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Social norms and superorganisms

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Abstract

Normativity is widely regarded as the ability to make evaluative judgments based on a shared system of social norms. When normativity is viewed through the cognitively demanding lens of human morality, however, the prospect of finding social norms innonhuman animals rapidly dwindles and common causal structures are overlooked. In this paper, I develop a biofunctionalist account of social normativity and examine its implications for how we ought to conceptualize, explain, and study social norms in the wild. I propose that we think of social normative systems as behavior-regulatory power structures that resolve conflicts between nested levels of selection in favor of the higher level. I argue that the best case for social norms outside of humans is not in the animals one might expect, such as primates or other large-brained vertebrates, but rather in social insects. Finally, I engage with a number of potential objections to this unorthodox proposal.

Keywords Convergence · Cooperation · Hymenopterans · Major transitions · Morality · Normativity · Punishment · Norms · Superorganisms

Introduction

Normativity is inherent to the adaptive organization of life. It underlies everything from the goal-directed behavior of living things to the exquisite functional match between the traits of organisms and the ecological design problems they need to solve. But this is not what most naturalistic philosophers and evolutionary anthropologists have in mind when they speak of "normativity." Rather, they mean the ability to make explicit evaluative judgments based on a shared system of social norms, or rules of interaction that regulate behavior in social groups. So conceived, normativity is a sophisticated cognitive and cultural phenomenon, rather than a broadly biological one. Human morality is taken as the paradigmatic case, with evaluative

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capacities thought to underwrite the unusually high levels of cooperation in humans as compared to other primates. When normativity is viewed through the cognitively demanding lens of human morality, however, the prospect of finding social norms in nonhuman animals rapidly dwindles, and common causal structures are overlooked.

In this paper, I shift explanatory aims away from evolutionary divergence and toward convergence. That is, rather than adverting to normativity to explain the unique cooperative feats of humans among vertebrates, I show that social insects have also converged on ultracooperation and propose that social norms figure in a unifying explanation of this phenomenon. Although striking parallels between human and insect societies have been discussed in detail by social evolution theorists (e.g., Maynard Smith and Szathmary 1997; Anderson et al. 2001; Wilson and Wilson 2007; Wilson 2012; Birch 2017), no sustained attention has been devoted to the possibility of normative convergence in these groups. This lacuna is due partly to the dominance of cognition-heavy approaches to normativity modeled on human moral psychology and culture, which this paper will push back against, and partly to the slow uptake of insect cognition and behavior into broader theories of comparative cognition, which this paper aims to accelerate. The broad goal is to sketch out a biofunctionalist account of social normativity and its implications for how we ought to conceptualize, explain, and study social norms in the wild.

I begin by considering prevailing evolutionary approaches to normativity and their explanatory limitations ("Evolutionary approaches to social normativity" section). I then sketch my positive view according to which social normative systems are behavior-regulatory power structures that resolve conflicts between nested levels of selection in favor of the higher level ("Positive proposal" section). From there I go on to argue that the best case for social norms outside of humans is not in the animals one might expect, such as primates or other large-brained vertebrates, but rather in social insects ("Social norms in superorganisms" section). Finally, I anticipate and diffuse several potential objections to my unorthodox proposal ("Objections Conjured and Parried" section).

Evolutionary approaches to social normativity

The gold standard

Although evidence is building for proto-normative traits like empathy (De Waal 2008) and a sense of fairness (Brosnan and De Waal 2014) in other social mammals and birds, *Homo* appears to be the only "genuinely" moral animal (Wright 1994). *Homo* is the only taxon capable of making moral judgments conceived as propositional attitudes like "it's wrong that X" or "it's good that Y" (Joyce 2007). Only humans take social norms as explicit reasons for action, and only humans believe that fellow group members believe that their fellow group members ought to follow norms (Bicchieri 2016). Only humans feel a sense of obligation to others (Tomasello 2016). Only humans are capable of simulating the world as it could and should be (Suddendorf and Corballis 2007). If these high-end cognitive and cultural abilities are taken to be preconditions for normativity, then humans are almost surely alone in the normative project.

On its face, this anthropocentric approach to normativity looks suspiciously self-serving. It offers up yet another progressivist metric that places humans at the pinnacle of the living world. Yet there are significant explanatory advantages to conceiving of social norms in this restrictive way. No other *vertebrate* (italicized for reasons that will be clear later on) has achieved the ecological prominence that *Homo* has, and there are good reasons to think that social norms are a crucial ingredient in the recipe for human evolutionary success.

The received view is that human moral normativity is an adaptation for enhanced cooperation (Kitcher 2011; Sterelny 2012; Henrich 2015; Tomasello 2016; Buchanan and Powell 2018; Campbell and Kumar 2022). Cooperation is ubiquitous among animals ("Contrast classes" section), but ultracooperation of the sort we see in humans is exceedingly rare in nature. Although “ultracooperation” has no precise definition in the literature, it generally refers to obligate intergenerational cooperation in many parallel dimensions of social living, including foraging, food-sharing, parenting, defense, communication, information transmission, industry, pedagogy, political power structures, and the like. Nearly everything about humans—from our lifeways, life histories, and morphologies to our technologies, communication, and niche-constructing abilities—is the result of intergenerationally scaffolded cooperation powered by social norms (Melis and Semmann 2010).

In combination with language, impulse control, and the ability to read the intentions of others in cooperative contexts (Burkhart et al. 2009), social normativity enabled early humans to transmit complex technological skillsets (Birch 2021) and solve coordination and innovation-retention problems that place strict limits on cooperation and technological accumulation in chimpanzee societies (Tennie et al. 2009). These newfound cooperative abilities allowed *Homo* to assume the mantle of apex predator and to exert an increasingly profound influence on global ecosystems, from the Neolithic extinction of megafauna (Sandom et al. 2014) to the current anthropogenic pressures on climate and habitat.

It is not surprising that we have found building-blocks of human morality in other animals. But if what we are looking for are difference-making adaptations that account for the great divergence of human behavioral ecology and lifeways from that of other primates (and vertebrates more broadly), then it’s the *lack* of normative cognitive and cultural capacities in these other animals that holds the greatest explanatory potential. The explanatory power of this “divergence explanation” comes at the cost of scope, however. It is limited to a one-off, historically contingent outcome of human evolution that has never been replicated in the 4-billion-year history of life (Powell 2020). Conceived in familiar human terms, normativity is unlikely to shed much light on the general laws that govern the evolution of complex social organization. The gold standard may illuminate a self-important bit of natural history, but it gives us little in the way of nomological purchase.[1]

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[1] Of course, unification is not useful if it is achieved ad hoc or at the cost of obscuring other valuable explanations; we ought to let biological phenomena speak for themselves in determining whether a nomic framework is warranted or desirable in any given case. In "Evolutionary approaches to social normativity" section, I propose a unified account of social norms that sheds light on the convergent evolu-

More expansive accounts of social norms and their limitations

Humans adhere to countless social norms in their mundane daily life without realizing it (Kelly and Davis 2018). Why, then, should we hold animals to standards that humans themselves often fail to meet? This thinking has motivated recent attempts to develop more phylogenetically inclusive accounts of social norms. For instance, Andrews's (2020) account of "naïve normativity" eschews metacognition and does not require that animals represent norms qua norms, and thus it avoids some of the higher-cognitive bells and whistles that human moral normativity entails. Nevertheless, naïve normativity retains demanding cognitive preconditions. It requires, for instance, that species have explicit group identities, cultural traditions, and expectations that fellow group members will follow certain rules (*cf.* Fitzpatrick 2020). This results in several limitations.

