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# Towards an integrative understanding of social behavior: new models and new opportunities

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**Running title:** Integrating studies of social behavior

47 Social interactions among conspecifics are a fundamental and adaptively significant  
48 component of the biology of numerous species. Such interactions give rise to group living  
49 as well as many of the complex forms of cooperation and conflict that occur within  
50 animal groups. Although previous conceptual models have focused on the ecological  
51 causes and fitness consequences of variation in social interactions, recent developments  
52 in endocrinology, neuroscience, and molecular genetics offer exciting opportunities to  
53 develop more integrated research programs that will facilitate new insights into the  
54 physiological causes and consequences of social variation. Here, we propose an  
55 integrative framework of social behavior that emphasizes relationships between ultimate-  
56 level function and proximate-level mechanism, thereby providing a foundation for  
57 exploring the full diversity of factors that underlie variation in social interactions, and  
58 ultimately sociality. In addition to identifying new model systems for the study of human  
59 psychopathologies, this framework provides a mechanistic basis for predicting how social  
60 behavior will change in response to environmental variation. We argue that the study of  
61 non-model organisms is essential for implementing this integrative model of social  
62 behavior because such species can be studied simultaneously in the lab and field, thereby  
63 allowing integration of rigorously controlled experimental manipulations with detailed  
64 observations of the ecological contexts in which interactions among conspecifics occur.

65

66 **Keywords: integrative models of social behavior; behavioral neuroendocrinology;**  
67 **behavioral genetics; psychopathology; model systems**

68

69

70 **Introduction**

71 Social behavior is comprised of interactions among conspecifics and results in  
72 relationships of variable form, duration, and function. Social interactions provide the  
73 foundation for a broad array of behavioral phenomena, including many of the complex  
74 forms of cooperation and conflict that are of particular interest to behavioral biologists  
75 (Nowak, 2006). For example, group living and communal rearing of young are forms of  
76 sociality that arise from social interactions among individuals. Sociality (broadly defined  
77 as group living) presents an apparent evolutionary paradox in that individuals may incur  
78 fitness costs by engaging in these interactions (Alexander, 1974; Griffin and West, 2002).  
79 Collectively, these phenomena form the basis for some of the most intricate and  
80 intriguing societies observed in nature (Wilson, 1975). In humans, social relationships are  
81 essential components of well-being (House et al., 1988).

82 While not all forms of social interaction are as complex or challenging to interpret as  
83 cooperative behaviors, social behavior is a fundamental attribute of the biology of many  
84 species and has been the focus of extensive research by scientists from multiple  
85 disciplines. Despite widespread application to basic and applied science, developing a  
86 comprehensive framework for explaining the proximate and ultimate bases for social  
87 interactions -- a rapidly emerging theme in behavioral research (Owens 2006) -- has  
88 proven troublesome (Johnstone, 2000). Traditional models of social variation have  
89 focused primarily on the ecological and evolutionary factors that lead to specific forms of  
90 social interaction (e.g., group living: Emlen and Oring, 1977; Emlen, 1995; Brashares  
91 and Arcese, 2002; Cahan et al., 2002). However, recent advances in neuroscience,  
92 endocrinology, and genetics have generated the knowledge and the toolkit required for

93 more integrative approaches to understanding social interactions (Young and Wang,  
94 2004). Developing a conceptual framework that incorporates these new resources is  
95 essential; in addition to informing research at multiple levels of organization (e.g., from  
96 molecular to evolutionary processes), such advances in our understanding of social  
97 interactions should have applications to human welfare and health, including improved  
98 diagnosis and treatment of psychopathologies such as autism, schizophrenia and  
99 depression (Bartz and Hollander, 2006; Lim and Young, 2006; Bosch et al., 2009;  
100 McGraw and Young, 2010).

101 Here, we outline an integrative framework for studying social behavior that addresses  
102 four important elements of modern behavioral biology. First, the framework highlights  
103 recent genetic, endocrine, and neurobiological advances that are creating new  
104 opportunities to study mechanisms of social behavior in an ecological context. By so  
105 doing, the framework integrates well developed, but traditionally distinct areas of inquiry  
106 and fosters the use of new technologies to explore social interactions in non-traditional  
107 study organisms and in non-laboratory settings. Second, the framework helps generate  
108 predictions about social relationships that can be tested in either the field or the  
109 laboratory and that aid discrimination between the causes and consequences of social  
110 interactions. Third, the framework explores the diversity of mechanisms that underlie  
111 social variation, thereby facilitating identification of large-scale patterns in the evolution  
112 of the genetic, endocrine, and neural bases for social behavior. Fourth, using non-  
113 traditional and natural systems is key to understanding natural variation in social behavior  
114 and sociality, and doing so will shed light on mechanisms maintaining social variation.

