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SYMPOSIUM INTRODUCTION

Introduction to Symposium: The Developmental and Proximate Mechanisms Causing Individual Variation in Cooperative Behavior

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Synopsis Nearly all animals interact with members of their own species at some point during their lives. These behavioral interactions range from courtship, mating, and parental care to the complex cooperative behavior among related or unrelated individuals in group-living species. A number of theoretical models have attempted to explain how cooperation can evolve through natural selection. Although tremendously influential in animal behavior research, these traditional models have largely ignored individual variation in cooperative behavior and its underlying developmental and proximate mechanisms. However, a set of emerging models suggest that the evolution of cooperation can be heavily influenced by the degree of individual variation in cooperative behavior, as well as the complexity of the underlying mechanisms. Yet, while theoreticians argue the importance of studying individual variation in cooperation and the mechanisms underlying it, empiricists have not focused upon these aspects. The main objectives of our symposium at the 2017 meeting of the *Society for Integrative and Comparative Biology* is to establish new research avenues to study variation in cooperative behavior using both proximate and ultimate explanations and to produce a road map to study the developmental and proximate mechanisms in generating individual variation in cooperative behavior. This symposium brought together empiricists and theoreticians investigating cooperative behavior in diverse taxa and across multiple levels of analysis. Here we briefly describe the rationale for this symposium and why we thought it was needed as well as provide a brief overview of the contributions.

Introduction

Most animals spend a large proportion of their time interacting cooperatively with conspecifics over courtship, mating, parental care, and other behaviors. In some group-living species, these behaviors become more complex as individuals perform cooperative behaviors among related or unrelated individuals. The evolutionary causes and consequences of such cooperative behavior have been a focus of biological research for nearly two centuries. Theoretical models such as those based on reciprocity (Trivers 1971; Axelrod and Hamilton 1981) or kin selection (Hamilton 1964) predict the conditions under which cooperation is likely to evolve through natural selection. Although these traditional models have resulted in productive research paradigms that have shaped the formal study of animal behavior for >50 years, more recent models suggest that the evolution of cooperation is also heavily influenced by the degree of individual variation in cooperative behavior (McNamara et al. 2004, 2008; McNamara and Leimar 2010; Johnstone and Manica 2011; van den Berg et al. 2015), as well as by their underlying developmental (i.e., how the current or past environment alters behavior) and proximate mechanisms (i.e., control mechanisms such as the genomic or physiological causes of the behavior) (van den Berg and Weissing 2015).

Despite their potential importance for the evolution of cooperation and social organization, individual variation in cooperative behavior and the mechanisms underlying it are understudied by empiricists (Réale et al. 2007; Bergmüller et al. 2010; Hofmann et al. 2014).

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Much of the empirical research on cooperative behavior to date has focused upon the ultimate factors shaping the evolution of social behavior (e.g., understanding the direct and indirect fitness benefits accrued through cooperation). Moreover, traditional theoretical models tend to focus upon the mean values of cooperative behavior within a population while ignoring the variation. While insightful, the next generation of studies of cooperative behavior must quantify the presence and importance of variation in cooperative behavior as well as integrate the study of the mechanisms underlying this individual variation in social behavior. Here, we illustrate the importance of this symposium in setting the research agenda for future studies of cooperative behavior both in the laboratory and in wild animals.

