

Innovative problem solving by wild spotted hyenas

Sarah Benson-Amram and Kay E. Holekamp

Proc. R. Soc. B published online 8 August 2012
doi: 10.1098/rspb.2012.1450

Supplementary data

["Data Supplement"](#)

<http://rsob.royalsocietypublishing.org/content/suppl/2012/08/01/rspb.2012.1450.DC1.html>

References

[This article cites 59 articles, 11 of which can be accessed free](#)

<http://rsob.royalsocietypublishing.org/content/early/2012/08/01/rspb.2012.1450.full.html#ref-list-1>

P<P

Published online 8 August 2012 in advance of the print journal.

Subject collections

Articles on similar topics can be found in the following collections

[behaviour](#) (826 articles)

[cognition](#) (173 articles)

[ecology](#) (1133 articles)

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

Advance online articles have been peer reviewed and accepted for publication but have not yet appeared in the paper journal (edited, typeset versions may be posted when available prior to final publication). Advance online articles are citable and establish publication priority; they are indexed by PubMed from initial publication. Citations to Advance online articles must include the digital object identifier (DOIs) and date of initial publication.

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

* Author for correspondence (bensonam@msu.edu).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2012.1450> or via <http://rsob.royalsocietypublishing.org>

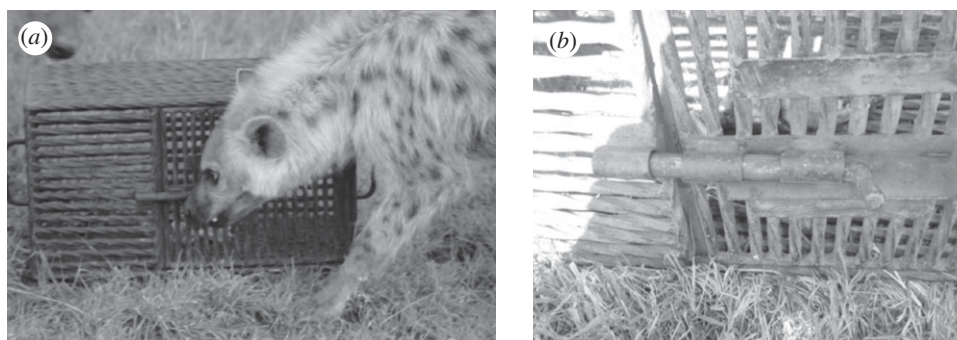


Figure 1. (a) An image of the puzzle box apparatus used in the experiment. (b) A close-up image of the latch bolt that hyenas had to move laterally in order to access the meat inside the puzzle box.

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 temperamental 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 $60 \times 31 \times 37$ cm puzzle box of welded 10.5 mm steel reinforcing bar (figure 1) for presentation to the hyenas. The box had a single 1020 cm^2 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.

(e) *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.

(f) *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 \pm 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 ($F_{18,63} = 2.31$, $p = 0.0076$; 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

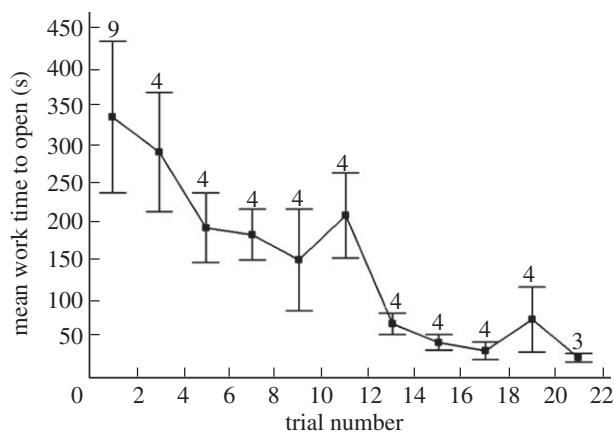


Figure 2. Average learning curve for successful wild hyenas when interacting with the puzzle box. The learning curve represents the mean \pm s.e. work time for all individuals who were successful in a given trial. Trial 1 represents the trial in which an individual was initially successful, and may not be the first time an individual interacted with the puzzle box. Sample sizes in trials 2–22 varied because not all seven hyenas that opened the puzzle box multiple times were successful in every trial.

