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OUTLOOK

Social tolerance in not-so-social pumas

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Summary
Elbroch, Levy, Lubell, Quigley, and Caragiulo (2017, *Science Advances, 3,* e170218) used GPS and motion-activated camera technology to track and rate the interactions between solitary wild pumas. They found that tolerance at feeding sites was not predicted by kinship but, rather, indicated the ability to engage in direct reciprocity, challenging previous assumptions about social cognition in solitary species.

Keywords Puma · Solitary · Carnivore · Social interactions · Reciprocity

Elbroch, Levy, Lubell, Quigley, and Caragiulo (2017) present potentially groundbreaking findings on the importance of social strategies in a relatively solitary species. This careful analysis of social interactions in a network of wild pumas (*Puma concolor*) may have implications for our understanding of social cognition specifically, and general cognition more broadly. Typically, researchers have assumed that the complexity of group living confers an advantage for cognitive sophistication relative to a more solitary lifestyle. This hypothesis is known as the social intelligence hypothesis. However, these new data suggest that relatively solitary species that come into contact with conspecifics on occasion may in fact have to remember and track social relationships over longer periods of time, perhaps necessitating the evolution of sophisticated memory and spatial skills. In addition, strategies for navigating intermittent relationships may lead to the emergence of social skills previously assumed to be reserved for group-living species. The authors do an excellent job describing the ecology of the puma and how various factors predict the existence of complex social strategies in this species. For example, they point to longevity and stable territories as important factors. In addition, they highlight the fact that pumas often kill prey larger than they can consume alone, reducing the element of competition that would make it advantageous to avoid or aggress against conspecifics. These observations provide a framework by which researchers can predict cognitive variability among taxa that differ according to factors such as longevity, territoriality, and foraging strategies.

As Elbroch and colleagues indicate, it is shortsighted to assume that animals with limited social interactions have failed to evolve adaptive social strategies for dealing with such interactions. These kinds of widespread assumptions have crippled progress in our understanding of the cognition of less social and more evasive species. The authors appropriately emphasize the importance of testing less social species in order to properly evaluate the importance of sociality for evolved cognitive abilities. The current bias toward testing group-living species for evidence of advanced cognition can provide only evidence in favor of the social intelligence hypothesis, where it is also necessary to rebut potentially refuting cases. A better understanding of the social networks of understudied species will help researchers devise appropriate tests of their cognitive capacities. The research reported by Elbroch et al. should stimulate further studies on carnivore cognition, including assessments of long-term memory, social learning, and reputation formation. In fact, in our lab, we are currently investigating reputation formation in domestic cats presented with human experimenters, but perhaps a better test would be to assess their attributions of reputation of each other, particularly for traits such as dominance and affiliation.

On a related note, whereas researchers sometimes treat sociality as a dichotomous variable in which animals are either social or asocial, sociality is better represented as a continuum where animals experience different types and degrees of sociality. Animals may, for example, live in groups, but do not need to track the relationships between individuals. Animals

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may form pairs, and these pairs may or may not include extended family members in their network. They may share some overlap in territory and monitor bordering occupants. Groups may exhibit fission–fusion dynamics. Elbroch and colleagues have embraced this multidimensional conceptualization of sociality and have shown that even relatively solitary animals may benefit from social cognitive skills.

In addition to the ramifications for understanding cognition broadly, Elbroch and colleagues' results may inform the study of cooperative behavior more specifically. Researchers have long theorized about ecological factors (e.g., agricultural vs. hunter-gatherer foraging strategies) that give rise to cooperative behavior in human societies. The finding of tolerated shared feeding among nonkin in pumas suggests that, even in species that do not exhibit cooperative hunting, tolerance at feeding sites requires a system of direct reciprocity, which may set the stage for the cognitive hardware necessary to track such interactions. The lack of a correlation between kinship and tolerance in Elbroch et al.'s data is interesting and flies in the face of traditional hypotheses that explain cooperation as a function of relatedness, inasmuch as tolerance is related to cooperation. However, it is consistent with previous work on food sharing in vampire bats, which has propelled researchers to move beyond assumptions that cooperation is restricted to kin to reveal the possibility of long-term social bonds and reciprocity in nonhumans (for review, see Wilkinson, Carter, Bohn & Adams, 2016). Although Elbroch and colleagues did not consider Wilkinson and colleagues' views, this approach can be extended to investigate hypotheses regarding nepotistic biases under conditions of perceived risk.