Individual variation in social behavior

Over the past 20 years, it has become widely appreciated that individual variation in animal behavior has important ecological and evolutionary consequences (Wilson et al. 1994; Bolnick et al. 2003; Dall et al. 2012; Wolf and Weissing 2012). Today, this is often studied under the theme of consistent differences in behavior (i.e., animal personality, temperament: Réale et al. 2007) or correlations among different behaviors (i.e., behavioral syndromes: Sih et al. 2004). Theory suggests that individual-variation in cooperative behavior or social responsiveness plays a primary role not only in determining if cooperation evolves, but also the degree of cooperation that evolves (McNamara et al. 2004, 2008; McNamara and Leimar 2010; Johnstone and Manica 2011; van den Berg et al. 2015). That is, the presence of individual variation in behavior makes the evolution of cooperation more likely and increases the overall level of cooperation among individuals (Wolf and Krause 2014). Despite intense focus on individual variation and cooperation, surprisingly few studies have investigated consistent individual differences in social behaviors or correlations among different types of social or other behaviors, particularly in vertebrates. Individual differences in cooperative behavior likely exist in vertebrates, but we know comparatively little about the existence of pro- or anti-social personalities in non-human animals as well as the presence of individual variation in cooperative behaviors (Réale et al. 2007; Réale and Dingemanse 2010; Bergmüller et al. 2010; Carere and Maestripieri 2013).

Mechanisms underlying social behavior

The mechanisms underlying behaviors are often ignored by behavioral ecologists despite many calls for their integration in a diversity of disciplines (McNamara and Houston 2009; Blumstein et al. 2010; MacDougall-Shackleton 2011; Hofmann et al. 2014; Taborsky et al. 2015). Theoretical models examining the conditions under which cooperation evolves often assume a simple map from genotype to behavioral phenotype (e.g., a 1:1 relationship between an allele and a cooperative phenotype). Although such simplifying assumptions are necessary, theory suggests that the outcome in the evolution of cooperation can be very different if more complex mechanisms underlie cooperative behavior (van den Berg and Weissing 2015). Despite extensive research on the ultimate causes of the evolution of cooperation, we know relatively little about the underlying mechanisms from both psychological (i.e., learning, memory of past experiences) and physiological perspectives (i.e., genomic, epigenomic, neuroendocrine) in wild or non-model animals. In studies of laboratory animals, the situation is very different, as mechanisms underlying social behaviors such as maternal care or pair-bonding behavior have been explored in detail, though only in a few species (Goodson 2005; Curtis et al. 2007; Donaldson and Young 2008; Renn et al. 2008; O'Connell and Hofmann 2011, 2012). Most empiricists studying cooperative behavior from an evolutionary perspective do not integrate the study of the mechanisms potentially underlying its expression (Hofmann et al. 2014). Thus, we must begin to understand not only how different early life experiences mechanistically influence developmental trajectories that affect social behavior, but how these mechanisms impact variation in social behavior and ultimately variation in fitness.

Recent work indicates that there may be common mechanisms underlying individual variation in social behavior across taxa. Laboratory studies suggest the possibility of general genomic or physiological mechanisms that explain variation in the expression of cooperative behavior. Although much attention has been focused upon the roles of vasopressin and oxytocin in causing differences in cooperative behavior (Donaldson and Young 2008; Goodson et al. 2009; Okhovat et al. 2015), there are a number of other candidate neural and neuroendocrine systems that may regulate the expression of cooperative behavior involving dopamine, steroid hormones, glutamate, or GABA (Curtis et al. 2007; Aragona and Wang 2009; Blumstein et al. 2010; O'Connell and Hofmann 2011, 2012). These mechanisms may be separate from those involving vasopressin/oxytocin or interact with these other neural or neuroendocrine pathways. Although there has been growth in our understanding of the mechanisms underlying social behavior in laboratory animals, the integration of studies of mechanisms of cooperative behavior in wild animals has lagged. As such, the generality of some of these mechanisms to explaining variation in social behavior is restricted to a few species. Studies on species used as model systems for investigations of the function of cooperative behavior rarely integrate mechanisms and the number of taxa in which mechanisms of cooperative behavior are investigated needs to be enlarged (Rubenstein and Hofmann 2015a; Taborsky et al. 2015).