115 One outcome of the integrative approach that we describe is to shift attention to  
116 studies of new animal systems, some of which have been well studied by ecologists, but  
117 that have not previously been considered as subjects for more mechanistic studies of  
118 social relationships. Overall, this review should encourage new collaborations between  
119 behavioral biologists from multiple disciplines, thereby leading to exciting developments  
120 in our understanding of social behavior, including the social interactions that underlie  
121 multiple human disorders.

122

### 123 **Levels of analysis: Tinbergen revisited**

124 Traditional studies of social behavior have tended to follow the framework established by  
125 Niko Tinbergen (1963), who outlined four orthogonal explanations for the diversity of  
126 behavior observed in nature: (1) immediate causation, (2) development, (3) function, and  
127 (4) evolutionary history. Immediate causes of behavior include physiological, genetic or  
128 ontogenetic factors, as well as the interactions among these aspects of an organism's  
129 biology. Developmental explanations include any changes in behavior resulting from  
130 ontogenetic processes or experiences. Functional causes describe how behavior currently  
131 influences survival and reproduction. Finally, historical explanations use a species'  
132 phylogenetic relationships to generate insights into the evolutionary gain or loss of a  
133 behavioral trait. These four approaches to the study of behavior can be divided into two  
134 levels of analysis (Sherman, 1988). Immediate causation and development comprise  
135 *proximate* explanations that answer questions regarding *how* behaviors occur  
136 mechanistically. Function and evolutionary history comprise *ultimate* explanations that  
137 reflect on *why* behaviors have evolved or are maintained. The four explanations are

138 complementary -- not exclusive -- and any trait can be studied at any (and likely all) of  
139 these level(s) of inquiry (Bolhuis and Verhulst, 2009). We propose that incorporating  
140 each of these levels of analysis will lead to a more integrative understanding of social  
141 behavior that will benefit all disciplines.

142       Historically, behavioral ecologists have emphasized ultimate-level questions, while  
143 biomedical researchers have focused on proximate-level phenomena, creating a  
144 conceptual and practical divide between these research settings that includes the  
145 emergence of distinct terminologies, methodologies, and study organisms. Recently,  
146 however, traditionally field-based behavioral ecologists have re-discovered the  
147 importance of studying proximate mechanisms (e.g., genetic, physiological,  
148 neuroendocrine, and neurophysiological processes) underlying behavior in order to better  
149 understand the evolution of behavior (Stamps, 1991; Owens, 2006). This increased  
150 recognition of the importance of proximate-level research has been facilitated by  
151 technical advances that have made mechanistic studies more tractable and that have  
152 opened up new lines of inquiry for understanding social behavior. In particular, recent  
153 advances linking physiology, genomics, and behavior offer exciting new opportunities to  
154 integrate ultimate- and proximate-level questions to explore social interactions, thereby  
155 forging new links between social behavior and potential causes of human behavioral  
156 dysfunction (Robinson et al., 2008). We feel strongly that likewise, biomedical research  
157 could benefit tremendously from incorporating the perspectives of behavioral ecologists  
158 to discover new model organisms and to refine experimental paradigms in an  
159 ethologically relevant manner.

160

161 **The importance of natural populations**

162 As an ethologist, Tinbergen’s studies of behavior were based largely upon observations  
163 of free-living animals faced with the challenges of surviving and reproducing in complex,  
164 “real world” environments. While studies of natural populations typically lack the  
165 rigorous control of environmental and inter-individual variation characteristic of  
166 laboratory-based research, data from free-living animals are critical to a comprehensive  
167 understanding of variation in social behavior for several reasons. First, observations of  
168 free-living individuals, behaving in species-typical ways, can be used to validate data  
169 from laboratory studies by confirming that behavioral interactions observed in captivity  
170 are characteristic of those observed in natural environments (Holmes and Sherman, 1982;  
171 Schradin and Pillay, 2003). Second, when observations of captive and free-living  
172 conspecifics differ, comparisons of data obtained in these two distinct contexts can be  
173 used to generate new insights into the factors regulating behavior (Calisi and Bentley,  
174 2009). Third, studies of free-living animals provide the ecological context required to  
175 evaluate the functional consequences of social behavior. Specifically, data from natural  
176 populations allow investigators to assess the reproductive and survival (functional)  
177 consequences of behavior under the selective conditions in which it normally occurs; in  
178 the absence of such information, it can be difficult to determine the functional and, hence,  
179 potential evolutionary significance variation in social interactions. Thus, while many of  
180 the recent endocrine, neural and genetic advances in our understanding of behavior have  
181 necessarily begun in the lab, applying these ideas and technologies to natural populations  
182 is essential to generating a complete understanding of the causes of variation in social  
183 behavior.

