

Taxon matters: promoting integrative studies of social behavior

NESCent Working Group on Integrative Models of Vertebrate Sociality: Evolution, Mechanisms, and Emergent Properties

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The neural and molecular mechanisms underlying social behavior – including their functional significance and evolution – can only be fully understood using data obtained under multiple social, environmental, and physiological conditions. Understanding the complexity of social behavior requires integration across levels of analysis in both laboratory and field settings. However, there is currently a disconnect between the systems studied in the laboratory versus the field. We argue that recent conceptual and technical advances provide exciting new opportunities to close this gap by making non-model organisms accessible to modern approaches in both laboratory and nature.

Understanding the astonishing diversity of social behavior displayed by animals – including humans – is a central goal of biological research [1,2]. Such diversity has been studied from multiple, often non-overlapping perspectives. For example, behavioral ecologists and evolutionary biologists have long sought to understand the ultimate (functional) explanations for social interactions. By contrast, psychologists, endocrinologists, and neurobiologists have typically focused on the proximate (mechanistic) bases for these behaviors. These distinct and often unconnected approaches have impeded efforts to understand how natural selection (and thus evolution) shapes the mechanisms underlying social behavior, leading to several recent calls for greater integration of studies of mechanism and function [2–5].

Social interactions among free-living animals are remarkably rich, ranging from intensely-aggressive contests and cooperative exchanges to the complex, higher-order patterns of behavior associated with group living and reproduction [1,2]. Such interactions are influenced by multiple factors, including variation in individual phenotypes, life-history stages, and the social contexts in which encounters occur. Each of these variables may, in turn, be modulated by a range of genetic, epigenetic, developmental, endocrine, and neural mechanisms that are shaped by environmental conditions. Because these mechanisms affect Darwinian fitness, they must evolve via natural selection [6].

Although the evolution of the neural mechanisms underlying vertebrate social behavior is a rapidly growing area of research, surprisingly little is known about how selection acts to shape these mechanisms [7,8], in part because few studies have been able to fully integrate proximate and ultimate analyses regarding this aspect of behavioral biology [2,4] (Box 1). One crucial impediment to such integration is the frequent use of different model organisms by researchers pursuing ultimate- versus proximate-level questions [9,10]. Currently, the most detailed ecological and evolutionary datasets typically lack complementary neural, endocrine, and genetic information, and, conversely, laboratory species or traditional ‘model organisms’ whose neural substrates have been studied in detail are typically missing from datasets regarding ecology and adaptive function. Indeed, the taxonomic foci of these different approaches to the study of social behavior are so markedly divergent that there are strong negative relationships between the numbers of papers published on popular model species in neural versus in behavioral and ecological research (Figure 1).

The gulf between these research strategies has become increasingly anachronistic and counterproductive, for

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Box 1. New systems, new models of study

Biologists interested in the mechanisms underlying social behavior, and those interested in the evolution of behavior have long used different criteria for choosing study species. For example, neuroscientists have focused on species well suited to the laboratory, meaning that they respond well to captivity, have high fecundity and short development times, and are amenable to artificial selection to reduce intraspecific variation or to enhance desired phenotypic traits. Over time, this focus has resulted in the development of a highly-specialized tool kit that allows ever-deeper exploration of the mechanistic underpinnings for social behavior in this subset of organisms, causing strong specialization on a small number of model organisms. By contrast, evolutionary biologists have favored studies of free-living organisms, particularly those that display distinct patterns of social behavior, occur in diverse habitats, and represent a broad range of phylogenetic clades. Evolutionary biologists aim to identify principles that generalize across many species and ecological circumstances [1]. Hence, rather than exploring a limited number of species in detail, they have sought – often through the use of comparative studies – to broaden the range of organisms for which data regarding social behavior are available. The result is a pattern of selecting study species that is nearly orthogonal to that employed by neuroscientists (see Figure 1 in main text).

To capitalize on emerging opportunities to integrate studies of mechanism and function, new systems are required. In fact, we argue that we should move away from the concept of ‘model’ systems altogether. We suggest that these new systems should be characterized by several important attributes. First, they should consist of

species that can be studied in both captivity and in the field. Although it may not be possible to employ the same procedures for captive and free-living animals, the complementary information generated in these distinct settings is crucial for understanding how selection forms the mechanisms of social behavior. Second, these new systems should be species for which we have some understanding of the ecology and the adaptive value of social behavior; these foundations are crucial to linking neuroendocrine mechanisms to the selective contexts in which they occur in nature. Third, these new systems should be drawn from clades of animals that vary in their patterns of social structure and life history strategies; this variation is essential for exploring both the generality of neural and endocrine pathways and how such mechanisms have responded to environmentally induced changes in selective pressures. Collectively, these attributes represent a significant change in the nature of the study organisms used to probe mechanisms of social behavior.

