

Social models

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Abstract

Animal societies are remarkably diverse. These social systems are often categorized based on features such as group size, stability, and sex ratio, amongst others. However, such coarse properties overlook the unique challenges each species has faced throughout evolution—challenges that have shaped the distinct ways in which they perceive and navigate their social landscape. To better capture these differences, I propose a comparative framework for quantifying how species construct social models of others. This approach comprises four modules, each designed to measure a distinct facet of how different taxa interpret and overcome the unique complexities of their social worlds.

Keywords

Comparative approach; Ethology; Evolution; Social behavior; Social brain; Social cognition; Social group; Social identity; Social learning; Social model; Umwelt

Key points

- Social models are acquired cognitive constructs that guide predictions of others behavior.
- Each distinct module within the social model framework reveals differences between species.
- Social models offer insights into the key challenges of each species social world by revealing the information pertinent to navigating their societies and options available to decision-making.
- Ego- and Allocentric social models reflect suites of social cognitive mechanisms that differ between taxa.

1 Introduction

Nearly all animals on the planet are social (Krause et al., 2009; Scott, 1956). Only the handful of asexually reproducing species could potentially live their entire lives without interacting with conspecifics, but they are clear outliers (Dolmatov, 2014; Engelstädter, 2008). Even a casual survey of animal sociality will reveal a truly remarkable spectrum of diversity, as each species' sociality evolved in response to the myriad selective forces acting on these dynamical systems and the individuals within them (Alexander, 1974). Whether individuals live in stable social groups comprising hundreds of individuals with frequent, repeated interaction or engage with conspecifics only for mating or during territorial encounters, these social interactions pose clear challenges to their evolutionary imperatives to survive and propagate genes. Because the brain networks that generate adaptive behaviors and social systems evolved in parallel, a relationship is expected to exist between a species most idiosyncratic social behaviors and the neural circuits that support them (Miller et al., 2019; Sewall, 2015; Varela et al., 2020). This relationship is elegantly illustrated by classic neuroethological systems (Nottebohm, 2005), but it is not limited to such highly specialized cases. Although some behavioral similarities may be evident across taxa, a closer look at the strategies employed by individuals of two species to navigate seemingly similar social scenes often reveals meaningful differences. This occurs because no two species perceive or respond to social challenges in exactly the same way. While this idea is intuitively correct, developing a scientifically rigorous and quantifiable approach to compare these differences has been elusive. To this end, I propose a framework for elucidating how different species construct social models that are based on experience with individual conspecifics and leveraged to predict

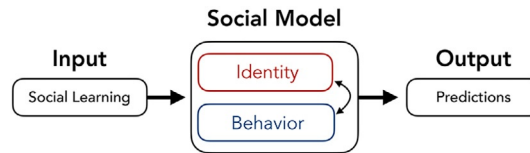


Fig. 1 Social Model Framework. The framework comprises three separable modules: Input - Model - Output. Information about conspecifics identity and behavior is acquired through social learning and observation (the input). Information about Identity and Behavior is integrated (social model) to construct predictions (output) about of how individuals will behave in different social settings.

how different individuals will behave in various contexts to guide the innumerable, continuous social decisions inherent to social living (Fig. 1).

Social models are acquired cognitive constructs that guide probabilistic determinations of how conspecifics will behave in novel contexts. In other words, they are our internal representations of specific, recognizable individuals in our social network that are built by observing how those individuals behave in distinct contexts and then making inferences about their behaviors and social interactions. These models predict the behavior of each conspecific in dynamic social settings and, as such, guide the continuous decision-making of individuals within these societies. Given the fluid nature of social scenes and the fact that no two contexts are the same, social models are effective if they build on prior experiences, retain specificity for individuals and context but adapt flexibly to each situation. The nature of social models, therefore, should reflect the challenges individuals face in the society. Importantly, 'challenge' in this context is not necessarily limited to the coarse characterizations of groups that have traditionally analyzed as correlates of cognitive faculties (i.e., size, composition, etc.) (Ashton et al., 2018; Byrne and Bates, 2007; Dunbar, 1995). Rather they reflect the species-specific dynamics of social interactions and the processes that govern the continuous decision-making in these societies. For example, chatters of budgerigars can number up to a hundred while a school of herrings can be one to two orders of magnitude greater in size. While at a coarse level of analysis these species are similar in that their respective groups are cohesive with opportunities for repeated interactions with conspecifics and collective behaviors that could be considered broadly consistent social behaviors, their respective social models are likely to be different because of the key differences in the challenges each faces for social living (Levin et al., 2016; Wyndham, 1980). Social models are expected to vary widely between taxa because the species-specific challenges to navigating each respective social landscape will differ as widely as the societies themselves. As such, comparing social models between species offers the potential for insight into species-specific, social-cognitive faculties and the variants of supporting neural mechanisms.

