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In search of animal normativity: a framework for studying social norms in non-human animals

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ABSTRACT

Social norms – rules governing which behaviours are deemed appropriate or inappropriate within a given community – are typically taken to be uniquely human. Recently, this position has been challenged by a number of philosophers, cognitive scientists, and ethologists, who have suggested that social norms may also be found in certain non-human animal communities. Such claims have elicited considerable scepticism from norm cognition researchers, who doubt that any non-human animals possess the psychological capacities necessary for normative cognition. However, there is little agreement among these researchers about what these psychological prerequisites are. This makes empirical study of animal social norms difficult, since it is not clear what we are looking for and thus what should count as behavioural evidence for the presence (or absence) of social norms in animals. To break this impasse, we offer an approach that moves beyond contested psychological criteria for social norms. This approach is inspired by the animal culture research program, which has made a similar shift away from heavily psychological definitions of 'culture' to become organised around a cluster of more empirically tractable concepts of culture. Here, we propose an analogous set of constructs built around the core notion of a normative regularity, which we define as a socially maintained pattern of behavioural conformity within a community. We suggest methods for studying potential normative regularities in wild and captive primates. We also discuss the broader scientific and philosophical implications of this research program with respect to questions of human uniqueness, animal welfare and conservation.

Key words: animal normativity, norm psychology, social norms, animal culture.

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I. INTRODUCTION

In human communities, social norms are typically understood as rules that dictate which behaviours are deemed appropriate or inappropriate. Thus construed, social norms govern a vast and variable array of human behaviours across all cultures, from customs of polite greeting, to rituals surrounding death and mourning, to the way that people form and maintain social hierarchies. Such rules are typically enforced by other members of the community through sanctions and rewards. Social norms are thought to play a number of important functions in human communities: they facilitate cooperation between unrelated individuals, create regularities that render complex social environments more navigable, and provide agents with guidelines for how to behave and live around one another in harmony.

Because social norms play such an important role in modern human societies, many researchers have inferred that social norms must stem from uniquely human forms of cognition. For example, some have argued that social norms are grounded in what they take to be uniquely human capacities for shared intentionality (Tomasello, 2016a, 2022; Schmidt & Rakoczy, 2019). Rochat (2015) traces norms to uniquely human forms of self-consciousness. Henrich (2015) attributes 'the secret of our success' in part to a uniquely human 'norm psychology' shaped by a history of hominin gene-culture coevolution (see also Richerson & Boyd, 2005; Sripada & Stich, 2006; Kitcher, 2011; Kumar & Campbell, 2022). Recently, Birch (2021) and Sterelny (2021) have argued that social norms evolved from cognitive control mechanisms that were originally selected for complex tool manufacturing in hominins. While these proposals vary in their details, they share the common assumption that human beings are the only 'normative animal' (Roughley & Bayertz, 2019). Most philosophical and social scientific

accounts of the nature and origins of social norms also make this assumption (e.g. Bicchieri, 2006, 2017; Sellars, 1949).

However, a number of philosophers, cognitive scientists, and ethologists have recently begun to approach this topic from a comparative perspective, asking whether or not social norms might be found in certain non-human animal communities (Andrews, 2020; Bekoff & Pierce, 2009; Danón, 2019; Fitzpatrick, 2017, 2020; de Waal, 2014; Kappeler, Fichtel & van Schaik, 2019; Lorini, 2018; Powell, 2023; Rudolf von Rohr, Burkart & Schaik, 2011; Rudolf von Rohr et al., 2015; Vincent, Ring & Andrews, 2018; Westra & Andrews, 2021; Whiten, Horner & de Waal, 2005). This growing literature (on what we shall refer to as the 'animal normativity debate') is motivated by a number of examples of non-human animal behaviours that evoke the concepts associated with social norms and rules, and by ethological reports that have identified animal behaviours that appear to be regulated by the presence of other group members.

Evidence suggesting that animal communities may possess social norms has emerged in a number of domains. The dominance hierarchies found in many species have been analysed in terms of 'convention-based societies' (Strauss & Holekamp, 2019), leading some researchers to speculate that the normatively governed social hierarchies of our species have important commonalities with certain non-human animal social hierarchies, and that both might be constituted by basic norms about who gets to do what, when, and with whom (de Waal, 2014; Nishida et al., 1995). Observations and experiments examining responses to potential acts of infanticide or mishandling of infants have been interpreted as evidence of rules against infanticide in chimpanzee (Pan troglodytes) communities (Rudolf von Rohr et al., 2011, 2015). Social play and play fighting in species such as chimpanzees (Flack, Jeannotte & de Waal, 2004) and dogs

(Bekoff, 2001) has been described as involving 'rules' governing play, signalling to potential rule enforcers, and modifying actions when playing with a younger or weaker partner. Instances of conformity to local cultural traditions, including traditions of tool preferences in chimpanzees (Luncz & Boesch, 2014; Whiten et al., 2005), food preferences in vervet monkeys (Chlorocebus pygerythrus) (van de Waal, Borgeaud & Whiten, 2013), vocal traditions in birds and cetaceans (Aplin, 2019; Watson et al., 2015; Whitehead & Rendell, 2015), as well as traditions of more arbitrary behaviour like chimpanzees wearing grass in their ear (van Leeuwen, Cronin & Haun, 2014) or dolphins tailwalking (Bossley et al., 2018) have been suggested as potential non-human social norms. Apparent expectations about resource distribution, first identified in captive brown capuchin monkeys (*Cebus apella*) (Brosnan & de Waal, 2003), also invite descriptions in terms of protesting rule violations.

Such examples notwithstanding, the suggestion that non-human animals may have social norms has been met with considerable scepticism. While critiques of the alleged behavioural evidence for social norms have been offered (e.g. Schlingloff & Moore, 2017), these doubts mostly stem from the aforementioned inference that norms must require uniquely human cognitive capacities (e.g. Schmidt & Rakoczy, 2019). Proponents of the view that non-human animals may possess social norms (hereafter, 'animal normativity') have pushed back against these critiques in several ways. Some have argued that evidence from non-human animals like chimpanzees might in fact be consistent with some common psychological criteria for social norms (Fitzpatrick, 2020; Westra & Andrews, 2021), while others have argued for a different set of psychological criteria that animals do meet (Andrews, 2020), or that some animals at least possess 'precursors' to human social norms (Rudolf von Rohr et al., 2011, 2012, 2015). However, progress in these debates is hindered by a general lack of consensus about both the psychological criteria for social norms and the kinds of behavioural data that would provide compelling evidence of animal normativity (or lack thereof).

Here, we describe a way to make progress on the question of whether other animals have social norms (and, if so, how they compare to human social norms). We outline an approach that moves away from disputes over contested psychological criteria and towards a diagnostic framework that refocuses attention on what we will call 'normative regularities' and the behavioural indicators of their presence. Our proposal is inspired by advances in the adjacent empirical literature on animal culture. We argue that the animal normativity debate today is much like the animal culture literature when it was at a stalemate in the 1990s, characterised by messy disagreements over whether animals possessed what researchers took to be the requisite psychological capacities for being genuinely 'cultural' learners. For instance, sceptics argued that cultural learning requires teaching and imitation, and so apparent instances of cultural behaviour in animals could not really be 'culture' (e.g. Galef, 1992; Laland & Galef, 2009). Over the course

of the early 2000s, however, the literature began to move beyond these disagreements over the psychological criteria for culture and converged upon standardised approaches for identifying cultural practices in animal behaviour - for instance, by developing more operationalised and less psychologically loaded definitions of the notion of a behavioural tradition. This reorientation contributed to the emergence of a burgeoning and fruitful empirical literature that has identified cultural practices in species as diverse as chimpanzees and fruit flies (Whiten, 2021). Because the approach shifted to probing psychological mechanisms only after identifying robust behavioural traditions, scholars converged upon a pluralist view about the psychological underpinnings of culture whereby culture can exist at different levels of complexity and be sustained by a variety of different social learning processes (Hoppitt & Laland, 2013). The result was a much richer research program that was both more productive and, despite a more inclusive definition, ultimately more nuanced and comprehensive than it had been.

Herein, we present an analogous framework for studying animal normativity and propose a new lexicon with which to discuss the phenomena involved. In Section II, we critique the current state of the animal normativity literature and draw lessons from the animal culture debate. In Section III, we build upon those lessons and offer a diagnostic behavioural approach to characterising social norms that is intended to be analogous to how animal culture researchers have come to approach identifying behavioural traditions in non-humans. In Section IV, we offer proposals for investigating potential social norms in wild and captive animals, with particular focus on great apes and monkeys. We conclude in Section V with a discussion of why this topic is of broader scientific and philosophical importance.

II. RESTRUCTURING THE ANIMAL NORMATIVITY DEBATE

(1) Limitations of the current approach

As it stands, the debate about animal normativity mostly centres on whether or not non-human animals possess a particular psychological capacity that is present in humans – a 'normative sense'. So understood, the animal normativity debate would seem to resemble familiar debates in comparative cognition, such as whether non-human animals can represent false beliefs (Krachun *et al.*, 2009; Krupenye *et al.*, 2016) or are capable of numerical reasoning (Matsuzawa, 2009; Pepperberg & Carey, 2012). As in these other debates, establishing animal normativity would seem to require testing various predictions about how animals might behave if they had a normative sense, and systematically controlling for whatever alternative non-normative explanations might be given (e.g. Lurz *et al.*, 2022).

The problem is that there is little agreement in the existing literature about the cognitive architecture that underlies the human normative sense (O'Neill & Machery, 2018).

