Innovative problem solving by wild spotted hyenas

Sarah Benson-Amram* and Kay E. Holekamp

Department of Zoology, Michigan State University, East Lansing, MI 48824, USA

Innovative animals are those able to solve novel problems or invent novel solutions to existing problems. Despite the important ecological and evolutionary consequences of innovation, we still know very little about the traits that vary among individuals within a species to make them more or less innovative. Here we examine innovative problem solving by spotted hyenas (Crocuta crocuta) in their natural habitat, and demonstrate for the first time in a non-human animal that those individuals exhibiting a greater diversity of initial exploratory behaviours are more successful problem solvers. Additionally, as in earlier work, we found that neophobia was a critical inhibitor of problem-solving success. Interestingly, although juveniles and adults were equally successful in solving the problem, juveniles were significantly more diverse in their initial exploratory behaviours, more persistent and less neophobic than were adults. We found no significant effects of social rank or sex on success, the diversity of initial exploratory behaviours, behavioural persistence or neophobia. Our results suggest that the diversity of initial exploratory behaviours, akin to some measures of human creativity, is an important, but largely overlooked, determinant of problem-solving success in non-human animals.

Keywords: innovation; problem solving; technical intelligence; trial-and-error learning; neophobia; spotted hyena

1. INTRODUCTION

Innovation—solving a novel problem or finding a new solution to an existing problem—allows animals to exploit novel resources or to use current resources more efficiently [1–3]. Innovation thus improves the ability of animals to survive in complex or changing environments, and to explore and create new niches [4]. Despite the important ecological and evolutionary consequences of innovation [1,5], within-species variation in innovative tendencies remains poorly understood [6]. Innovations are rarely observed in the field both because of their rare and unpredictable nature, and also because recognizing an act as an innovation requires a comprehensive knowledge of the behaviour of the study species, which may require thousands of hours of behavioural observations [7]. In order to better understand the behavioural and cognitive processes underlying innovation among captive animals, researchers have adopted the strategy of inducing innovation by presenting individuals with a novel problem-solving task [3,8–13]. Although a few studies have now demonstrated individual variation in problem-solving abilities [3,6,11,14,15], we still know very little about the characteristics that vary among individual conspecifics to make them more or less innovative [13].

Here we test a hypothesis suggesting that individuals who initially confront a novel problem with the greatest range of behavioural strategies are most likely to eventually solve that problem [16–18]. Although this has been shown in human infants [16,19], to our knowledge it has never been experimentally confirmed in non-human animals. To do so, we presented wild hyenas with a novel food-access puzzle, measured the diversity of exploratory behaviours each individual employed when interacting with the puzzle for the first time and related this diversity to whether the individual ever managed to solve the problem.

Along with initial exploratory diversity, we also examined the relative contributions of persistence and neophobia to problem-solving success. Persistence has been shown to influence problem-solving success in woodpecker finches and meerkats [20,21]. In addition, individuals must inhibit neophobic responses when approaching novel objects and entering novel feeding situations to successfully solve foraging problems and use new food resources [22]. Neophobia is defined as avoidance of novel stimuli [23–25]; several studies have found that neophobic individuals are less likely than others to participate in novel problem-solving tasks, and are thus unlikely to innovate or solve problems [8,9,14,26–28]. Finally, because learning is necessary for a one-time innovation to become a successful longer-term, we examined patterns of response acquisition among individuals who were successful at solving the problem, and who were tested in multiple trials.

Exploration is typically quantified by examining the extent to which an individual investigates a novel area or object, including measures such as the time spent in the novel area, the amount of space the individual covers, the amount of time spent near the novel object, the number of sides or parts of the object contacted, or the latency to approach novel objects in their environment [8,13,14,28–32]. In this study, we focused on the variety of behaviours that hyenas exhibited when interacting for the first time with a novel problem-solving apparatus, and thus we did not rely exclusively on these traditional temporal or
spatial measures. Previous studies have examined whether exploratory tendency is positively correlated with innovativeness among species [8] and among individuals within a species [13,14,29], though the results of these studies are mixed. Some studies found that variation in exploration of a novel environment was unrelated to variation in problem-solving success [14,29], whereas others found a positive correlation between exploration and innovation [8,13,28]. Although exploratory behaviour is often regarded as a necessary precursor to innovation [1,33], it is not sufficient for the emergence of an innovation [29]. For an innovation to occur, it is likely that innovators must exhibit additional cognitive abilities, such as the ability to behave flexibly [34–36]. Here, we suggest that the diversity of behavioural responses an animal exhibits when first confronted with a novel problem-solving task may reflect its ability to respond flexibly to the problem [18].