Here I propose a conceptual framework for the quantitative study of social models comprising four distinct modules: Input - Identity - Behavior - Output (Fig. 1). The social model itself comprises the pair of interrelated Identity and Behavior modules that incorporate these streams of critical information and collectively yield valuations (Chang et al., 2015; Tremblay et al., 2017) for how conspecifics will act in distinct (novel) settings, while the other two modules of the framework pertain to how information pertinent to the social model is acquired - the input - and how one's model of others is applied to predict conspecifics behavior in distinct contexts - the output. Mechanisms for identity and behavioral recognition are necessary for a species to have a social model of others. Specific details of these respective recognition systems, as well as how information from these two independent processes is merged into a cohesive model that represents how individuals behave in different contexts, are critical to distinguishing social models between species. Social models could, for example, be differentiated between species based on measurable properties such as the number and breadth of social categories across which conspecifics can be recognized and/or the size of the species' behavioral repertoire that can be recognized in different settings, including its related sources of variance. While elephants can recognize over 100 individuals and the relative social relationships between these individuals (McComb et al., 2000, 2001), recognition of nestmates and relative social cast in the hive is sufficient to navigate honey bee societies (Breed, 1981, 1983). Likewise, the precision with which species can predict conspecific behavior reveals details about how identity and behavior are integrated in their social model. A coordinated hunt in giant river otters (Lodé et al., 2021), for example, is likely possible because each individual can anticipate each other's behavior while pursuing prey, suggesting they possess detailed social models of each individual member of their family group based on extensive observations of their individual hunting behavior and prosocial tendencies (Schmelz et al., 2017). A final consideration for this framework further emphasizes the relationship between the different modules. The mechanisms for acquiring information - Input - used to construct social models ultimately constrains its content, and by extension determines the types and specificity of the predictions that can be made of others' behavior - Output. Because of the constraints and relationships between the different modules in this framework, one need not have data for each of the modules to make informed characterizations about how these models may differ between species.

The social model framework is, in a sense, a quantitative approach to capture what ethologists refer to as the Umwelt of the species (Bueno-Guerra, 2018; Nagel, 1974). This well-known concept pertains to the fact that each species experiences the world through different perceptual systems that have shaped their distinct behavior and cognition, and that these distinct sensory viewpoints should be considered when comparing how animals engage with the world (and those in it). Here we apply this notion to the social domain and consider the intertwined relationships that exist between the challenges of each species unique social world and the mechanisms selected over evolution to enable individuals to overcome them. By identifying measurable properties of social models, this framework provides a roadmap to quantify and compare an integral foundation of the social cognitive faculty as well as explicating its underlying neural mechanisms at the computational, systems and circuit levels - across species

(Miller et al., 2019). While our discussion will focus primarily on behavior, the framework is similarly applicable to understanding the supporting neural mechanisms and computations. Brain and behavior, after all, are simply two sides of the same coin. Indeed, each of the components of the social model, including its input and output will have distinct, identifiable underlying neural processes. Species exhibiting recognition of multiple learned social categories, for example, are expected to exhibit neural mechanisms that support these behaviors (Báez-Mendoza et al., 2021; Rose et al., 2021; Tyree et al., 2023). In other words, studies of the different behavioral mechanisms underlying each facet of the social model can guide investigations of the related brain processes (Miller et al., 2022).