First, although such accounts endeavor to be more inclusive, they wind up replicating some of the major drawbacks of anthropocentric approaches. It is onerous enough to show that *concepts* of group identity, explicit normative expectations, and distinct cultural traditions are present in our sister taxa the chimpanzees, let alone in more distant vertebrate groups like cetaceans, carnivores, elephants, or corvids. But even if proto psychological norms of this sort could be established in a few nonhuman vertebrates, they are unlikely to play a pronounced role in the ecology and evolution of these groups, let alone in the evolution of sociality writ large. The solution is not merely to devise keener means of detecting human-like norms in non-human animals (though that, too, is a worthy project), but rather to re-conceptualize norms in a more thoroughly non-anthropocentric way that allows for broader applications and admits of deeper evolutionary insights. Finding shades of normativity in other animals would do something to blur the anachronistic boundary between humans and other animals that lingers in the annals of popular consciousness. It might even reveal some minimal preadaptations for normativity in humans that were present in and transmitted from a common primate ancestor. But what important patterns would it explain? What phenomena would it unify? The problem, then, is not that these approaches stray too far from the human case, but that they do not stray far enough, and as a result they land in an explanatory valley.[2]

Footnote 1 (continued)

tion of ultracooperative societies (the phenomena) across the deepest chasms of animal evolution. Importantly, this unified "convergence explanation" does not preclude finer-grained "divergence explanations" of the sort that have given evolutionary accounts of human morality their explanatory punch. In fact, the convergence framework can suggest new hypotheses and bring new credences to bear on existing evolutionary theories of human-specific normativity ("The "collateral kin selection" objection" section).

[2] Another possibility is that the parochial approach to social norms is motivated by ethical rather than scientific considerations. Some have argued that it is social normativity that sets the higher moral status of human beings in relation to other animals (e.g., Machan 2004), and so perhaps discovering human-like social normativity in other animals would have direct implications for their moral standing or moral status. I find this dubious, because traits like empathy and norm acquisition are clearly not necessary for being a moral patient, nor do they rise to the level of moral agency or mutual accountability that could plausibly give rise to a higher moral status (Powell et al. 2021). They are relevant, however, to the conditions under which a being can flourish above and beyond its experience of pleasure and pain—and understanding those conditions is an affirmative obligation of any plausible theory of animal ethics (Rowlands

A more fundamental limitation of all prevailing approaches is that they treat social norms as products of sophisticated cognitive mechanisms. This is presumably because they are modeled on, or at least inspired by, human cooperative frameworks in which culture and higher-order cognition play a central role. It makes good sense to begin an investigation with familiar examples of the explanandum. But the problem with building specialized modes of cognition into a definition of social norms is that doing so overlooks the possibility of functional convergence. Functions can be multiply-realizable, and selection will often tap different proximate mechanisms to achieve the same function, especially where distantly related lineages have evolved solutions to the same design problem under very different developmental constraints. These robust cases of convergence can reveal the specific functions of (Currie 2012) and nomological constraints on (Powell 2020; Powell and Mariscal 2015) adaptation.

For instance, camera-type eyes evolved more than a dozen times in vertebrates, mollusks, spiders, jellyfish, and even in a group of single-celled algae called dinoflagellates which have microscopic eyeballs fashioned out of subcellular organelles like mitochondria and chloroplasts. Imagine the scientific disservice of building vertebrate-specific mechanisms into our definition of "eye" or "vision" and then concluding that because octopuses employ different proximate mechanisms, they do not have eyes or cannot see. So it is with social norms. Because anthropocentric approaches all but foreclose the possibility of normative convergence, they hold no potential for disentangling contingent from law-like features of social evolution.

Positive proposal

The basic idea

What would a more expansive, convergence-friendly account of social norms look like? A good place to begin is with adjacent contrast classes. Animals use all sorts of signals and rituals to coordinate their behavior: think of the synchronous flash patterns of fireflies, the mating dance of peacock jumping spiders, or coral reef fish soliciting the hygienic services of a cleaner wrasse. If these simple coordination devices implicated social norms, this would either gut the concept or collapse it into the well-studied phenomenon of biological signaling. The way to avoid this, however, is not to make sophisticated cognition or culture a precondition for social norms (as existing accounts do), but rather to look for behavioral coordination in a more specific evolutionary context.

That context has to do with the way life is organized. A major insight of contemporary biological theory is that organisms do not merely comprise groups—they *are* groups. Animals, plants, and protozoans are essentially cooperatives that have

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Footnote 2 (continued)
2015). For present purposes, however, I will set these moral issues aside and focus solely on scientific payoff.

reduced their rates of evolutionary conflict to miniscule levels by effectively transferring fitness to a higher level of adaptive organization (Michod 2005, 2007; Okasha 2009). They have achieved this through immune systems, germline bottlenecks, divisions of labor, and other devices that ensure the only way for lower-level units to maximize their fitness is to support the home team. What might have looked normative in the context of a social group presents to us as the routine self-maintenance of the organism. But in reality, it's groups all the way down (Levin 2019).

What I will suggest here is that social normativity plays a key role in the formation of certain kinds of groups: namely *ultracooperative groups*, some of which have gone on to evolve into full-blown superorganisms. The dual notion of organism-as-society and society-as-organism has enjoyed a resurgence in recent years, thanks to work on major evolutionary transitions and the reinvigoration of group-selection theory (Birch 2017), especially in the superorganism context (Wilson 2012; Nowak et al. 2010; Hölldobler and Wilson 2009; Wilson and Wilson 2007). Principles of social evolution have proved useful to understanding many of the parallels between multicellular organisms and eusocial insect colonies, including their formation, maintenance, and internal specialization (Birch 2017, ch. 7). The analysis here will focus on the role of social norms in driving these convergent outcomes.

Life on Earth has a "nested" organization akin to Russian dolls: genes are nested within chromosomes, simple cells are nested within complex cells, complex cells are nested within multicellular organisms, and multicellular organisms are nested within societies. These nested levels, which McShea (2001) calls "hierarchy," are the legacies of major evolutionary transitions (Maynard Smith and Szathmary 1997): formative events in the history of life in which the fitness of lower-level units was transferred to a higher-level evolutionary individual. Developmental innovations in information transmission then allowed for the differentiation of parts within levels, resulting in specialized divisions of labor that increased functional efficiency and opened up new adaptive zones.