The cognitive evolutionary approach to the psychology of norms, for example, holds that it is grounded in a domainspecific 'norm system' for acquiring, representing, and enforcing intrinsically motivating rules (Chudek & Henrich, 2011; Kelly & Davis, 2018; Sripada & Stich, 2006). Alternatively, others have suggested that the normative sense develops from skills and motivations for shared intentionality - a cooperative capacity grounded in the sharing and representation of others' intentions. This capacity enables children first to understand each person's role in a collaborative activity and later to understand what 'we', qua group, demand from each other (Schmidt & Rakoczy, 2019; Tomasello, 2016a, 2019). Birch (2021) proposed that the human normative sense is supported by model-based control systems that underpin expert performance in skilled action, such as tool manufacture, which involve standards for correct and incorrect performance (see also Sterelny, 2021). Still others have proposed that human norm psychology stems from basic domain-general processes, such as reinforcement learning, prediction-error minimization, and the maintenance of allostasis (Colombo, 2014; Theriault, Young & Barrett, 2021), or that norm psychology is a culturally evolved 'cognitive gadget' built upon domain-general foundations (Heyes, 2023). Andrews' (2020) naïve normativity model points instead to a set of basic cognitive prerequisites for social norms in humans, such as the detection of agents, the ability to distinguish between ingroup and outgroup members, and experiencing evaluative emotions. Bicchieri's (2006, 2017) influential account of social norms, meanwhile, seems to presuppose some advanced forms of belief-based mental-state attribution – specifically, the ability to think about what others think ought to be the case.

Each model makes different claims about the psychological prerequisites for social norms and their underlying cognitive and motivational basis. This lack of consensus about the cognitive architecture underpinning the human normative sense creates significant methodological challenges for researchers attempting to study social norms in non-human animals, making it extremely difficult to determine which species are good or bad candidates for having a normative sense.

Consider the divergent roles that third-party punishment plays in each of these theories. Many theorists hold that third-party punishment by uninvolved bystanders constitutes positive evidence for the existence of social norms (Rudolf von Rohr et al., 2011). Norm system theories generally hold that third-party punishment played an important role in the evolution of the norm system and in stabilising cooperative norms at the community level (Chudek Henrich, 2011; cf. Boyd & Richerson, 1992; Mathew, Boyd & van Veelen, 2013). However, some of these accounts also suggest that the motivation to punish third-party norm violators is a feature of the norm system itself, a key component of the 'norm execution mechanism' (Kelly & Davis, 2018; Sripada & Stich, 2006). Notably, this disposition to punish is thought to stem from an intrinsic motivation, rather than any sort of instrumental calculation about individual payoffs.

With similar assumptions about the centrality of punishment to norm psychology in mind, some sceptics have suggested that the apparent dearth of evidence for third-party punishment in chimpanzee populations is evidence for the absence of social norms (Riedl et al., 2012; Schmidt & Rakoczy, 2019; Powell, 2023). [We note that there are reports of third-party punishment in chimpanzees (reviewed in Rudolf von Rohr et al., 2011, 2012) and vervet monkeys (Arseneau-Robar et al., 2016, 2018). Third-party 'policing' has also been identified in chimpanzees (Rudolf von Rohr et al., 2012) and pigtailed macagues (Macaca nemestrina) (Flack et al., 2006). Outside of the primate order, there is evidence of third-party punishment in cleaner fish (Labroides dimidiatus) (Deutchman et al., 2023; Raihani, Grutter & Bshary, 2010) and in eusocial insects (Singh & Boomsma, 2015). For example, in cleaner fish pairs, females who cheat by eating client fish mucus are punished by their male partner by being aggressively chased.] However, other models place hardly any emphasis upon the role of thirdparty punishment in the evolution of the normative sense, or upon the motivation to engage in third-party punishment in response to norm violations. For example, Theriault et al. (2021) treat third-party punishment as a completely distinct mechanism for enforcing social conformity, existing in parallel with the force of social expectations. Meanwhile, Birch (2021) views third-party punishment as just one among many types of normatively regulated behaviour. Construed this way, third-party punishment only plays a peripheral role in the psychology of norms. While its presence might serve as evidence of socially normative thinking, its absence would by no means be indicative of the absence of social norms.

Some of these disagreements may perhaps be seen not so much as disputes about the nature of normative cognition itself, but rather about how the normative sense evolved and whether it is subserved by domain-specific or domain-general mechanisms. Several of these theories agree that central to normative cognition is some kind of representational contrast between what *is* and what *ought* to be the case. This creates its own significant methodological challenges, since representations of oughtness, appropriateness, and so forth, are extremely difficult to identify in behaviour, and make the difficulties of operationalising theory of mind seem easy by comparison (although this is also why many researchers have focused on third-party punishment, as at least one potentially tractable behavioural indicator of such representations).

There is, however, also a key disanalogy between questions about social norms and questions about whether animals possess a theory of mind or a sense of number. The latter sort of question is explicitly about whether or not individual animals have a particular cognitive capacity, whereas the former is about a property that can only be had by a *group* of individuals. Questions about cognitive capacities can be answered by measuring the behaviours of individual animals (albeit in a social context, in the case of theory of mind). But when we ask whether or not animals have social norms, we are interested, at least in part, in questions about the way

animal *communities* are structured. These questions cannot be answered solely by examining capacities on an individual level. Their answers lie in the study of social interactions and community-level patterns of behaviour (Westra & Andrews, 2022).

In short, the model of comparative psychology that has been successful for the study of capacities like theory of mind is a poor fit for the study of animal normativity. There is, however, another empirical literature that offers a better model for the study of social norms in non-human animals: the study of animal culture.

(2) Lessons from the animal culture debate

In the 1990s and early 2000s, there was a heated debate about whether or not the term 'culture' could be applied legitimately to non-humans (Kendal, Laland & Galef, 2009; Hill, 2009) - for instance, McGrew (2003) referred to the 'chimpanzee culture wars'. One major strand of scepticism came from psychologists, who insisted that genuine culture requires active teaching and imitation (Galef, 1992), and/or perspective-taking and intersubjectivity (Tomasello, Kruger & Ratner, 1993). Without evidence for such psychological capacities, putative instances of 'cultural' practices in animals – such as the practice of potato washing in Japanese macaques (Macaca fuscata) spreading from one juvenile to others in the troop (Kawai, 1965) and the diversity of behavioural repertoires across populations of wild chimpanzees (Whiten et al., 1999) - were summarily dismissed. For instance, Tomasello et al. (1993, p. 495) proclaimed, 'Many animal species live in complex social groups; only humans live in cultures'.

Some decades later, the conversation is guite different. Although there remains some scepticism, attributions of 'culture' to animals are now commonplace and widely accepted in the scientific literature, and an increasing range of taxa are recognised as having cultural practices, or behavioural traditions, in some form or another (see e.g. Whiten, 2021). First, animal culture researchers broadened their conception of the explanatory target, so that it included not just individuallevel psychological capacities but also patterns of interaction within animal communities. They additionally developed a set of constructs with which to describe those patterns. Second, in characterising these different types of 'culture', researchers converged upon psychological pluralism, allowing that similar cultural phenomena in different species can be sustained by a variety of different underlying psychological mechanisms with distinct evolutionary histories (e.g. Kendal, Galef & van Schaik, 2010; Haidle et al., 2015; Heyes, 2018). Third, comparative researchers and cognitive scientists interested in the evolution and phylogenetic distribution of culture across the animal kingdom came to recognise that 'culture' is a phenomenon that can exist at different levels of complexity. For instance, Heyes' (2020) recent primer on 'culture' describes how the different strands of the literature have coalesced around three current approaches to thinking about, and identifying, cultural practices that can be ordered in terms of restrictiveness, each serving different but complementary theoretical goals: Culture-1, Culture-2, and Culture-3 (see also Kelly & DeBlock, 2022).

Culture-1 is the most inclusive use of 'culture' in the literature, and it refers to socially inherited patterns of behaviour and information. At the heart of this conception of culture is social learning: the acquisition of behavioural dispositions and information from other agents and/or their products. Notably, this definition does not require any particular type of social learning, such as imitation or teaching. It just requires that the learning process is indeed social, rather than a process of entirely independent individual learning of the behaviour.

A more restrictive use of 'culture' – Culture-2 – requires that the relevant information or behaviour is not just acquired from others, but is also group typical, persistent over time, and variable such that it cannot be explained by genetic or environmental differences between groups of the same species. This corresponds with the common idea of cultures as traditions that are passed on from one generation to the next and differentiate one group of otherwise very similar animals from another. This is probably the most commonly used definition in the animal culture literature [e.g. van Schaik *et al.*, 2003; Laland & Janik, 2006; Koops *et al.*, 2015; van Leeuwen, 2021; although see Schuppli & van Schaik (2019) and Hopper & Carter (2020) for important qualifications about excluding environmental differences].

Heyes' (2020) third, and most restrictive, definition of 'culture' - Culture-3 - corresponds to what is often referred to as 'cumulative culture', where the relevant information or behavioural patterns are not just transmitted via social learning and are group typical, but also accumulate – i.e. they accrue modifications over time as they are passed down through successive instances of social learning. Over time, this process produces a body of cultural variants that are more refined, and often complex enough that many could not be independently reinvented by a culturally naïve individual. The process requires individual innovators to modify existing cultural variants (perhaps intentionally or by accident) and pass them on to others (Mesoudi, 2011). It also requires that those variants survive in the relevant population for long enough that they can accumulate further modifications. This is, of course, an extremely important feature of human cultures and lies behind our remarkable cumulative technological and other achievements as a species (Henrich, 2015).