Linking individual variation and mechanisms of social behavior

Despite its importance, we do not yet fully understand the existence and origins of individual variation in cooperative behavior. This includes the role of developmental experiences in creating variation, as well as its underlying genomic, epigenomic, neural, and physiological mechanisms (Hofmann et al. 2014). The availability of new laboratory tools and their application in non-model organisms should permit new studies about the proximate causes of individual variation in cooperative behavior in wild animals. These tools will allow investigation into whether variation in cooperative behavior is caused by common mechanisms across taxa (Rubenstein and Hofmann 2015b). Simultaneously, there has been widespread recognition of the theoretical importance of individual variation in behavior for the evolution and maintenance of cooperation through natural selection. This has been supplemented by recent theoretical evidence that the complexity of the mechanisms underlying cooperative behavior can also shape its evolution. Despite repeated pleas to integrate functional and mechanistic studies in animal behavior, this has rarely occurred. This is perhaps best illustrated by the study of cooperative behavior where mechanisms are traditionally studied in a few model organisms and humans in the laboratory even though the evolution and function of cooperative behavior has been studied in wild animals for nearly two centuries (Taborsky et al. 2015). This symposium aimed to promote more integrative studies of social behavior by focusing attention on the causes and consequences of individual variation in cooperative behavior.

SICB 2017 symposium: moving forward

A practical aim of this symposium is to gather both empiricists and theoreticians studying the mechanisms and consequences of individual variation in cooperative behavior in both invertebrate and vertebrate taxa. It includes a mixture of researchers studying cooperative behavior in non-model animals and those who study species where a genomic or neuroscience toolkit to study cooperative behavior is available. We have three primary goals for this symposium:

(1) To connect empiricists and theoreticians studying cooperative behavior, as well as those studying cooperative behavior in laboratory and wild animals.

(2) To identify emerging methods to study proximate mechanisms underlying cooperative behavior that will produce new studies in non-model animal species that are often the focus of studies of cooperative behavior.

(3) To identify "big questions" that need to be addressed through studying individual variation in cooperative behavior as well as the methodological framework and professional network to address these questions.

Overview of symposium contributions

The eight contributions to this symposium range from an overview of theoretical models regarding the evolution of cooperation to the neural and endocrine causes of variation in cooperative behavior in a variety of taxa, including insects, fish, and mammals. We begin by summarizing the theoretical contributions. Van Cleve (2017) describes the conditions where cooperation can evolve through different combinations of relatedness, reciprocity, and the non-linearity of fitness payoffs associated with cooperation. This model produces new testable predictions about the causes of variation in the expression of cooperation that may ultimately aid in our understanding of variation in the expression of cooperative behavior across species or within populations or social groups. Using a simple population genetic approach, Sheehan et al. (2017) developed a model to show how genetic diversity for individual recognition signals can be maintained. Although individual discrimination is essential for mediating cooperation in models for the evolution of cooperation either through kin selection or reciprocity, a longstanding assumption has been that genetic variation for identity signals that facilitate such discrimination should be reduced and therefore individuals should instead use identity cues. Genetic variation in identity signals is crucial if individuals are to identify others with whom to cooperate either in kin selection or reciprocity models. Sheehan et al. (2017) use a simple population genetic model to show how genetic diversity for individual recognition signals can be maintained, a broadly applicable result.

After this series of models describing the mechanisms of cooperation and principles of individual recognition in social species, the remaining papers are empirical in nature. Charbonneau et al. (2017) emphasize understanding the causes of individual variation in non-cooperative behavior (laziness) in social ants. Although worker inactivity in social insect colonies has been widely documented, few studies have investigated whether there is individual-variation in laziness. The authors test five non-mutually exclusive hypotheses to explain the presence of individual-variation in laziness in the ant *Temnothorax rugatulus*. They review the evidence for four existing hypotheses and propose a new hypothesis based on the life histories of worker ants. They find some support for these different hypotheses and suggest that lazy workers are not yet fully developed, instead either reproducing on their own at the expense of the colony, or acting as a method of food storage for the colony (i.e., laying eggs that served as a source of food for colony members).