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 ($\chi^2_1 = 4.67$, $p = 0.031$; figure 3a). More persistent hyenas—those who spent more time working on the box during their first trial before giving up—tended to be somewhat more successful than less persistent hyenas, although this effect was not significant ($\chi^2_1 = 1.99$, $p = 0.16$; figure 3b). Individuals who were eventually successful in opening the puzzle box also had lower latencies to approach the puzzle box, and so were less neophobic, than individuals who were never successful ($\chi^2_1 = 4.14$, $p = 0.042$; 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.

Table 1. Summary of model comparison results investigating problem-solving success. The inclusion of the following factors as predictors of problem-solving success failed to further improve the fit of our best model: age, sex and social rank of the focal hyena, the presence or absence of conspecifics, and all two- and three-way interactions involving work time, exploration diversity and latency to approach the puzzle box. The model was based on data from the initial trial on all 62 hyenas that participated in the experiment.

predictor	χ^2	d.f.	p	AIC
best model				35.41
work time	1.99	1	0.16	
exploration diversity	4.66	1	0.031	
latency to approach	4.14	1	0.042	
not retained in best model				
age	0.058	1	0.81	37.35
rank	0.77	1	0.38	36.69
sex	0.59	1	0.44	36.32
conspecific present or absent	0.68	1	0.41	36.73
work time \times exploration diversity	0.13	1	0.72	40.92
work time \times latency to approach	0.36	1	0.55	40.92
exploration diversity \times latency to approach	0.0066	1	0.94	40.92
work time \times exploration diversity \times latency to approach	0.26	1	0.61	42.66

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: $F_{1,54} = 1.75$, $p = 0.19$; 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: $F_{1,34} = 1.79$, $p = 0.19$).

(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 ($\chi^2_1 = 88.18$, $p < 0.0001$; 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

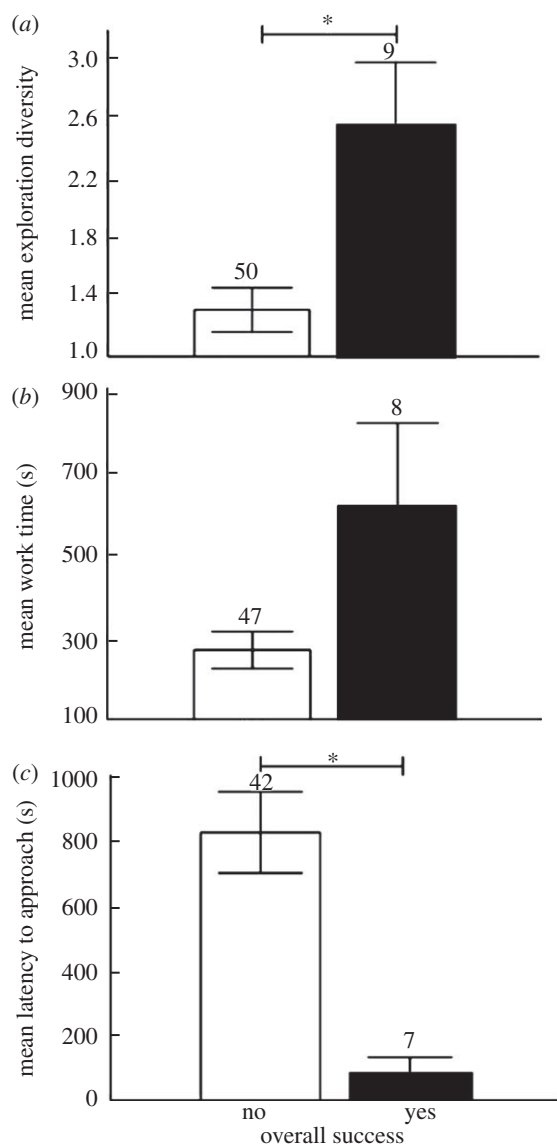


Figure 3. Mean \pm s.e. (a) exploration diversity, (b) work time (indicating persistence) and (c) latency to approach in the initial trial with the puzzle box for all individuals for whom these measures could be scored. Bars indicate whether an individual was ever successful in opening the puzzle box. Asterisks represent significant differences where $*p < 0.05$.