It is currently unclear whether variation in innovation stems in part from temperament differences, and should thus be considered a personality trait, such that some individuals are more innovative than others regardless of their social status, age or sex [6,14,37]. It is also unclear whether developmental or social environmental factors such as age and social rank might affect innovation, or whether state-dependent variables such as motivation influence innovation. In the latter case, we would expect body condition to be correlated with the diversity of initial exploratory behaviours exhibited, as well as with the frequency of problem-solving success [1,6,9,14,38–41]. To address these possibilities, we tested effects of individual identity, social rank, age, sex and body condition on initial exploratory diversity, neophobia and problem-solving success among wild spotted hyenas.

We chose to study innovation in hyenas because they exhibit species characteristics that are postulated to be closely associated with innovation [1,10]. For instance, innovation is thought to be vital for generalist and opportunistic species [10]. Spotted hyenas are generalist carnivores that use a variety of tactics to hunt a diverse array of prey, including at least 30 different species [42–44]. Furthermore, innovation rates among invasive species are generally positively correlated with colonization success [10,45,46]; spotted hyenas are the most abundant large carnivore in sub-Saharan Africa, with a wide distribution that suggests great invasion success [47,48]. Finally, spotted hyenas have demonstrated complex social cognitive abilities. For example, hyenas recognize third-party relationships [49], form coalitions [50], reconcile after fights [51] and demonstrate cooperative problem solving [52]. However, although hyenas excel cognitively in the social domain, no one has previously assessed their technical problem-solving skills.

2. METHODS

(a) Subjects and study site

The subjects were individuals from two neighbouring clans of spotted hyenas in the Masai Mara National Reserve, Kenya. Individuals were identified by unique spot patterns and other natural markings such as ear notches. Observations were conducted daily, from 05.30 to 09.00 and from 17.00 to 20.00, on an average of 23.5 days per month between May 2007 and May 2008. Hyenas were considered juveniles prior to reproductive maturity; post-dispersal males and breeding females were considered adults [53]. During the study period, the Talek West clan contained 46–48 members, including 12–13 adult females with their juvenile offspring and 10 adult males, and the Fig Tree clan contained 36–38 members, including 10 adult females with their juvenile offspring and 7–8 adult immigrant males. Additional information about the study subjects, methods and materials is given in the electronic supplementary material.

(b) Apparatus

We built a 60 × 31 × 37 cm puzzle box of welded 10.5 mm steel reinforcing bar (figure 1) for presentation to the hyenas. The box had a single 1020 cm² door on one long side, large enough to allow for a hyena to put its head inside the box, and handles in the centre of each short side (see figure 1; electronic supplementary material, movie S1). When it was baited with roughly 2 kg of raw meat, the box weighed more than 35 kg. The spacing between the bars of the box was sufficient to allow hyenas to see and smell the meat inside. To obtain access to the meat, a subject had to slide a 12 cm steel bolt latch laterally, and swing open the door (see electronic supplementary material, movies S1 and S2). The hyenas could also see and touch the entire latch mechanism, which could be opened using either the mouth or the forepaws. The end handles allowed the animals to drag the apparatus, to up-end it and in some cases even to flip it into the air as part of their exploratory behaviour (see electronic supplementary material, movie S2).

(c) Procedure

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

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

Lone hyenas were preferentially selected for inclusion in our experiments, but conspecifics sometimes also approached and participated in the trial. If multiple hyenas were present within a 20 m radius of the puzzle box at any point during a trial, it was defined as a ‘group trial’, and behavioural data were extracted for each focal individual who approached within 5 m of the puzzle box (see §2f for a description of how group trials were analysed). In total, we conducted 417 trials on 62 individuals; 88 trials were conducted with lone hyenas, and 329 trials were considered group trials. The number of trials per individual ranged from 1 to 30, and the mean number of trials per individual was 6.71 ± 1.01 s.e. Eighteen individuals participated in at least eight trials during the 12 month study period.

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

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

We counted the number of different exploratory behaviours hyenas exhibited when interacting with the puzzle box, and we used this number as the individual’s ‘exploration diversity’ score. Focal hyenas exhibited up to five exploratory behaviour patterns when interacting with the puzzle box; these behaviours were defined as biting, digging, flipping the box, investigating the box and pushing or pulling the box (all defined in the electronic supplementary material). Thus, the exploration diversity score for any focal individual in each trial could range from 0 to 5.