Equipped with these conceptual tools, research on animal culture has clearly made enormous progress over the last few decades. While it remains highly controversial whether there are any instances of Culture-3 in non-human animals (Sasaki & Biro, 2017; Schofield *et al.*, 2018; Gruber *et al.*, 2021; Dean *et al.*, 2014; Tennie *et al.*, 2020; Whiten *et al.*, 2021), there is an increasing number of clear examples of non-human culture in the sense of social inheritance (Culture-1) and group traditions (Culture-2) across the animal kingdom (Aplin, 2019; Danchin *et al.*, 2018; Laland, Atton & Webster, 2011; Whitehead & Rendell, 2015; Whiten, 2021).

Researchers have thus moved beyond the semantic gatekeeping that characterised the early years of the debate by carving the phenomenon of interest into multiple, finergrained constructs which focus primarily on behavioural patterns within and among subpopulations and their genesis. In this respect they have anticipated the project of conceptual engineering in philosophy (e.g. Chalmers, 2020), which has among its aims the design, implementation, and evaluation of concepts as needed for specific tasks. They have additionally followed the advice of McGrew (2003, p. 434): 'Definitions are only useful if they clarify matters. All else is pedantry. Define culture as you must to tackle the question at hand, just make it clear, fair, and most of all productive'.

The move towards psychological pluralism has also been key. Defining 'culture' in terms of psychological capacities like imitation, teaching, or perspective-taking stifled progress because it assumed too much about the psychology underlying human cultural transmission. While some remain convinced that active teaching and/or imitation are important, perhaps necessary, in producing Culture-3 (e.g. Tomasello, 2016b; Tennie, 2019), there is now general recognition that if so-called 'simple' social-learning capacities like emulation, stimulus and local enhancement, affordance learning, and so on, are sufficient for the acquisition of complex, community-specific behavioural practices in animals, there is reason to suppose that these more basic capacities are operative in much human cultural transmission as well (Zwirner & Thornton, 2015; Heyes, 2018). And, even if it is the case that some aspects of human cultural transmission are subserved by some special set of 'cultural' learning processes (e.g. Lucas et al., 2020; Montrey & Shultz, 2020), the assumption that these processes alone must underpin all forms of cultural behaviour has come to be seen as unjustified. Crucially, this move towards psychological pluralism has allowed researchers to pursue more productively psychological questions about exactly how different cultural practices may come about and be sustained – for instance, the role and type of copying in producing primate cultures (Tennie et al., 2020) - without making too many assumptions about what form the answers to those questions should take.

(3) Take-aways for the animal normativity debate

Although there is currently a much smaller body of empirical work on normativity than existed on animal culture, from our view, the animal normativity debate is now in much the same place, methodologically, as the animal culture debate was in the 1990s: being held back by an unproductive focus on psychological processes and definitions that are difficult to operationalise and that stack the deck in favour of human uniqueness. Instead of treating the capacity for social norms as a monolithic psychological phenomenon, animal normativity researchers must be open to the possibility that it may turn out to be quite graded and multidimensional. Just as significant parts of the animal culture debate have benefited from a shift towards more fine-grained distinctions like

Culture-1, Culture-2, and Culture-3, we suggest that the animal normativity debate would benefit from a shift towards a more ecumenical, pluralistic approach to social norms that would make them easier to conceptualise and identify empirically. In particular, we draw three lessons from the framework developed to study animal culture better.

First, we need a working conception of social norms that allows researchers to identify and refer to patterns of social behaviour of interest that is psychologically neutral and does not entail strong assumptions about the cognitive faculties or mechanisms that produce them or their specific evolutionary histories. The psychological elements in this construct should be framed in broad, functional terms that could, in principle, admit of many possible realisations by different types of psychological process, much like the notion of 'social learning' invoked in Culture-1. In other words, social norms should be conceptualised in a way that is *pluralistic*.

Second, while any such construct should not privilege human social norms *a priori*, it should be able to capture paradigmatic social norms in human communities. Just as Culture-1 and Culture-2 are defined in such a way that their extensions include most forms of human culture, any minimal conception of social norms should include in its extension common examples of human social norms, such as social dominance hierarchies, prohibitions against theft and violence, food taboos, sartorial norms, and greeting norms

Third, this conception of social norms should be able to support the development of a taxonomy of different social-norm constructs. Just as behaviours falling under Culture-3 can be understood as a subset of the behaviours falling under Culture-2, and likewise the behaviours designated by Culture-2 are a subset of the behaviours designated by Culture 1, an analogous approach to social norms should initially cast a wide net, but also be capable of accommodating further fine-grained distinctions between different kinds of norms or different degrees of normative complexity.

Importantly, this project is not one of conceptual analysis. We are not analysing the concepts of social norm or normativity, nor is our aim to capture folk intuitions about the proper usage of any associated terms. Rather, we are carrying out the kind of conceptual engineering that led to progress in the animal culture debate. The goal is to fashion readily operationalisable terms with which to describe the core explanatory and descriptive targets of the cognitive science of social norms.

III. NORMATIVE REGULARITIES

In this section, we introduce a new basic construct for the animal normativity debate, which should be understood as roughly analogous to the notion of Culture-1 (Heyes, 2020). To distinguish this construct from other commonsense and theoretical uses of the term 'social norm', we will use the term *normative regularity*. Following Westra & Andrews (2022),

we define a normative regularity as a socially maintained pattern of behavioural conformity within a community. This definition has three elements: the concept of patterns of behavioural conformity, the concept of social maintenance, and the concept of a community.

(1) Patterns of behavioural conformity

One of the main things that the cognitive science of social norms aims to explain is individuals' conformity to behavioural practices that are common in their local group. Appeals to patterns of behavioural conformity are common across different accounts of normative cognition. Bicchieri's (2006, 2017) model of socially normative motivation, for example, hinges on individuals' beliefs about whether a given behaviour is common in their community. Similarly, Kelly & Setman (2020) characterise the psychological 'norm system' as producing behaviours that have 'stabilising group-level effects on patterns of collective social organisation'. The propensity for 'overimitation' in human children, where children imitate arbitrary and nonfunctional patterns of behaviour of those around them, is also often understood in the context of social norms, as a mechanism for ensuring conformity (Kenward, Karlsson & Persson, 2011; Keupp, Behne & Rakoczy, 2013). And, in the animal normativity literature, conformity to local practices, such as food colour preferences in vervet monkeys (van de Waal et al., 2013) are common examples of possible social norms (Andrews, 2020; Luncz & Boesch, 2014; Luncz & van de Waal, 2021; van Schaik, 2012).

Patterns of behavioural conformity can be recognised even when we do not know the psychological mechanisms that cause members of a community to adhere to them, and regardless of whether those patterns are attributed to biology (e.g. incest avoidance) or culture (e.g. sartorial practices). In this respect we can think of them as what Dennett (1991) called *real patterns*: readily discernible empirical regularities that support robust predictions and generalisations, whose existence does not depend upon us knowing the underlying mechanisms that produce them. The first stage in identifying a normative regularity is thus finding a robust pattern of behavioural conformity.

Not all paradigmatic human social norms require all members of a community to perform exactly the same behaviour in the same context. Many involve different types of agents performing role-specific behaviours (e.g. gender norms and norms that apply differently to different positions in a social hierarchy), or individuals abstaining from certain behaviours (e.g. incest prohibitions or food taboos). Others apply only in very specific contexts (e.g. norms governing ritual ceremonies). 'Conformity', then, may look different across cases, and some patterns of behavioural conformity will be much more obvious than others. However, all genuine instances will be real patterns in the behaviours of group members, which in turn provide the basis for robust predictions and generalisations about how individuals will behave in the relevant context(s).

(2) Social maintenance

However, not all patterns of behavioural conformity qualify as normative regularities. For example, if a group of animals all congregate at the same water source in an otherwise dry landscape, this needn't imply that drinking at that water source is a social norm. There is nothing particularly social about this kind of behavioural conformity: a solitary animal unaware of any conspecifics faces a pressing biological need to find water, and facts about the local environment dictate how that need is satisfied. Similarly, researchers often distinguish between social norms and 'statistical regularities' (Rudolf von Rohr et al., 2011) or 'descriptive norms' (Cialdini, Reno & Kallgren, 1990), i.e. group-level patterns produced merely by individuals copying the behaviour of those around them (Deutsch & Gerard, 1955). In contrast to such cases of mere conformity by coincidence, copying or imitation, the patterns we are calling normative regularities are explained in terms of some kind of social pressure to conform.

Our notion of social maintenance offers a minimally psychological way of describing this social pressure. A pattern of behavioural conformity is socially maintained when individual adherence to the pattern is explained by the way that members of the community react to cases of conformity and non-conformity. Social maintenance thus consists of behaviours in the relevant community that collectively incentivise conformity to a behavioural pattern and disincentivize non-conformity.