Many animal systems that meet these new criteria are already under investigation by behavioral ecologists. Thus, the most efficient strategy for advancing the integration of mechanistic and functional studies would be to promote collaborations between neuroscientists and behavioral ecologists by encouraging coordination of research and training activities in ways that transcend disciplinary and organizational boundaries (including collaborative networks and synthesis centers, workshops, and summer schools for all career stages). In conclusion, to understand social behavior within an integrative framework, we not only need to identify new study systems, we also need new models of study.

instance impeding efforts to understand the evolution of mechanisms because the absence of comparative data from a range of species makes it challenging to study homologies in neural structure and function [2]. During the past decade, many issues of homology have been resolved for broad classes of species [5], and many of our most powerful analytical procedures have shifted from reagent-based to sequence-based tools, thereby tremendously reducing barriers to studies of mechanisms in non-traditional taxa. For example, neuroanatomists have mapped the distributions of major transcription factors, neuromodulators, and neural pathways to identify homologs of major brain regions across all major vertebrate lineages [11]. Moreover, the identification of common neuromodulators (e.g., monoamines,

nonapeptides) that underlie the coordination of behaviors in taxa as diverse as insects and humans suggests a very conserved core set of mechanisms that can be studied in many species [5,12]. Finally, major new technologies based on characterizing and manipulating gene sequences – ranging from early examples of gene therapy vectors and RNAi to the more recent methods of optogenetics, RNAseq, and CRISPR-based genome editing – can be applied as powerfully in non-traditional species as in traditional laboratory models, creating exciting new opportunities to investigate the immense diversity of social phenotypes found in the natural world. In short, we are no longer limited to studying traditional ‘model’ organisms to probe the mechanistic bases of social behavior.

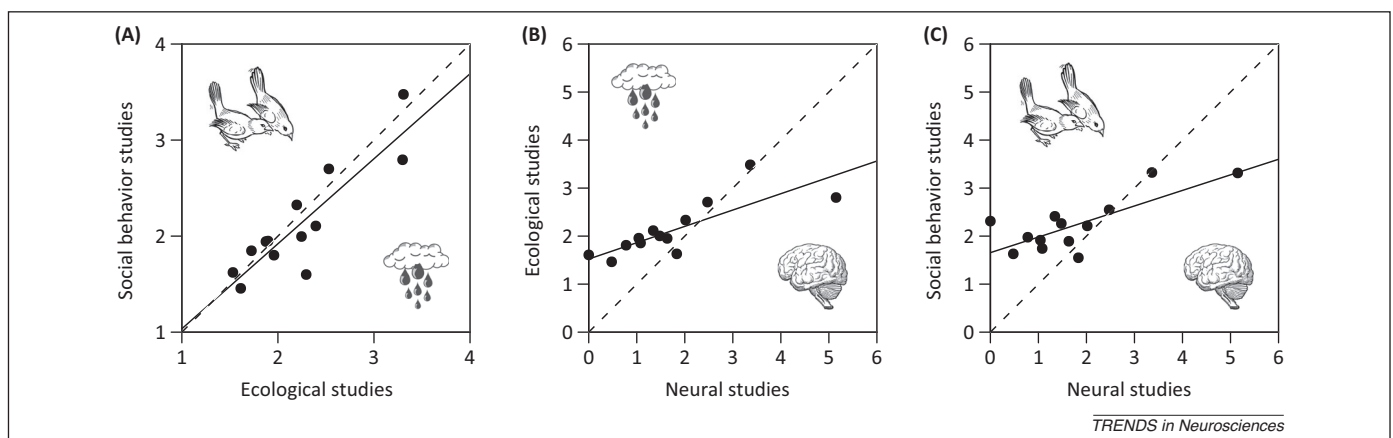


Figure 1. Disparity in the vertebrates used in studies of social behavior, ecology, and neuroscience. Research effort (numbers of studies, \log_{10} -transformed) summarized from a literature survey of representative model systems in behavioral ecology, reproductive biology, social behavior, and behavioral neuroscience. Panels illustrate correlations (continuous lines; $R^2 = 0.59\text{--}0.78$; all $P < 0.005$) between the numbers of studies per species compared to the assumption of similar research effort across these disciplines (broken lines; slope = 1). These analyses reveal (A) close correspondence between the number of studies on a species' behavior (reproductive and social) and ecology, but significant deviations [comparison of observed slopes with expectation (similar research effort): $P < 0.0001$] between (B) the relative number of ecological versus brain and neural studies and (C) the relative number of behavioral versus brain and neural studies from the same species. The raw data, including the species and search terms used, are provided in Table S1 in the supplementary material online.