184

185 **Genetic and genomic advances: new opportunities to explore natural systems**

186 Studies of humans as well as traditional non-human animal models (e.g., *Drosophila*  
187 *melanogaster*, *Caenorhabditis elegans*, *Mus musculus*, *Rattus norvegicus*) have been  
188 invaluable for identifying genes involved in the regulation of social behavior (Robinson  
189 et al., 2005). Given that gene function is often conserved, we expect that numerous  
190 homologous loci await study in non-traditional model systems, thereby allowing  
191 exploration of gene expression in free-living animals subject to variable environmental  
192 conditions. For example, in lab populations of *D. melanogaster*, the *foraging* gene is  
193 responsible for differences in locomotor activity related to securing food; homologues of  
194 *foraging* have been shown to influence the age of onset of foraging in free-living  
195 honeybees (*Apis mellifera*) (Robinson et al., 2008; Amdam and Page, 2010). Among  
196 humans, allelic variants of the gene *Drd4* are associated with personality traits and  
197 novelty seeking; this locus appears to play a similar role in natural populations of birds,  
198 such as great tits (*Parus major*; Fidler et al., 2007). Finally, polymorphisms in the  
199 vasopressin receptor gene, *Avpr1a*, are associated with pair bonding behavior in both  
200 humans and prairie voles (*Microtus ochrogaster*) (Hammock and Young, 2005;  
201 Donaldson and Young, 2008) This conservation of gene function across sometimes  
202 disparate taxonomic groups provides an important foundation for expanding studies of  
203 the genetic bases of social behavior to natural populations of animals

204 At the same time, the ever-expanding toolkit for genetic research makes it  
205 increasingly possible to undertake experimental studies of the genetic mechanisms  
206 underlying social behavior. For example, use of siRNA to knock down gene expression

207 in zebra finch (*Taeniopygia guttata*) has revealed that a homologue of *FoxP2* (a gene  
208 thought to be involved in human language) also plays an important role in vocal learning  
209 in songbirds (Haesler et al., 2007). Viral vector-mediated gene transfer has been used to  
210 over-express genes in specific brain regions to determine gene function in species such as  
211 prairie voles, yielding critical insights into the causes of social and mating system  
212 variation across species (Lim et al., 2004; Ross et al., 2009). Transgenic technologies,  
213 although currently limited to a few species, are being developed for non-traditional model  
214 organisms as diverse as prairie voles, three-spine sticklebacks (*Gasterosteus aculeatus*)  
215 and non-human primates (Hosemann et al., 2004; Donaldson et al., 2009; Sasaki et al.,  
216 2009). As such technologies become easier to employ, the range of species to which they  
217 are applied should grow, yielding an increasingly rich picture of the genetic bases for  
218 variation in social behavior.

219 Finally, for organisms lacking a fully sequenced genome, transcriptome studies (i.e.,  
220 quantification of gene expression on a genome-wide scale) provide a tractable means of  
221 identifying genes underlying social behavior. DNA microarrays for honeybees were used  
222 to develop one of the first genome-wide views of social structure (Robinson et al., 2008)  
223 and studies of ants have demonstrated that similar genes underlie social variation (Ingram  
224 et al., 2005) in both insect lineages. Microarrays have also been used in swordtails  
225 (*Xiphophorus nigrensis*) to determine how gene expression differs between social and  
226 sexual signals (Cummings et al., 2008) and in African cichlids (*Astatotilapia burtoni*) to  
227 identify candidate genes related to social behavior, including loci that are up-regulated in  
228 dominant but not subordinate individuals (Renn et al., 2008). The rapid development of  
229 high-throughput, low-cost, “next generation” genomic sequencing technologies make it

230 increasingly feasible to explore gene activity in a variety of non-traditional animal  
231 systems.

232

233 **Neuroendocrine advances: improving understanding of social variation**

234 Greater understanding of how neuroendocrine processes regulate behavior represents  
235 another area in which studies of natural populations may complement our rapidly  
236 expanding knowledge of traditional animal models. In particular, predicting how  
237 neuroendocrine activity should affect the social behavior of free-living animals is central  
238 to the development of an integrative model of sociality (Nunes et al. 1999; Ryan and  
239 Vandenberg, 2002). Below, we highlight several exciting areas of research into the  
240 neuroendocrine bases for social behavior. Two of these (circulating hormone levels,  
241 receptor density and expression) are pathways for which evidence is already accruing  
242 regarding neuroendocrine or neuroanatomical influences on social behavior. While few  
243 empirical data are available for the third pathway (binding globulins), this aspect of  
244 neuroendocrine function appears to hold great potential for future research into the  
245 proximate bases for social variation.