The most familiar example of social maintenance is the enforcement of behavioural conformity through third-party punishment. It is well established that third-party punishment of non-conformers can sustain cooperation and other behavioural regularities in social groups by rendering the costs of non-conformity greater than the costs of conformity (Boyd & Richerson, 1992). Third-party punishment is viewed as a signature of social normativity by several researchers in the animal normativity debate (e.g. Riedl et al., 2012). There are, however, important questions about what 'punishment' amounts to. In the human social norm literature, it is largely agreed that punishment need not involve direct, physically aggressive responses to non-conformity. For example, Kelly & Setman (2020) write that 'Enforcement and punishment are broad categories, and can include correcting, withholding cooperation, communicating disapproval through body language or explicit criticism, ostracising or gossiping about norm violators, or even physical violence'. Likewise, Bicchieri (2017, p. 35) writes that 'the reaction to nonconformity may range from slight displeasure to active or even extreme punishment'. Standard examples of punishment also tend to involve intent on the part of community members (e.g. intentionally punishing or gossiping about a norm violator), but from a functional perspective there is no reason to require this: for instance, if an act of nonconformity causes other community members to be confused or surprised, they may avoid non-conformers, which may in turn incentivize conformity. Nor is there any strong reason

to insist on an essential role for third parties: if a pattern of behavioural conformity emerges because the threat of second-party retaliation deters non-conformity, it would still fit our definition of a normative regularity. These 'punitive' behaviours, despite their differences, all incentivize conformity by imposing a cost on individuals who deviate from behavioural regularities. We will refer to the class of behaviours with this basic feature as *negative social maintenance*.

Imposing costs on non-conformity is just one way that the behaviour of an individual can be socially incentivised. Another is via rewards for conformity, or positive social maintenance. Examples could include explicit verbal praise for conformity to a norm (in humans), as well as social rewards like inclusion in cooperative endeavours, continued inclusion in social relationships and group activities, and increased social status. It could also include modelling or teaching (e.g. by parents) as a proactive way of encouraging norm adoption and maintenance. Empirically, signs of positive social maintenance can serve as evidence that a normative regularity is present when researchers suspect the presence of a normative regularity but lack evidence of negative social maintenance. However, evidence of positive social maintenance behaviours may need to be supplemented by evidence of observed or experimentally induced negative social maintenance behaviours to establish strongly that a given behavioural regularity is socially maintained.

(3) Community

Some accounts of the psychology of social norms have explicit definitions of who counts as a member of a given normative community. For example, Bicchieri's (2017) account of social norms invokes the notion of a reference network, which she defines as 'the range of people whom we care about when making particular decisions' (Bicchieri, 2017, p. 14). This definition is too psychologically laden for our purposes. However, it is also a useful way of illustrating some of the inevitable context sensitivity that arises when identifying the social scope of a given normative regularity. For example, the same individual may simultaneously belong to one or more minimal, dyadic communities with their own idiosyncratic norms, which exist within a slightly larger normative community consisting of a single family unit, which is in turn part of a larger tribe or clan with its own normative regularities. Social norms from these overlapping communities can also conflict. such that an individual might abide by one community's norm in one context and by the other community's norm in the other.

In practice, this context sensitivity can make identifying normative communities on the basis of some general empirical criterion difficult. However, researchers often have their own methods for individuating communities and subcommunities within an animal population (e.g. Sosa, Sueur & Puga-Gonzalez, 2020), which are justified independently of questions about animal normativity. We recommend that, when aiming to study normative regularities, researchers

employ whichever means of distinguishing between social groups is ecologically and socially appropriate.

IV. IN SEARCH OF NORMATIVE REGULARITIES

In this section, we will describe how researchers might study normative regularities, with a specific focus on the study of great apes and monkeys. This is not because these taxa are necessarily the most likely to display normative regularities. It may be, for instance, that whales and dolphins (Whitehead & Rendell, 2015) or eusocial insects (Powell, 2023) are equally good candidates for having normative regularities. Rather, our focus on primates reflects our own expertise and the abundance of relevant research. We will however discuss both observational and experimental contexts, which will allow for an optimal combination of experimental control and ecological validity (Andrews, 2020; Janson & Brosnan, 2013).

(1) Evidence for social maintenance

According to our framework, investigation into any type of normative regularity will begin with the identification of a pattern of behavioural conformity within a community. Such patterns may be discovered via observational methods in the wild or captivity, or they might be artificially introduced into a community. The key task would then be to determine whether this pattern is socially maintained. Researchers could investigate whether a given pattern of behavioural conformity is socially maintained in two ways. First, researchers could observe bystander responses to individuals who conform to or violate the regularity; positive responses to conformers and/or negative responses to violators would constitute evidence of social maintenance (Table 1). Second, researchers could observe whether or not degree of actor conformity correlates with the presence or absence of conspecific observers. If decisions to conform are contingent upon the possibility of being observed by other community members, this constitutes evidence that the relevant behaviours are socially maintained (Table 2).

One domain ripe for this kind of investigation is the study of primate culture. Primate culture researchers have uncovered a wide range of distinctive patterns of behavioural conformity, but as yet it is unclear whether or not any of these behaviours are socially maintained. This makes primate cultural behaviours prime candidates for the investigation of normative regularities. For example, in the Taï Forest of Côte d'Ivoire, there is a striking difference in chimpanzees' tool material selection between groups, with some communities preferring stone and others preferring wooden tools for the same foraging task. When chimpanzee females immigrate from groups with more efficient tool-use behaviours, they nonetheless adopt the less-efficient tool-use behaviours of their new communities (Luncz & Boesch, 2014). The fact that these individuals adopt inefficient tools despite the fact that more efficient alternatives are readily available is

Table 1. Candidate dependent variables for investigating social maintenance via bystander behaviours.

Withdrawing from participation	Withdrawing from participation creates a cost to a potential partner. For example, in inequity a version studies, one subject receives a lower value reward for performing the same task as a neighbour, and may refuse to cooperate in later rounds (Brosnan & de Waal, 2003; Brosnan et al., 2006). Such a refusal may be a form of negative social maintenance by the harmed
Eavesdropping and partner choice	party. Eavesdropping on third-party interactions allows animals to learn about the behaviour, dispositions, and relationships of their group-mates. Experimental paradigms have demonstrated that eavesdropping informs the decisions that animals make about whom to interact with in the future (Anderson et al., 2013; Bshary & Grutter, 2006; Krupenye & Hare, 2018). These findings position partner choice as a potentially powerful mechanism for rewarding (through cooperation and affiliation) norm-conformers and disincentivizing (through avoidance, aggression, or refusal to cooperate) norm-violators. Partner choice tasks are therefore ripe for examining these social maintenance mechanisms.
Protest	Protest takes the shape of a behaviour that appears to indicate displeasure with an action. Protests have been identified in a number of primate species [see Rudolf von Rohr et al. (2012) for a list], including head-shaking 'no' which has been observed to be used by bonobos in some contexts (Schneider et al., 2010). In symbol-trained apes, protests may also be indicated through the use of lexigrams or American Sign Language (ASL) signs which are translated as 'no' or 'bad'. For example, in the bonobo and chimpanzee lexigram project, apes have been observed to use the lexigram 'bad' to describe their own naughty behaviour (Lyn et al., 2008). Social maintenance could be studied via both natural protests and introduced symbols.
Paying to watch non-conformers incur costs	Paying to watch non-conformers incur costs has been demonstrated in chimpanzees, who observed humans who acted prosocially by giving food to another human, or antisocially by teasing another individual and not giving them food. When the antisocial actor was later attacked, the chimpanzee audience would open a door to allow them to continue watching the punishment, more so than when the prosocial actor was attacked (Mendes et al., 2018).
Differential treatment of naïve and knowledgeable individuals	Differential treatment of naïve and knowledgeable individuals can also be measured as evidence of social maintenance. If there is a normative regularity that is learned, we may predict that responses to infant violations would be weaker than responses to adult violations (de Waal, 2014).
Pedagogy	Teaching/demonstrations/tolerance towards observers and for unskillful attempts can offer evidence of positive social maintenance, and can be measured by considering tolerance levels of knowledgeable individuals as they allow naïve individuals to observe putative normative behaviour. For example, female bonobos have been observed to permit juveniles to try out sexual behaviours on them (Clay et al., 2022)
Reconciliation and repair	Reconciliation and repair can be demonstrated by a bystander facilitating a reconciliation after a violation, such as when a female chimpanzee leads two males together after an altercation (de Waal & van Roosmalen, 1979).

inherently puzzling, and it is unclear what sorts of incentives are driving these patterns of conformity.

One plausible hypothesis is that there is some kind of social maintenance mechanism at work. To explore this possibility, researchers could investigate links between the rate of conformity and the rate and extent of social integration (e.g. Brosnan, Schiff & de Waal, 2005) or the relative social status of innovators versus adopters (Hopper et al., 2011; Matsuzawa & Yamakoshi, 1996). Goldsborough et al. (2021) provide anecdotal evidence for such an 'integration effect' of increased cultural conformity: when two female chimpanzees were introduced to a community of zoo-housed chimpanzees that practiced a female-specific cultural behaviour known as the 'cross-armed walk', one female quickly adopted this behaviour, while the other did not. The researchers report that 2 years later, 'the female who copied the local tradition appeared more socially integrated than the other immigrant female' (Goldsborough et al., 2021, p. 547). Determining whether such a correlation between conformity and social integration is in fact evidence of social maintenance of the behavioural regularity would require precise temporal analyses linking changes in immigrant conformity to changes in group member responses over time, as well as controls for independent strategies relevant to relationship-building and integration, such as the amount of grooming given.