2 Constructing social models

The framework described here outlines the general process by which social models are constructed and the respective role of each module. Below I briefly discuss each of these modules, while distinguishing the Identity and Behavior components of the social model itself. The rationale behind this organization is to highlight how differences within each module can yield functionally different models that support the spectrum of sociality evident throughout the animal kingdom.

2.1 Input: Observing others and their behavior

The principal input for models of others is through social learning. In other words, the process by which individuals gather information from observing the behaviors of other agents (Heyes, 2012). It is possible that recognition of some behaviors could occur with little to no learning, particularly for species with highly stereotyped and/or relatively limited species-typical behavioral repertoires. Likewise, some categories of social recognition could be possible without explicit learning, such as an individual's sex, family, nestmate, or species (Brandstaetter et al., 2008; Miller et al., 2004; Nelson, 1989; Ryan, 1983; Singer, 1998; Stuart and Herbers, 2000). However, constructing social models for many species—including most vertebrates—relies heavily on observing and learning about conspecifics and their behavior through experience. This does not necessarily mean that an observer has no model for conspecific behavior in the absence of interacting with a particular individual. Rather the observer could have a generic social model that can be applied for the first interaction based on prior experience with a conspecific of a similar social category but transitions to a model specific to that individual after an interaction occurs. Social learning comprises a number of different discrete processes (Laland, 2004; Reed et al., 2010), but here we are concerned specifically with the acquisition of information about socially-relevant categories (i.e. identity, dominance, etc.) and conspecifics' behavior. Moreover, we distinguish between mechanisms for first-person and third-person observations of others as they reflect meaningful differences in types of information available to construct social models. Differences between these learning mechanisms provide insight into the social lens through which the species 'see' conspecifics by revealing the features of social identity and behavior most relevant to their sociality.

Social learning from the first- and third-person perspectives primarily differs in the reference point(s) from which observers can acquire information about conspecifics. First-person learning refers to the process by which an observer acquires knowledge about conspecifics only through direct interactions with others. Observers in these species may encode many facets of an individual conspecific's behavior, but it would solely be limited to their own reference point. A conspecific may be dominant, helpful, larger and/or female, but those behavioral properties would be only relative to the individual observer, not to other conspecifics. Third-person social learning, by contrast, allows observers to encode behavioral events and interactions between conspecifics independent from their own perspective. A well-known example of third-person social learning is eavesdropping, whereby observers can learn about others' social relationships by watching/listening to conspecifics interact with each other. Notably, eavesdropping has been observed in a wide range of species (Johnstone, 2001; Martínez et al., 2022; Otter et al., 1999). Another example of third-person social learning from more laboratory based experiments would be the paradigms such as the social defeat witness paradigms (Allsop et al., 2018; Carnevali et al., 2020; Warren et al., 2013), in which an observer learns about the aggressiveness and dominance of conspecifics by watching pairs of conspecifics interact.

The advantage of third-person learning from a social modeling perspective is simply that these mechanisms enable individuals to encode information about each conspecific's various social interactions with other group members and not only relative to the observer. This could include family relationships, relative dominance, friendships, mates, etc.; each of which are categories of social identity that could enrich the model for a particular individual by providing information about their respective social network. While some species may only be endowed with mechanisms for first-person social learning, others may have both first and third person mechanisms. It is important to note, however, that evidence of third-person social learning in different species does not necessarily mean that their respective social models are equivocal, as the pertinent information learned by each species can differ. Perhaps one analogy is the distinction between linear or non-linear neural coding mechanisms. Whereas the former accounts for a singular process, there are seemingly countless forms of nonlinear coding mechanisms (Grossberg, 1988). Likewise, third-person learning is not an omnibus process, but denotes a broad suite of potential observational mechanisms for acquiring information about conspecifics from multiple social reference frames.