My basic idea is that norms are social interactive structures that are adaptively designed to resolve conflicts between nested levels of selection in favor of the higher level by regulating the behavior of lower-level units in ultracooperative groups that have gone some ways, but not all the way, down the asymptotic path to a new evolutionary individual. I say "asymptotic" because even paradigmatic organisms—units of near-unanimous cooperation—have not fully eliminated conflicts between levels. Animal immune systems still need to patrol the body for defectors in the form of cancerous cell lines, and "genetic societies" within cells must police meiotic drive to block selfish genes from being overrepresented in the gametes. My empirical thesis (canvassed in "Social norms in superorganisms" section) is that social norms arose convergently in distantly related animal groups to stabilize ultracooperation at the group level.

On the account I propose, institutionalized punishment is crucial to establishing a social norm. As I understand it here, "institutionalized punishment" has a many-against-one power structure that I call "policing." This is a somewhat unorthodox usage in biological circles, where "policing" often refers to any form of cheater punishment in the service of group stability (Singh and Boomsma 2015). On that more capacious usage, policing can include (e.g.) the bullying of subordinates by dominant individuals and evolutionarily partial third-party interventions, so long as these actions aid in the production of public goods. The narrower conception of policing that I employ here, which lies closer to the sociological meaning of the term, better captures the specific social structures and group-level processes that underpin the convergent evolution of ultracooperation.

Although some accounts of social norms do not require enforcement broadly construed (e.g., Westra and Andrews 2023), let alone in the narrower sense used here, I think that policing is necessary to establish a social norm for several reasons. First, communal enforcement is what gives norms their *normative force*. Legal philosophers dating back to John Austin have argued that enforcement is an identity-making feature of law—that unenforced laws are not "laws" in any meaningful sense of the term. This is because social rules are designed to bring about certain states of affairs in a community of actors, and the actualizing power of enforcement is essential to achieving these goals (Kleinfeld 2012). Laws and norms are of course enforced by individuals, but for social rules to have an actualizing power of their own, they must be *institutionalized*. The same, I submit, goes for social norms in the wild: institutionalized enforcement is not merely evidence for norms—it is constitutive of them. It is important here to distinguish the conditions necessary to establish the existence of a norm from the circumstances in which that norm is enforced in any given case. Norms can be enforced through dyadic (one-on-one) interactions, but this punitive behavior must be widely distributed in a community or tasked to a dedicated subset of specialized enforcers for it to be meaningfully institutionalized.

Second, enforcement must not be conditioned on self-interest, rank, or relatedness to the violator, as this is what makes a society "normative" in the literal sense—i.e., governed by rules rather than sheer power or self-interest. If one reacts negatively toward an action when it is directed at oneself or one's kin but remains indifferent when the same action is directed at other members of one's community, then one is acting out of prudence or self-interest; and if one opposes an action merely out of self-interest, then one does not *disapprove* of that action in any meaningful social sense, and hence one does not act on the basis of communal norms. Different norms can apply to different individuals in a society given their particular social roles and relations, but in a normative society no one is exempted from compliance unless it is a norm that they be exempted. That said, social rules are never perfectly enforced, and policing can be subtle or otherwise hard to detect. As we shall see, the clearest cases of policing outside of humans are found in advanced species of social insects.

Contrast classes

Before we dive into the hive, however, it will be useful to underscore several further points. First, although cooperation is ubiquitous in nature, only a tiny fraction of it involves social norms. For instance, there is evidence for tit-for-tat-style reciprocal altruism in a wide range of animals, from grooming in primates (Brosnan and De Waal 2002), to blood-meal sharing in vampire bats (Wilkinson 1984), to raptor-mobbing in birds (Wheatcroft and Price 2008), to a panoply of mutualisms between species. But there is no evidence in any of these cases that the failure to reciprocate garners a retaliatory response apart from merely ending a cooperative relationship (Riehl and Frederickson 2016). Indeed, cooperation often just continues despite obvious defection. Consider lions, the honorary chimpanzees of the cat clade: lions are intensely social, they form coalitions, alloparent their cubs, compete aggressively against neighboring prides, and cooperatively hunt the most dangerous game on the African savannah. These conditions are similar in many ways to early human ecology and are ostensibly ripe for the evolution of norms; and yet studies show that lion laggards—individuals who blatantly freeride on the efforts of other pride members—are not retaliated against in any way (Grinnell 2002).

In cases where we do see retaliation, there is no evidence that these tit-for-tat interactions are properly policed. Dominant individuals sometimes harass subordinates to induce their cooperation—something that has been observed in cooperatively brooding cichlid fish, paper wasps, and naked mole rats. And in larger cichlid groups consisting of a breeding pair and subordinate helpers, bystanders have been shown to individually punish experimentally-induced defectors, though this likely provides direct fitness benefits by enhancing the rank of the bystander vis-à-vis the defector (Fischer et al. 2014). The same holds true for species dyads in the context of symbioses. Cleaner wrasses can cheat by cheekily plucking off their client's beneficial mucus instead of their ectoparasites, and cleaners that are operating in male–female pairs have been found to chase off their partner if she picks at mucus and thereby loses clients (Raihani et al. 2010). Yet even there, cleaners are thought to personally benefit from punishing their partner, and there is no many-against-one power structure propping up public goods. In cases like these, individualized punishment may incentivize cooperation, but one member of a social dyad retaliating against a non-cooperating partner is not, on the view presented here, sufficient to establish a social norm. It is third-party disapproval of an action that distinguishes socially normative behavior from self-interested behavior (where "disapproval" is cashed out in functional terms). As noted earlier, if retaliation against a noncooperative behavior only occurs when that behavior is directed at oneself or one's offspring, then social norms are not implicated on my view. Dyadic interactions can of course be structured by social norms, but there must be a wider community that takes an interest in those interactions for them to be framed as normatively appropriate or not.

Another problem with the idea of dyadic norms is that it lacks ecological validity. It is of little explanatory value to conceive of norms as operating among two individuals in isolation from their broader community. Two individuals might technically constitute a 'group' for decision-theoretic purposes, but hominoid societies have never been structured in a pairwise fashion. For most or all of human evolution, social groups have been tight-knit units in which norms are taught, enforced, and to some extent internalized at the community level. Norms of egalitarianism in early humans, for instance, arose when subordinates joined forces to prevent dominant individuals from monopolizing resources or hording the spoils of collaborative foraging (Wrangham 2019). The same community-level power structures that suppress domination and defection in human groups also configure norms in other ultracooperative animal societies, as we shall see in the next section.[3]

A further implication of this account is that cultural traditions per se do not constitute social norms. Local behavioral regularities can emerge due to conformity biases without any need for policing. For example, a chimp who joins a foreign group with a different style of nut-cracking may adopt the local style even if her new compatriots do not give a hoot whether she uses their homegrown method or a different one (Luncz et al. 2014). The same goes for other mere traditions, such as hand-clasping cultures. Although we cannot say for sure that chimpanzees are unbothered by non-conformity in such cases, there is at present no evidence that they are. Indeed, we might not expect enforcement in such cases as there are ostensibly no cooperative goods to be disrupted by nonconformity. Conforming to local practices may help integrate a migrant into their new group (Goldsborough et al. 2021), and traditions may coordinate behavior in ways that increase group efficiency, but these patterns of interaction do not involve norms if they do not involve policing.

