showed higher rates of innovation than did wild primates (Reader & Laland 2003). Likewise, wild baboons demonstrated very low success rates on three novel problem-solving tasks, which were similar, but not identical, to problems that captive baboons solved successfully (Laidre 2008). Thus, it appears that studies of innovative problem-solving among captive animals may suffer from low external validity (Webster & Lefebvre 2001; Ramsey et al. 2007).

If by-products of a captive lifestyle, such as reduced neophobia towards man-made objects, bias the abilities of captive individuals such that they consistently perform better on novel technical problems than their wild counterparts, then we should incorporate this bias into our interpretation of existing studies of captive animals, and potentially focus future work on animal innovation in wild populations. To determine how captivity changes innovation and whether captive studies of animal innovation do indeed suffer from low external validity, we need experimental investigations of innovation in both wild and captive populations of the same species across a range of taxa. To date, only three studies have compared innovative problem-solving abilities in wild and captive populations of the same species using a single experimental paradigm, and all three of these studies were conducted on birds (Webster & Lefebvre 2001; Gajdon et al. 2004; Bouchard et al. 2007). Interestingly, these studies all found that captive individuals had better technical problem-solving skills than their wild counterparts. Here, we test the external validity of captive studies of animal innovation by comparing the performance of wild and captive spotted hyaenas in solving a novel technical problem.

Higher innovation rates among captive animals might result from several different processes, none of which are mutually exclusive. First, excess energy may enable captive animals to innovate solutions to problems in their environment (Kummer & Goodall 1985), as captive animals need not cope with the demands of foraging. If this hypothesis is correct, then success rates should differ between individuals with high food intake and those that are more food deprived. For example, we should expect to see differences in problem-solving success between high- and low-ranking wild individuals where social rank determines priority of access to resources. We should also find little or no variation in problem-solving success among captive individuals when they all have the same food intake. Second, captive animals may have more frequent exposure to the novel problem due to shorter and more consistent intertrial intervals resulting from the human experimenter's guaranteed access to the animals; captives may thus learn faster than wild animals with more sporadic exposure to the problem. If this is true, then differences in problem-solving success between captive and wild populations should only emerge after individuals have had several trials with the novel problem and there should be no difference in success between wild and captive animals in initial trials. Third, captive individuals have far more exposure to man-made objects than do wild individuals; this may result in low neophobia among captives when exposed to a novel apparatus (Huber & Gajdon 2006; van de Waal & Bshary 2010). Several studies have found that neophobic individuals are less likely than others to participate in novel problem-solving tasks, and are thus unlikely to solve problems (Seferta et al. 2001; Webster & Lefebvre 2001; Greenberg 2003; Bouchard et al. 2007; Cole et al. 2011). If it is true that reduced neophobia among captive individuals allows them to solve problems more successfully than wild individuals, then we should see a negative relationship between neophobia and problem-solving success among individuals from any single population, and wild animals should show considerably more neophobia than captive conspecifics. Fourth, captive individuals may be more successful because they have more time to spend working on a novel problem than do wild individuals (Kummer & Goodall 1985). Unlike wild individuals, lone captive animals do not have to contend with competing demands on their time, such as antipredator behaviour or social interactions, and they can devote all of their time and attention during a trial to solving the novel technical problem. If this hypothesis is correct, then there should be no difference in problem-solving success between wild and captive populations when each individual interacts with the novel problem for the same amount of time. Overall, if captivity influences either the amount or quality of time that individuals spend interacting with a novel problem, or their likelihood of responding to a test situation by approaching a novel apparatus, then captive animals will probably be more successful at problem solving than will individuals in their natural habitat.

We previously reported the results of an experimental study on wild hyaenas, which found that only 15% of wild individuals tested were able to solve a novel problem-solving task, even when many of them had multiple opportunities to do so (Benson-Amram & Holekamp 2012). That study also investigated determinants of problem-solving success in wild hyaenas and found that individuals showing the greatest diversity of exploratory behaviours in their initial encounter with the problem were eventually most successful (Benson-Amram & Holekamp 2012). We also observed a slight trend for more persistent individuals, those that spent more time in their initial trial working on the problem before giving up, to be more successful than less persistent individuals. Additionally, neophobia was a major inhibitor of innovative problem-solving success among wild hyaenas. Specifically, individuals that took longer to approach the problem in their initial trial were significantly less successful than individuals that approached the apparatus more quickly (Benson-Amram & Holekamp 2012). Here, we tested captive hyaenas on the same novel technical problem that we previously presented to the wild hyaenas and asked whether captive hyaenas differ from wild hyaenas in their overall ability to solve the problem. We also inquired whether the diversity of initial exploratory behaviours, persistence and neophobia had the same influences on technical problem solving among captives as was demonstrated in the wild.