Beyond these investigations of potential normative regularities in naturally occurring cultural behaviours, researchers could also attempt to 'seed' new cultural behaviours experimentally in primate populations and then observe whether or not these behaviours are socially maintained. This kind of approach would build upon methods like that of van de Waal et al. (2013), who provisioned groups of vervet monkeys with both pink and blue corn, and initially rendered one of these types of corn distasteful by treating it with quinine. These preferences were acquired by group members and passed onto offspring, even after the corn was no longer treated with quinine. Upon immigration to a new group with a different corn-colour preference, however, the authors found that offspring tended to shift their corn-colour

Table 2. Candidate dependent variables for investigating social maintenance via degree of actor conformity.

'When in Rome' behaviours When in Rome behaviours occur when individuals move between different communities with distinct normative regularities. This is true whether there are differences regarding communicative signals, material culture, or arbitrary conventions. Measures can include degree and speed of conformity to the new group behaviours. Immigration is a particularly fruitful area of study, even occurring in captivity where animals of the dispersing sex are routinely moved between groups at least once during their lives to simulate natural patterns and to minimise inbreeding. It is telling that conformity seems persistently to reappear when we study immigration in the wild across animal species such as birds (Aplin, 2019), monkeys (van de Waal et al., 2013) and apes (Luncz et al., 2015, 2018). Scenarios that involve an individual moving back and forth between two communities with different behavioural regularities could also be a context for measuring differential responses by actors. Costs to conform are sometimes evident in immigrant actors who have to forgo an efficient or less costly Costly conformity behaviour in order to conform to the new community, but can also occur when an individual forgoes individual preferences in order to conform, as in the case of chimpanzees trading tokens for carrots when the alpha female did so (Hopper et al., 2011). Costs can be apparent in terms of fitness, which can involve sacrificing short-term benefits such as more efficiently cracking nuts (as in the Taï chimpanzee case; Luncz et al., 2018) or gaining access to undisputed food items (as in the coloured corn vervet monkey case; van de Waal et al., 2013). Overcoming self-interest to follow behavioural regularities could be investigated when new individuals are introduced into an established group, either through immigration or through experimental manipulation, or by experimentally introducing new patterns into captive communities. Socially contingent non-conformity, which refers to contexts in which social enforcement is likely versus unlikely, could Socially contingent reveal animals' sensitivity to normative regularities and to the social maintenance mechanisms that enforce non-conformity them. For example, animals may be more likely to violate norms when they cannot be observed by groupmates or specifically when the individuals most likely to enforce the norm are not present.

preference to that of the group. As with naturally occurring cultural behaviours such as chimpanzee tool-use practices, it is unclear whether or not the adoption of these experimentally induced feeding habits was socially maintained in any way. To answer these questions, future studies replicating this methodology should closely monitor rates of integration among immigrant individuals and measure how they relate to the adoption of group-specific feeding habits.

Experimental contexts offer further opportunities for investigating normative regularities. For example, in one study of social transmission of food preferences, the alpha females of two chimpanzee social groups were taught to trade one of two token types for food rewards. One alpha female was rewarded with a less-preferred carrot for doing so, while the other got a more preferred grape. Most of the subordinate chimpanzees in the carrot group came to discover that they could trade the other token for a grape. Interestingly, despite their individual preference for the grape, the subordinate chimpanzees continued to select the carrot-yielding token, following the pattern set by the alpha female (Hopper et al., 2011). Evidently, for these (well-fed, captive) chimpanzees, conforming to this social pattern was more valuable than acquiring their preferred food. Had these researchers been investigating whether or not this pattern was socially maintained, one possible strategy would have been to give subordinate chimpanzees the chance to obtain either grape or carrot tokens either in view of the other chimpanzees (as was the case in the original study) or in a private setting. If subordinate chimpanzees' choices varied depending on whether or not they were being observed by the other chimpanzees, this would indicate that their incentive to conform to the regularity was shaped by social factors, which

suggests the presence of some form of positive or negative social maintenance.

Communicative behaviours provide another domain for studying primate normative regularities (Hobaiter & Byrne, 2014). For example, chimpanzees learn to provide rough grunts that signal the presence of food to affiliates (Watson *et al.*, 2015). However, in some cases chimpanzees do not rough grunt in response to the pant hoot of an approaching chimpanzee, thereby violating the regularity (Schel *et al.*, 2013). If giving rough grunt signals were a normative regularity, then we might expect conspecifics to respond to violations by imposing some kind of social cost upon the violator – perhaps some form of physical aggression, denying the violator valuable social opportunities, or failing to respond to their calls.

Other potentially fruitful areas of investigation include behaviours surrounding resource allocation and sharing. Among dyads, resource allocation behaviours are often reciprocal over some timeframe, with the apparent expectation that behaviours will be returned, as well as a recognition of contexts in which they will likely not be. For example, chimpanzees are sensitive to individual differences in willingness to cooperate and share the spoils of cooperation, and choose partners who share more tolerantly (Melis, Call & Tomasello, 2006a; Melis, Hare & Tomasello, 2006b). Capuchins, too, choose not to cooperate in contexts in which their partners can dominate (de Waal & Davis, 2003). Intriguingly, they maintain these partner preferences outside of specific contexts in which they could be under-benefited, to the degree that they will refuse to cooperate with a partner who took more than their share in the past, even when the rewards are presently equal and cheating isn't possible (Brosnan, Freeman & de Waal, 2006). These partner-choice behaviours could constitute social maintenance responses to conformity with, and deviations from, patterns of behavioural conformity in the domain of sharing and resource allocation. These are just a few examples of the contexts in which researchers might investigate normative regularities in primates. In Table 3 we suggest other fruitful contexts for investigating primate social norms.

(2) A note on physiological approaches to studying animal norms

Prior research on social norms in primates allowed subjects to view a scene in which a hypothesised normative regularity was violated, but in a controlled way, and observed thirdparty responses to violations. Rudolf von Rohr et al. (2015) presented captive chimpanzees with videos of infanticide taken from documentary film footage to probe whether these chimpanzees regarded attacking infants as violating a norm. They used a looking-time measure and reported that subjects looked longer at the infanticide videos than at other videos, such as those that featured violence between adults. Recent advances in technology for non-invasively assessing the physiological responses of animals to stimuli, such as eye-tracking, infra-red thermography and pupillometry (Ermatinger, Brügger & Burkart, 2019; Brügger, Willems & Burkart, 2021; Krupenye, Köster & Clay, 2021; Montes-Lourido et al., 2021; Lewis & Krupenye, 2022), provide a potentially powerful enhancement to this approach. Many of these methods are capable of remotely and non-invasively measuring outputs of the autonomic nervous system, such as increases in pupil dilation (Joshi & Gold, 2020) or decreases in nasal skin temperature (Kano et al., 2016), that correlate with arousal. This approach is well suited for assaying animals' expectations (and violations thereof), illuminating the patterns of behavioural conformity that animals are aware of, their sensitivity to violations of these patterns, and potentially their expectations of third-party social maintenance. For example, studies presenting closely matched visual or auditory stimuli that conclude in expected versus unexpected ways (e.g. an agent conforming to or violating a behavioural regularity, a bystander responding to a violation with or without some form of social maintenance) can identify animals' expectations, if animals show greater patterns of arousal in response to putatively unexpected events (Krüger, Bartels & Krist, 2020). Some measures, like pupillometry, can only be continuously recorded if the animal remains in a relatively constrained area but there are now both contact (e.g. wearable devices for monitoring heart rate or skin conductance) and contact-free (e.g. infra-red thermography, video-based heart rate estimation) metrics with the potential to index animals' internal states in unconstrained contexts, provided that the appropriate confounds of each method are controlled for. This makes these tools potentially suitable for assaying animals' expectations not just in video but also in live, interactive social contexts (Barrault et al., 2022).

While suggestive, the Rudolf von Rohr et al. (2015) approach itself does not provide direct evidence for social maintenance, which is key for identifying normative regularities.

Table 3. Potential normative regularities in non-human primate communities.

Domain	Potential normative regularities
Infants	Parental care, cooperative care, weaning, infanticide prohibition, tolerance for non-conformity in their actions
Juveniles	Acquisition of adult behaviour patterns, copulations, consortship, tolerance of proximity, demonstrations, corrections, play, declining tolerance for non-conformity
Elders	Deference, helping, baby-sitting, granted expertise
Death	Treatment of dying and dead individuals, responses to death
Disability, infirmity	Provisioning disabled individuals, supporting travel or movement (potentially mediated by age and rank)
Feeding	Tolerance of others, distributive practices/inequity aversion, signalling, food preference, food processing, hunting roles, facilitated learning of hunting, interventions in hunts, rescuing prey animals
Immigration	Conformity to in-group, increased proximity while resting
Social status/dominance	Access to others for grooming or copulation, access to food or preferred locations, deference, reconciliation, tolerated aggression
Out-group engagements	Standing ground, boundary patrols, incursions, territory modifications, kidnapping, killing, castrating, play, food-sharing, integration
Travel	Traditional travel routes, coordinated movement and travel timing, deference to knowledgeable individuals
Communication	signals about food, predators, play, consortship, immigrant acceptance, greetings, reconciliation, consolation, song change, deceptive signals
Affiliation	Patterns of play, grooming, proximity, sex, social support, relationship-building strategies, reconciliation, consolation
Cultural traditions	Group-specific socially learned behaviours
Sex	Sex roles for males and females, access to sex partners
Political style	Despotic versus egalitarian leadership styles, pacifistic versus aggressive cultures

Looking-time and physiological measures such as thermography used with individuals cannot by themselves tell us how participants would behave towards violators or communicate their displeasure to naïve individuals. To use such methods to explore social maintenance, a communicative partner is needed. Social maintenance requires the presence of other group members, and the measurable response would have to impact another individual. If the other group member is the violator, the subject's response could be taken as a form of punishment, and if the group member is a naïve individual the subject's expression of displeasure would be an opportunity for learning. Focusing exclusively on implicit measures such as looking time or thermography also presumes a particular understanding of the underlying psychology of social norms that ties responses to norm violators to negative affect, which, while not implausible, should no more be presumed than any of the models of normative cognition discussed earlier. Hence, such paradigms need to be supplemented with methodologies that identify social maintenance behaviours more directly, like those previously described. For example, physiological measures could test first whether bystanders detect violations of behavioural regularities in live scenarios. But, even more critically, they can assess whether variation in bystanders' awareness of the norm violation (as measured by physiology) predicts bystanders' decisions to enact or forego social maintenance, accounting for other relevant factors (audience composition, participant status/power to act). For example, one might find consistent evidence for norm violation detection in both low- and high-status individuals but evidence that norm violation detection predicts social maintenance only in high-status individuals with power to act. Such a pattern would also illuminate the mechanisms underlying social norms, since arousal patterns that are shared by both low- and high-status subjects but compel action only in highstatus subjects would clearly reflect cognition rather than a non-cognitive driver of behaviour.