Social models are data hungry. Learning conspecifics behavior benefits from the frequency of the observed interactions. The priors of a social model are modified with each successive observation (Gale and Kariv, 2003). A single interaction with a group member is not likely to carry the predictive power of 1000 interactions, even if the initial observation is consistent with their modal behavior. This is simply because contexts in which individuals interact are highly variable and even seemingly subtle differences can

lead to significant increases in the predictability of a conspecific's behavior. As a result, factors such as a species' gregariousness, group size, and social cohesion directly impact how often individuals have opportunities to observe interactions amongst conspecifics. This in turn affects the predictability of their social models. A territorial species whose group comprises only their immediate family of 3–4 will have frequent interactions with those individuals, but only irregular interactions with members of the adjacent groups. Ultimately a species' respective social model of group members would be significantly richer than for the non-group members. While a species may have a capacity for particular details in their social models, it does not necessarily mean that a model of that nature will be evident because of the experienced based social learning needed to optimize these models.

2.2 Identity

Social identity is a cornerstone of social models. As such, mechanisms for social recognition are necessary in any species with a social model because it allows for observers to distinguish between conspecifics. Without recognition, all individuals would be equivocal and all predictions about behavior would be limited and general, likely resulting largely in reactions to events rather than probabilistic predictions about potential outcomes. While some forms of social recognition could be innately or genetically guided - such as for species, kin, sex or nestmates - likely due to generationally consistent phenotypic and/or molecular properties used to recognize these categories (Brandstaetter et al., 2008; Miller et al., 2004; Nelson, 1989; Ryan, 1983; Singer, 1998; Stuart and Herbers, 2000), many other social categories are likely learned through social observations (Bielsky and Young, 2004; Gherardi et al., 2012; Insley et al., 2003; Ward et al., 2007). The types of social categories evident in each species provides insight into their social models as it reveals the different ways that each species can categorize others.

The most well-studied facet of learned social identity is that of the individual (Beecher, 1989; Gokcekus et al., 2021; Tibbetts and Dale, 2007). Because each individual is unique, recognition for most species is only possible by learning their respective idiosyncratic features through direct interactions or observations of a specific animal and perceptual mechanisms attuned to the sensory features that distinguish conspecifics (Tibbetts and Dale, 2007). This sensory information can be acoustic, visual or olfactory, as all have been reported to be integral to individual recognition in different species (Beecher, 1989; Brennan and Kendrick, 2006; Bruce and Young, 1986; Carlson et al., 2020; Chang and Tsao, 2017). Given its significance for animal societies, it is perhaps unsurprising that this cornerstone of social models is largely ubiquitous across animals (Bee and Gerhardt, 2002; Beecher, 1989; Johnston and Bullock, 2001; Mason and Parker, 2010; Miller et al., 2005; Miller and Wren Thomas, 2012; Sayigh et al., 1999; Tibbetts and Dale, 2007; Wiley, 2013). Moreover, the breadth of species shown to exhibit individual recognition span the range of social diversity, indicating that this cognitive process is not tethered to the number of individuals in a group nor their degree of gregariousness.

Social identity is not limited to the individual level. Other social categories (e.g. sex, family, age, etc.) covary with an individual's identity are integral to social living for many species. Although dominance in some species is evident in phenotypic traits (Caro and Mallarino, 2020; Howell and Caro, 2024; Thoß et al., 2019), in most species dominance hierarchies are learned through behavioral interactions (Heyes, 1994; Scheibler et al., 2004). One of these relates to dominance. As there are no egalitarian animal societies, social groups are organized hierarchies of relative dominance (Barnard and Burk, 1979; Tibbetts et al., 2022). Notably, the particular details of these dominance hierarchies can vary across taxa (Broom et al., 2009), including separate hierarchies for males and females in some species (Cowlshaw and Dunbar, 1991; Hemelrijk et al., 2008; Rutberg, 2010; Wittemyer and Getz, 2007). Though dominance may be a byproduct of sociality, it remains a powerful factor driving behavior in social groups. Moreover, these hierarchical structures are not necessarily permanent, as animals may rise or fall in rank over time. As a result, this social identity is constantly being relearned.