Based on findings from earlier work with other species (Webster & Lefebvre 2001; Gajdon et al. 2004; Bouchard et al. 2007), we predicted that captive hyaenas would be more successful at solving a novel technical problem, and thus more innovative, than wild hyaenas. We predicted that captive hyaenas would be more persistent, show a greater diversity of exploratory behaviours and be less neophobic than wild hyaenas. Despite these predicted differences, we expected that captive hyaenas would learn the solution to the novel technical problem via trial-and-error learning, which is the same method of learning demonstrated by wild hyaenas (Benson-Amram & Holekamp 2012). Thus we predicted that captive hyaenas, like their wild counterparts, would fail to show insightful problem solving, which in contrast to trial-and-error learning, occurs when an individual has a sudden comprehension, or an 'aha' moment, leading to a rapid solution to the problem (Kounios & Jung-Beeman 2009; Shettleworth 2010).

Lastly, like many primates, wild hyaenas show a strong effect of age on exploration diversity, persistence and neophobia (Benson-Amram & Holekamp 2012). Juvenile primates are thought to be more innovative and less neophobic than adults, perhaps because they have more spare time to devote to exploration and problem solving (Kummer & Goodall 1985; Reader & Laland 2003). Here we predicted that captive juvenile hyaenas would act like wild juveniles, and that they would therefore show greater exploration diversity and less neophobia than adults.

METHODS

Subjects and Study Site

Wild subjects were 62 spotted hyaenas from two neighbouring clans in the Masai Mara National Reserve, Kenya. Benson-Amram & Holekamp (2012) provide complete details on the identification of individual hyaenas, assignment to rank, sex and age categories, and methods used to assess problem-solving success, neophobia, exploration diversity and persistence among wild hyaenas.

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

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

Experimental Apparatus

The experimental apparatus was a reinforcing steel, 'rebar', puzzle box baited with raw meat; it had a simple bolt latch that the hyaenas needed to slide laterally for the door to swing open (see Supplementary Material, Movie S1), thereby allowing the hyaena access to the meat inside. The box was designed such that subjects could both see and smell the meat inside the box. The hyaenas could also see and touch the entire latch mechanism, which could be opened using either the mouth or the forepaws. The puzzle box was designed so that hyaenas would have to use behaviours in their existing repertoire in a novel fashion. Hyaenas often pull carcasses, or pull limbs off of carcasses. Therefore, moving the bolt latch laterally to open the door of the puzzle box represents a novel application of an existing behaviour in the hyaena repertoire.

Because of logistical constraints, we used slightly different puzzle boxes for the wild and captive hyaenas. Both puzzle boxes had two rebar handles, one located centrally on each short side and a single door on one long side. The puzzle boxes for the two groups were nearly the same size (L × H × W dimensions: wild hyaenas: 60 × 31 × 37 cm, with a 34 cm long door; captive hyaenas: 63.5 × 33 × 33 cm, with a 39 cm long door). However, because different materials were available in Kenya and the U.S., the puzzle box used in captivity weighed 45 kg whereas the puzzle box used in the wild weighed 35 kg. Despite the weight of these boxes, both captive and wild hyaenas were able to lift, flip and drag them around (see Supplementary Movie S1).

Experimental Procedure

We presented a baited puzzle box opportunistically to wild hyaenas. In total, we conducted 417 trials on 62 wild hyaenas, including 19 adult females, 9 adult males, 15 juvenile females, 17 juvenile males and 2 juveniles of unknown sex. Complete details of the experimental procedure used with wild hyaenas are given in Benson-Amram & Holekamp (2012).

We gave each captive individual a 10 min habituation period in the 39 m^2 test enclosure just prior to its first trial of the day. This allowed subjects to investigate the test enclosure in the absence of the puzzle box, and minimized the amount of time they spent investigating the enclosure during the experimental trial. After the habituation period, captive hyaenas were moved back into a holding pen while we set up the puzzle box. Hyaenas at the field station were trained before testing to move from one enclosure to another (Drea & Carter 2009). As had been done with the wild hyaenas, the puzzle box was baited with raw meat (approximately 1 kg of beef ribs) and the latch handle was left protruding at 90° from the box.