Studies of a greater variety of taxa and phenotypes promise to broaden as well as deepen our understanding of the social brain. We argue emphatically that systematic disparities in the taxonomic foci of the two research approaches outlined above preclude attempts to integrate our understanding of social behavior, its neural substrates, and their evolution. These disparities are largely vestiges of past technical and conceptual obstacles that are rapidly being eliminated. To capitalize upon these opportunities and to promote greater synthesis of behavioral research, we recommend that neuroscientists and behavioral ecologists jointly (i) develop predictive models of social interactions that integrate function and mechanism, thereby allowing improved understanding of why a given species displays a particular set of behavioral outcomes [3]; (ii) generate testable predictions regarding the role of neural and other mechanisms in shaping social phenotypes in natural environments [13]; (iii) gather data and employ multivariate analyses in appropriate developmental and historical contexts to identify patterns of covariance across traits at multiple levels of organization, thereby generating crucial insights into the evolution of genetic, neural, and endocrine mechanisms of social behavior [2]. These goals can only be achieved if we identify suitable systems that allow concurrent study of social behavior in the laboratory and field [14] (Box 1).

The type of integrative analyses that we propose require behavioral, ecological, genetic, and neuroendocrine data from the same species. While there has been a tremendous bias towards studies of rats and mice as model organisms in neuroscience and endocrinology (>90% of non-human mammals) [15], it is time to expand the taxonomic scope of this work to explore the neural and molecular substrates of behavioral variation in species that can also be studied in their natural ecological and social contexts. While this review has emphasized vertebrates, our call for greater integration extends to all animal lineages with social phenotypes, including insects and other invertebrates. Such integrative research is essential to determine how intra- and inter-specific differences in social behavior are influenced by variation in the underlying mechanisms, as well as to identify the roles of ecological and evolutionary forces in shaping the mechanistic bases for complex social behavior in all animals.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.tins.2015.01.004>.

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SPECIES		SEARCH TERMS														Total number of studies	
Latin name	Common name	habitat	Ecology							Reproductive & Social Behavior			Brain & Neural Studies				
			(resource* OR food OR shelter*) AND NOT (neur* OR OR	predat* OR	distribut* OR spac* AND NOT (brain OR neur*)	kinship OR relatedne	demograp h*	(resource* AND acqui*) OR forag*	predat* AND	mat* OR reprod* OR spawn* AND NOT (brain OR neur*)	"parent* care" OR "brood care" OR "offspring care" AND NOT (brain OR neur*)	(reprod* OR sexual) AND mat* AND NOT (brain OR neur*)	"white matter" OR neuroanat* OR ("brain region" AND (size OR volume))	(neuromod* OR neuroendocrin* OR neuropeptid* OR hormon*) NOT receptor	receptor AND (neur* OR brain)	"neural activity" OR "immediate early gene" OR "firing rate"	
<i>Neolamprologus pulcher</i>	Princess of Lake Tanganyika	5	27	22	8	11	1	3	1	47	19	20	0	9	1	0	174
<i>Astatotilapia burtoni</i>	Burton's mouthbrooder	7	10	5	9	0	0	1	1	32	0	8	9	31	27	0	140
<i>Danio rerio</i>	Zebrafish	64	411	209	1251	12	7	32	41	2688	1	242	116	518	1617	57	7266
<i>Peromyscus californicus</i>	California mouse	28	11	28	19	0	2	2	0	47	8	6	0	1	4	0	156
<i>Microtus ochrogaster</i>	Prairie vole	36	41	29	26	4	11	5	4	149	8	49	6	17	50	30	465
<i>Cynomys ludovicianus</i>	Black-tailed prairie dog	75	17	29	40	1	9	22	3	36	0	2	0	0	0	0	234
<i>Rattus norvegicus</i>	Rat	355	404	613	490	8	30	61	23	551	4	55	5854	54982	73867	6385	143682
<i>Junco hyemalis</i>	Junco	59	57	52	38	1	1	32	7	98	5	21	10	2	9	0	392
<i>Taeniopygia guttata</i>	Zebra Finch	15	159	52	57	6	1	47	1	357	12	121	44	27	132	93	1124
<i>Physalaemus pustulosus</i>	Tungara frog African clawed	8	5	21	15	0	1	1	1	46	0	22	1	2	3	5	131
<i>Xenopus laevis</i>	frog	5	17	13	37	0	1	1	0	71	0	14	1	8	28	5	201
<i>Cnemidophorus inornatus</i>	Whiptail lizard	40	31	31	42	0	2	27	2	71	0	25	3	6	20	0	300
<i>Anolis carolinensis</i>	Green Anole	10	8	9	10	0	2	1	0	22	1	4	0	0	2	0	69
Total Number of studies		707	1198	1113	2042	43	68	235	84	4215	58	589	6044	55603	75760	6575	154334

Table S1: Results of the literature review of model systems for which detailed ecological, reproductive, and/or neurobiological information are available. The search terms used are listed in the second row of the table; we searched for publications containing these terms in the title and abstract using the SCOPUS Database (search conducted 11 March 2013). Relative research effort in ecology, reproductive biology, and neurobiology was estimated for each model system from the number of hits for the indicated Boolean combination of search terms.