Social groups typically comprise closely related individuals, a feature of sociality likely linked to the advantages of kin selection (Michod, 1982; West-Eberhard, 1975). From the perspective of social recognition, this provides the opportunity to recognize individual conspecifics as well as their respective family members - i.e. mother, father, brother, sister, cousin, aunt, uncle, grandmother etc. For example, one can recognize the individual X but also that her mother is Y and brother is Z. This is significant for social models because species whose social recognition extends to these social categories allows for a richer representation of identity and increased predictability of their behavior in different social contexts based on the other individuals present and their respective relatedness. Recognition of multiple social categories for each individual would be particularly powerful in species whose societies consist of multiple families living within single stable groups. Here recognizing individuals as well as which related and unrelated individuals are present in a social scene can have a profound influence on what potential outcomes may arise from that context.

2.3 Behavior

The second cornerstone of social models is behavior. More specifically, this refers to the corpus of ethological behaviors in a species repertoire. Like most observable species characteristics, behavior is an evolved phenotype; a target of selection. Like other phenotypes, similarities in behavior may exist between closely related taxa but species can be distinguished by the idiosyncrasies evident in their repertoire. Many are likely to include behaviors related to feeding/foraging, traveling, mating, and social interactions, amongst many others, though the structure of individual behaviors are likely to vary considerably between distantly related species. For example, a bottlenose dolphin and a peregrine falcon both travel from one location to another, but the former will swim while the latter will fly. Even within a broad behavioral category there are likely to be multiple distinguishable actions. The increased

use of modern pose-estimation technology is transforming our understanding of biomechanics by providing the level of precise quantification needed to more fully characterize ethological behaviors that have been difficult to do with more traditional methods (Bala et al., 2020; Han et al., 2024; Pereira et al., 2020, 2022). Consider the prey-capture behavior of arboreal marmoset monkeys in the wild, which was parsed into numerous fine details for different positional, manual and visual related actions using these advanced methods (Ngo et al., 2022). This example highlights that subtle but meaningful differences in posture and position that occur within rich ethological behaviors, including in dynamic social interactions, will likely require cutting-edge computer vision approaches to effectively quantify (Pereira et al., 2022).

Like identity, mechanisms to recognize the behaviors within a species repertoire are necessary for social models. This suite of mechanisms must correctly identify each ethological behavior in a species repertoire as well as the source and range of variance of each behavior. While some behaviors may be highly stereotyped, others may vary considerably based on context. Motor actions, for example, can have many sources of variance (Cohen and Sternad, 2009; Dhawale et al., 2017), but not all may be meaningful to an observer learning about a conspecific's behavior. Behavioral recognition mechanisms, therefore, are tasked with integrating these features of the behavioral process quickly and reliably. Moreover, many behaviors occur within a sequence rather than as isolated events. This adds a further level of analysis for behavior recognition because the meaningful information about each behavior may be present with respect to the sequence itself, and not only the individual behaviors, similarly to social categorization of identity. Comparisons across species for this facet of constructing social models can distinguish both the breadth of a species repertoire, and the sensitivity of observers to recognize conspecifics' behaviors including their respective variants. This is particularly important for social behaviors in their repertoire, as they are likely to be particularly powerful for effectively modeling the ethological actions of conspecifics in the pertinent social contexts.

At the core of social models is the integration of behaviors with identity. Recognition of behaviors is key, but a primary function of this faculty is distinguishing how each individual conspecific behaves. After all, one of the key sources of variance for any behavioral phenotype is the individual executing it. As a result, mechanisms for behavioral recognition must be closely aligned with those for social recognition, such that models for different conspecifics can be constructed in accordance with their idiosyncratic behaviors. The more precise the mapping between behavior and individual, the more robust the social model and the effectiveness of its output. In effect, the model evaluates a conspecific's identity and behavior based on prior experiences and applies that information to generating a prediction for the immediate context. The observed behavior of the individual could be consistent or deviate from that prediction, thereby generating additional social observations that can augment the model.