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

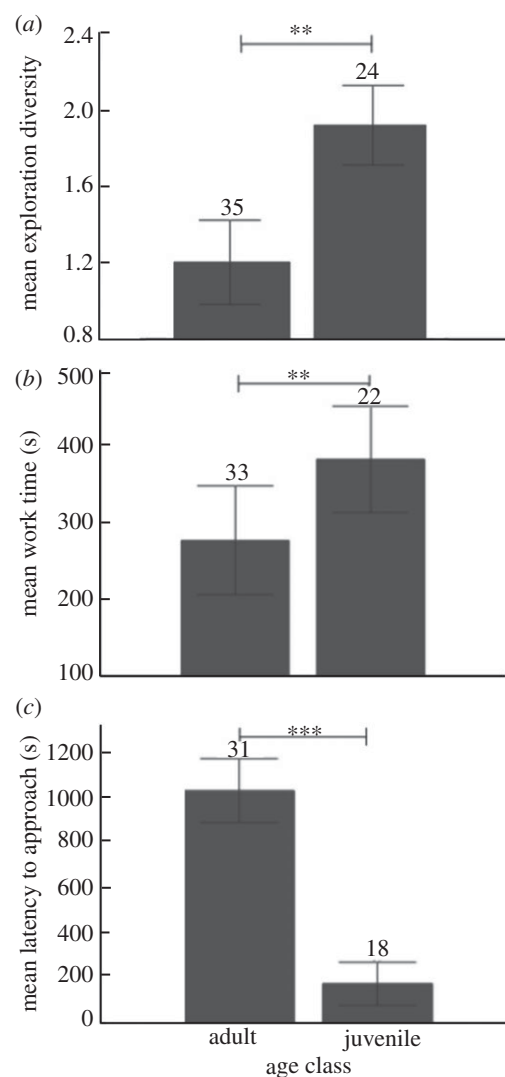


Figure 4. Mean \pm s.e. (a) exploration diversity, (b) work time and (c) latency to approach the puzzle box during the initial trial for focal hyenas sorted by age class. Asterisks represent significant differences where $**p < 0.01$ and $***p < 0.001$.

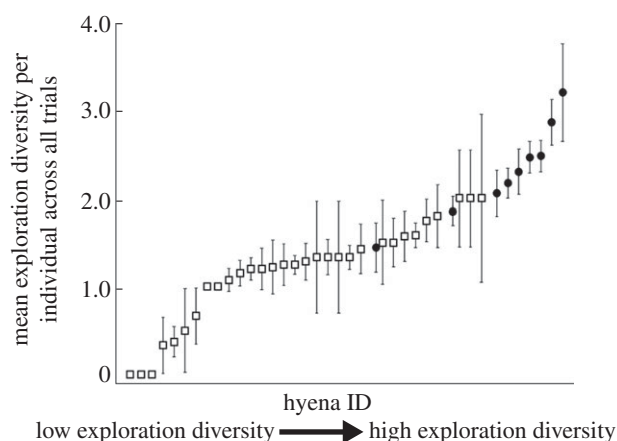


Figure 5. Mean \pm s.e. exploration diversity across all trials for each individual hyena that participated in multiple puzzle box trials ($n = 40$). Individual hyenas are listed along the x-axis. Box colour and shape indicate whether the individual ever opened the puzzle box. Black circles, successful; white squares, unsuccessful.

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 behaviour could have been used to solve the task, then successful individuals would have displayed only one or a few behaviours. Additionally, our data are consistent with those from previous studies on other taxa showing that neophobia 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 behavioural 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.

5. CONCLUSION

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.

The research presented here was described in Animal Research Application no. 07/08-099-00, approved most recently on 4 June 2010 by the All University Committee on Animal Use and Care at Michigan State University.

We thank the Kenyan Ministry of Education, Science and Technology for permission to conduct this research. We also thank Kenya Wildlife Service, Narok County Council, and the senior warden and rangers of the Masai Mara National Reserve for their assistance. This research was supported by National Science Foundation grant nos IOB0618022, IOS0819437, IOS1121474 and DBI-0939454. Michigan State University, the Animal Behavior Society and Sigma Xi provided funding to S.B.-A. We are grateful to Tom Getty, Steve Glickman, Jeff Clune, Eli Swanson and other members of the Holekamp lab for their advice and suggestions on how to improve the manuscript. We thank Redouan Bshary and two anonymous referees for their insightful comments on earlier drafts of this manuscript. Finally, Alan Bond has provided support, advice and feedback on all stages of this work, and we are very grateful for his guidance.