Both Withee and Rehan (2017) and Weitekamp et al. (2017) then describe the genomic and neural causes of variation in cooperation in insects and fish, respectively. Withee and Rehan (2017) describe how winning or losing dominance contests or a changing social rank can alter brain gene expression in the subsocial bee *Ceratina calcarata*. They show that consistently winning dominance contests explained most of the variation in brain gene expression followed by change of social rank. They also identify candidate genes for aggression using comparative transcriptomics across 21 invertebrate and 6 vertebrate taxa, and show that *cis*-regulatory elements may play an important role in mediating aggression during social contests. Weitekamp et al. (2017) then describe the neuromolecular causes of elevated aggressive behavior during group defense in the social African cichlid fish *Astatotilapia burtoni*. When the territory of a social group is invaded, both group members and neighboring males will exhibit aggression to defend the territory. The authors investigated several neuroendocrine mechanisms that may mediate this aggression during territory defense, showing that in neighboring males but not residents, gene expression (especially of the serotonin receptor) in the area of the fish brain that may be homologous to the mammalian basolateral amygdala (medial part of the dorsal telencephalon) is correlated with aggression during territory defense. This suggests that the neural mechanisms modulating aggression of neighbors and residents may differ. In addition, they find that during aggression there is positive co-regulation of gene expression of multiple genes implicated in modulating social behavior (e.g., serotonin receptor, dopamine receptor 1 and 2, androgen and estrogen receptor α, and isotocin receptor ITR2) within but not across different brain regions that are the putative homologs to the mammalian basal lateral amygdala and hippocampus, both of which are parts of the Social Decision-making Network (O'Connell and Hofmann 2011).

These contributions are followed by several others examining the neuroendocrine causes of individual variation in cooperation across different taxa. Smith et al. (2017) present results from a literature review regarding how the peptide hormone oxytocin affects the expression of cooperative behavior in free-living animals, including the results from a field study of how oxytocin influenced social behavior in free-living yellow-bellied marmots (*Marmota flaviventris*). As is frequently the case, the effects of oxytocin on cooperation are much more complicated than is typically presented. Specifically, the authors show that in some circumstances oxytocin plays a role in anti-social—rather than social—behavior and the effects of oxytocin on marmot social behavior may be sex-specific.

Finally, Saltzman et al. (2017) and Kelly et al. (2017) provide discussion, new results, and new hypotheses about the causes of individual variation in parental behavior. Saltzman et al. (2017) present a thorough overview of the developmental and proximate causes of variation in paternal care in five species of bi-parental rodents where males provide paternal care. They describe several future areas of research that are needed, including the hypothesis that vasopressinergic signaling in the brain is modulated by gonadal hormones and causes individual variation in paternal care. In contrast, Kelly et al. (2017) describe the possible neural mechanisms causing shifts in the parental behavior of mothers and fathers toward their offspring across ontogeny in prairie voles (*Microtus ochrogaster*). They focus upon the effects of two peptide hormones (vasopressin and oxytocin) on shifting maternal and paternal behavior as offspring get older.

Conclusion

Discussions on the integration of mechanism and social behavior are not new (e.g., Réale et al. 2007; Bergmüller et al. 2010; Hofmann et al. 2014). In this symposium, however, we specifically emphasize the role of mechanism in driving individual differences in behavior that could have significant fitness consequences. It became clear that the causes of variation in cooperative behavior are a field of study that can unify those that approach it from both theoretical and mechanistic perspectives. We succeeded in bringing together a diversity of researchers from theoreticians and neuroscientists (Objective 1) and emphasized the diversity of research on the causes of individual variation in cooperative behavior in a variety of model and non-model systems. The contributions here illustrate the variety of approaches from theory to mechanism to better understand the causes of individual variation in cooperation that can be investigated in both model and non-model organisms (Objective 2). As we look forward, it is clear that new empirical research on the genomic, epigenomic, and neuroendocrine mechanisms of individual differences in social behavior in a greater diversity of natural systems is clearly needed. This symposium helps to generate a list of the next set of research questions that should be addressed in this discipline (Objective 3). These studies must be undertaken in the context of the emerging theoretical models that explore the factors that influence the evolution of cooperation (e.g., reciprocity, kin selection), and they must consider the large role that developmental processes play in the origins of individual variation in behavior. Ultimately, a focus on individual variation may be one way in which researchers can better integrate studies of mechanism and social behavior.