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

In total, we conducted 170 trials on 19 captive hyaenas, including 9 adult males, 7 adult females and 3 juvenile females. Twenty-two wild and 15 captive hyaenas participated in at least six trials during the 12-month study period, and the number of trials per individual ranged from 1 to 39 (mean ± SE = 7.23 ± 0.96 trials per individual).

Data Extraction from Videotaped Trials

All puzzle box trials were videotaped in their entirety, and behavioural data were extracted from the videotaped trials. The puzzle box was initially a wholly novel stimulus for the hyaenas, so we estimated neophobia by examining the latency of each focal hyaena to contact the box once it entered a 5 m radius around the box during its initial trial, or for the captive hyaenas, once they entered the enclosure with the baited puzzle box. Individuals who participated in trials but never contacted the box were assigned a contact latency of 1800 s (30 min).

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

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We calculated the number of different exploratory behaviours by hyaenas when they were interacting with the puzzle box, and we used this number as the individual's 'exploration diversity' score. Wild hyaenas showed up to five exploratory behaviour patterns when interacting with the puzzle box: these behaviours were defined as 'biting', 'digging', 'flipping the box', 'investigating' and 'pushing or pulling the box' (Benson-Amram & Holekamp 2012). To have a direct comparison of the exploratory behaviour shown by wild and captive hyaenas, we examined the same set of five exploratory behaviours in the captive hyaenas as well. If a hyaena demonstrated all five of these behaviours at least once during a trial, it received the maximum exploration diversity score of 5. If a hyaena showed none of these behaviours, it received an exploration diversity score of 0.

From each videotaped record, we extracted the amount of 'work time' for the subject, which was the time it spent with its head down working on the puzzle box, until it either opened the box and retrieved the meat or stopped working and ended the trial. We used work time as our measure of persistence in this study.

Social Influences

Previous analyses of data from the wild hyaenas, which controlled for pseudoreplication, revealed no effect of social context on problem-solving success (Benson-Amram & Holekamp 2012). However, we did find that the presence of conspecifics by the box decreased neophobia among naïve wild hyaenas (Benson-Amram & Holekamp 2012). Therefore, we considered social context for the wild hyaenas in our analyses of neophobia, but not in our analyses of problem-solving success.

The social context experienced by the captive hyaenas during their puzzle box trials was different from that experienced by the wild hyaenas. In captivity, only the focal hyaena was present in the test enclosure during a puzzle box trial. However, we did initially set up the captive study to investigate social learning in spotted hyaenas. Thus, 11 captive hyaenas were 'observers' that had the opportunity to watch a conspecific or 'demonstrator' open the puzzle box just prior to each of their trials. Five hyaenas served as 'controls' and had no opportunity to observe conspecifics interact with the puzzle box. Two hyaenas served as demonstrators. The demonstrators were not trained to open the puzzle box, but were consistently successful in all of their trials. We therefore included social treatment group (demonstrator, observer, and control) in our analyses of captive hyaenas.

Statistical Analyses

We used generalized linear models (GLM; R v.2.13.0, R Foundation for Statistical Computing, Vienna, Austria) to test effects of social influences, captivity, age, social rank and sex on problem-solving success, exploration diversity, persistence and neophobia. Following analyses previously conducted with data from wild hyaenas (Benson-Amram & Holekamp 2012), we used GLM to examine the influence of exploration diversity, persistence and neophobia on problem-solving success among the captive hyaenas. Work time and latency to approach the puzzle box were log transformed to achieve normal distributions. To ensure that individuals were not simply more diverse in their exploratory behaviour because they spent more time working on the puzzle box, work time was included as the first covariate in all analyses that included exploration diversity. One outlier was excluded from our analyses on neophobia among captive hyaenas because this individual did not receive a 10 min habituation period prior to the start of its first trial. However, we ran all tests on neophobia with and without this outlier, and found that the relative significance of the results and the effect direction were the same in all cases.

