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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.

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, & Lundrigran, 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 starboard 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.