Social norms in superorganisms

The original ultracooperators

Essays on the evolution of human cooperation often begin by noting that *other than the social insects*, humans are the most complexly cooperative animals on Earth; but the parallels between human and insect societies are rarely explored any further (exceptions include Wilson 2012, Wilson and Wilson 2007, and Birch 2017, which are discussed below). Are the human and social insect cases entirely orthogonal? This paper will answer with a resounding “no.” Although the lifecycles and lifeways of social insects are almost maximally alien, their ultacooperative achievements—from agriculture and architecture to communication and organized warfare—are eerily familiar. And as we shall see, so too are their systems of norm enforcement. Arthropods (the phylum to which insects belong) evolved the first centralized nervous systems and active visual lifestyles in the history of animal evolution, before vertebrates had even developed eyes or brains—and more recently, during their conquest of land, they developed the first civilizations on Earth.

Eusociality has three distinctive features: cooperative brood care, overlapping generations, and two basic castes: a reproductive caste (akin to the germline in animals and plants) and a worker caste devoted to colony maintenance who, as a rule, do not reproduce (akin to the soma or body of animals). The term “superorganism” is usually reserved for complex eusocial insect societies, mainly the hymenopterans

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[3] Consider a dyad within a larger social group that comes to operate on different rules of conduct than the rest of the community. At that point, no norms are configured; it is only once a third individual joins the group and all three individuals engage in third-party policing to suppress defection and domination that *incipient* norms would emerge. For present purposes, however, I am less interested in one-off instances like these and whether they meet stipulated definitions, and more in the normative causal structures that shape the ecology and evolution of highly cooperative species.

(ants/bees/social wasps) and the more distantly related termites. Like the specialized cell types of animal bodies, superorganism worker castes have highly specialized morphologies and behaviors that suit them to a variety of colony roles, from nannies and nest-builders to warriors and waste managers (Hölldobler and Wilson 2009).

Superorganisms are the original ultracooperators. They exhibit nearly every feature of the cluster of traits associated with ultracooperation (summarized in Box 1), which they evolved via between-colony selection (Wilson and Wilson 2007; see also "The “collateral kin selection” objection" section) many millions of years before humans came onto the scene and without any fancy mental representations to boot. Superorganisms are obligate cooperative foragers, food-sharers, brooders, and warmongers without parallel in the animal kingdom. They have elaborate communication systems and behavioral immune systems. They have political power structures designed to suppress dominant individuals whose selfish activities would otherwise disrupt group performance. Many superorganisms are structured around agricultural practices, exhibit regular tool use, and provide some of the clearest examples of peer-to-peer pedagogy in the animal kingdom. Given that many of these features have been proposed as the ecological impetus for the evolution of social normativity in humans, it is worth taking a serious look at whether insect societies might be organized around social norms as well.

Box 1

The Original Ultracooperators

Social insects exhibit many cooperative behaviors linked to the evolution of social norms in humans.

Foraging

The evolution of punishment in human hunter-gatherers is thought to have been crucial for stabilizing food-sharing norms that underpinned the cooperative hunting of large game and the equitable distribution of the spoils (Sterelny 2012; Boehm 2001). Like humans, ant workers collaborate in gathering and hunting, tracking, ambushing, and subduing dangerous prey thousands of times their size and jointly transporting large foraging bounties over complex terrain back to the nest for processing and triage. Food-sharing is essential to colony success: procured nutrients are stored in "social stomachs" (gasters) and shared between members of all castes and larvae via regurgitation (trophallaxis).

Brooding

Cooperative brooding has been proposed as the original social problem that human normativity was adaptively designed to solve (Burkhart, Hrdy & Van Schaik 2009). Social insects are cooperative brooders par excellence: workers forgo their own reproduction and tend conscientiously to the colony's highly vulnerable brood—feeding and cleaning them, optimizing temperature and moisture in nurseries, defending the brood from interspecific predators and intra-colony threats, and safely relocating eggs and larvae to new nest sites. Collaborative brooding is likely the repeated driver of complex eusociality in insects (see "The "collateral kin selection" objection" section).

Warfare

Intergroup conflict was probably a key factor in the evolution of altruistic norms in humans (Bowles 2008; Buchanan & Powell 2018). In insects, too, collaborative hunting skills would have been readily extended to organized warfare between societies. Superorganisms are the only nonhuman animals to wage existential wars that can last for months and result in millions of casualties, replete with warfare specialists, troop transport, reconnaissance, formations, supply lines, and rescue operations to retrieve the wounded. Their battles involve suicide bombing, projectiles, barricades, and even the appeasement of superior forces to ward off an impending invasion (Moffett 2011).

Immunity

Many aspects of human moral and political psychology can be understood as behavioral adaptations for pathogen avoidance (Navarrete and Fessler 2006). Superorganisms typically live in large underground populations in close quarters, which makes them susceptible to infectious disease. They have thus evolved elaborate defenses against pathogens that include social distancing, allogrooming, destructive disinfection, the generation of colony-level "fevers," and the safe disposal of the dead; they have mechanisms of innate and acquired immunity, inoculating nest-mates with doses of pathogen, and they patrol the colony for interlopers and illicit reproduction (Aanen 2018; Pull & McMahon 2020).

Politics

Social insects live in distinct societies with tightly controlled boundaries. Unlike other political animals, such as wolves or chimps, whose social interactions are grounded in personal familiarity, superorganisms live in large anonymous societies that require abstract markers of group identity. In humans, these take the form of language, symbols, and dress (McElreath et al. 2003); in superorganisms, they involve a colony scent—a hydrocarbon signature embedded in the exoskeleton cuticle which colony members imprint upon as hatchlings and maintain over time through allogrooming. Superorganisms also have elaborate social hierarchies and deploy coalitions to suppress exploitation by high-ranking group members (see "Policing in insect societies" section).

Communication

Humans are quintessential informavores with an intrinsic motivation to share information with conspecifics through language. Superorganisms do not have anything like the infinitely combinatorial linguistic system of humans, but they do have the most advanced multi-modal communication system in the non-human animal world. Chemosensory, motor, tactile, auditory, and visual signals are combined in syntax-like permutations to recruit specific workers to problems that require specific sorts of collective action. Information crucial to colony homeostasis is acquired through experience, passed from worker to worker in the field, stored at the level of the group, and transmitted down generations of individual workers (Gordon 2016).

Industry

Normative cognition is likely key to the mastery of technical skills (Birch 2021) and scaffolded learning environments (Powell 2020; Sterelny 2012) that underpin technological industry in humans. Although social insects do not rely on normative learning structures, they have nevertheless developed exquisite agricultural practices that include the domestication of various fungi (Ramadhar et al. 2014) and a range of hemipteran insects (Hölldobler and Wilson 2009); and some ants have been shown to collect and flexibly deploy tools used for transporting food (Banschbach et al. 2006).

Pedagogy

Pedagogical interactions in ants are manifest during "tandem runs"—social interactions that enable knowledgeable, experienced workers to teach naïve foragers the location of resources (Frank and Richardson 2006). Tandem runs involve bidirectional feedback that keeps a pair together as they progress toward a target, with the teacher modifying her behavior as needed with the goal of teaching her naïve partner the location of the resource. Interesting, tandem running occurs in smaller colonies that are unable to rely wholly on mass recruitment via pheromone deposit trails.