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

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

RESULTS

We found no difference in success ($\chi^2_1 = 2.52$, $P = 0.11$), exploration diversity ($F_{1,16} = 0.060$, $P = 0.81$), neophobia ($F_{1,17} = 4.0$, $P < 0.062$) or persistence ($F_{1,17} = 2.82$, $P = 0.11$) between captive hyaenas that observed a conspecific open the box and those that did not. Thus, watching another hyaena solve the problem did not improve performance. There was no effect of previous experience in a cooperative problem-solving experiment or hormone treatment group on success (experience: $\chi^2_1 = 1.63$, $P = 0.20$; hormone: $\chi^2_2 = 1.77$, $P = 0.41$), exploration diversity (experience: $F_{1,13} = 0.12$, $P = 0.73$; hormone: $F_{2,14} = 0.54$, $P = 0.59$), persistence (experience: $F_{1,14} = 2.59$, $P = 0.13$; hormone: $F_{2,15} = 1.14$, $P = 0.35$) or neophobia (experience: $F_{1,13} = 0.22$, $P = 0.65$; hormone: $F_{2,14} = 0.38$, $P = 0.69$) among the captive hyaenas. We therefore did not consider previous experience in cognition experiments or hormone treatment group any further.

Problem Solving and Exploration Diversity in Captive and Wild Hyaenas

As predicted, captive hyaenas were significantly more successful than wild hyaenas ($\chi^2_1 = 23.39$, $P < 0.0001$). Only 14.5% of wild hyaenas (9 of 62) ever succeeding in opening the puzzle box, whereas 73.7% of captive hyaenas (14 of 19) were successful. Captive hyaenas were also more persistent during their initial trial than wild hyaenas ($t_{72} = -2.67$, $P = 0.0094$). On average, unsuccessful captive hyaenas spent 14.9 ± 2.8 min working on the puzzle box during their first trial, whereas the average work time for wild hyaenas in their first trial was only 5.3 ± 0.9 min. We compared the percentage of captive and wild hyaenas that opened the puzzle box during only the first 5 min of the initial trial and found that captive hyaenas were still significantly more successful than their wild counterparts ($\chi^2_1 = 20.41$, $P < 0.0001$). Interestingly, all successful captive hyaenas were able to open the puzzle box in their initial trial, whereas only two of the nine successful wild hyaenas succeeded in their first trial.

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

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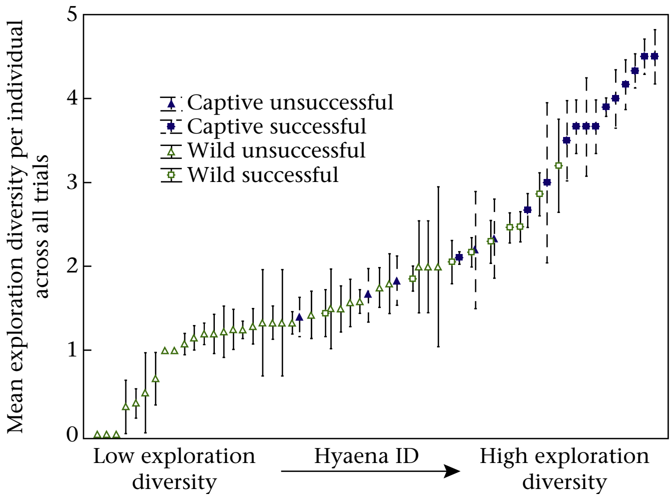

Figure 1. Mean ± SE exploration diversity score across all trials for each individual hyaena that participated in multiple puzzle box trials ($N = 58$). Individual hyaenas are listed along the *X* axis. Symbol shape indicates whether the individual was captive or wild. Symbol shading indicates whether the individual ever opened the puzzle box.

Characteristics Associated with Problem-solving Success among Captive Hyaenas

Similar to what was found in the wild (Benson-Amram & Holekamp 2012), exploration diversity was a strong predictor of success among captive hyaenas. Successful captives spent less time working on the puzzle box ($\chi^2_1 = 4.65$, $P = 0.031$) but were still significantly more diverse in their exploratory behaviours ($\chi^2_1 = 17.25$, $P < 0.0001$; Fig. 2) than unsuccessful individuals during their initial trial with the puzzle box. Neophobia also had a significant negative effect on success among the captives ($\chi^2_1 = 5.05$, $P = 0.025$), with successful individuals showing less neophobia in their initial trial than unsuccessful individuals. Neophobia had a similar inhibitory effect on problem-solving success in the wild hyaenas (Benson-Amram & Holekamp 2012).