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

(e) Statistical analyses
We used logistic regression, generalized linear mixed models (GLMMs) and likelihood ratio tests to investigate determinants of problem-solving success, learning and the effects of individual ID, age, social rank and sex on exploration, neophobia and work time. Exploration diversity, latency to approach the puzzle box and work time were each log-transformed to achieve normal distributions. To account for the influence of social factors in analyses of individual performance, we also included whether the trial was a group trial and whether a higher-ranking conspecific was present during the trial as predictor variables in relevant models. Alternative models were compared using Akaike’s information criterion (AIC) values. A smaller AIC value indicates a better-fitting model [54], and the results from the model with the lowest AIC value are reported here. Mean values are given ± s.e. Differences between groups were considered significant when $p \leq 0.05$.

3. RESULTS
(a) Problem-solving success and individual learning
Of the 62 individuals who interacted with the puzzle box, nine (or 14.5% of subjects) opened the puzzle box at least once, and seven of these opened the puzzle box multiple times. To investigate learning, we used GLMMs to examine how work time and exploration diversity changed over successive trials for successful and unsuccessful individuals. Figure 2 presents a learning curve showing the average work time for all individuals who were successful in a given trial. Trial number was a significant predictor of work time ($F_{1,18.63} = 2.31, p = 0.0767$; figure 2) and exploration diversity ($F_{21,101} = 2.72, p < 0.0001$), indicating that successful hyenas improved their performance with experience. Specifically, successful hyenas became significantly faster at opening the puzzle box and exhibited significantly fewer exploratory behaviours as they learned how to solve the problem. In contrast, unsuccessful individuals did not show a reduction of effort across trials ($F_{13,122} = 0.55, p = 0.89$), nor did they alter their exploratory behaviour with additional experience ($F_{13,120} = 0.82, p = 0.63$).

(b) Characteristics associated with problem-solving success
To investigate determinants of success in problem solving, we used logistic regression with immediate or eventual success (Y/N) as the binomial response variable, and
with the following predictor variables that were scored during the participant’s initial trial: (i) work time, exploration diversity and latency to approach the puzzle box; (ii) the age, social rank and sex of the focal hyena; and (iii) all two- and three-way interaction terms between work time, exploration diversity and latency to approach. To ensure that individuals were not simply more exploratory because they spent longer working on the puzzle box, work time was included as the first covariate in all analyses that included exploration diversity. Only exploration diversity, work time and neophobia were retained in the best-fitting model explaining variation in problem-solving success (table 1). Individuals who exhibited a greater diversity of exploratory behaviours during their first trial were significantly more successful than individuals with lower initial exploration diversity ($\chi^2 = 4.67, p = 0.031$; figure 3a). More persistent hyenas—who were eventually successful in opening the puzzle box also had lower latencies to approach the puzzle box ($\chi^2 = 4.14, p = 0.042$; figure 3c). All two- and three-way interaction terms involving work time, exploration diversity and latency to approach were non-significant (table 1), indicating that all three of these measures independently influenced variation in problem-solving success and that exploration diversity did not depend on work time. Neither sex, social rank nor age of the focal hyena significantly predicted variation in success, and none were included in the best-fitting model (table 1). Neither time between trials nor body condition significantly explained variation in any response variable (see electronic supplementary material).

We used GLMMs to inquire how age, social rank and sex affected exploration, neophobia and work time. Juveniles exhibited significantly greater exploration diversity ($F_{1,50} = 8.026, p = 0.0066$; figure 4a), spent significantly more time working ($F_{1,51} = 7.65, p = 0.0079$; figure 4b) and were less neophobic ($F_{1,44} = 23.11, p < 0.0001$; figure 4c) than adults during initial trials. However, neither sex nor social rank of the focal hyena significantly affected exploration diversity (sex: $F_{1,51} = 1.75, p = 0.19$; rank: $F_{1,54} = 0.64, p = 0.43$), work time (sex: $F_{1,49} = 0.18, p = 0.68$; rank: $F_{1,47} = 2.38, p = 0.13$) or neophobia (sex: $F_{1,46} = 0.69, p = 0.41$; rank: $F_{1,34} = 1.79, p = 0.19$).