Policing in insect societies

Several types of norms are ostensibly policed in insect societies. One concerns egg laying (Wenseleers and Ratnieks 2006). In ants, bees, and wasps, when a fertile queen is present, workers are functionally expected to forego reproduction. The queen does not personally enforce this norm biomechanically: instead, low-ranking workers play the heavies, fastidiously attacking offenders and destroying any eggs they lay. This policing can be 99% effective and does not depend on the offender's social rank or genetic relatedness to the enforcers (Ratnieks and Wenseleers 2005), conforming to the definition of "institutionalized punishment" discussed above.

A second type of policing concerns caste-fate. One remarkable finding of superorganism research is that the caste and sub-caste that a superorganism larva develops into is determined by differences in rearing, not genetics—much as cell specialization in animal bodies is accomplished through epigenetic mechanisms acting on the same genetic profile. Because caste-fate is manipulable, female larvae are evolutionarily incentivized to develop into reproductive queens rather than sterile workers, and if not kept in check, this would undermine the colony's division of labor. Low-ranking workers police larva by controlling the food they are permitted to eat to ensure they develop into needed workers rather than supernumerary queens, and any unauthorized queens that emerge are promptly executed (Wenseleers et al. 2005a; b).

Third, there is social status policing. Like members of the Victorian underclass who could be fired or demoted for dressing above their station, some ant societies are organized around elaborate social hierarchies that are rigorously enforced. In queenless societies, individuals who engage in false dominance displays or feign a high social status that might move them up in line for reproduction can be sprayed with a secretion that marks them as an offender, which then prompts coordinated attacks by low-status worker police (Hölldobler and Wilson 2009). Policing has evolved convergently in ants, bees, and wasps (Foster and Ratnieks 2001), and recently has been shown to have arisen in termites as well, with subordinates acting in concert with older reproductives to attack and kill younger reproductives who lose in the competition for the dominant breeding position (Sun et al. 2020).

In all of these cases, subordinates use biochemical cues and context-sensitive fixed-action patterns to coordinate efforts to prevent individuals of any rank or caste from performing behaviors that threaten to derail group performance. Importantly, these interactions are not the result of asymmetrical power dynamics that enable dominant individuals to induce cooperation in weaker subordinates. Rather, they are many-against-one power structures, maintained by subordinates, that benefit the collective in its evolutionary struggle against competing collectives. The need for policing (and by implication norms) may be obviated where castes have internalized their altruistic roles, such as where workers have come to lack reproductive organs entirely (Wenseleers et al. 2005b)—a point of no return analogous to the loss of reproductive functions in the somatic cells of multicellular organisms. At that point, conflict between levels of selection disappears entirely (Birch 2017; Okasha 2009), and with it, the need for social norms.

Although both human and insect societies are structured around norms, there are important differences in the way that normativity underpins ultracooperation in these respective groups. For one thing, positive reinforcement—rewarding individuals for compliance with social norms—is far less important in insect societies (if not non-existent), likely due to the fact that cooperative behaviors in insects are under stronger genetic control. For another, in humans, social norms coordinate individually costly collaborative efforts like foraging, food-sharing, teaching, and warfare, whereas there is no evidence at present that norms directly underpin these sorts of collaborations in social insects. However—and this point is crucial—such complex cooperative endeavors are only evolutionarily stable in social insects (and hence amenable to selective canalization) thanks to norms that successfully constrain individual reproduction. With individual reproductive success effectively transferred to the group level, a collective evolutionary fate is sealed, and an individual has no choice (functionally speaking) but to contribute to group vegetative and reproductive functions for their own persistence and propagation. Once unauthorized reproduction is under normative control, selection can canalize a whole range of cooperative behaviors without normative input into those activities. By contrast, norms systematically regulating reproduction have never stabilized in human groups (and may never do so), leaving the transfer of fitness to the group level incomplete. As a consequence, cooperative motivations have not fully canalized in humans, making normative input during ontogeny critical for nearly all cooperative human endeavors.

Hölldobler and Wilson (2009) quote Harvard University president Abbott Lowell as saying, tongue-in-cheek, that the ants, "like human beings, can create civilizations without the use of reason." Social insects probably have no conception of the norms they are following, but this is probably true of all nonhuman animals governed by social norms, and on occasion it is true of humans as well.

Objections conjured and parried

The "slimy slope" objection

If, as I have suggested, social norms supervene on diverse cognitive capacities and modes of inheritance, then what would prevent us from finding social norms in biological cooperatives like bacterial biofilms, amebic slime molds, and brainless colonial animals, all of which have mechanisms that regulate cheating? And if that is an implication of my view, is this not a good reason to fall back on the stipulation that norms are necessarily the product of demanding cognitive mechanisms?

My response is twofold. First, although cheater detection is sometimes described by biologists as "policing," it rarely has the many-against-one power structure necessary for establishing a norm on my view. Second, social norms do not exist where lower-level units cooperate but do not "behave" in any meaningful sense of the term. Whether we find ourselves slipping down the slimy slope, therefore, will depend on how we think about "behavior." Biologists hold different views about what counts as a behavior (Levitis et al. 2009), but there is general agreement that it does not include purely developmental processes like producing insulin in response to sugar.

And because the mechanisms that regulate cheating in microbial cooperatives involve things like producing or withholding a metabolite to control cellular processes, they do not regulate behavior properly understood. At this stage, however, we cannot rule out social norms in microbes or brainless animals—but nor should we want to. Some may see these possibilities as reductios; I see them as explanatory strengths.

The "freedom to choose" objection

If behavioral compliance is rigidly determined by "genetic programs," rather than learned and freely chosen by individuals, does it really count as norm-following? Humans are robust agents, and so enculturation and coercion are necessary to ensure they adhere to altruistic norms. Superorganisms, in contrast, do not need an insect equivalent of the Soviet NKVD to ensure that workers sacrifice themselves in service to the Great Mother. Indeed, social insects do not need norms at all!

My response is that rather than thinking of behavior in binary terms of free versus fixed, it is better to see behavior as falling along a continuum of plasticity and canalization. Even in humans, norm compliance and content are to some degree innately prepared (Haidt 2012, 325–28); and what is not canalized by genes is stabilized by culture, which equally undermines the freedom to choose. So, it is misleading to say that humans "choose" to conform while other animals follow rigid genetic programs or instincts.

At the same time, it is important to recognize the considerable flexibility of insect behavior. Much has been made of the hive mind and swarm intelligence, but the individual workers of superorganisms turn out to be surprisingly cognitively adept in their own right. Although the stereotype of insects as mindless automatons lingers on, the last two decades have seen an overhaul in our understanding of insect cognition, casting doubt on the assumption that absolutely small brains cannot support sophisticated mental processes. Social insects can acquire complex unnatural skills (e.g., string pulling to get a reward), learn abstract concepts (e.g., "sameness/difference") and transfer them across sensory modalities, exhibit emotion-like states (e.g., negative arousals) that modulate their decision-making, acquire innovations through social learning, and perhaps even reason about causation (reviewed in Chittka 2017; Mikhalevich and Powell 2020).