Individual Learning

We found no difference in the rate at which successful captive and wild hyaenas learned the problem-solving task ($F_{1,21} = 0.34$, $P = 0.57$; Fig. 3). Figure 3 presents the learning curves from the first six successful trials for both wild and captive hyaenas by showing the average work time to open the box for all individuals who were successful during a given trial. Trial number was a significant predictor of work time to open the box among captive hyaenas ($F_{5,52} = 6.083$, $P < 0.0001$; Fig. 3), which matches the findings previously reported for the wild hyaenas (Benson-Amram & Holekamp 2012). Thus, successful wild and captive hyaenas improved their performance with experience and became significantly faster at opening the box over time (Fig. 3). Unsuccessful captive hyaenas showed a steady decline in their box-oriented behaviour across successive trials and showed a near extinction of any box-oriented behaviour by their sixth trial ($F_{5,18} = 9.20$, $P < 0.001$). Interestingly, this result differs from what we found in the wild population, where unsuccessful hyaenas showed no reduction in effort over time (Benson-Amram & Holekamp 2012).

Effects of Age and Sex on Problem Solving, Exploration Diversity and Neophobia

We found interesting differences between wild and captive populations with respect to the influence of age on problem solving, exploration diversity and neophobia. Although we found no age effect on success in the wild population (Benson-Amram & Holekamp 2012), here we found that captive adults were significantly more successful than captive juveniles ($\chi^2_1 = 9.84$, $P = 0.0017$; Fig. 4a). In fact, although over 80% of captive adults were able to open the puzzle box, no captive juveniles were successful. Captive juveniles also had significantly lower exploration diversity scores ($F_{1,16} = 11.13$, $P = 0.0042$; Fig. 4b) and were more neophobic ($F_{1,16} = 20.22$, $P = 0.00037$; Fig. 4c) than adults, which is the opposite of what we found in the wild population (Benson-Amram & Holekamp 2012; Fig. 4b, c). Because of this strong effect of age, and because all of the captive juveniles we tested were female, we only used data from adults when examining the effect of sex on success, exploration diversity and neophobia

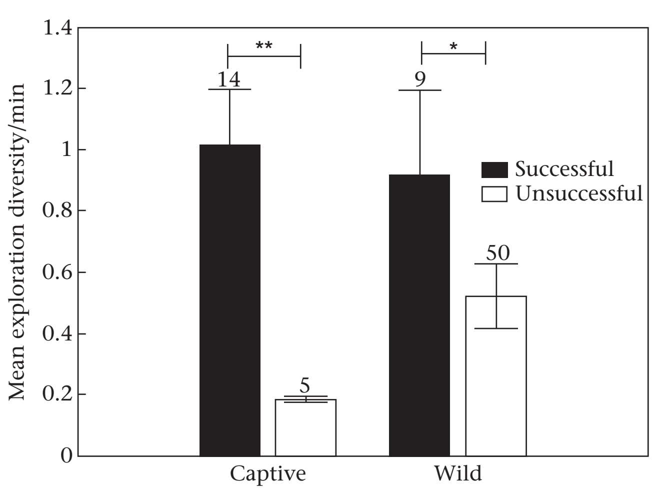

Figure 2. Mean ± SE exploration diversity score per min for each captive and wild focal hyaena during the initial trial for all individuals for whom this measure could be calculated ($N = 78$). Exploration diversity score per min is calculated by dividing the number of different box-oriented exploratory behaviours by work time, and is given in the number of behaviours per min. Bar shading indicates whether or not an individual was ever successful in opening the puzzle box. Asterisks represent significant differences: *$P < 0.05$; **$P < 0.001$.