2.4 Output: Predicting the behaviors of others

The output of social models are the predictions of conspecifics' behavior by the observer. More specifically, it is the capacity to apply probabilistic determinations based on prior experience about the outcome of social events involving individual conspecifics in diverse contexts, including those comprised of different conspecifics. This is particularly important because sociality is an ever-changing landscape, with no two contexts being identical. One's ability to accurately predict how each conspecific is likely to behave on a continuous basis is directly related to the social model itself. Will individual A attack me when she approaches? What will be the outcome when Individual X moves closer to Individual Y? If an observer's social model of a particular individual has limited information, either due to input constraints and/or sparse observations, they will likewise have poor predictions about that individual's behavior during an encounter. This relationship highlights how the input to social models directly impacts its output. One cannot act on information that is has not represented. Ultimately the output of social models guides the breadth of ongoing decision-making inherent to social living. But the available options are determined by the model itself. To illustrate this point, we distinguish between ego- and allocentric social models and the predictions of others behavior that each can generate (Fig. 2). Importantly, this distinction aims to determine whether a species has the capacity to construct allocentric models or if species are limited in egocentric models and related predictions of conspecific behavior. Species with allocentric social models are likely able to change the respective reference frame based on the social context and apply the most optimal model for the particular social scene (Chang, 2013). However, like third-person social learning, allocentric models are not a singular process but comprise many different types. A capybara and a grey parrot may both have allocentric social models, for example, but they will likely differ in important ways that reflect the unique challenges each faces in their societies.

Egocentric social models are constructed solely from the reference point of the individual observer (i.e. first-person social learning). As such, the predictions individuals with egocentric models can make about conspecifics is only relative to themselves (Fig. 2A). For example, individual X is dominant to me, therefore she is likely to perform behavior 1 in the current context (Fig. 2B). Such egocentric social models allow individuals to predict the outcome of various interactions ranging from dyads to multi-individual collective behaviors, provided all interactions are guided from their own reference point. Egocentric models, however, cannot afford individuals the capacity to predict the behavior of others from those individuals' perspective independent of their own. It is pertinent to point out that complex social behaviors can arise in species that possess only egocentric models. Some collective behaviors, for example, are produced based on immediate social interactions that give rise to seemingly dynamic group-level interactions. The seemingly complex dynamics emerge from relatively simple principles related to individuals responding to the movements of their immediate neighbors (Aoki, 1982; Cavagna et al., 2010; Okubo, 1986; Young et al., 2013). Phenotypic complexity is not necessarily a proxy for the sophistication of the underlying mechanisms.

Allocentric social models are constructed from the reference point of multiple individuals, rather than only from the perspective of the observer. Such information can only be acquired through third-person mechanisms attuned to the interactions between other

