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Social carnivores outperform asocial carnivores on an innovative problem



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The social intelligence hypothesis proposes that social complexity selects for cognitive complexity. However, the role of social complexity in the evolution of nonsocial cognition remains unresolved, resulting in disparate hypotheses. The domain-specific hypothesis posits that sociality only bolsters cognition associated with social challenges and contends that ecological complexity drives the evolution of nonsocial cognition. Alternatively, the domain-general hypothesis argues that the unmatched selective pressures of sociality favour greater cognitive flexibility and ultimately superior general cognition. We tested these hypotheses through experimental comparisons of nonsocial cognition in social and asocial carnivores: lions, *Panthera leo*, spotted hyaenas, *Crocuta crocuta*, leopards, *Panthera pardus*, and tigers, *Panthera tigris*. We tested subjects using a technical task, a puzzle-box, designed to test innovation. Social species were more successful innovators than asocial species. We also observed a positive association between sociality, persistence and innovation; social species spent significantly more time engaged in the task, and persistent individuals were more successful in solving the task. Thus, our findings support the domain-general hypothesis; social carnivores outperformed asocial carnivores on an innovative problem.

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Many social taxa demonstrate complex cognitive abilities, indicating that cognition has convergently evolved in several lineages (Emery & Clayton, 2004; van Horik, Clayton, & Emery, 2012; Marino, 2002; Wasserman, 1993). The social intelligence hypothesis attributes the convergent evolution of cognitive complexity to shared selective pressures imposed by the challenges of navigating social landscapes (Byrne, 1994, 1997; Byrne & Whiten, 1988; Whiten, 2008). Social animals must keep track of dynamic relationships, anticipate and appropriately respond to conspecifics' behaviour, and profit from exploiting the skills of group members through cooperation and competition. Individuals derive benefits from cognitive abilities facilitating these challenges, and the resultant fitness advantage engenders an evolutionary link, whereby social complexity selectively favours cognitive complexity.

The social intelligence hypothesis predicts that social species are cognitively advanced, and accordingly, social taxa have demonstrated impressive cognitive tool-boxes (Byrne & Bates, 2007; Reader & Laland, 2002). However, the extent to which sociality

bolsters cognition in nonsocial (e.g. ecological) domains remains unclear. The domain-general social intelligence hypothesis argues that sociality selects for overall cognitive complexity, including cognitive abilities associated with ecological challenges (Byrne & Whiten, 1988). Proponents of this hypothesis argue that the unique selective pressures of social interactions serve as a bootstrap for the evolution of superior general cognition. In contrast, the domain-specific social intelligence hypothesis proposes that specific domains of cognition evolve in response to domain-related challenges; sociality selects only for, or especially for, cognitive abilities in a social domain (Byrne & Whiten, 1988). Proponents of this interpretation argue that species facing similar ecological complexity will not differ in ecological domain cognition, regardless of social complexity. Both hypotheses predict that social species are cognitively advanced in social domains and neither hypothesis excludes social or nonsocial species from showing advanced cognition in ecological domains. The hypotheses diverge in their interpretation of the selective pressure that 'sociality' places on the evolution of cognition in ecological domains.

The majority of studies investigating the social intelligence hypothesis have focused on indirect measures of cognitive ability (i.e. neocortex to whole brain ratio) and on tests of cognition only in social taxa. In agreement with the domain-general social

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intelligence hypothesis, social group size is positively correlated with measures of brain size and social taxa adeptly solve experimental tests of cognition (Byrne & Bates, 2007; Dunbar, 1998; Dunbar & Bever, 1998; Perez-Barberia, Shultz, & Dunbar, 2007; Reader & Laland, 2002; Roth & Dicke, 2005; Shultz & Dunbar, 2007). These results support an evolutionary link between social complexity and cognitive complexity but fail to exclude ecological complexity as an equal or superior selective pressure in nonsocial domains. Recently, researchers have begun to address the potential role of ecological complexity by investigating how cognition varies with ecological complexity and group size in primate lineages. In primates, dietary breadth, but not social group size, is positively associated with performance on tasks requiring self-control, a nonsocial cognitive domain (MacLean et al., 2014). Similarly, in lemurs, group size predicts species performance on tasks requiring social cognition but not tasks requiring nonsocial cognition (MacLean et al., 2013). These findings support the domain-specific social intelligence hypothesis and suggest that ecological complexity is an additional stimulus to cognitive evolution.