Data from studies tracking wild animal movements and interactions are important for assessing the quality of animal relationships, as researchers question whether other species are capable of "friendships" (Seyfarth & Cheney, 2012). There are also implications for the self-domestication hypothesis. Hare (2017) suggests that selection for tolerance over aggression led to the emergence of a particular suite of social-communicative skills in humans, serving as the foundation for our uniquely human capacity for mentalizing. Thus, the observation that pumas have the capacity to selectively exhibit tolerance of other pumas may yield important insight into their developing cognition. Furthermore, individual differences in tolerance may be associated with reproductive success. Such findings may also have interesting implications for mate choice in a relatively solitary species.

There are, of course, untested assumptions arising from Elbroch and colleagues' findings. Future research should focus on larger networks and present pumas with unfamiliar conspecifics to examine whether aggression/tolerance is really wielded flexibly as a function of familiarity or prior experience. If so, such findings would support a new form of behavioral flexibility in which animals can adjust their behaviors according to their knowledge of a complex system of interactions rather than being constrained to respond in fixed ways to cues of relatedness. Perhaps this ability would predict a capacity for cooperation, which is only recently being examined in feline species.

In addition to its theoretical contributions, this article is also an excellent example of how technological advances, such as the Global Positioning System (GPS), permit researchers to observe previously hidden phenomena and, thus, to ask previously impenetrable questions. Historically, inaccessibility created a bias in the species studied by comparative researchers, especially in wild habitats. Video-recording technology through the use of motion-activated video cameras has also greatly improved the ability of researchers to surreptitiously observe natural behaviors. Use of GPS along with motion-activated video cameras allowed Elbroch and colleagues to place cameras efficiently at sites where repeated movements were detected to maximize the likelihood of observing interactions at prey sites. Without the capacity to hone in on such patterns, it would not have been possible to detect important patterns in the pumas' interactions.

Lastly, one of the highlights of the Elbroch et al. article is the implication for trophy hunting. The authors suggest that territorial males drive the pattern of tolerance within triads consisting of two females and one male. Trophy hunters that often target large males of a species may disrupt these relationships in a way that undermines the ability of individuals to coexist across territory boundaries. A recent paper on social bet-hedging supports the idea that vampire bats benefit from a larger number of nonkin relationships when food-sharing partners are lost (Carter, Farine, & Wilkinson, 2017). Analyzing the puma data similarly, particularly in light of potential loss of territorial males, would be illuminating. A better understanding of how removal of one individual can impact the network and social relations of remaining individuals can better inform decisions on which animals to protect in natural environments and perhaps can be informative in captive husbandry decisions as well.

References

Carter, G. G., Farine, D. R., & Wilkinson, G. S. (2017). Social bet-hedging in vampire bats. *Biology Letters, 13*, 20170112. https://doi.org/10.1098/rsbl.2017.0112

Elbroch, L. M., Levy, M., Lubell, M., Quigley, H., & Caragiulo, A. (2017). Adaptive social strategies in a solitary carnivore. *Science Advances, 3*, e170218.

Hare, B. (2017). Survival of the friendliest: *Homo sapiens* evolved via selection for prosociality. *Annual Review of Psychology, 68*, 155–186.

Seyfarth, R. M., & Cheney, D. L. (2012). The evolutionary origins of friendship. *Annual Review of Psychology*, 63, 153–177.

Wilkinson, G. S., Carter, G. G., Bohn, K. M., & Adams, D. M. (2016). Non-kin cooperation in bats. *Philosophical Transactions of the Royal Society B, 371*, 20150095. https://doi.org/10.1098/rstb.2015.0095