REFERENCES

- Reader, S. M. & Laland, K. N. 2003 *Animal innovation*. Oxford, UK: Oxford University Press.
- Kummer, H. & Goodall, J. 1985 Conditions of innovative behaviour in primates. *Phil. Trans. R. Soc. Lond. B* **308**, 203–214. (doi:10.1098/rstb.1985.0020)
- Morand-Ferron, J. & Quinn, J. L. 2011 Larger groups of passerines are more efficient problem solvers in the wild. *Proc. Natl Acad. Sci. USA* **108**, 15 898–15 903. (doi:10.1073/pnas.1111560108)
- Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P. & Lefebvre, L. 2005 Big brains, enhanced cognition, and response of birds to novel environments. *Proc. Natl Acad. Sci. USA* **102**, 5460–5465. (doi:10.1073/pnas.0408145102)
- Nicolakakis, N., Sol, D. & Lefebvre, L. 2003 Behavioural flexibility predicts species richness in birds, but not extinction risk. *Anim. Behav.* **65**, 445–452. (doi:10.1006/anbe.2003.2085)
- Laland, K. N. & Reader, S. M. 1999 Foraging innovation in the guppy. *Anim. Behav.* **57**, 331–340. (doi:10.1006/anbe.1998.0967)
- Van Schaik, C. P., Van Noordwijk, M. A. & Wich, S. A. 2006 Innovation in wild Bornean orangutans (*Pongo pygmaeus wurmbii*). *Behaviour* **143**, 839–876. (doi:10.1163/156853906778017944)
- Webster, S. J. & Lefebvre, L. 2001 Problem solving and neophobia in a columbiform–passeriform assemblage in Barbados. *Anim. Behav.* **62**, 23–32. (doi:10.1006/anbe.2000.1725)
- Bouchard, J., Goodyer, W. & Lefebvre, L. 2007 Social learning and innovation are positively correlated in pigeons (*Columba livia*). *Anim. Cogn.* **10**, 259–266. (doi:10.1007/s10071-006-0064-1)
- Lefebvre, L. & Bolhuis, J. J. 2003 Positive and negative correlates of feeding innovations in birds: evidence for limited modularity. In *Animal innovation* (eds S. M. Reader & K. N. Laland), pp. 39–61. Oxford, UK: Oxford University Press.
- Morand-Ferron, J., Cole, E. F., Rawles, J. E. C. & Quinn, J. L. 2011 Who are the innovators? A field experiment with 2 passerine species. *Behav. Ecol.* **22**, 1241–1248. (doi:10.1093/beheco/arr120)
- Liker, A. & Bókony, V. 2009 Larger groups are more successful in innovative problem solving in house sparrows. *Proc. Natl Acad. Sci. USA* **106**, 7893–7898. (doi:10.1073/pnas.0900042106)
- Overington, S. E., Cauchard, L., Côté, K. A. & Lefebvre, L. 2011 Innovative foraging behaviour in birds: what characterizes an innovator? *Behav. Processes* **87**, 274–285. (doi:10.1016/j.beproc.2011.06.002)
- Cole, E. F., Cram, D. L. & Quinn, J. L. 2011 Individual variation in spontaneous problem-solving performance among wild great tits. *Anim. Behav.* **81**, 491–498. (doi:10.1016/j.anbehav.2010.11.025)
- Pfeffer, K., Fritz, J. & Kotrschal, K. 2002 Hormonal correlates of being an innovative greylag goose, *Anser anser*. *Anim. Behav.* **63**, 687–695. (doi:10.1006/anbe.2001.1949)
- Caruso, D. A. 1993 Dimensions of quality in infants' exploratory behavior: relationships to problem-solving ability. *Infant Behav. Dev.* **16**, 441–454. (doi:10.1016/0163-6383(93)80003-Q)
- Skinner, B. F. 1981 Selection by consequences. *Science* **213**, 501–504. (doi:10.1126/science.7244649)
- Parker, C. E. 1974 Behavioral diversity in ten species of nonhuman primates. *J. Comp. Physiol. Psychol.* **87**, 930–937. (doi:10.1037/h0037228)
- Siegler, R. S. 1995 How does change occur: a microgenetic study of number conservation. *Cogn. Psychol.* **28**, 225–273. (doi:10.1006/cogp.1995.1006)
- Tebich, S., Sterelny, K. & Teschke, I. 2010 The tale of the finch: adaptive radiation and behavioural flexibility. *Phil. Trans. R. Soc. B* **365**, 1099–1109. (doi:10.1098/rstb.2009.0291)
- Thornton, A. & Samson, J. 2012 Innovative problem solving in wild meerkats. *Anim. Behav.* **83**, 1459–1468. (doi:10.1016/j.anbehav.2012.03.018)
- Tebich, S., Fessl, B. & Blomqvist, D. 2009 Exploration and ecology in Darwin's finches. *Evol. Ecol.* **23**, 591–605. (doi:10.1007/s10682-008-9257-1)
- Bergman, T. J. & Kitchen, D. M. 2009 Comparing responses to novel objects in wild baboons (*Papio ursinus*) and geladas (*Theropithecus gelada*). *Anim. Cogn.* **12**, 63–73. (doi:10.1007/s10071-008-0171-2)
- Greenberg, R. 1983 The role of neophobia in determining the degree of foraging specialization in some migrant warblers. *Am. Nat.* **122**, 444–453. (doi:10.1086/284148)
- Greenberg, R. 1990 Feeding neophobia and ecological plasticity: a test of the hypothesis with captive sparrows. *Anim. Behav.* **39**, 375–379. (doi:10.1016/S0003-3472(05)80884-X)
- Seferta, A., Guay, P. J., Marzinotto, E. & Lefebvre, L. 2001 Learning differences between feral pigeons and