Carnivores offer a socially diverse and ecologically complex model system for further resolving the relationships among social, ecological and cognitive complexity. We used Carnivora as a model system to compare nonsocial cognition in closely related, but socially distinct, species: spotted hyaenas, *Crocuta crocuta*, lions, *Panthera leo*, leopards, *Panthera pardus*, and tigers, *Panthera tigris*. Spotted hyaenas (hereafter, hyaenas) live in primate-like hierarchical societies and are adept at tasks requiring both social and nonsocial cognition (Benson-Amram, Heinen, Dryer, & Holekamp, 2011; Benson-Amram, Heinen, Gessner, Weldele, & Holekamp, 2014; Benson-Amram & Holekamp, 2012; Drea & Carter, 2009; Holekamp et al., 1997; Holekamp, Sakai, & Lundrigan, 2007). The genus *Panthera* is a monophyletic group of both social and asocial felids. Sociality evolved only once within the *Panthera* lineage, and lions are the only social felids (Finarelli & Flynn, 2009; Perez-Barberia et al., 2007). Lions live in large (up to 21 individuals), permanent social groups, and akin to many species of monkeys, group membership is maternally inherited (Mosser & Packer, 2009; Packer, 1986). Similar to other complexly social species, lion sociality is characterized by a high degree of cooperation (Grinnell, 2002; Heinsohn & Packer, 1995; Packer & Pusey, 1982; Scheel & Packer, 1991; Stander, 1992a). However, unlike hyaenas, lions' social structure lacks a strict dominance hierarchy and is instead egalitarian (Packer, Pusey, & Eberly, 2001). Hierarchical species face additional challenges associated with keeping track of one's own rank and the ranks of other group members. Leopards and tigers are asocial and only associate during mating or with dependent offspring (Schaller, 1972; Seymore, 1989). Thus, hyaenas and lions are more socially complex than their asocial relatives, leopards and tigers.

Although socially distinct, all four species occupy similar environments, and thereby encounter similar ecological challenges. Lions, leopards and hyaenas are endemic to Africa, and throughout Africa, their ranges often overlap (Hayward & Kerley, 2008; Schaller, 1972). Lions, leopards and tigers are also endemic to Asia and occupy the same habitat types (Karanth & Sunquist, 2000; Meena, 2009; Sunquist, 1981). All four species encounter ecological complexity through habitat heterogeneity, resulting in patchily distributed resources and prey (Karanth & Sunquist, 2000; Mosser, Kosmala, & Packer, 2015; Pickett, Cadenasso, & Benning, 2003). The successful capture of prey requires nonsocial cognitive abilities enabling individuals to successfully locate prey, avoid detection and use techniques to counter prey escape and take down a prey animal (Hayward & Kerley, 2008; Schaller, 1972; Stander, 1992a,b). Successful hunting techniques likely vary according to prey species, and the broad diets of lions, leopards, tigers and hyaenas require

flexible hunting strategies (Hayward, 2006; Hayward et al., 2006; Hayward & Kerley, 2005; Karanth & Sunquist, 2000). Thus, both social and asocial carnivores face ecological complexity.

In hyaenas and lions, cognition evolved in the presence of both social and ecological complexity. In tigers and leopards, cognitive abilities were selected for in the absence of social complexity but in the presence of ecological complexity. According to the domain-general social intelligence hypothesis, social complexity is positively associated with cognitive complexity and more socially complex species should outperform less socially complex species in all cognitive tasks, regardless of ecological complexity (hyaenas and lions > leopards and tigers). Alternatively, the domain-specific social intelligence hypothesis predicts that species facing similar ecological complexities should not differ in tasks requiring nonsocial cognition related to ecological challenges.

We used a nonsocial challenge (innovative problem solving) to experimentally compare cognition in hierarchical, egalitarian and asocial carnivores. Innovation has been defined as 'a solution to a novel problem or a novel solution to an old one' (Kummer & Goodall, 1985, page 205). Animals depend on innovation to adapt to changing environments, exploit novel resources and/or expand their niche (Day, Coe, Kendal, & Laland, 2003; Huebner & Fichtel, 2015; Lefebvre, Reader, & Sol, 2004; Reader & Laland, 2001). Innovation is associated with cognitive complexity, and in primates, innovation is positively correlated with relative brain size (Lefebvre et al., 2004; Manrique, Völter, & Call, 2013; Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005). Retrieving food from a difficult matrix is a commonly encountered ecological challenge, and retrieving food from a novel matrix requires innovative problem solving. Extractive foraging tasks (e.g. puzzle-tasks) are an effective means of testing innovation and other cognitive processes associated with problem solving (Griffin & Guez, 2014). We used a puzzle-box task to compare social and asocial carnivores' innovative problem solving in the context of resource acquisition.