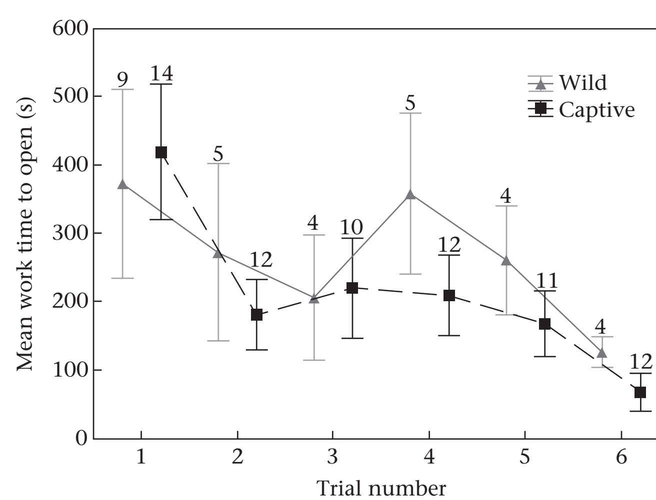

Figure 3. Average learning curve for successful wild and captive hyaenas when interacting with the puzzle box. The learning curve represents the mean ± SE work time for all individuals who were successful in a given trial. Trial 1 represents the trial in which an individual was initially successful, and may not have been the first time an individual interacted with the puzzle box. Sample sizes varied because not all hyaenas that opened the puzzle box multiple times were successful in every trial.

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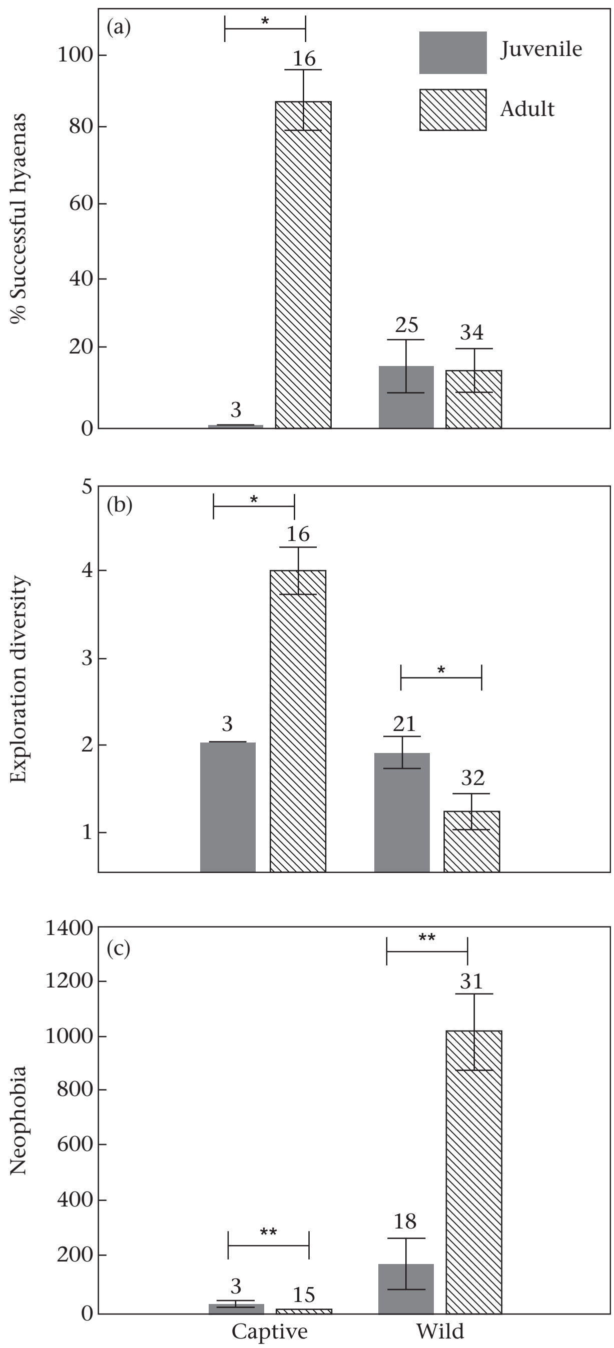

Figure 4. Comparison of juvenile and adult hyaenas tested in the wild and in captivity with respect to (a) the percentage of individuals that were ever successful in opening the puzzle box, (b) mean ± SE exploration diversity score during the initial trial, and (c) mean ± SE latency to approach the puzzle box during the initial trial. Asterisks represent significant differences: *$P < 0.01$; **$P < 0.001$.

among captive hyaenas. Sex did not significantly affect exploration diversity ($F_{1,13} = 0.46$, $P = 0.51$) or neophobia ($F_{1,13} = 0.65$, $P = 0.43$) among captive adults, which matches results from the wild population (Benson-Amram & Holekamp 2012). However, we did find a trend for captive adult females to be less successful than captive adult males ($\chi^2_1 = 3.68$, $P = 0.055$). Two of the 16 captive adults tested failed to open the puzzle box and both were female. As in the wild population (Benson-Amram & Holekamp 2012), there was no effect of social rank on success ($\chi^2_1 = 0.01$, $P = 0.91$), exploration diversity ($F_{1,16} = 0.09$, $P = 0.77$), persistence ($F_{1,17} = 1.55$, $P = 0.23$) or neophobia ($F_{1,16} = 0.60$, $P = 0.45$) among captive hyaenas. Note, however, that social ranks among captives could achieve values of only 1 or 2, which is quite different from the situation in the wild.