- zenaida doves: the role of neophobia and human proximity. *Ethology* **107**, 281–293. (doi:10.1046/j.1439-0310.2001.00658.x)
- 27 Greenberg, R. 2003 The role of neophobia and neophilia in the development of innovative behaviour of birds. In *Animal innovation* (eds S. M. Reader & K. N. Laland), pp. 175–196. New York, NY: Oxford University Press.
- 28 Auersperg, A. M. I., von Bayern, A. M. P., Gajdon, G. K., Huber, L. & Kacelnik, A. 2011 Flexibility in problem solving and tool use of kea and New Caledonian crows in a multi access box paradigm. *PLoS ONE* **6**, e20231. (doi:10.1371/journal.pone.0020231)
- 29 Biondi, L. M., Bó, M. S. & Vassallo, A. I. 2010 Inter-individual and age differences in exploration, neophobia and problem-solving ability in a Neotropical raptor (*Milvago chimango*). *Anim. Cogn.* **13**, 701–710. (doi:10.1007/s10071-010-0319-8)
- 30 Mettke-Hofmann, C., Winkler, H. & Leisler, B. 2002 The significance of ecological factors for exploration and neophobia in parrots. *Ethology* **108**, 249–272. (doi:10.1046/j.1439-0310.2002.00773.x)
- 31 Greenberg, R. 1984 Differences in feeding neophobia in the tropical migrant woodwarblers *Dendroica castanea* and *D. pensylvanica*. *J. Comp. Psychol.* **98**, 131–136. (doi:10.1037/0735-7036.98.2.131)
- 32 Drent, P. J. & Marchetti, C. 1999 Individuality, exploration and foraging in hand raised juvenile Great Tits. In *International Ornithological Congress* (eds N. J. Adams & R. H. Slowtow), pp. 896–914. Johannesburg, South Africa: BirdLife South Africa.
- 33 Kendal, R. L., Coe, R. L. & Laland, K. N. 2005 Age differences in neophilia, exploration, and innovation in family groups of callitrichid monkeys. *Am. J. Primatol.* **66**, 167–188. (doi:10.1002/ajp.20136)
- 34 Wallach, M. A. & Kogan, N. 1965 *Modes of thinking in young children a study of the creativity-intelligence distinction*. New York, NY: Holt, Rinehart and Winston.
- 35 Bonk, C. 2003 *Creativity tests: Guilford's alternative uses task (1967)*. Bloomington, IN: Department of Educational Psychology, School of Education, Indiana University. See http://www.indiana.edu/~bobweb/Handout/sub/Bob_CT_Uses.html.
- 36 Christensen, P. R., Guilford, J. P., Merrifield, P. R. & Wilson, R. C. 1960 *Alternate uses*. Beverly Hills, CA: Sheridan Psychological Service.
- 37 Verbeek, M. E. M., Drent, P. J. & Wiepkema, P. R. 1994 Consistent individual differences in early exploratory behaviour of male great tits. *Anim. Behav.* **48**, 1113–1121. (doi:10.1006/anbe.1994.1344)
- 38 Lefebvre, L. 2000 Feeding innovations and their cultural transmission in bird populations. In *The evolution of cognition* (eds C. Heyes & L. Huber), pp. 311–328. Cambridge, MA: MIT Press.
- 39 Reader, S. M. & Laland, K. N. 2001 Primate innovation: sex, age and social rank differences. *Int. J. Primatol.* **22**, 787–805. (doi:10.1023/A:1012069500899)
- 40 Russon, A. E. 2003 Innovation and creativity in forest-living rehabilitant orangutans. In *Animal innovation* (eds S. M. Reader & K. N. Laland), pp. 279–306. Oxford, UK: Oxford University Press.
- 41 Box, H. O. 2003 Characteristics and propensities of marmosets and tamarins: implications for studies of innovation. In *Animal innovation* (eds S. M. Reader & K. N. Laland), pp. 197–219. Oxford, UK: Oxford University Press.
- 42 Cooper, S. M., Holekamp, K. E. & Smale, L. 1999 A seasonal feast: long term analysis of feeding behaviour in the spotted hyaena (*Crocuta crocuta*). *Afr. J. Ecol.* **37**, 149–160. (doi:10.1046/j.1365-2028.1999.00161.x)