METHODS

Subjects and Study Sites

We conducted experiments with captive lions ($N = 21$), leopards ($N = 11$), tigers ($N = 7$) and hyaenas ($N = 9$) located in Florida and South Africa at Lion Country Safari, Big Cat Rescue, Zoo Miami and The Kevin Richardson Wildlife Sanctuary. All study subjects were individually identifiable and were adults older than 4 years of age. Experiments were conducted from May 2012 to May 2015. We conducted trials in the subjects' outdoor enclosures. Lions, leopards and tigers were individually presented the puzzle-box. Because of the design of the sanctuary facilities and the social dynamics of captive hyaenas, we tested hyaenas with one to four subjects present in the enclosure. For hyaena trials, we collected data on the first successful individual in the group.

Testing Apparatus

We constructed a $61 \times 91 \times 89$ cm puzzle-box of flexible star-board marine grade polymer (Fig. 1). The box had a spring-loaded hinge door and a spring latch held the door closed. Subjects opened the door by grasping a pull attached to the latch and pulling away from the box at a 180° angle; pulling at an angle other than 180° did not engage the latch (Fig. 1). Pulling in the correct direction engaged the spring-latch and the spring-loaded hinge popped the door open. A subject could easily grasp the pull using either its paws or its mouth. We baited the box with each subject's normal dietary portion of raw meat. We drilled holes into the six sides of the box and subjects could see and smell the meat inside.

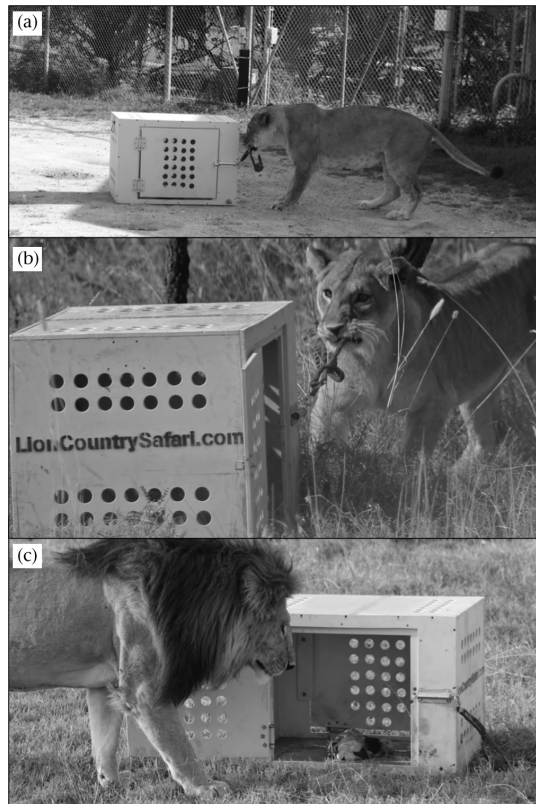


Figure 1. Images of the puzzle-box apparatus used in the experiments. (a) Unsuccessful solution; lion pulling at an incorrect angle. (b) Successful solution; lion pulling at the correct (180°) angle. (c) Successful lion accessing the food reward.

Experimental Procedure

Subjects were not fed for at least 24 h before testing to ensure food motivation. Prior to the start of a trial, we sequestered the focal subject in a night pen or an enclosure adjacent to the testing area, then we baited the puzzle-box and placed it inside the testing area. Trials started when a subject was released from the adjacent enclosure/pen into the testing area. Subjects were given three trials and 10 min per trial to successfully open the puzzle-box. In cases where a subject was actively working on the pull at the 10 min mark, the trial ended when the subject ceased interacting with the pull. All trials were videotaped.

The research presented was reviewed and approved by the University of Miami's Internal Animal Care and Use Committee under protocol number 11-051.