246 (1) *Circulating hormone levels*. Much of the research linking environmental  
247 variation, neuroendocrine function, and social behavior in vertebrates has focused on  
248 circulating concentrations of steroids (Wingfield et al., 1990; Schoech et al., 2004; Pfaff,  
249 2005), particularly glucocorticoids (Creel, 2001; Pfaff, 2005). For example, singular  
250 breeding societies with communal care of offspring (i.e., one female dominates  
251 reproduction and non-breeders care for non-descendent offspring; Silk, 2007) may be a  
252 selectively advantageous social strategy in stressful environments in which independent

253 reproduction is rarely successful (Moehlman, 1979). Under these conditions, group  
254 members may produce lower levels of glucocorticoids when groups are at or below  
255 threshold size (Silk, 2007), which in turn reduces social stress and enhances cooperative  
256 rearing of offspring. Alternatively, social animals may experience chronically high levels  
257 of stress hormones which could have negative fitness consequences and possibly explain  
258 habitat-specific fitness outcomes of group-living and the establishment of social  
259 hierarchies (Creel, 2001; Young et al., 2006; Rubenstein, 2007). Whether variation in  
260 glucocorticoids causes or results from social variation needs experimental demonstration  
261 (Rubenstein and Shen, 2009). There is some evidence of reduced androgens in non-  
262 breeding male alloparents, but as with glucocorticoids, patterns of androgen variation are  
263 not consistent across species (Schoech et al., 2004). For example, in striped mice  
264 (*Rhabdomys pumilio*) — a socially flexible species in which males exhibit alternative  
265 mating tactics and varying levels of parental care — subordinate ‘roamer’ males have  
266 higher levels of testosterone than dominant territorial males (Schradin et al., 2009).  
267 There is also some evidence that prolactin may play a causal role in subordinate helping  
268 behavior in some birds (Buntin, 1996; Schoech et al., 2004).

269       (2) ***Receptor density and expression.*** In rodents, intraspecific variation in social  
270 organization and in behaviors such as social bonding and parental care has been linked to  
271 variation in neuropeptide receptor densities in the brain (Hammock and Young, 2004;  
272 Olazábal and Young, 2006a,b; Beery et al., 2008). Highly social and monogamous  
273 species have oxytocin and vasopressin receptors concentrated in regions of the brain  
274 associated with reward and reinforcement, while non-monogamous species do not  
275 (Young and Wang, 2004). Viral vector gene transfer has been used to manipulate

276 neuropeptide receptor expression in these brain regions in voles (*Microtus* spp.), thereby  
277 demonstrating a causal link between receptor expression and these aspects of behavior  
278 (Lim et al., 2004). At a genetic level, polymorphisms in the promoter regions of the genes  
279 encoding these receptors appear to contribute to diversity in receptor expression patterns  
280 (Hammock and Young 2004). Oxytocin-like receptors may also influence sociality in  
281 birds (Goodson et al. 2009). The remarkable plasticity of the oxytocin and vasopressin  
282 receptor systems provides a potential mechanism for creating diversity in social  
283 phenotypes of both males and females. Future studies are needed to determine the  
284 relevance of these receptor systems in shaping social and reproductive interactions in  
285 natural populations of other taxa. Species with populations that exhibit intraspecific  
286 geographic variation in social mating systems (Roberts et al., 1998) may be particularly  
287 strong candidates to study variation in neuropeptide systems.

288 (3) ***Binding globulins***. Steroid-binding proteins are glycoproteins that transport  
289 hormones of the hypothalamic-pituitary-adrenal (HPA) and hypothalamic-pituitary-  
290 gonadal (HPG) axes to target tissues (Westphal, 1983; Breuner and Orchinik, 2002). The  
291 function of binding globulins is much debated. It is not clear whether binding globulins  
292 act simply to transport steroids to target tissues (carrier hypothesis) or whether they act  
293 like a sponge to bind excess steroids to prevent them from reaching target tissues, thereby  
294 buffering tissues from high circulating steroid levels (buffer hypothesis) (Romero, 2002).  
295 Moreover, the function of steroid-binding proteins could differ among taxa. For  
296 example, in contrast to mammals, birds appear to lack a sex steroid-specific binding  
297 globulin; instead sex steroids (e.g., testosterone) are bound to corticosteroid-binding  
298 globulins (CBG) (Deviche et al., 2001). In captive rats, subordinate individuals had

299 lower CBG concentrations than dominant individuals (Spencer et al., 1996; Stefanski,  
300 2000) while in horses social stress caused a decrease in CBG binding capacity  
301 (Alexander and Irvine, 1998). These results suggest a potentially crucial link between  
302 stress, CBG, and inter-individual variation in social behavior. Consequently, the role of  
303 CBG and other binding globulins deserves further consideration in studies of vertebrate  
304 social behavior.