This is not to suggest that social insects have mental representations of the norms they are following or that they experience indignance toward norm-violators. But their cognitive flexibility raises the intriguing possibility that compliance is shaped during the lifetime of individual colony members by the reactions of conspecifics to norm violations. Indeed, "execution" is not the only result of policing: injury and demotion in rank are also frequent outcomes (Helanterä and Ratnieks 2019), and they could serve to rehabilitate offenders or deter future norm violations. We should not assume, therefore, that insect policing is limited to the evolutionary "pruning" of genetically determined norm violators.

Having said that, we are sitting here today writing about our own evolution thanks to a great deal of human pruning. Ultracooperation is only possible in humans because we have massively reduced rates of aggression within groups as compared to common chimpanzees. This is thanks to a process that Wrangham (2019) calls “self-domestication.” The idea is that the human lineage imposed selection pressures for prosociality on itself by way of coalitions of normative egalitarians who reliably dispatched violent, power-hungry individuals through “targeted conspiratorial killing”—a cheap form of pruning made possible by language and joint intentions. This process of self-domestication looks strikingly similar to what happened in superorganisms, except with olfaction, context-sensitive fixed-action patterns, and females playing the enforcement-coordinating role that language, metacognition, and males played in early humans. These are, of course, very different solutions to the same design problem, but their ecofunctional structure is the same.

The “scare quotes” objection

A third objection maintains that all allusions to “punishment,” “policing,” and “institutions” in social insects should be in scare quotes, because they are at best metaphorical and at worst category mistakes. There is no genuine punishment in insect societies because these animals lack moral emotions like indignance, anger, empathy, and shame. There is no policing because insect workers have no conception of their social role. There are no institutions because there is no insect culture of which to speak. Metaphors have proven epistemologically useful in evolutionary science, from the “fossil record” (Currie forthcoming) to the theory of “natural selection” itself. Nevertheless, one might be tempted to see this whole discussion as a mere verbal quibble, and to maintain that since the social sciences already have a rich cognitive account of social norms on the table, we should just call what insects have “schnorms” and go our merry way.

In fact, we can put the scare quotes objection in even stronger terms. Returning to convergent eyes, we can say that the eyeball (qua morphological structure) is convergent in single-celled dinoflagellates, but that vision is not, because “vision” implies a kind of cognitive-representational architecture that dinoflagellates lack. In the same vein, one might argue that social norms entail a cognitive-representational architecture that social insects lack. It is right that explaining visual ecology requires adverting to a cognitive-representational architecture that is lacking in brainless organisms with eyes. But the situation is different for social norms, since as we have seen, ultracooperation—the presumed function of social normativity—has been realized by social structures underpinned by radically different cognitive-representational formats, motivations, and sensory modalities. One palatable solution to the “schnorms objection” would be simply to call the normative structures I have described “functional social norms,” with human and insect societies exhibiting different proximate realizations of this adaptive organization. This would allow anthropologists and psychologists to retain the cognition and culture-grounded meaning of “social normativity” in human-specific explanatory contexts, while providing the conceptual space needed for a unified account of social normativity.

The value of the convergentist approach gets lost when the project of explaining social normativity boils down to identifying the cognitive difference-makers of human success. Henrich and Muthukrishna (2021), for instance, frame the challenge of explaining social norms as one of providing a difference-making account of human cooperation where the contrast class is other *mammals* and where cooperation and social identity are conceived in terms of *choices* and *expectations*. Meeting this challenge will undoubtedly involve adverting to sophisticated mental representations. Integrating higher-order cognition into models of norm adherence may be useful for understanding the conditions of norm compliance in humans, but it lacks the nomological generality of behavior-based accounts of the sort I have proposed here. Because evolutionary theory subsumes rational choice theory (Okasha 2009), it provides a more general framework for understanding social evolution.

A broader mistake in play here is to assume that there is only one level of description for any given trait, when in fact the multiple realizability of function allows for different generalizations at different levels of specificity. Human moral normativity is simply one specific instantiation of social norms, and social norms are only one type of cheater-regulating mechanism in animals (immune systems, developmental bottlenecks, and programmed cell death are others). Therefore, to say that the function of social norms is to "promote cooperation," a standard refrain in the literature on the evolution of normativity, is an imprecise characterization. There are many adaptations that promote cooperation, and most of them do not involve social norms.

If, as Henrich and Muthukrishna (2021, 209) put it, "the question to focus on is how our social environments have become structured such that the smart move is often to cooperate and help rather than to exploit and harm", then we must look beyond primates, mammals, and even vertebrates to develop a broader functionalist understanding of social normativity. This does not stop us, of course, from investigating finer-grained research questions about the psychological and cultural realizers of cooperation in humans. And there may be limited degrees of convergence in the cognitive realizers of putatively normative behavior across mammals and birds. But such approaches should be understood as having more targeted explanatory aims, and they should be informed by broader parallels between human and insect societies.

Another benefit of studying patterns of convergence is that it allows us to separate law-like causation from contingent confabulation. Consider undertaking. Explanations of why early cave-inhabiting humans started burying their dead usually advert to belief in an afterlife. But then one notices something interesting: superorganisms like termites, which live in close-quartered populations that are forced to contend with infectious disease, also bury their dead. In termites, undertaking is a response to chemical cues and diminished vital signs rather than supernatural propositions. But the "real" reason why both humans and superorganisms bury their dead is to guard against infectious disease—selection is simply working with whatever proximate mechanisms are on hand. The biofunction explains all cases of undertaking, whereas human-specific proximate mechanisms figure in only one. What makes a social interaction fundamentally normative is not its proximate motivators, but the functional structure of the interaction taken in ecological and evolutionary context.

As Birch (2017, p. 186) cautions, however, it is important not to overstate the parallels between human and insect societies, some of which arose only recently with the advent of post-Neolithic human populations. In a detailed evolutionary comparison of human and insect sociality, Wilson (2012, p. 24) characterizes human societies as “eusocial” in the thin sense that they contain overlapping generations and tend to perform altruistic acts as part of a division of labor. But whereas complex eusocial insects betray the hallmarks of a transition to a higher-level individual (McShea 2002), humans have not differentiated into reproductive and vegetative castes, as they lack the extreme morphological plasticity that allows the same genome in social hymenopterans to differentiate into vastly different castes and subcastes via simple environmental modulations. Instead, task specialization in human societies has been offloaded from genes onto culturally transmitted skills and technology. And because human individuals retain high behavioral plasticity throughout ontogeny, the bulk of human normativity is spent wrangling selfish, nepotistic, and individualistic behavior that tends to undermine group performance.

Human sociality thus has a long evolutionary distance to travel before it could rise to the level of superorganism; and given the life cycles and mixed-motivational nature of human beings, there is a good chance it will never get there. As Wilson (ibid, p. 74) concludes, it may be that “no insect-like social system can be created in the theater of mammalian social evolution.” The deep structural similarities between human and insect societies are owed not to the fact that both are superorganisms, but rather to the fact that both are ultracooperative societies underpinned by social norms.