DISCUSSION

Demonstrating that a captive animal can solve a novel problem shows us that a species has the capability to innovate in that domain. Our results confirm, however, that captive studies tell us little about whether individuals from the same species would regularly show, or benefit from, innovative behaviour in the wild. As predicted, we found a striking difference in the percentage of captive and wild hyaenas that were able to solve a novel technical problem, even when members of both populations were allowed multiple opportunities to do so. These results match previous findings in other taxa indicating that captive animals outperform their wild counterparts on novel problem-solving tasks (Webster & Lefebvre 2001; Gajdon et al. 2004; Bouchard et al. 2007). Our results also support our prediction that captive hyaenas would show more diverse exploratory behaviours than wild hyaenas during their interactions with the puzzle box. A similar finding has been reported for hamadryas baboons, *Papio hamadryas*, in which captives invented several behaviours that had never been seen in the wild (Kummer & Kurt 1965). Not surprisingly, here captives were also more persistent than wild hyaenas, probably because captive individuals were in a confined space with the puzzle box for up to 30 min, whereas wild hyaenas could choose to leave the puzzle box at any time. Additionally, captive hyaenas were significantly less neophobic than the wild hyaenas. In fact, on average, captives approached the novel puzzle box nearly 100 times faster than did the wild hyaenas.

All of the successful captive hyaenas solved the problem in their initial trial. Although this result might appear to indicate insight in the captive hyaenas, we think the captive hyaenas were demonstrating trial-and-error learning. The captive hyaenas approached the experimental apparatus quickly and immediately proceeded to investigate and manipulate the apparatus. We saw no behavioural indications that the hyaenas were engaging in insightful problem solving (Köhler 1925; Yerkes 1927; Beck 1967); in other species such indications include 'hesitation, pause, or attitude of quiet concentration', the 'appearance of a critical point at which the organism suddenly, directly and definitely performs the required act', or 'ready repetition of adaptive response after once performed' (Yerkes 1927, page 156). When we examined the individual learning curves of each successful captive hyaena, we found that only two individuals, Scooter and Zawadi, showed near mastery of the solution after their initial trial. All other successful captive hyaenas learned the solution more slowly and showed patterns that clearly indicated trial-and-error learning.

Opportunities for social learning had no significant effect on problem-solving success in either the captive or the wild hyaenas. However, further analyses are needed before we can definitively conclude anything about the social learning abilities of hyaenas. In a future study we will extend this work by examining in greater depth whether social learning opportunities influence exploration and other aspects of problem-solving behaviour besides overall problem-solving success.

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

Hypothesis 1: Excess Energy

Excess energy may enable captive animals to innovate solutions to problems in their environment (Kummer & Goodall 1985).

Captive individuals in our study had daily access to food whereas food availability to wild hyaenas was far less predictable. Furthermore, high-ranking wild individuals have far better access to food resources in the wild than do their low-ranking counterparts (Frank 1986; East & Hofer 2001). If differential food access influenced problem-solving ability, then social rank should have had a significant effect on problem-solving success among the wild hyaenas, but that was not the case. Furthermore, although this hypothesis predicts that there should be no difference in success between individuals with equivalent food intake, and although all captive hyaenas experienced identical feeding conditions, captive adults were much more successful here than captive juveniles. Thus, neither the captive nor the wild data support the hypothesis that excess energy enabled the captive individuals to be more successful than the wild hyaenas.

Hypothesis 2: Shorter Intertrial Intervals among Captives

Captive hyaenas may have been more successful because they participated in six trials in a 2-day period, compared to the wild hyaenas, which on average had significantly longer intervals between trials. The shorter time between trials among the captive individuals may have led to a more rapid learning of the problem and its solution. However, 73.7% of captive individuals opened the puzzle box in their initial trial compared with only 3.2% of wild individuals. Additionally, we saw no difference in the rate at which captive and wild individuals learned the novel problem-solving task (Fig. 3). Thus, our results suggest that the greater success of captive hyaenas was not simply a result of the frequency with which they interacted with the puzzle.