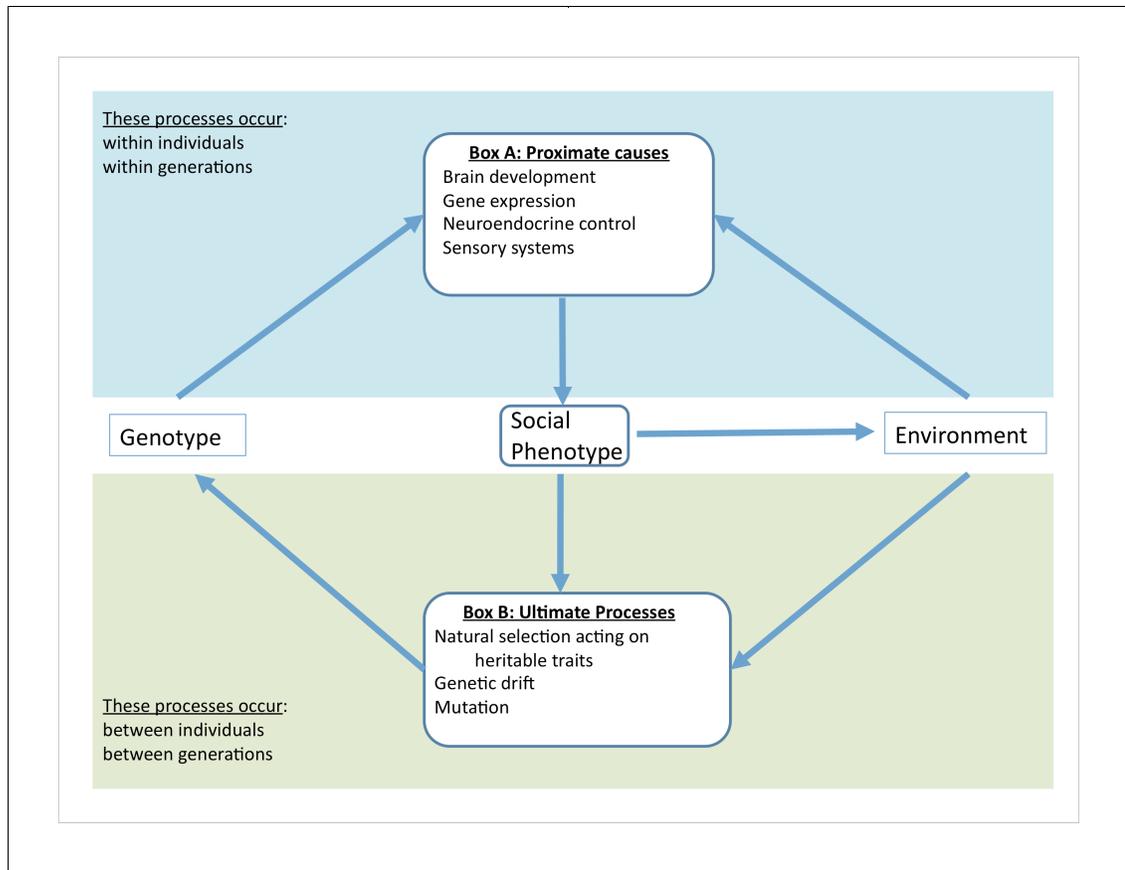
305 Continued research into how neuroendocrine mechanisms influence social behavior  
306 in diverse organisms will lead to improved understanding of the evolution of mechanistic  
307 diversity. When coupled with data regarding the adaptive context of social behavior  
308 obtained from studies of free-living animals, this understanding will allow us to identify  
309 ideal model systems for human psychopathologies. These predictive abilities will emerge  
310 from the study of a diversity of species, engaged in a diversity of social behaviors.

311

### 312 **An integrative approach: guiding future research**

313 Figure 1 illustrates how environmental conditions and natural selection may interact to  
314 shape the proximate mechanisms underlying variation in social interactions and, in turn,  
315 how those mechanisms may affect the fitness consequences of differences in social  
316 behavior. Pathways link social and ecological responses to physiological and behavioral  
317 changes in the individual. We believe that both disciplines (behavioral ecology and  
318 biomedical research) could benefit tremendously from adopting this integrative  
319 perspective.