(3) Communal and recursive normative regularities

Up to this point, we have focused on a single construct: normative regularities. Notably, the class of normative regularities is quite wide. While such a broad construct might suit certain comparative projects (especially those interested in the ways in which social norms might be realised by many different psychological mechanisms) others might prefer a narrower way of operationalising the norms construct. One way to do this would be to introduce further psychological criteria into the definition of normative regularities, requiring (for example) that social maintenance be motivated by an explicit representation of a rule, or that communities understand themselves as such. This kind of modification would, however, run contrary to our core methodological proposal: the comparative study of social norms must be psychologically neutral. Instead, we recommend that researchers build upon the analogy with the animal culture literature. Just as Culture-2 and Culture-3 constitute increasingly restrictive (yet still psychologically neutral) subsets of Culture-1 behaviours, animal normativity researchers can introduce a corresponding taxonomy that carves out increasingly restrictive subsets of normative regularities.

One possible taxonomy might be:

Norms-1: socially maintained patterns of behavioural conformity within a community, or normative regularities.

Norms-2: suites of normative regularities that serve to distinguish different animal communities behaviourally within a given species, or communal normative regularities.

Norms-3: normative regularities that govern the social maintenance of other normative regularities, or recursive normative regularities.

Unlike bare normative regularities, which may hold across all communities that belong to a given species and include a substantial biological component (such as incest taboos in humans), the above Norms-2 construct emphasises the way that norms - much like cultures (Whitehead & Rendell, 2015) are often invoked to explain behavioural variability across distinct populations (e.g. Gelfand, 2018). In this sense, Norms-2 may be thought of as *communal normative regularities*. But importantly, social maintenance remains a distinctive feature of normative – as opposed to cultural – behaviours. This means that a group-typical behaviour might count as an instance of Culture-1, Culture-2, or even Culture-3, and yet fail to qualify as a normative regularity if there is no evidence that it was socially maintained. Note also that the difference between Norms-1 and Norms-2 is in some ways a matter of degree: the more that an animal community is behaviourally distinguished by its distinctive normative regularities, the more 'communally normative' it will become.

Norms-3 – which would provide an analogue to the notion of cumulative culture - captures the fact that humans have social norms about social norms (and social norms about social norms about social norms, etc.) (e.g. Mathew, 2017). For example, when a child violates a norm, it is usually understood in Western populations that the child's parents are permitted to punish them, but a stranger is not. However, certain strangers can enforce norms about appropriate and inappropriate forms of punishment on the parents of other children. In principle, normative regularities could exhibit indefinitely many such levels of recursion, corresponding with increasingly complex systems of social maintenance and behavioural conformity. Notably, while this construct does not build in any particular cognitive prerequisites, it is very plausible that greater degrees of recursion at the level of normative regularities might require correspondingly recursive representational capacities (e.g. Hauser, Chomsky & Fitch, 2002; Camp, 2009).

In order for these more restrictive constructs to be empirically useful, they too must be operationalisable. In this regard, the implementation of something like Norms-2 would be relatively straightforward, as it would hinge upon the operationalisation of multiple normative regularities, which has already been described in detail. Something like Norms-3 would be more challenging, as it is not immediately obvious how we might distinguish a recursive normative regularity from an especially complex non-recursive one.

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Researchers would need to approach this question in an interactive fashion. First, a base-level normative regularity would need to be identified, including the positive or negative social behaviours that maintain it. Research would then need to examine whether or not these latter behaviours are themselves subject to positive or negative social maintenance: do norm enforcers enjoy greater degrees of social inclusion than non-enforcers? Are non-enforcers subject to social exclusion or third-party punishment? Employed systematically within a given community, this method could permit researchers to map out complex systems of normative regularities, and thereby gain insight into the overall regulative structure of that population.

We believe that such a taxonomy could provide researchers with some useful constructs for distinguishing between different classes of normative regularities. However, some caution is in order: as in the study of culture, there are many possible ways that such a hierarchy could be constructed. Normative regularities vary along all kinds of dimensions of complexity, from the number of individuals governed by a given norm, to the persistence of a given normative regularity across generations, to the relative 'tightness' or 'looseness' in a given community's pattern of negative social maintenance (Gelfand, 2018). There is no a priori reason to privilege one of these dimensions over another, only the pragmatic utility of a particular set of constructs for pursuing a particular comparative project. What is crucial, however, is that any hierarchical framework for thinking about norms be specified in minimally psychological terms and not build in strong assumptions about their underlying cognitive architecture (Westra & Andrews, 2022).

V. SCIENTIFIC AND ETHICAL IMPLICATIONS

To be clear, while we have highlighted examples that suggest the presence of normative regularities that are worthy of further exploration, our goal in this paper has not been to take a definitive position on the existence or non-existence of social norms in any species. Rather, our aim has been to sketch out and illustrate an approach for moving forward with empirical research on a cluster of questions about animal normativity. In this section, we step back and consider the significance of this kind of research and provide further support for the importance of the less psychologically presumptive, more open-ended framework we have articulated.

First, and most obvious, the question of whether and to what degree normative regularities are present in other species is crucial to our understanding of human evolution. A growing number of authors have placed significant emphasis on the importance of social norms and 'norm psychology' in explaining the evolution of supposedly uniquely human forms of cooperation, prosociality, cumulative culture, and morality (e.g. Kitcher, 2011; Haidt, 2012; Henrich, 2015; Tomasello, 2016a, 2019, 2022; Wrangham, 2019; Sterelny, 2021; Kumar & Campbell, 2022). These accounts

all assume that social norms are uniquely human. It therefore matters for assessing the tenability of these accounts, and for thinking more broadly about the role that social norms may have played in human evolution, whether that assumption is correct, or whether social norms are, in fact, more widely distributed in the animal kingdom. Identifying and precisely characterising the types of normativity found in other species, and their underlying mechanisms, is critical to determining the types of normativity that set humans apart and the evolutionary changes responsible for them.

Second, just as research into culture in non-human animals has informed our understanding of the psychological underpinnings of culture in humans (Boesch, 2012; Heves, 2018), research into the possibility of normative regularities in non-humans may inform our understanding of the psychology of social norms in humans. This is why it is so problematic that authors have tied questions of the existence of social norms to particular models of human norm psychology, since the nature of that underlying psychology remains unsettled (Heyes, 2023). In particular, comparative research provides an important check on the tendency of philosophers and psychologists to over-intellectualise human cognition (Hume, 1739; Shettleworth, 2010; Andrews, Buckner, 2013), allowing us to examine what kinds of psychological capacities are or are not necessary for manifesting particular traits. Research with animals may help us move forward with questions such as whether we do indeed possess an innate domain-specific norm system (Sripada & Stich, 2006; Chudek & Henrich, 2011), or whether norm cognition is subserved by more domain-general processes (Theriault et al., 2021; Heyes, 2023), whether norm cognition is linked with capacities for shared intentionality (Tomasello, 2016a; Schmidt & Rakoczy, 2019), selfconsciousness (Rochat, 2015), and so forth, or whether norm cognition is supported by a multitude of different psychological capacities (Westra & Andrews, 2022). These pursuits require us to have a framework for identifying the existence of normative regularities in other species that does not presuppose answers to these questions and can then be used to probe further the psychological underpinnings of social norms where they have been identified. Negative findings would also be informative. Recent models of norm learning accord a role to capacities such as reinforcement learning (Morris & Cushman, 2018; Nichols, 2021), strategic copying of high-status individuals and majority behaviours (Henrich & Henrich, 2010), and so forth - capacities we know are shared with other animals (Heyes, 2023; Kendal et al., 2018). Our failing to find normative regularities in species with these capacities would therefore be instructive with respect to the scope and limits of these models.

Third, determining whether normative regularities are present in the behaviour of particular animals is important for understanding the animals themselves. If populations of animals do what they do because of social maintenance, then that has significant implications for human—animal interactions both in the wild and in captive settings. Behaviour sustained by normative regularities will need to be understood

differently to other kinds of behaviour. For example, it is possible that groups of animals may persist with potentially maladaptive behaviours because they are socially maintained in some of the ways we have described (e.g. Cloutier et al., 2002; Hopper, Freeman & Ross, 2016; Laland & Williams, 1998). It is also potentially important for conservation efforts (Greggor, Thornton & Clayton, 2017). Animal culture researchers have emphasised the role animal culture can play in effective conservation interventions, such as introducing green corridors or other novel travel routes, discouraging animals from eating agricultural products, and designing successful reintroduction projects (Brakes et al., 2021). If some of these cultural behaviours are sustained or otherwise linked to normative regularities, that is important information to know. For instance, take the puzzling case of migrating wildlife continuing to use a fence gap to cross into neighbouring habitats, even after large portions the surrounding fencing had been removed (Dupuis-Desormeaux et al., 2018). If social maintenance is discouraging individuals from exploring other crossing routes, conservation efforts may benefit from thinking of the challenge as one of changing norms, rather than just changing behaviour.