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References

Aragona BJ, Wang Z. 2009. Dopamine regulation of social choice in a monogamous rodent species. Front Behav Neurosci 3:1–11.

Axelrod R, Hamilton WD. 1981. The evolution of cooperation. Science 211:1390–6.

Bergmüller R, Schürch R, Hamilton IM. 2010. Evolutionary causes and consequences of consistent individual variation in cooperative behaviour. Philos Trans R Soc Lond B Biol Sci 365:2751–64.

Blumstein DT, Ebensperger LA, Hayes LD, Vásquez RA, Ahern TH, Burger JR, Dolezal AG, Dosmann A, González-Mariscal G, Harris BN, et al. 2010. Toward an integrative understanding of social behavior: new models and new opportunities. Front Behav Neurosci 4:1–9.

Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML. 2003. The ecology of individuals: incidence and implications of individual specialization. Am Nat 161:1–28.

Carere C, Maestripieri D. 2013. Animal Personalities: Behavior, Physiology, and Evolution. Chicago (IL): University of Chicago Press.

Charbonneau D, Poff C, Nguyen H, Shin MC, Kierstead K, Dornhaus A. 2017. Who are the 'lazy' ants? Testing multiple hypotheses for the function of inactivity in social insects reveals a possible role of constraint—inactive ants are corpulent and may be young and/or selfish. Integr Comp Biol 57:649–67.

Curtis JT, Liu Y, Aragona BJ, Wang Z. 2007. Neural regulation of social behavior in rodents. In: Wolff JO, Sherman PW, editors. Rodent societies: an Ecological and Evolutionary Perspective. Chicago (IL): University of Chicago Press. p. 185–94.

Dall SR, Bell AM, Bolnick DI, Ratnieks FL. 2012. An evolutionary ecology of individual differences. Ecol Lett 15:1189–98.

Donaldson ZR, Young LJ. 2008. Oxytocin, vasopressin, and the neurogenetics of sociality. Science 322:900–4.

Goodson JL. 2005. The vertebrate social behavior network: evolutionary themes and variations. Horm Behav 48:11–22.

Goodson JL, Schrock SE, Klatt JD, Kabelik D, Kingsbury MA. 2009. Mesotocin and nonapeptide receptors promote estrilid flocking behavior. Science 325:862–6.

Hamilton WD. 1964. The genetical evolution of social behavior I. J Theor Biol 7:1–16.

Hofmann HA, Beery AK, Blumstein DT, Couzin ID, Earley RL, Hayes LD, Hurd PL, Lacey EA, Phelps SM, Solomon NG, et al. 2014. An evolutionary framework for studying mechanisms of social behavior. Trends Ecol Evol 29:581–9.

Johnstone RA, Manica A. 2011. Evolution of personality differences in leadership. Proc Natl Acad Sci U S A 108:8373–8.

Kelly A, Hiura L, Saunders A, Ophir A. 2017. Oxytocin neurons exhibit extensive functional plasticity due to offspring age in mothers and fathers. Integr Comp Biol 57:603–18.

MacDougall-Shackleton SA. 2011. The levels of analysis revisited. Philos Trans R Soc Lond B Biol Sci 366:2076–85.

McNamara JM, Houston AI. 2009. Integrating function and mechanism. Trends Ecol Evol 24:670–5.

McNamara JM, Leimar O. 2010. Variation and the response to variation as a basis for successful cooperation. Philos Trans R Soc Lond B Biol Sci 365:2627–33.

McNamara JM, Barta Z, Houston AI. 2004. Variation in behaviour promotes cooperation in the Prisoner's Dilemma game. Nature 428:745–8.