320



321

322

323 Fig 1. An integrative framework for studying social behavior. This framework is  
 324 consistent with the recursive evolutionary paradigm (Feder et al., 2000) wherein the  
 325 genotype of an individual works in concert with the environment to produce a given  
 326 phenotype (Box A). This has adaptive and non-adaptive consequences that determine the  
 327 genotypes in the next generation (Box B). Social phenotypes may influence the  
 328 environment in multiple ways, indicating a dynamic bi-directional relationship that can  
 329 affect processes in both boxes. Since the environment in turn influences both proximate  
 330 mechanisms and ultimate processes, it is important to study both to gain an integrative  
 331 understanding of social behavior. For example, if a social behavior decreases predation  
 332 threat, behavioral biologists should examine how that decrease affects the neuroendocrine

333 mechanisms underlying that behavior in addition to how it affects the selective landscape.  
334 Moreover, because proximate mechanisms (Box A) are themselves subject to  
335 evolutionary dynamics (Box B), there is a need for research measuring selection on and  
336 heritability of that neuroendocrine mechanism rather than simply the direct effect on the  
337 social behavior. This model, while not exhaustive, provides a framework and guidance  
338 for synthetic research of sociality.

339

#### 340 **Integrative research directions**

341 Below, we highlight several important areas of research that are being enhanced by an  
342 integrative approach to social behavior; we expect that other, new lines of inquiry will  
343 emerge as additional mechanisms and techniques are incorporated into an integrative  
344 framework such as we propose. To underscore the utility of this framework in uniting  
345 traditional and emerging perspectives on social behavior, we cast our review in terms of  
346 the four orthogonal research questions outlined by Tinbergen nearly 50 years ago:

347       **(1) Immediate causation.** The environment may contribute to intraspecific variation  
348 in behavioral phenotypes by altering proximate mechanisms governing behavior,  
349 including allelic variation, gene expression, and neural activity. For example, prairie  
350 voles found in ecologically distinct populations exhibit marked differences in social  
351 behavior (Roberts et al., 1998). Young and colleagues (Young and Wang, 2004) have  
352 shown that this variation in vole social behavior is linked to variation in  
353 oxytocin/vasopressin receptor densities in the brain, with the expression of these  
354 receptors being mediated by the *oxtr* and *avpr1a* genes. Our model integrates this  
355 information, generating the following predictions: (a) the immediate ecological causes of

356 habitat-specific social behavior include factors such as the distribution of food resources  
357 or habitat openness, (b) differential selection resulting from this ecological variation leads  
358 to population-level differences in the frequency of *avr1a* alleles, and (c) allelic  
359 differences in *avr1a* gene expression explain population-specific neuropeptide receptor  
360 densities.

361       **(2) Ontogeny.** Variation in the physical or social environment may influence the  
362 timing of ontogenetic changes (nervous system development, endocrine function, gene  
363 expression) that mediate social behavior. For example, natal philopatry is widely  
364 recognized as an important process leading to the formation of social groups (Emlen,  
365 1995). The ecological causes of natal philopatry are usually attributed to benefits of  
366 philopatry (e.g., indirect fitness) or ecological constraints on dispersal (e.g., habitat  
367 saturation). Nunes et al. (1999) demonstrated that Belding's ground squirrel (*Urocitellus*  
368 *beldingi*) dispersal is mediated by organizational effects of testosterone during early  
369 postnatal development. Within such a mammalian system, our framework could integrate  
370 these ideas, generating the following predictions: (a) limited resources lead to reduced  
371 hypothalamic production of GnRH, pituitary responsiveness to GnRH, and leutenizing  
372 hormone receptor expression during early post-natal development, resulting in fewer  
373 dispersers and greater natal philopatry, (b) individuals staying in the group have higher  
374 inclusive fitness than those that disperse or do not form groups, and (c) social group  
375 formation decreases testosterone during early post-natal development, resulting in greater  
376 dispersal and reduced philopatry. Other areas of exploration include how (i) ecology  
377 influences maternal condition and, therefore, offspring development and adult behavior  
378 (e.g., intrauterine position effects on social behaviors; Ryan and Vandenberg, 2002) and

379 (ii) ecological and social variation influence the genetic and hormonal pathways leading  
380 to the development of alloparental care.

381       **(3) *Function.*** The fitness consequences of social behavior are often habitat-specific  
382 (Silk, 2007). Individuals encounter environmental variation and respond accordingly both  
383 during ontogeny (that determines phenotype) and through day-to-day, seasonal and  
384 facultative experience. The resulting social behavior (a phenotype) has costs and benefits,  
385 the magnitudes of which determine fitness (lifetime reproductive success). These ideas  
386 can be tested in the context of social behavior such as group foraging, which is thought to  
387 reduce the risk of predation. Under this hypothesis, social foraging is selectively  
388 advantageous in open habitats or in habitats with abundant predators (Ebensperger, 2001;  
389 Brashares and Arcese, 2002). However, social foraging has costs and thus, may occur  
390 less in habitats with low predation pressure. Different neural and sensory pathways are  
391 expected to be activated in these ecological and social conditions (*sensu* Hermes et al.,  
392 2009). For example, if the function of social foraging is to reduce predation risk, then  
393 reduced allostatic loads are expected when individuals forage together. This hypothesis  
394 predicts that (a) individuals have higher circulating glucocorticoid levels in populations  
395 with abundant predators and (b) circulating glucocorticoid levels decrease with increasing  
396 number of individuals per foraging group in populations with high levels of predation  
397 risk.