### Table 1. Summary of model comparison results investigating problem-solving success.

<table>
<thead>
<tr>
<th>predictor</th>
<th>$\chi^2$</th>
<th>d.f</th>
<th>$p$</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>best model</strong></td>
<td></td>
<td></td>
<td></td>
<td>35.41</td>
</tr>
<tr>
<td>work time</td>
<td>1.99</td>
<td>1</td>
<td>0.16</td>
<td></td>
</tr>
<tr>
<td>exploration diversity</td>
<td>4.66</td>
<td>1</td>
<td>0.031</td>
<td></td>
</tr>
<tr>
<td>latency to approach</td>
<td>4.14</td>
<td>1</td>
<td>0.042</td>
<td></td>
</tr>
<tr>
<td><strong>not retained in best model</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>age</td>
<td>0.058</td>
<td>1</td>
<td>0.81</td>
<td>37.35</td>
</tr>
<tr>
<td>rank</td>
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<td>1</td>
<td>0.38</td>
<td>36.69</td>
</tr>
<tr>
<td>sex</td>
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<td>1</td>
<td>0.44</td>
<td>36.32</td>
</tr>
<tr>
<td>conspecific present or absent</td>
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<td>1</td>
<td>0.41</td>
<td>36.73</td>
</tr>
<tr>
<td>work time $\times$ exploration diversity</td>
<td>0.13</td>
<td>1</td>
<td>0.72</td>
<td>40.92</td>
</tr>
<tr>
<td>work time $\times$ latency to approach</td>
<td>0.36</td>
<td>1</td>
<td>0.55</td>
<td>40.92</td>
</tr>
<tr>
<td>exploration diversity $\times$ latency to approach</td>
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<td>1</td>
<td>0.94</td>
<td>42.66</td>
</tr>
<tr>
<td>work time $\times$ exploration diversity $\times$ latency to approach</td>
<td>0.26</td>
<td>1</td>
<td>0.61</td>
<td>42.66</td>
</tr>
</tbody>
</table>

### (c) Individual variation in exploration diversity

We inquired whether there were consistent individual differences in exploration diversity for all 40 individuals who participated in multiple trials. We used a likelihood ratio test to compare generalized linear models with and without the ID of the focal hyena as a random effect. We found consistent variation in exploration diversity among individuals ($\chi^2 = 88.18, p < 0.0001$; figure 5). As figure 5 shows, exploration diversity ranged among individuals from those who exhibited no exploratory behaviours in any trial to one individual who averaged more than three exploratory behaviour types per trial. Successful individuals were concentrated at the more diverse end of the range (figure 5).

### (d) Social effects

The presence of a conspecific at the puzzle box during a hyena’s initial exposure to the novel object significantly decreased its latency to approach the puzzle box ($F_{1,35} = 4.51, p = 0.041$). However, the social environment during a trial may also have had inhibitory
influences on work time and access to the latch side of the puzzle box for lower-ranking hyenas. Although the effects were not statistically significant, the presence of higher-ranking conspecifics during a trial tended to decrease the amount of time lower-ranking focal hyenas worked on the puzzle box before giving up ($F_{1,180} = 3.08, p = 0.081$), and also tended to decrease the percentage of time spent by successful hyenas on the latch side of the puzzle box before opening it ($F_{1,75} = 2.99, p = 0.088$).

There was no significant difference in success (Fisher exact probability test, $p = 0.40$), exploration diversity ($T_{38} = 1.38, p = 0.18$) or work time ($T_{38} = 0.76, p = 0.45$) between hyenas that had seen the puzzle box opened and those that had not.

4. DISCUSSION

Our results support the hypothesis that the diversity of initial exploratory behaviours plays a vital role in innovative problem solving by animals in their natural habitat. In fact, the finding that individuals using more diverse actions were more successful is evidence that the...
task required innovation, because if a pre-existing hyena behavior could have been used to solve the task, then successful individuals would have displayed only one or a few behaviors. Additionally, our data are consistent with those from previous studies on other taxa showing that neophilia can have an inhibitory effect on innovation [27], and that adults are more neophobic than juveniles in the wild [1].

(a) Traits associated with problem-solving success
Although individuals who give up quickly are less likely to be successful than more persistent individuals [21], persistence alone does not necessarily lead to greater problem-solving success. Perseverative errors occur when individuals repeat the same behavioral response over and over, despite the absence of any stimulus or reward, and such perseveration is thought to inhibit problem solving and learning [55]. To solve problems reliably, individuals must avoid such errors and instead seek out alternative solutions to the problem. Thus, it may be that individuals who are able to act flexibly will be more successful at solving novel problems than individuals who are neither behaviourally flexible nor persistent. Our results support this idea. Exploration diversity and persistence were major behavioural attributes of successful hyenas.