Finally, the account of social norms I have put forward is discordant with ordinary intuitions about normativity, and it presents a significant departure from how the concept is standardly used in philosophy and the human sciences. But the history of science is a story of exploding (rather than vindicating) our intuitive understandings of the causal structure of the world in the service of deeper explanation. We should thus welcome attempts to reconceptualize distinctive human traits in a broader and more humbling evolutionary context, even if we ultimately find those efforts unpersuasive.

The “maladaptive norms” objection

One might object to the account of social norms put forward in this paper by pointing out that many social norms in humans do not in fact facilitate cooperation, and some may be straightforwardly maladaptive at the group level—and yet, they are still norms. Some elaborate rites, rituals, and food taboos that provide no obvious utility may actually serve as honest signals or bonding mechanisms that maintain the cohesion of cooperative groups. It is undeniable, however, that some norms benefit a few dominant individuals and their kin at the expense of the group, such as the deliberately inept bureaucracies and legal systems that bolstered colonialist rule (Buchanan and Powell 2017) and that continue to bolster autocracies. Still other norms are deleterious to everyone in a society, such as those grounded in magical thinking that can impede causal inference. Norms like these may proliferate like cultural viruses at the expense of individual and group fitness by exploiting psychological biases of human beings (Dennett 2007; Sperber 1996). Or they could simply be a byproduct of the dynamics of cultural transmission, which allow for the rapid spread of maladaptive variants: mathematical models show that punishment can stabilize any norm no matter how maladaptive it might be (Boyd and Richerson 1992). Either way, the point is that maladaptive norms are still norms. If this is right, then norms cannot be indexed to group-level functions, if they can be indexed to any functions at all.

There are several things to say in response. First off, it is important to distinguish the generic norm acquisition and enforcement system from the specific, contentful norms that it outputs (Machery and Mallon 2010). Whereas norm acquisition and enforcement are human universals, the content of normative systems varies widely across cultures and ecological contexts. This adaptive flexibility makes the evolution of social norms susceptible to parasitism by powerful individuals and creates a tendency to throw-off deleterious byproducts. But this in no way affects the adaptive etiology of the underlying norm acquisition-enforcement system itself. By way of analogy: The fact that slave-making ants invade host colonies, kill their native reproductives, and coopt the host workforce into altruistically raising the invaders' brood is not evidence that collaborative brood care in ants is not a group-level adaptation; instead, it illustrates how that adaptive system can be parasitized in ways that result in a group's destruction. Bicchieri (2016) is right that the proliferation of many social norms in humans cannot be *explained* by the cooperative functions they perform. But just as a malfunctioning heart is still a heart, maladaptive norms are still norms, for they emanate from a system that proliferated because, on the whole, it tends to generate norms that facilitate cooperation.

The key question then becomes: cooperation *at what level*? In a recent extended discussion of the evolution of human normative psychology and culture, Henrich and Muthukrishna (2021) argue that social normative systems arose via within-group processes early in human evolution; only more recently, they suggest, were norms coopted for binding kin groups into larger clans, tribes, and nations by regulating nepotism, cronyism, and other forms of kin-based cooperation that tend to undermine group solidarity (2021, 213, 228). If this "exaptation" view is correct, then social normative systems predate the multilevel selection context, and so they must be delineated and explained independently of their effects on group performance. Henrich and Muthukrishna's view recognizes a role for social norms in solving multilevel cooperation conflicts; our main point of disagreement turns on the etiology of this role. Whereas I take multilevel selection to be the ecological impetus for social norms, they see multilevel selection as a recent twist on a normative capacity that arose much earlier in an individual-selection context.

Although the question of levels at the point of origin cannot at present be answered definitively, the convergent ultracooperation cluster may provide some clues over and above what we can glean from modeling work on the evolution of punishment and what we know about the social ecology of early humans. If the ultracooperation cluster is a natural cluster kind, then the fact that kin selection, reciprocity, honest signaling, and reputational systems appear to have been neither necessary nor sufficient to sustain ultracooperative functions in hymenopterans suggests that individual-level selection may have taken a backseat to group-level processes in the evolution of human ultracooperation as well.

The “synchronic cause” objection

A related challenge to the present view, and indeed to any adaptationist account of social norms, holds that social norms should be defined solely in virtue of their synchronic effects. Policing is policing, with the same proximate effects on cooperative behavior, regardless of its adaptive origins and irrespective of whether it arose under group-level or individual-level processes. If synchronic policing structures are sufficient to configure social norms, then we can recognize norms as such even when they are maladaptive for the group and even if they have no adaptive function at any level. What, then, do we gain by tying social norms to specific adaptive hypotheses and levels of selection?

What we gain, I think, is a unified explanatory account of social norms and their role in the evolution of ultracooperative groups at various locations in the meandering (and eminently defeasible) trajectory toward a higher-level individual. Although it is possible in principle that normative societies could arise through kin selection or even non-adaptive processes, social norms in the wild are, as an empirical matter, intimately tied up with certain group-level processes ("The “collateral kin selection” objection" section). These processes form an integral part of my *account* of social norms, if not part of their *definition*. Even the very broad biological notion of policing excludes punishment behaviors that do not disrupt group stability (Singh and Boomsma 2015). Yet until the underlying evolutionary processes are decisively established, it is important to keep the phenomenon distinct from the processes that are hypothesized to have produced it. This remains true even if there is a give-and-take between how norms are delineated and how they are explained, with novel explanations revealing features of social norms that might otherwise have gone unnoticed.

If, for the time being, social norms are to be defined by their ontogenetic rather than phylogenetic structure, then it is fruitful to delineate this structure in behavioral rather than cognitive terms, as it is behavior that natural selection “sees,” not its multiple cognitive realizers. In effect, behavior "screens off" proximate causes with respect to fitness consequences. The ultracooperative capacities that humans have achieved with complex normative cognition and culture, social insects have achieved with complex hydrocarbons and fixed-action patterns. Thinking about social normativity in terms of adaptive behavior, rather than in terms of the proximate cognitive realizers of adaptive behavior, is epistemically valuable for the same reasons that thinking about cooperation, politics, agriculture, and warfare in behavioral terms is fruitful: namely, it reveals law-like continuities that transcend the historical contingencies of body plans, life cycles, and lifeways. It explains why normative features arose and what role they play in living societies, human, insect, or otherwise. At even grander scales, it shows how social norms form evolutionary bridges from individuals to groups and back again, driving up the hierarchical organization of life.

This is a fresh boon for moral naturalism. For it suggests that not only is human normativity an adaptation for group-level cooperation (a standard position), but also that it is merely one expression of a law-like process which produced civilizations millions of years before humans appeared on the scene and that will continue to do so long after we are gone.

The "collateral kin selection" objection

Collateral kin selection refers to selection for behaviors that decrease the survival prospects of an individual but enhance the fitness of that individual's relatives beyond the parent–offspring relation. If collateral kin selection can explain away all conflicts between levels of selection, then this would obliterate the present proposal insofar as it attempts to ground social norms in solutions to multilevel selection conflicts. How much of a threat is this to the general framework offered here or to the specific example of social normativity in insects?