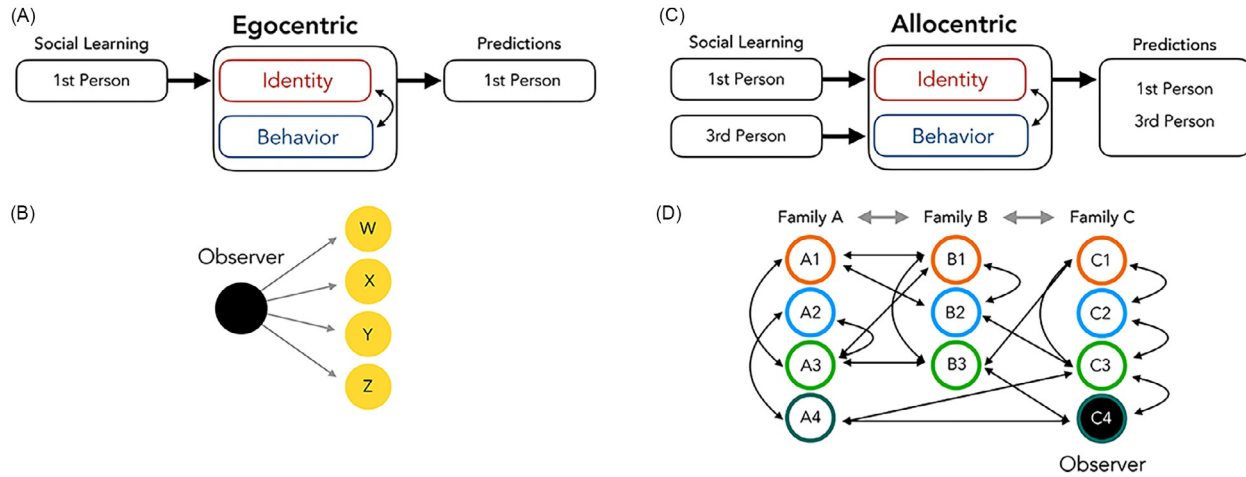


Fig. 2 Ego- and Allocentric Social Models. (A) Plots a schematic illustration of an Egocentric model, including the core modules for constructing these models and illustrates how 1st Person social learning input constrains its output. (B) Highlights this further by schematizing how the Observer is the sole reference point for making behavioral predictions about each individual (W-Z). (C) Plots a schematic illustration of an Allocentric social model, including the core modules and illustrates how both 1st and 3rd Person social learning can drive similar predictive outputs. (D) Schematized allocentric social models more detail. These models allow the Observer to make predictions about conspecifics' behavior from the reference point of any individual in any of the families in this representative social group because the Observer has learned about those respective relationships through 3rd person social learning.

members of the group and applied to predict the outcome of the myriad possible social interactions that occur in different contexts (Fig. 2C). In other words, an observer can recognize that Individual A1 and Individual C2 are not only cousins but frequent partners when foraging. Therefore, when a larger male (Individual B2) threatens Individual C2, the observer can predict that there is a high probability that Individual A1 will support Individual C2 to combat the threat. Importantly, at no point is the observer directly involved in the interaction (Fig. 2D). Clear experimental evidence of allocentric models is somewhat sparse, though this is more likely due to the challenges of designing experiments that reveal these processes than to their actual presence or absence in different animal species (Wittig et al., 2014). A series of creative and elegant playback experiments in baboons is one of the strongest demonstrations. In typical baboon social interactions, the grunt is produced by the dominant female as she approaches a subordinate, who produces a fear bark in response. Other than the most dominant and subordinate females, all other females have the potential to be either dominant or subordinate depending on the particular dyadic interaction. To test other females' social knowledge, subjects were broadcast social consistent or inconsistent sequences (i.e. the subordinate female produces a grunt and the dominant producing a fear bark). Cheney, Seyfarth and colleagues observed that the female baboons were highly sensitive to the relative rank of all individuals in the group (Cheney et al., 1995), even between families (Bergman et al., 2003), suggesting that these primates had a detailed understanding of the relative social ranks and individuals identities of all females in their large social groups (i.e. an allocentric social model) and that they can apply their social model to make precise predictions about how interactions between any of those individuals should unfold depending on their relative place in the hierarchical social network. This creative experimental design is based on a thorough understanding of both the species sociality and the identity and relative social relationships of all the animals in the social group. This work illustrates how the study of allocentric social models will likely necessitate that detailed ethology be combined with innovative experimental design.

3 Discussion

Sociality confers many advantages to individuals, ranging from kin selection to protection from predators, amongst many others (Alexander, 1974; Clutton-Brock, 2009; Fryxell et al., 2007; Palla et al., 2007; West-Eberhard, 1975). But whatever the forces are that drive the evolution of group living in different taxa, once together, individuals now live in proximity and interact with each other regularly, requiring selection for a suite of mechanisms for navigating the intricacies of these interactions and emergent dynamics. Given the breadth of social organizations evident in different animals, the challenges of navigating these social landscapes vary widely, as do mechanisms that enable individuals to succeed in their respective society. Here we sought to provide a framework to better quantify the similarities and differences in these cognitive faculties across species. Rather than determine whether species have classic cognitive capacities in their repertoire (i.e. cooperation, tool-use, theory of mind, etc.), the social model framework outlined here seeks to explicate how individuals 'see' their social challenges and overcome them. It follows that the content of a species social models should reflect the information most pertinent for success in their society, both in the features that are represented and how it is implemented to predict specific facets of others behavior. For example, an observer will learn about and represent each individual in a conspecific's family network only if that information is needed to make advantageous social decisions. If an individual can navigate their society using only information about their rank relative to conspecifics, then their social model will be constructed

primarily through first-person learning. This does not imply that such models are inherently simple or complex; rather it asserts that species' social faculties evolve in response to the demands of their respective societies. Moreover, egocentric and allocentric models are not necessarily mutually exclusive. Many species likely possess both and switch between them depending on the demands of the immediate context.