398       **(4) *Evolutionary history.*** While such studies are largely lacking, each of the above  
399 topics can be addressed through comparative studies conducted in a phylogenetic context.  
400 By examining patterns of mechanistic diversity across a broad array of taxa for which  
401 phylogenetic relationships are known, it should be possible to identify previously

402 unrecognized examples of evolutionary divergence, convergence, and conservation of  
403 mechanisms of social behavior. Social phenotypes can be constrained by the genetic  
404 architecture of proximate mechanisms, which is dependent on evolutionary history.  
405 Once these phenomena have been comprehensively characterized, it will be possible to  
406 study the evolution of mechanism in novel and comprehensive ways. In particular, once  
407 these evolutionary patterns have been identified, we will be able to complete much more  
408 meaningful analyses of the ways in which ecological and life history factors affect  
409 mechanisms of social behavior, thereby linking studies of mechanism back to the  
410 ultimate-level questions most often addressed by behavioral ecologists. For example, as  
411 we gather more information on the link between mating systems and the expression of  
412 neuropeptide receptors underlying social variation, it will be possible to employ  
413 phylogenetically controlled comparative approaches. Based on ecological (Emlen and  
414 Oring, 1977) and neuroanatomical (Young and Wang, 2004) theory, we expect that  
415 across taxa, the expression of neuropeptide receptors underlying mating systems (e.g.,  
416 oxytocin, vasopressin) will be similar in species found in similar habitats.

417

#### 418 **An evolutionary context for understanding the mechanisms of social variation**

419 As noted above, an evolutionary approach to studies of the proximate mechanisms  
420 underlying social behavior may lead to new, comparative insights into how such  
421 mechanisms evolve and are maintained in animal populations. We believe that this  
422 outcome of an integrated approach to social behavior is so important that we wish to  
423 elaborate upon this topic with the following examples:

424       (1) **Divergence**. There are multiple ways to solve a mechanistic problem, leading to  
425 the potential for considerable evolutionary divergence in the mechanistic bases for social  
426 behavior. This variation may be evident, for example, in the ways that hormones are  
427 regulated; while some endocrine mechanisms are modulated at the secretory level, others  
428 are modulated at the level of receptor number or sensitivity (Bamberger et al., 1996).  
429 Temporal variation in neuroendocrine mechanisms is also evident. For example, in some  
430 birds, aggression (e.g., territory defense) during the mating season is regulated by  
431 circulating testosterone while territoriality during the non-breeding season is regulated by  
432 localized (i.e., non-circulating) production of testosterone and estradiol produced within  
433 the brain (Soma et al., 2008).

434       (2) **Convergence**. The variety of mechanisms associated with social behavior also  
435 raises the possibility of evolutionary convergence in hormonal and other proximate  
436 solutions to behavioral challenges. As a potential example of such convergence, bird song  
437 and fish acoustical signals – both of which are involved in territory defense -- involve  
438 very different sound-production organs (syrinx, swim bladder, electric organs), yet both  
439 systems are modulated by androgens and are regulated by distinct but similarly  
440 functioning neural circuitry (Smith et al., 1997; Zakon and Dunlap, 1999; Bass et al.,  
441 2008).

442       (3) **Conservation of function**. Particularly effective mechanisms may be retained  
443 over time and through speciation events because of the adaptive benefits that they confer.  
444 For example, oxytocin and vasopressin (or their homologs) are involved in maintaining  
445 affiliative relationships in songbirds (Goodson et al., 2009) and in voles (Donaldson and  
446 Young, 2008). Similarly, glucocorticoids have a generalized role in mobilizing energy

447 and redirecting behavior in many vertebrates and across many different social contexts  
448 (Denver, 2009). These observations suggest that these endocrine systems have deep  
449 evolutionary histories and that their functions have been conserved for extended periods  
450 of vertebrate evolution.

451 In general, these patterns will only emerge from a comparative, evolutionary  
452 approach. However, more information on the mechanisms of social behaviors is needed  
453 from a diverse range of taxa before such comparisons can be made. At this time, we lack  
454 evidence of mechanisms underlying social behaviors from sufficient taxa – until this  
455 information is discovered such comparative, evolutionary approaches are unattainable.  
456 Thus, we argue that behavioral ecologists and neuroscientists need to engage in more  
457 collaboration aimed at identifying the mechanisms of social behaviors in new model  
458 organisms, expanding on the limited number of traditional model organisms used to date.