- 43 Höner, O. P., Wachter, B., East, M. L. & Hofer, H. 2002 The response of spotted hyenas to long-term changes in prey populations: functional response and interspecific kleptoparasitism. *J. Anim. Ecol.* **71**, 236–246. (doi:10.1046/j.1365-2656.2002.00596.x)
- 44 Henschel, J. & Skinner, J. 1990 The diet of the spotted hyenas *Crocuta crocuta* in Kruger National Park. *Afr. J. Ecol.* **28**, 69–82. (doi:10.1111/j.1365-2028.1990.tb01138.x)
- 45 Sol, D., Timmermans, S. & Lefebvre, L. 2002 Behavioural flexibility and invasion success in birds. *Anim. Behav.* **63**, 495–502. (doi:10.1006/anbe.2001.1953)
- 46 Sol, D. & Lefebvre, L. 2000 Behavioural flexibility predicts invasion success in birds introduced to New Zealand. *Oikos* **90**, 599–605. (doi:10.1034/j.1600-0706.2000.900317.x)
- 47 Holekamp, K. E. & Dloniak, S. M. 2010 Intraspecific variation in the behavioral ecology of a tropical carnivore, the spotted hyena. *Adv. Stud. Behav.* **42**, 189–229. (doi:10.1016/S0065-3454(10)42006-9)
- 48 Funston, P. *et al.* 2010 Substrate and species constraints on the use of track incidences to estimate African large carnivore abundance. *J. Zool.* **281**, 56–65. (doi:10.1111/j.1469-7998.2009.00682.x)
- 49 Engh, A., Siebert, E., Greenberg, D. & Holekamp, K. E. 2005 Patterns of alliance formation and postconflict aggression indicate spotted hyenas recognize third-party relationships. *Anim. Behav.* **69**, 209–217. (doi:10.1016/j.anbehav.2004.04.013)
- 50 Smith, J. E., Van Horn, R. C., Powning, K. S., Cole, A. R., Graham, K. E., Memenis, S. K. & Holekamp, K. E. 2010 Evolutionary forces favoring intragroup coalitions among spotted hyenas and other animals. *Behav. Ecol.* **21**, 284–303. (doi:10.1093/beheco/arp181)
- 51 Wahaj, S. A., Guse, K. R. & Holekamp, K. E. 2002 Reconciliation in the spotted hyena (*Crocuta crocuta*). *Ethology* **107**, 1057–1074. (doi:10.1046/j.1439-0310.2001.00717.x)
- 52 Drea, C. M. & Carter, A. N. 2009 Cooperative problem solving in a social carnivore. *Anim. Behav.* **78**, 967–977. (doi:10.1016/j.anbehav.2009.06.030)
- 53 Holekamp, K. E., Smale, L. & Szykman, M. 1996 Rank and reproduction in the female spotted hyena. *J. Reprod. Fertil.* **108**, 229–237. (doi:10.1530/jrf.0.1080229)
- 54 Crowley, M. J. 2007 *The R book*. New York, NY: John Wiley & Sons.
- 55 Hauser, M. D. 1999 Perseveration, inhibition and the prefrontal cortex: a new look. *Curr. Opin. Neurobiol.* **9**, 214–222. (doi:10.1016/S0959-4388(99)80030-0)
- 56 Day, R. L., Coe, R. L., Kendal, J. R. & Laland, K. N. 2003 Neophilia, innovation and social learning: a study of inter-generational differences in callitrichid monkeys. *Anim. Behav.* **65**, 559–571. (doi:10.1006/anbe.2003.2074)
- 57 Frigaszy, D., Visalberghi, E. & Galloway, A. 1997 Infant tufted capuchin monkeys' behaviour with novel foods: opportunism, not selectivity. *Anim. Behav.* **53**, 1337–1343. (doi:10.1006/anbe.1996.0368)
- 58 Sigg, H. 1980 Differentiation of female positions in hamadryas one male units. *Zeitsch. Tierpsychol.* **53**, 265–302. (doi:10.1111/j.1439-0310.1980.tb01054.x)
- 59 Bunnell, B. N. & Perkins, M. N. 1980 Performance correlates of social behavior and organization: social rank and complex problem solving in crab-eating macaques (*M. fascicularis*). *Primates* **21**, 515–523. (doi:10.1007/BF02373840)
- 60 Boogert, N. J., Reader, S. M. & Laland, K. N. 2006 The relation between social rank, neophobia and individual learning in starlings. *Anim. Behav.* **72**, 1229–1239. (doi:10.1016/j.anbehav.2006.02.021)
- 61 Katzir, G. 1982 Relationships between social structure and response to novelty in captive jackdaws, *Corvus monedula* L. I. Response to novel space. *Behaviour* **81**, 231–263. (doi:10.1163/156853982X00157)