Data Collection

Successful trials were those in which the subject opened the box (see [Supplementary Video S1](#)). We used videotaped recordings to extract data on innovation, persistence and exploration for both successful and unsuccessful trials. To investigate innovative problem-solving ability, we measured whether a subject successfully solved the puzzle-box (innovation) on at least one trial. To

further explore innovative behaviour, we used measures of 'persistence' and 'exploratory' behaviours. We defined persistence as the proportion of total trial time that a subject spent oriented towards and actively working on the puzzle-box. We scored six exploratory behaviours: 'circling', 'digging', 'biting', 'paws on top of the box', 'pawing the sides of the box' and 'pushing the box'. We measured exploration by counting the number of exploratory behaviours that each subject used when working on the box; thus, individual scores ranged from 0 to 6 (see [Supplementary Material](#)).

Statistical Analysis

To test the overall hypothesis that innovative problem solving differs among species, we used a Fisher–Freeman–Halton test to analyse a 4×2 contingency table and compared success according to species. We used Welch's ANOVA to investigate overall interspecific differences in persistence. To account for unequal variances, we used a Kruskal–Wallis test to examine overall interspecific differences in exploration. Following overall hypothesis testing, post hoc comparisons were made to examine differences in innovation related to sociality and social structure. All tests were two tailed using an alpha criterion of 0.05 for significance. If overall t results did not meet our criterion for statistical significance of an effect, we employed a Bonferroni correction for analysing any subsets of the overall results in post hoc comparisons.

All statistical analysis were performed using JMP Pro12 (SAS Institute, Cary, NC, U.S.A.). Figures were generated using R (R Foundation for Statistical Computing, Vienna, Austria).

RESULTS

Innovation

Of the 48 subjects tested, 8 of 9 hyaenas (88%), 16 of 21 lions (76%), 6 of 11 leopards (54%) and 2 of 7 tigers (29%) successfully solved the puzzle-box in at least one of three trials ([Fig. 2](#), [Supplementary Video S1](#)), providing support for the overall statistical hypothesis that innovative problem solving differs among these species. We also observed a significant difference in innovative problem-solving success among species (Fisher–Freeman–Halton test: $df = 3$, $P = 0.047$). Our results agree with the domain-general social intelligence hypothesis, and social individuals (lions and hyaenas) innovated more successfully than their asocial (leopards and tigers) counterparts (Fisher's exact test: $P = 0.025$).

Hyaenas were the most successful, lions outperformed their asocial relatives, and overall asocial species were the least successful ([Fig. 2](#)). We found no significant difference in performance between hierarchical (hyaenas) and egalitarian (lions) individuals (Fisher's exact test: $P = 0.637$).

Persistence

The length of time spent actively working on a problem may influence success on novel problems (innovation). We investigated interspecific differences in persistence, defined as the proportion of time an individual spent actively working on the puzzle-box in their first trial. We were unable to calculate scores for two successful hyaenas because of video equipment failure; we calculated scores for six successful and one unsuccessful subject.

As expected, successful individuals spent a significantly higher proportion of time actively working on the puzzle-box (Welch's ANOVA: $1.32.38 = 17.33$, $P = 0.0002$). Once again, our overall statistical hypothesis, that innovative problem solving differs among species, was supported, and we observed a significant difference in

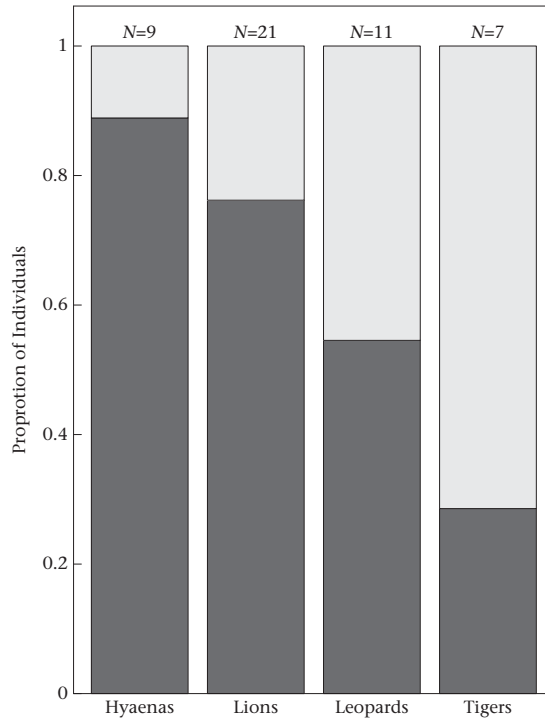


Figure 2. Innovative problem-solving performance of social species (hyaenas, lions) and asocial species (leopards, tigers). Dark grey bars show the proportion of individuals that successfully opened the puzzle-box on at least one of three trials. Light grey bars show the proportion of individuals that failed to open the puzzle-box within three trials.