McNamara JM, Barta Z, Fromhage L, Houston AI. 2008. The coevolution of choosiness and cooperation. Nature 451:189–92.

O'Connell LA, Hofmann HA. 2011. The vertebrate mesolimbic reward system and social behavior network: a comparative synthesis. J Comp Neurol 519:3599–639.

O'Connell LA, Hofmann HA. 2012. Evolution of a vertebrate social decision-making network. Science 336:1154–7.

Okhovat M, Berrio A, Wallace G, Ophir AG, Phelps SM. 2015. Sexual fidelity trade-offs promote regulatory variation in the prairie vole brain. Science 350:1371–4.

Réale D, Dingemanse NJ. 2010. Social behaviour: genes, ecology and evolution. In: Székely T, Moore AJ, Kamdeur J, editors. Personality and individual social specialisation. Cambridge: Cambridge University Press. p. 417–41.

Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. 2007. Integrating animal temperament within ecology and evolution. Biol Rev 82:291–318.

Renn SC, Aubin-Horth N, Hofmann HA. 2008. Fish and chips: functional genomics of social plasticity in an African cichlid fish. J Exp Biol 211:3041–56.

Rubenstein DR, Hofmann HA. 2015a. New frontiers for the integrative study of animal behavior. Curr Opin Behav Sci 6:1–182.

Rubenstein DR, Hofmann HA. 2015b. Proximate pathways underlying social behavior. Curr Opin Behav Sci 6:154–9.

Saltzman W, Harris B, De Jong T, Perea-Rodriguez J, Horrell N, Zhao M, Andrew J. 2017. Paternal care in biparental rodents: intra- and inter-individual variation. Integr Comp Biol 57:589–602.

Sheehan M, Miller C, Reeve H. 2017. Identity signaling and patterns of cooperative behavior. Integr Comp Biol 57:580–8.

Sih A, Bell A, Johnson JC. 2004. Behavioral syndromes: an ecological and evolutionary overview. Trends Ecol Evol 19:372–8.

Smith JE, Petelle MB, Jerome EL, Cristofari H, Blumstein DT. 2017. Oxytocin experiments shed light on mechanisms shaping prosocial and antisocial behaviors in non-human mammals: a review and field study. Integr Comp Biol 57:619–30.

Taborsky M, Hofmann HA, Beery AK, Blumstein DT, Hayes LD, Lacey EA, Martins EP, Phelps SM, Solomon NG, Rubenstein DR. 2015. Taxon matters: promoting integrative studies of social behavior: NESCent Working Group on Integrative Models of Vertebrate Sociality: evolution, mechanisms, and emergent properties. Trends Neurosci 38:189–91.

Trivers RL. 1971. The evolution of reciprocal altruism. Quart Rev Biol 46:35–57.

Van Cleve J. 2017. Stags, hawks, and doves: social evolution theory and individual variation in cooperation. Integr Comp Biol 57:566–79.

van den Berg P, Weissing FJ. 2015. The importance of mechanisms for the evolution of cooperation. Proc R Soc Lond B Biol Sci 282:20151382.

van den Berg P, Molleman L, Junikka J, Puurtinen M, Weissing FJ. 2015. Human cooperation in groups: variation begets variation. Sci Rep 5:16144.

Weitekamp CA, Nguyen J, Hofmann HA. 2017. Neuromolecular regulation of aggression differs by social role during joint territory defense. Integr Comp Biol 57:631–9.

Wilson DS, Clark AB, Coleman K, Dearstyne T. 1994. Shyness and boldness in humans and other animals. Trends Ecol Evol 9:442–6.

Withee J, Rehan S. 2017. Social aggression, experience, and brain gene expression in a subsocial bee. Integr Comp Biol 57:640–8.

Wolf M, Krause J. 2014. Why personality differences matter for social functioning and social structure. Trends Ecol Evol 29:306–8.

Wolf M, Weissing FJ. 2012. Animal personalities: consequences for ecology and evolution. Trends Ecol Evol 27:452–61.