459

#### 460 **Redefining model organisms**

461 Natural selection has generated an extraordinary diversity of behavioral adaptations to  
462 environmental variation. Behavioral ecologists have exploited this diversity to determine  
463 the ecological causes and fitness consequences of variation in social behavior in a wide  
464 range of species. However, our understanding of the genetic and neuroendocrine basis of  
465 social behavior is still limited and has been derived primarily from laboratory studies of  
466 inbred lines of classic model organisms (e.g., mice, rats and fruit flies; Sokolowski,  
467 2010). Indeed, there may be non-model systems that might be better models than these  
468 classic model organisms. To begin to use our integrative model to gain a comprehensive  
469 understanding of social interactions, it is time to rethink the traditional definition of a

470 model organism and to begin developing new model systems in which it is possible to  
471 study ultimate-level questions of function as well as the proximate-level neurobiological  
472 and genetic mechanisms that underlie social variation.

473 An ideal model system should exhibit marked spatial or temporal variation in social  
474 behavior that can be studied quantitatively both in the laboratory and in natural (or semi-  
475 natural) environments. Traditionally, traits that have made an organism valuable to  
476 laboratory studies have included short generation times, regular reproduction in the  
477 laboratory environment, ease of handling for experimental manipulations, and availability  
478 of tools for characterizing genetic, neural, and endocrine mechanisms. However, some  
479 free-living species might illustrate the ways human populations have spread throughout  
480 world, and hence they might provide an ideal model to analyze social variation and  
481 behavioral mechanisms that are uniquely shaped by this dispersal history and subsequent  
482 adaptation to a variety of ecological situations. As genetic and other technologies  
483 improve, the ability to study mechanisms in less traditional model species increases  
484 (Donaldson and Young, 2008; McGraw and Young, 2010). Other desirable traits such as  
485 ease of capture and observation in the wild will ensure that as these technologies become  
486 increasingly available and affordable.

487

#### 488 **Relevance to human social behavior**

489 The integrative approach we suggest, coupled with the development of new model  
490 organisms for the study of variation in social behavior may provide a powerful means to  
491 translate research findings into improved understanding human social cognitive function  
492 (Ebstein et al., 2010; Insel 2010). A variety of neuropsychiatric disorders are

493 characterized by disruptions in social behavior and social cognition, including depression,  
494 autism spectrum disorders, bipolar disorders, obsessive-compulsive disorders, and  
495 schizophrenia. Therefore, integrative research using more accurate animal models of  
496 social behavior may lead to the development of treatment strategies for  
497 psychopathologies. In other words, the perspectives of behavioral ecology may be lead  
498 to discoveries of animal models that are ideally suited for addressing questions relevant  
499 to psychiatry. For example, discoveries of the role of oxytocin in social attachment in  
500 socially monogamous prairie voles have already led to clinical therapy trials for the  
501 enhancement of social cognitive function in autism spectrum disorders through the use of  
502 oxytocin pharmacotherapies (Opar, 2008). Thus, by adopting a more ecological and  
503 evolutionary approach to biomedical research, we should enhance our biomedical  
504 discoveries.

505

## 506 **Conclusions**

507 Our integrative framework (Fig. 1) has broad implications for the study of social  
508 behavior. A fully integrative model for sociality has been the ‘holy grail’ of behavioral  
509 ecologists studying social relationships among individuals. By conducting studies with  
510 explicit links between proximate and ultimate levels of analysis, we gain a  
511 comprehensive and integrative understanding of these relationships, an advance that  
512 could generate a paradigm shift studying the study of social behavior. Additionally, this  
513 approach has many applications. First, an integrative view of sociality that includes  
514 genetic, neural, and endocrine mechanisms will provide insights into evolutionary  
515 potential and thus provides a powerful tool for predicting species responses to

516 environmental change. Second, such a fundamentally integrative understanding can yield  
517 insights into human psychopathological disorders that may improve treatment of these  
518 conditions. Third, an understanding of the links between ecological variation,  
519 mechanism, and sociality can lead to improvements in animal husbandry and welfare as  
520 part of both endangered species management and animal production. To achieve these  
521 benefits, we must train our next generation of students in integrative approaches to  
522 behavior and create a culture of interdisciplinary, collaborative work. This requires  
523 financial and logistical support by universities, medical facilities, and funding agencies.  
524 While difficult, these efforts will yield extraordinary benefits to the study of social  
525 behavior.

526

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535

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705

706 **Conflict of Interest Statement**

707 The authors declare that the research was conducted in the absence of any commercial or  
708 financial relationships that could be construed as a potential conflict of interest.

709