persistence among species (Welch's ANOVA: $F_{3,15.03} = 4.928$, $P = 0.014$). Social species spent the greatest proportion of time working on the puzzle-box (Fig. 3). In agreement with the domain-general social intelligence hypothesis, persistence differed significantly between social and asocial individuals, and social individuals showed significantly greater persistence than asocial individuals (Welch's ANOVA: $F_{1,30.58} = 9.849$, $P = 0.004$). Although lions spent the greatest amount of time working on the puzzle-box (Fig. 3), we observed no significant difference in persistence between lions (egalitarian) and hyaenas (hierarchical) (Tukey–Kramer HSD: $N = 28$, $P = 0.303$).

Exploration

Exploratory behaviour may facilitate innovative problem solving, as exploratory individuals are more likely to find novel solutions through trial and error. We investigated innovation as a measure of exploratory behaviour and compared exploratory scores from the first trial (Fig. 4). Of the nine hyaenas tested, we were only able to calculate innovation scores for five successful subjects because of video equipment limitations.

Lions were the most exploratory and were the only species to display all six exploratory behaviours (Fig. 4). However, lions ($N = 21$), leopards ($N = 11$), tigers ($N = 7$), and hyaenas ($N = 5$) did not significantly differ in their exploratory behaviours (Kruskal–Wallis test: $\chi^2_4 = 7.06$, $P = 0.070$). We also observed no evidence for differences in exploratory behaviours between social and

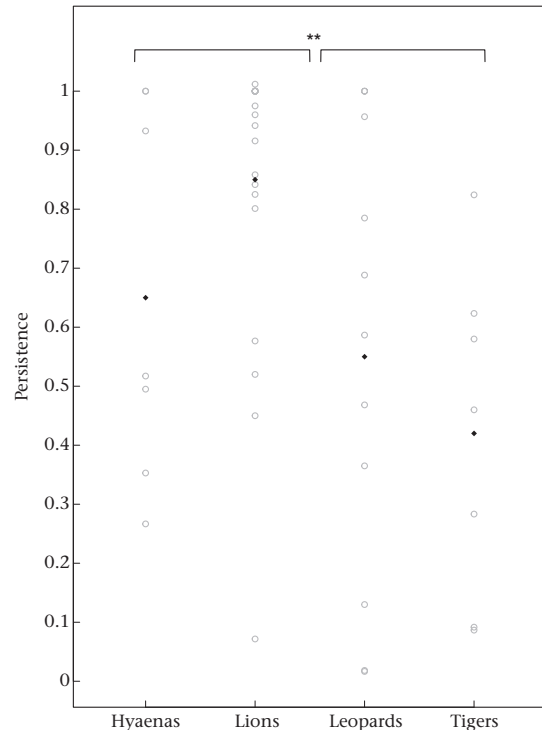


Figure 3. Individuals' persistence measured as the proportion of the first trial that social (hyaenas, lions) and asocial (leopards, tigers) individuals spent engaged in the puzzle-box. Open circles represent individuals. Black diamonds denote species mean persistence score. ** $P < 0.05$ (Welch's ANOVA).

asocial species; we conducted pairwise comparisons using a Bonferroni correction ($\alpha = 0.008$) and found no significant interspecific differences in exploration scores (Wilcoxon each pair tests: hyaena–lion: $Z = 2.29$, $N = 26$, $P = 0.022$; hyaena–tiger: $Z = 2.56$, $N = 12$, $P = 0.010$; hyaena–leopard: $Z = 1.80$, $N = 16$, $P = 0.072$; lion–leopard: $Z = 0.78$, $N = 32$, $P = 0.433$; lion–tiger: $Z = -0.89$, $N = 28$, $P = 0.37$; tiger–leopard: $Z = 0.00$, $N = 18$, $P = 1.00$).