Hypothesis 3: More Experience with Man-made Objects

Captive individuals have far more exposure to metallic man-made objects than do wild individuals, which may result in less neophobia among captive than wild animals when exposed to a novel apparatus like the one used here (Huber & Gajdon 2006; van de Waal & Bshary 2010). Previous work has shown that neophobia negatively affects problem-solving success (Seferta et al. 2001; Webster & Lefebvre 2001; Greenberg 2003; Bouchard et al. 2007; Cole et al. 2011; Sol et al. 2012). For example, 33% of vervet monkeys, *Chlorocebus aethiops,* with frequent access to human facilities and man-made objects solved a novel food-access puzzle, whereas only 7% of vervets in more isolated areas were able to solve the same problem (van de Waal & Bshary 2010). A similar result has also been reported in several bird species, where individuals from highly urbanized environments are less neophobic and more innovative than birds from less urbanized areas (Liker & Bókony 2009; Sol et al. 2011). Sol et al. (2011) postulated that these differences are due to lower predation levels in highly urbanized habitats.

Here we found evidence consistent with the hypothesis that the difference in performance between wild and captive hyenas is due to differential neophobia. Captive hyaenas were both significantly less neophobic and more successful than the wild hyaenas. In addition, captive juvenile hyaenas were significantly more neophobic, less diverse in their exploratory behaviour and less successful than captive adults. In contrast, adults were more neophobic and less diverse in their exploratory behaviours than juveniles in the wild. This interesting result, in which age had significant, but opposite, effects on innovative problem-solving in the two populations, may be due to a natural tendency for younger hyaenas to be more exploratory and less neophobic than adults, but in captivity the experience that adults have with man-made objects becomes relatively more important in terms of reducing neophobia towards a novel man-made apparatus.

Hypothesis 4: More Undisturbed Time with the Novel Problem

Captive individuals may be more successful at solving a novel problem simply because they have more time to spend working on the task than do wild individuals (Kummer & Goodall 1985). If true, then the difference in success rates between captive and wild populations should disappear when captive hyaenas have only a limited amount of time to work on the problem. Wild hyaenas spent an average of 5 min working on the puzzle box in their initial trial, so we limited our analyses to examine only the percentage of captive hyaenas that successfully opened the puzzle box during the first 5 min of their initial trial. However, even during this limited time period, captive hyaenas were still significantly more successful than their wild counterparts. Thus, it does not appear that the actual amount of time spent working on the problem caused the stark difference in success between the two populations. However, we cannot rule out the possibility that the time that captive individuals spent working on the problem was of higher quality. Wild hyaenas have many other distractions to which captive hyaenas are not exposed, such as conspecific interactions, potential predators and potential prey.

Conclusion

It appears that the significant difference in problem-solving success between the wild and captive populations was largely due to differences in exploration and neophobia. The captive hyaenas had fewer distractions and fewer conflicting motivations than did the wild hyaenas, which probably led to more focused and higher-quality work time for the captive individuals. Additionally, the captive hyaenas had more experience with, and exposure to, man-made objects and therefore were less neophobic and more innovative than the wild hyaenas. It also remains possible that captivity has an 'enculturation effect' whereby captive hyaenas develop greater cognitive capacities due to their interaction with humans and their experience with man-made objects (Tomasello & Call 2004; Whiten & van Schaik 2007; van de Waal & Bshary 2010), or that captive hyaenas have better learned the affordances of man-made objects and are therefore more adept at manipulating them in novel situations (Call & Tomasello 1996). Further experimental work is needed to elucidate the relative contributions of these factors to the superior problem-solving abilities and exploration diversity observed among captive animals.

Although captive populations offer many advantages in studies of problem solving, social learning and other sophisticated cognitive abilities in animals, our results support the claim that captive innovation research has low external validity, and suggests that animal innovation research should focus on wild populations if we want to address questions such as how innovations are discovered and which individuals innovate in natural populations. Indeed, our finding that wild/captive differences are largely due to differences in neophobia and exploration suggests that studies conducted in the wild will shed considerably more light on innovation than will captive studies.

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Supplementary Material

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