In addition to behavioural flexibility and persistence, in order to successfully solve novel problems, individuals must also be willing to engage with unfamiliar objects or situations in the first place. Although there are certainly costs associated with reduced neophobia, such as increased predation risk and disease transmission [56], our results clearly reveal benefits by demonstrating that less neophobic individuals are significantly more successful problem solvers than more neophobic individuals.

As expected, once the successful hyenas learned the solution to the problem, they became very efficient and reliable problem solvers. Specifically, successful hyenas became significantly faster and exhibited significantly fewer exploratory behaviours in later trials as they became proficient in solving the puzzle box task. In contrast, the behaviour of unsuccessful hyenas did not change as they gained experience with the problem. Although a floor effect might appear to be a likely explanation for this finding, this in fact seems unlikely. That is, unsuccessful hyenas spent an average of 267 s (almost 4.5 min) working on the puzzle box before giving up during their initial trial, and thus had ample opportunity to engage in exploratory behaviours and to solve the problem, yet failed to do so.

(b) Influences on exploration diversity, persistence and neophobia
Major factors thought to influence innovation include age, sex, social rank and individual differences [1,21,23,39,57–62]. Our results indicate that both state-dependent variables (such as age) and individual identity influence variation in innovation among spotted hyenas. As has been shown in primates [1,2,33,63], we found that juvenile hyenas exhibited significantly greater exploratory diversity, and were more persistent and less neophobic than adults. The greater exploratory behaviour of juveniles may be due to juveniles receiving more protection and having more free time than adults to devote to exploration and problem solving [1,2]. On the other hand, innovation in the current experiment may have required a degree of strength or level of physical ability or coordination that juveniles did not yet possess [1,21,40,41]. That is, the large size and weight of the puzzle box may have favoured adults over juveniles. This might explain why we found no effect of age on problem-solving success despite the greater exploration diversity and persistence exhibited by younger hyenas.

We observed significant variation among individuals in their exploration diversity across all trials, and their relative rankings on this trait could not be attributed to such factors as age, social status or sex. Successful individuals clustered at the most exploratory end of the range, supporting the idea that individuals vary in their ability to solve novel problems, and that variation in exploratory behaviour can have important consequences for an individual’s ability to solve a novel problem.

(c) Problem-solving success and individual learning
Although spotted hyenas are extremely adept at solving social problems [64], only 15 per cent of them managed to solve a technical food-acquisition problem in the wild, even when many of them had multiple opportunities to solve the problem. Those hyenas that were able to solve the problem became significantly faster at opening the puzzle box over successive trials. The shape of the learning curve (figure 2) also demonstrated that hyenas learned via trial and error. If the curve was steep and smooth, this might suggest the occurrence of insight learning; however, the jagged and shallow shape of the learning curve is more strongly indicative of trial and error [65,66].

Interestingly, the success rate that we observed in this study is similar to that documented in wild vervet monkeys (Cercopithecus aethiops) tested on a comparable novel problem-solving task in which they were asked to access out-of-reach food [67]. These monkeys occurred in social groups with either frequent or rare access to human facilities. The monkeys were able to open a baited box in order to access a fruit reward: 17 out of 53 individuals tested (32%) were able to solve the problem. However, only 2 out of 30 (7%) were successful in groups without frequent access to human facilities, suggesting that interactions with man-made objects improved the ability of these monkeys to solve the novel problem [67]. Hyenas and vervet monkeys both show remarkable social dexterity [64,68], so their similarly low success rates when encountering a novel food-acquisition problem suggest that these species may be much better at solving novel social than technical problems. These species have been tested with only one or a few technical problems to date, so we cannot generalize to draw conclusions about overall non-social intelligence. However, given that both vervets and spotted hyenas are generalists with broad distributions, we found it surprising that they performed so poorly when confronted with novel technical tasks. One possible explanation for the low success rates observed in these studies is that wild animals may be more strongly negatively affected by the novel technical problem-solving apparatus, and thus more constrained by neophobia, than we anticipated.
In summary, our study demonstrates that the diversity of initial exploratory behaviours is a critical determinant of innovative problem solving in non-human animals. A likely benefit of large brains is the ability to respond flexibly to novel situations and to innovate solutions to novel problems [69–73]. One behavioural mechanism that individuals might employ to increase the likelihood of discovering solutions to novel problems is simply to increase the variety of behavioural responses they exhibit when confronted with a novel object. In fact, measures of an individual’s ability to think flexibly about the possible functions of objects are a major component of tests of human creativity [34–36]. Just as larger groups of animals appear more innovative than smaller groups owing to the greater diversity of skill sets among individual group members [3,12], our work demonstrates that individual animals also benefit when they exhibit diverse exploratory responses.

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