What is a social brain? Or perhaps more generally, what does it mean to be social? While this manuscript has not explicitly discussed these questions, they were the primary motivation behind developing the conceptual framework outlined here. It is important to point out that any discussion of 'social brains' must first consider the behavior. After all, it is behavior - not the brain - that is the target of evolutionary selection. A consideration of these questions is fundamental to any discussion of sociality, particularly because there is no clear answer ... yet (Dunbar, 2009; Dunbar and Shultz, 2007; Lockwood et al., 2020). An alternative way to approach these questions is not to focus on sociality itself, but on the effects of its absence across different species. In other words, can a species truly be considered 'social' if isolating an individual from conspecifics has little impact on its behavior? This logic is consistent with common practices of removing, silencing or modulating specific cells, circuits or brain areas to determine their functional significance (Deisseroth, 2015; Vaidya et al., 2019). Evidence shows that the effects of social isolation on presumably 'social' animal species can range from minimal to extreme (Hawkley et al., 2012). Songbirds, for example, have long been studied in neuroscience for their remarkable social learning system that guides vocal development (Mooney, 2022; Nottebohm et al., 1976), but adults in some species can be tested in isolation for weeks with seemingly little impact on their non-song behavior (Comins and Gentner, 2015; Fehér et al., 2017). Likewise many rodent species exhibit stress responses only after being separated from conspecifics for two or more weeks (Hawkley et al., 2012). By contrast, the behavior of other 'social' species, such as primates and parrots, decays rapidly when socially isolated (Mitchell et al., 1966; Nicol and Pope, 1993; Polverino et al., 2015). In some cases the effects of social separation on primates are evident within minutes of separation (Cross et al., 2004), with long periods of isolation resulting in significantly impaired psychological well-being similar to what is observed in humans (Hawkley et al., 2012; McKinney Jr, 1974). The differential impact of social isolation on species likely belies fundamental differences in their social Umwelt - and by extension the supporting neural processes - but is rarely (if ever) mentioned in discussions of animal sociality. Social isolation should certainly not be the sole dimension upon which we reimage our concepts of sociality, but rather a bellwether that current common conceptions are inadequate to encapsulate multidimensional dynamics of social brain functions evident across species.

4 Conclusions

Our concepts of sociality must evolve if we are to penetrate the pervasive mysteries surrounding social brains. Broad characterizations based on coarse properties such as group size, composition, stability etc., and simplistic experimental paradigms are unlikely to provide the level of insight needed to address fundamental questions about social behavior, perception, and cognition—especially when it comes to capturing species' social models. For example, a classic paradigm in rodent research to assess social dominance involves placing two individuals and opposite ends of a narrow tube to measure which one advances and which one retreats (Fan et al., 2019). While experimentally effective in one sense, this task vastly oversimplifies a highly dynamic social behavior and the myriad ways it manifests in different contexts over time (Fulenwider et al., 2022; Varholick et al., 2019; Zilkha et al., 2023). Rather than simplify our paradigms to make them amenable to reductionistic frameworks, it is imperative that we quantify the more nuanced processes evident in the species social ethology that are integral to solving the ongoing challenges in each respective society and which shape the evolution of their brains (Miller et al., 2022). This may be particularly important for understanding the different dimensions of social brains because at least some of the neural computations may only be evident while individuals confront specific social challenges in real-time (Báez-Mendoza et al., 2021; Jovanovic et al., 2022; Lee et al., 2024; Li et al., 2024; McMahon et al., 2014; Rose et al., 2021). The social model framework presented here represents a first step towards bridging this gap. By better understanding how different species construct predictive models of others, we by extension gain a deeper window into how they experience their social world. By better quantifying a species' Umwelt, we will be better equipped to drive a paradigm shift in our understanding of social brains, and the mechanisms that make our own social experiences so phenomenologically unique.

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