Finally, there are ethical implications of our potentially discovering social norms in non-human animals. If a group of captive animals in our care have normative regularities, we may have ethical obligations not to disrupt them unnecessarily. Similarly, we may have a responsibility not to disrupt the normative regularities of wild communities or populations. We also need to consider how interactions between human caretakers and captive animals may create normative regularities – for instance, regularities surrounding feeding, treatment by caretakers, and so on - and cause potential harm to animals (e.g. distress, confusion, anxiety) when we violate them intentionally or unintentionally (Gottlieb, Coleman & McCowan, 2013; Ulyan et al., 2006). Seeking to understand the normative regularities in captive social groups may also be important for facilitating their welfare. For instance, what if eating faeces (coprophagy) or other putatively 'abnormal' behaviours in a group of captive chimpanzees is a normative regularity and is part of how this particular group does things? Current evidence suggests that such behaviours can spread through social learning (Hook et al., 2002; Hopper et al., 2016), and if such patterns qualify as norms, then they may not be indicative of negative welfare (Hopper et al., 2016; Goldsborough et al., 2022). Furthermore, just as humans may have difficulty learning the norms of new social groups they immigrate into, naïve animals who join established groups may have difficulty integrating if they do not learn the norms. Understanding the normative regularities that prevail in a social group could be extremely important for facilitating successful integration and for assessing the welfare impact of regrouping and rehousing practices. Animal welfare science is only just beginning to explore the implications of research on the complex social lives of non-human animals for thinking about their flourishing (Whitehead & Rendell, 2015; Benz-Schwarzburg, 2019),

and it is likely that research on animal culture and (potentially) normative regularities is an especially important area for furthering animal welfare research (Hopper, 2021; Fitzpatrick & Andrews, 2022).

VI. CONCLUSIONS

- (1) Non-human animal communities display a wide range of behaviours that resemble human social norms in important respects, yet most social norm researchers have dismissed or ignored the possibility of social norms beyond the human lineage. This seems to be motivated by the assumption that animals lack the psychological prerequisites for social norms.
- (2) There is no consensus about what kinds of psychological capacities underpin social norms in humans, let alone in non-human animals. The capacities that are hypothesised tend to be extremely difficult to identify in behaviour (e.g. representations of *ought*).
- (3) The animal culture literature overcame a parallel challenge by developing a set of minimally psychological and operationalisable constructs for characterising different kinds of non-human cultural behaviours.
- (4) We propose a set of minimally psychological, readily operationalised constructs for studying possible social norms in non-human animals, based on the central notion of a *normative regularity*.
- (5) We described how researchers can apply these constructs in observational and experimental settings to ascertain whether certain non-human primate behaviours constitute normative regularities.
- (6) This framework for studying social norms in non-human animals will shed light on longstanding questions about the evolution of social norms in humans, enhance the study of animal social behaviour, and inform how we act on our ethical obligations regarding animal welfare.

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VIII. AUTHOR CONTRIBUTIONS

E. W., S. F., and K. A. were equally responsible for the original conceptualization and drafting. S. F. B., T. G., C. H., L. M. H., D. K., C. K., L. V. L., and J. T. equally contributed to conceptualization, writing and editing.

IX. REFERENCES

- ANDERSON, J. R., KUROSHIMA, H., TAKIMOTO, A. & FUJITA, K. (2013). Third-party social evaluation of humans by monkeys. *Nature Communications* 4(1), 1561.
- ANDREWS, K. (2012). Do Apes Read Minds? Toward a New Folk Psychology. MIT Press, Cambridge, MA.
- ANDREWS, K. (2020). Naïve normativity: the social foundation of moral cognition. Journal of the American Philosophical Association 6(1), 36–56.
- APLIN, L. M. (2019). Culture and cultural evolution in birds: a review of the evidence. Animal Behaviour 147, 179–187.
- Arseneau-Robar, T. J. M., Müller, E., Taucher, A. L., van Schaik, C. P., Bshary, R. & Willems, E. P. (2018). Male monkeys use punishment and coercion to de-escalate costly intergroup fights. *Proceedings of the Royal Society B: Biological Sciences* 285, 20172323.
- Arseneau-Robar, T. J. M., Taucher, A. L., Müller, E., van Schaik, C., Bshary, R. & Willems, E. P. (2016). Female monkeys use both the carrot and the stick to promote male participation in intergroup fights. *Proceedings of the Royal Society B: Biological Sciences* 283, 20161817.
- BARRAULT, C., SOLDATI, A., HOBAITER, C., MUGISHA, S., DE MOOR, D., ZUBERBÜHLER, K. & DEZECACHE, G. (2022). Thermal imaging reveals social monitoring during social feeding in wild chimpanzees. *Philosophical Transactions of the Royal Society B: Biological sciences* 377(1860), 20210302.
- BEKOFF, M. (2001). Social play behaviour: cooperation, fairness, trust and the evolution of morality. *Journal of Consciousness Studies* 8, 81–90.
- BEKOFF, M. & PIERCE, J. (2009). Wild Justice: The Moral Lives of Animals. University of Chicago Press, Chicago.
- BENZ-SCHWARZBURG, J. (2019). Cognitive Kin, Moral Strangers? Linking Animal Cognition, Animal Ethics & Animal Welfare. Brill, Leiden.
- BICCHIERI, C. (2006). The Grammar of Society. Cambridge University Press, New York. BICCHIERI, C. (2017). Norms in the Wild: How to Diagnose, Measure, and Change Social Norms. Oxford University Press, New York.
- BIRCH, J. (2021). Toolmaking and the evolution of normative cognition. Biology and Philosophy 36(1), 4.
- BOESCH, C. (2012). From material to symbolic cultures: culture in primates. In *The Oxford Handbook of Culture and Psychology* (ed. J. Valsiner), pp. 677–692. Oxford University Press, Oxford.
- Bossley, M., Steiner, A., Brakes, P., Shrimpton, J., Foster, C. & Rendell, L. (2018). Tail walking in a bottlenose dolphin community: the rise and fall of an arbitrary cultural 'fad'. *Biology Letters* 14(9), 20180314.
- BOYD, R. & RICHERSON, P. J. (1992). Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethology and Sociobiology* 13(3), 171–195.
- BRAKES, P., CARROLL, E. L., DALL, S. R. X., KEITH, S. A., McGREGOR, P. K., MESNICK, S. L., NOAD, M. J., RENDELL, L., ROBBINS, M. M., RUTZ, C., THORNTON, A., WHITEN, A., WHITING, M. J., APLIN, L. M., BEARHOP, S., ET AL. (2021). A deepening understanding of animal culture suggests lessons for conservation. Proceedings of the Royal Society B: Biological Sciences 288(1949), 20202718.
- BROSNAN, S. F. & DE WAAL, F. B. M. (2003). Monkeys reject unequal pay. Nature 425(6955), 297–299.
- BROSNAN, S. F., FREEMAN, C. & DE WAAL, F. B. M. (2006). Partner's behavior, not reward distribution, determines success in an unequal cooperative task in capuchin monkeys. *American Journal of Primatology* 68(7), 713–724.
- BROSNAN, S. F., SCHIFF, H. C. & DE WAAL, F. B. (2005). Tolerance for inequity may increase with social closeness in chimpanzees. Proceedings of the Royal Society B: Biological Sciences 272(1560), 253–258.
- BRÜGGER, R. K., WILLEMS, E. P. & BURKART, J. M. (2021). Do marmosets understand others' conversations? A thermography approach. Science Advances 7(6), eabc8790.
- BSHARY, R. & GRUTTER, A. S. (2006). Image scoring and cooperation in a cleaner fish mutualism. *Nature* $\bf 441$ (7096), 975–978.
- BUCKNER, C. (2013). Morgan's Canon, meet Hume's Dictum: avoiding anthrofabulation in cross-species comparisons. *Biology and Philosophy* 28(5), 853–871.
- CAMP, E. (2009). A language of baboon thought? In The Philosophy of Animal Minds (ed. R. Lurz), pp. 108–127. Cambridge University Press, Cambridge, UK.