- 62 Katzir, G. 1983 Relationships between social structure and response to novelty in captive jackdaws, *Corvus monedula* L. II. Response to novel palatable food. *Behaviour* **87**, 183–208. (doi:10.1163/156853983X00426)
- 63 Hauser, M. D. 1988 Invention and social transmission: new data from wild vervet monkeys. In *Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes, and humans* (eds R. W. Byrne & A. Whiten), pp. 327–343. New York, NY: Clarendon Press/Oxford University Press.
- 64 Holekamp, K., Sakai, S. & Lundrigan, B. 2007 The spotted hyena (*Crocuta crocuta*) as a model system for study of the evolution of intelligence. *J. Mammal.* **88**, 545–554. (doi:10.1644/06-MAMM-S-361R1.1)
- 65 Thorndike, E. L. 1911 *Animal intelligence: experimental studies*. New York, NY: Hafner Publishing Company.
- 66 Werdenich, D. & Huber, L. 2006 A case of quick problem solving in birds: string pulling in keas, *Nestor notabilis*. *Anim. Behav.* **71**, 855–863. (doi:10.1016/j.anbehav.2005.06.018)
- 67 van de Waal, E. & Bshary, R. 2010 Contact with human facilities appears to enhance technical skills in wild vervet monkeys (*Chlorocebus aethiops*). *Folia Primatol.* **81**, 282–291. (doi:10.1159/000322628)
- 68 Cheney, D. L. & Seyfarth, R. M. 2007 *Baboon metaphysics: the evolution of a social mind*. Chicago, IL: University of Chicago Press.
- 69 Timmermans, S., Lefebvre, L., Boire, D. & Basu, P. 2000 Relative size of the hyperstriatum ventrale is the best predictor of feeding innovation rate in birds. *Brain Behav. Evol.* **56**, 196–203. (doi:10.1159/000047204)
- 70 Nicolakakis, N. & Lefebvre, L. 2000 Forebrain size and innovation rate in European birds: feeding, nesting and confounding variables. *Behaviour* **137**, 1415–1429. (doi:10.1163/156853900502646)
- 71 Lefebvre, L., Whittle, P., Lascaris, E. & Finkelstein, A. 1997 Feeding innovations and forebrain size in birds. *Anim. Behav.* **53**, 549–560. (doi:10.1006/anbe.1996.0330)
- 72 Sol, D., Lefebvre, L. & Rodríguez-Teijeiro, J. D. 2005 Brain size, innovative propensity and migratory behaviour in temperate Palearctic birds. *Proc. R. Soc. B* **272**, 1433–1441. (doi:10.1098/rspb.2005.3099)
- 73 Reader, S. M. & Laland, K. N. 2002 Social intelligence, innovation, and enhanced brain size in primates. *Proc. Natl Acad. Sci. USA* **99**, 4436–4441. (doi:10.1073/pnas.062041299)