For some time, it was thought that the unique haplodiploid genetics of social hymenopterans made it in the fitness interest of female workers to become sterile or voluntarily forego reproduction in order to spend their energies raising full worker sisters. In social hymenopterans, females develop from fertilized diploid eggs and males from unfertilized haploid eggs. Consequently, in colonies with a single, once-mated queen, workers are 0.75 related (*r*) to their sisters, whereas they are only 0.5*r* to their own diploid male and female offspring and 0.5*r* to their own haploid (unfertilized) sons. Eusociality thus became a classic illustration of Hamilton's inclusive fitness framework, explaining away the extraordinary altruism of social insects as a straightforward prediction of kin selection models. Additionally, other inclusive fitness models showed that genes for policing (including egg destruction and aggression toward reproductive workers) can spread in social insect colonies even if they do not confer any group-level benefits, so long as workers are more closely related to the queen's offspring then they are to the haploid offspring of their fellow workers (Ratnieks 1988).

This elegant theory of eusociality has since been toppled by less elegant data. It turns out that many queens are multiply-mated and many colonies have multiple, distantly related queens, resulting in uneven patterns of inheritance among colony members that renders relatedness a nonfactor in the selection for altruistic behavior (including self and other policing). Even in singly-mated, single-queen colonies, inclusive fitness theory predicts that reproductively totipotent workers should favor having sons (0.5*r*) over brothers (0.25*r*)—and yet, when a fertile queen is present, these selfish behaviors are markedly reduced thanks to policing by third-party subordinates. In some cases policing may have selfish evolutionary motivations, such as in primitive wasp and bumblebee colonies where workers destroy the eggs of their sisters in order to secure a future for their own offspring (Sing and Boomsma 2015). But there would presumably be no need for the altruistic policing characteristic of more advanced superorganisms were fitnesses between levels of selection harmoniously aligned. Such an alignment has only occurred in highly derived superorganisms whose workers have lost their reproductive organs entirely, effectively driving their individual fitnesses to zero ("Policing in insect societies" section).

Another problem for kin-based theories of eusociality is that altruistic norms have evolved in diploid organisms. Humans are the obvious case, but the critical insect case is termites, which are more closely related to cockroaches than to other eusocial insects. Because termites have diploid genetics (like humans), overall genetic relatedness cannot account for policing or sterile castes in this ultracooperative clade. Complex eusociality cannot be explained away, therefore, as a quirk of hymenopteran genetics. Coercion-based theories of altruism, whether cashed out in a multilevel selection or an inclusive fitness framework, offer an alternative to kin selection when it comes to explaining the evolution of cooperation (Queller 2016). Although it has been argued that kin selection and multilevel selection are formally (mathematically) equivalent (Lehmann et al. 2007), this does not imply that these frameworks offer equally adequate *causal explanations* of cooperation in any given case, as several theorists have noted (Birch 2020; Okasha and Martens 2016).

But if kin selection was not the predominant driver of eusociality in hymenopterans, then what was? One view is that cooperative brooding was the repeated ecological driver of eusociality in ants, bees, and social wasps (Hölldobler and Wilson 2009). The hypothesis is that eusociality arose several times in solitary parasitic wasps, which provision their larvae with paralyzed insects to leisurely consume in their brood chamber. Wilson (2012) conjectures that initial stages of eusociality involved selection for genes that inhibited the instinct to disperse, keeping overlapping generations at the mother nest and creating a redundancy in parental care that reduced the cost of parental death. Female wasps took turns foraging, feeding, cleaning, and guarding their nests from a panoply of predators and parasites. Then, under colony-level selection, further epigenetic modifications to life cycle and behavior allowed brood care to be taken over by non-reproductive workers, which in turn paved the way for further caste-based differentiation into specialized reproductives, foragers, soldiers, nurses, and so on.[4] Punishment for unauthorized reproduction, initially carried out by dominants in smaller groups amenable to cheater-monitoring, gave rise to enormous colonies patrolled by teams of third-party policers. If this is right, then the relatedness component of inclusive fitness—which forms the core of kin selection theory—falls short of explaining ultracooperation.

Although the cooperative brooding hypothesis is merely one among several ecofunctional theories of eusociality on offer (cooperative foraging is another), the present argument does not hinge on any particular ecofunctional hypothesis being true. The point is that the inclusive fitness framework supplies no ecofunctional explanation at all. Further, understanding the convergent adaptive etiology (Currie 2012) of functional social norms in insects could inform the relative credences we assign to adaptationist accounts of human normativity, such as cooperative alloparenting (Burkhart et al. 2009), foraging (Sterelny 2012; Wrangham 2019), and skill transmission theories (Birch 2021).

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[4] There are many cases of cooperative breeding in both vertebrates and insects in which facultative "helper" subordinates are not closely related to the dominant breeders they serve, exchanging their services for the survivorship benefits of group membership and a chance to become a dominant breeder in the future (the so-called "pay-to-stay" model). By serving a dominant breeding individual or pair, helpers benefit from gaining access to a communal territory, lower predation pressures, and mating opportunities. These relationships are fluid: defections and evictions are common and governed by market forces (Grinsted and Field 2017).

The "scientistism" objection

Another potential worry about human-insect comparisons concerns their ethical undertones. Referring to morally loaded categories like "warfare," "slave-making," and "aggressive policing" in superorganisms could be read as a scientistic attempt to naturalize morally deplorable human practices and institutions, which in turn could appear to justify and thereby perpetuate them. This inductive risk remains even if the comparisons are theoretically defensible, even if "adaptation" does not imply environmentally unalterable, and even if the inference from description to justification is a straightforward logical fallacy (Weaver 2019). After all, human atrocities have rarely thrived on logical consistency and empirical coherence, and the dehumanization strategies employed by architects of ethnic cleansing and genocide have often made effective use of human-insect comparisons (Navarrete and Fessler 2006).

On the other hand, coming to see defining human traits like normativity as continuous with those of nonhuman animals—including small-brained ones—does a great service to the battle against anthropocentric views of life, making good on the "decentering" and "dethroning" project that Darwin began (Powell and Mikhalevich forthcoming). The crux of the issue is whether finding social normativity in insects will make us think of humans as more insect-like or insects as more human-like. On balance, I suspect that establishing human-animal continuity (whether due to convergence or common ancestry) provides a more robust impetus for moral inclusivity than it does exclusivity, though it would take a more detailed analysis to make this case decisively.

Conclusion

Philosophical investigations of normativity are no longer confined to the armchair. But attempts to extend the concept of social norms to the living world are still prone to many of the same pitfalls that saddle anthropocentric approaches. Biotheoretical work on minimal agency and cognition have vastly expanded research programs long tethered to inimitable features of human psychology (Fulda 2017; Moreno and Mossio 2015; Lyon 2006). I have advocated a similar shift in thinking about social norms, sketching a convergentist alternative that abstracts away from contingent proximate cognitive details to reveal large-scale causal structures in social evolution. The striking parallels between human and insect societies, recognized by keen observers of nature for thousands of years, are neither accidental nor metaphorical. They're owed to the fact that both are normative societies.

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