DISCUSSION

Our results support the domain-general social intelligence hypothesis in that we found a positive association between sociality and cognition in a nonsocial task requiring innovation (Fig. 2). Our findings differ from results reported for primates, where innovation was not associated with sociality (measured as group size; Day et al., 2003). A potential explanation for the differing results is that even primates living in small groups must contend with social complexity, indicating that group size alone may be an insufficient proxy for social complexity. The social intelligence hypothesis proposes that sociality places unique selective pressures on cognition through complex social interactions (Byrne & Whiten, 1988). Complex societies require individuals to constantly monitor group members, accurately predict group members' reactions, appropriately time behaviour towards group members and cooperate and/or compete for resources (Humphrey, 1976). Thus, social complexity is governed by social structure and the nature of social relationships within a group; larger group size does not

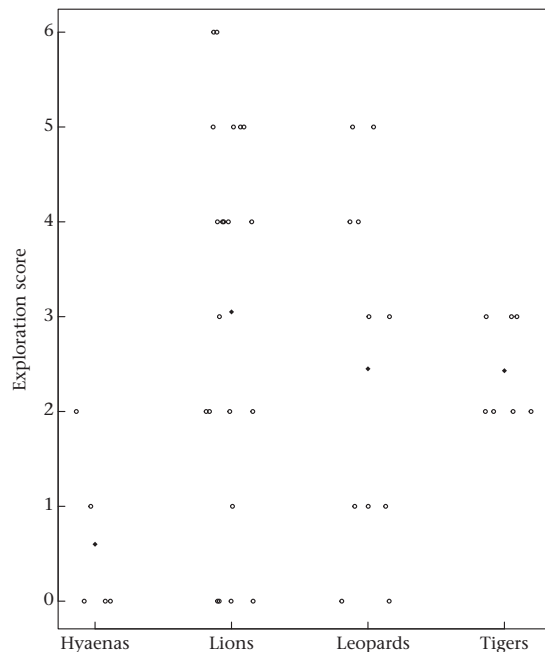


Figure 4. Exploration diversity measured as the number exploratory behaviours displayed during an individual's first trial. Six exploratory behaviours were scored (score range = 0–6 per subject). Open circles denote individuals. Black diamonds denote species mean exploration scores.

necessarily translate to greater social complexity. Individuals navigating ranks and relationships in a small group may face many of the same social challenges as individuals navigating ranks and relationships in a larger group. Consequently, in addition to comparisons based on group size, research on social intelligence should include comparisons of social and asocial species.

Our results confirmed that social species significantly outperform asocial species on an innovative task, and social carnivores most adeptly solved an innovative problem (Fig. 2). Leopards and tigers are the least socially complex, and as predicted by the domain-general social intelligence hypothesis, were significantly less likely to solve the puzzle-box. Our findings support the domain-general social intelligence hypothesis in carnivore lineages.

Innovation is influenced by neophobia/neophilia (Biondi, Bo, & Vassallo, 2010; Bouchard, Goodyer, & Lefebvre, 2007; Sol, Griffin, Bartomeus, & Boyce, 2011), and our results support an association between neophilia (persistence), innovation and sociality (Fig. 3). Innovating enables animals to better cope with environmental change and acquire novel resources but also exposes animals to unknown risks (Benson-Amram et al., 2011). For example, invasive species must adapt to novel environments and/or adopt new foraging strategies, but in doing so, risk encountering unfamiliar enemies and/or poisonous foods (Biondi et al., 2010; Bouchard et al., 2007; Sol et al., 2011). Animals must balance the cost of approaching a potentially dangerous novel resource (neophilia) with the cost of avoidance (neophobia), as avoiding novel resources may prevent animals from successfully adapting to a new/changing environment (Greenberg, 2003). Neophilic animals take greater risks but are also more successful innovators. In hyaenas, innovation is related to neophilia and persistence/work effort (Benson-

Amram & Holekamp, 2012). In primates, socially complex species (chacma baboons, *Papio ursinus*) display greater neophilia than less socially complex species (geladas, *Theropithecus gelada*; Bergman & Kitchen, 2009). In the present study, more successful innovators were also more neophilic and spent more time interacting with the puzzle-box; compared to unsuccessful individuals, successful individuals spent a significantly higher proportion of time interacting with the puzzle-box. In addition, we found that successful species were also more socially complex, thereby linking neophilia and success with sociality. Social carnivores were more successful and displayed greater persistence/neophilia than their less successful asocial counterparts.

Our comparisons did not reveal an association between exploratory behaviour (an additional measure of neophilia) and sociality or success. Hyaenas displayed the least exploratory diversity (Fig. 4). Additionally, within *Panthera*, we did not observe a link between sociality and exploration. Although lions displayed the greatest exploratory diversity, they did not significantly differ from tigers and leopards (Fig. 4). In agreement with findings in other species, sociality was linked to lowered neophobia but not to exploratory behaviour (Bergman & Kitchen, 2009; Biondi et al., 2010; Carere & Locurto, 2011).

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Supplementary Material

Supplementary material associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2016.01.013>.

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