- CHALMERS, D. J. (2020). What is conceptual engineering and what should it be? Inquiry 1–18. https://www.tandfonline.com/doi/full/10.1080/0020174X.2020. 1817141.
- CHUDEK, M. & HENRICH, J. (2011). Culture–gene coevolution, norm-psychology and the emergence of human prosociality. Trends in Cognitive Sciences 15(5), 218–226.
- CIALDINI, R. B., RENO, R. R. & KALLGREN, C. A. (1990). A focus theory of normative conduct: recycling the concept of norms to reduce littering in public places. *Journal of Personality and Social Psychology* 58, 1015–1026.
- CLAY, Z., MOSCOVICE, L. & GRUBER, T. (2022). Bonobo sexual behavior and psychology. In *The Cambridge Handbook of Evolutionary Perspectives on Sexual Psychology* (ed. T. SHACKELFORD), pp. 370–400. Cambridge University Press, Cambridge.
- CLOUTIER, S., NEWBERRY, R. C., HONDA, K. & ALLDREDGE, J. R. (2002). Cannibalistic behaviour spread by social learning. *Animal Behaviour* 63(6), 1153–1162.
- COLOMBO, M. (2014). Two neurocomputational building blocks of social norm compliance. Biology and Philosophy 29(1), 71–88.
- DANCHIN, E., NÖBEL, S., POCHEVILLE, A., DAGAEFF, A.-C., DEMAY, L., ALPHAND, M., RANTY-ROBY, S., VAN RENSSEN, L., MONIER, M., GAZAGNE, E., ALLAIN, M. & ISABEL, G. (2018). Cultural flies: conformist social learning in fruitflies predicts long-lasting mate-choice traditions. *Science* 362(6418), 1025–1030.
- DANÓN, L. (2019). Animal normativity. Phenomenology and Mind 17, 17.
- DE WAAL, F. B. M. (2014). Natural normativity: the 'is' and 'ought' of animal behavior. Behaviour 151, 185–204.
- DE WAAL, F. B. M. & DAVIS, J. M. (2003). Capuchin cognitive ecology: cooperation based on projected returns. Neuropsychologia 41(2), 221–228.
- DE WAAL, F. B. M. & VAN ROOSMALEN, A. (1979). Reconciliation and consolation among chimpanzees. Behavioral Ecology and Sociobiology 5(1), 55–66.
- DEAN, L. G., VALE, G. L., LALAND, K. N., FLYNN, E. & KENDAL, R. L. (2014). Human cumulative culture: a comparative perspective. *Biological Reviews* 89(2), 284–301.
- DENNETT, D. C. (1991). Real patterns. The Journal of Philosophy 88(1), 27-51.
- DEUTCHMAN, P., AELLEN, M., BOGESE, M., BSHARY, R., DRAYTON, L., GIL, D., MARTIN, J., PŘĚTÔT, L., RAIHANI, N., SANTOS, L. & McAULIFFE, K. (2023). Punishment is sensitive to outside options in humans but not cleaner fish (*Labroides dimidiatus*). *Animal Behaviour* 205, 15–33.
- DEUTSCH, M. & GERARD, H. B. (1955). A study of normative and informational social influences upon individual judgment. The Journal of Abnormal and Social Psychology 51, 629–636.
- Dupuis-Desormeaux, M., Kaaria, T. N., Mwololo, M., Davidson, Z. & MacDonald, S. E. (2018). A ghost fence-gap: surprising wildlife usage of an obsolete fence crossing. *PeetJ* 6, e5950.
- ERMATINGER, F. A., BRÜGGER, R. K. & BURKART, J. M. (2019). The use of infrared thermography to investigate emotions in common marmosets. *Physiology & Behavior* 211, 112672.
- FITZPATRICK, S. (2017). Animal morality: what is the debate about? *Biology and Philosophy* 32(6), 1151–1183.
- FITZPATRICK, S. (2020). Chimpanzee normativity: evidence and objections. *Biology and Philosophy* 35(4), 45.
- FITZPATRICK, S. & Andrews, K. (2022). Animal culture and animal welfare. Philosophy of Science 89(5), 1104–1111.
- FLACK, J. C., GIRVAN, M., DE WAAL, F. B. & KRAKAUER, D. C. (2006). Policing stabilizes construction of social niches in primates. *Nature* 439(7075), 426–429.
- FLACK, J. C., JEANNOTTE, L. A. & DE WAAL, F. B. M. (2004). Play signaling and the perception of social rules by juvenile chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* 118, 149–159.
- Galef, B. G. (1992). The question of animal culture. Human Nature 3(2), 157-178.
- GELFAND, M. J. (2018). Rule Makers, Rule Breakers: How Culture Wires our Minds, Shapes our Nations and Drive our Differences. Scribner, New York.
- GOLDSBOROUGH, Z., STERCK, E. H. M., DE WAAL, F. & WEBB, C. E. (2022). Individual variation in chimpanzee (*Pan troglodytes*) repertoires of abnormal behaviour. *Animal Welfare* **31**(1), 125–135.
- Goldsborough, Z., Webb, C. E., de Waal, F. B. M. & van Leeuwen, E. J. C. (2021). Zoo-housed female chimpanzee adopts local female-specific tradition upon immigrating into a new group. *Behaviour* **158**(6), 547–564.
- GOTTLIEB, D. H., COLEMAN, K. & McCOWAN, B. (2013). The effects of predictability in daily husbandry routines on captive rhesus macaques (*Macaca mulatta*). Applied Animal Behaviour Science 143(2–4), 117–127.
- GREGGOR, A. L., THORNTON, A. & CLAYTON, N. S. (2017). Harnessing learning biases is essential for applying social learning in conservation. *Behavioral Ecology and Sociobiology* 71(1), 16.
- GRUBER, T., CHIMENTO, M., APLIN, L. M. & BIRO, D. (2021). Efficiency fosters cumulative culture across species. *Philosophical Transactions of the Royal Society B: Biological Sciences* 377(1843), 20200308.
- HAIDLE, M. N., BOLUS, M., COLLARD, M., CONARD, N., GAROFOLI, D., LOMBARD, M., NOWELL, A., TENNIE, C. & WHITEN, A. (2015). The nature of culture: an eight-grade model for the evolution and expansion of cultural

capacities in hominins and other animals. Journal of Anthropological Sciences 93, 43-70

- HAIDT, J. (2012). The Righteous Mind: Why Good People Are Divided by Politics and Religion. Knopf Doubleday Publishing Group, New York.
- HAUSER, M. D., CHOMSKY, N. & FITCH, W. T. (2002). The faculty of language: what is it, who has it, and how did it evolve? *Science* **298**(5598), 1569–1579.
- HENRICH, J. (2015). The Secret of our Success: How Culture Is Driving Human Evolution, Domesticating our Species, and Making us Smarter. Princeton University Press, Princeton.
- HENRICH, J. & HENRICH, N. (2010). The evolution of cultural adaptations: Fijian food taboos protect against dangerous marine toxins. Proceedings of the Royal Society B: Biological Sciences 277(1701), 3715–3724.
- HEYES, C. (2018). Cognitive Gadgets: The Cultural Evolution of Thinking. Harvard University Press. Boston.
- HEYES, C. (2020). Culture: a primer. Current Biology 30, R1246-R1250.
- HEYES, C. (2023). Rethinking norm psychology. Perspectives on Psychological Science. 19, 12–38 (doi: 10.1177/17456916221112075).
- HILL, K. (2009). Animal "culture"? In The Question of Animal Culture (eds K. N. LAIAND and B. G. GALEF), pp. 269–287. Harvard University Press, Cambridge, MA.
- HOBAITER, C. & BYRNE, R. W. (2014). The meanings of chimpanzee gestures. Current Biology 24(14), 1596–1600.
- HOOK, M. A., LAMBETH, S. P., PERLMAN, J. E., STAVISKY, R., BLOOMSMITH, M. A. & SCHAPIRO, S. J. (2002). Inter-group variation in abnormal behavior in chimpanzees (*Pan troglodytes*) and rhesus macaques (*Macaca mulatta*). *Applied Animal Behaviour Science* **76**(2), 165–176.
- HOPPER, L. M. (2021). Leveraging social learning to enhance captive animal care and welfare. *Journal of Zoological and Botanical Gardens* 2(1), 1.
- HOPPER, L. M. & CARTER, A. J. (2020). Methods to study chimpanzee social learning from a comparative perspective. In *Chimpanzees in Context: A Comparative Perspective on Chimpanzee Behavior, Cognition, Conservation, and Welfare* (eds L. M. HOPPER and S. R. Ross), pp. 167–188. Chicago University Press, Chicago.
- HOPPER, L. M., FREEMAN, H. D. & Ross, S. R. (2016). Reconsidering coprophagy as an indicator of negative welfare for captive chimpanzees. *Applied Animal Behaviour Science* 176, 112–119.
- HOPPER, L. M., SCHAPIRO, S. J., LAMBETH, S. P. & BROSNAN, S. F. (2011). Chimpanzees' socially maintained food preferences indicate both conservatism and conformity. *Animal Behaviour* 81(6), 1195–1202.
- HOPPITT, W. & LALAND, K. N. (2013). Social Learning: An Introduction to Mechanisms, Methods and Models. Princeton University Press, Princeton.
- HUME, D. (1739). A Treatise of Human Nature. Oxford University Press, Oxford.
- JANSON, C. H. & BROSNAN, S. F. (2013). Experiments in primatology: from the lab to the field and back again. In *Primate Ecology and Conservation: A Handbook of Techniques* (eds E. J. Sterling, N. Bynum and M. E. Blair), pp. 177–194. Oxford University Press, Oxford.
- JOSHI, S. & GOLD, J. I. (2020). Pupil size as a window on neural substrates of cognition. Trends in Cognitive Sciences 24(6), 466–480.
- KANO, F., HIRATA, S., DESCHNER, T., BEHRINGER, V. & CALL, J. (2016). Nasal temperature drop in response to a playback of conspecific fights in chimpanzees: a thermo-imaging study. *Physiology & Behavior* 155, 83–94.
- KAPPELER, P. M., FICHTEL, C. & VAN SCHAIK, C. P. (2019). There ought to be roots: evolutionary precursors of social norms and conventions in non-human primates. In *The Normative Animal? The Anthropological Significance of Social, Moral and Linguistic Norms* (eds N. ROUGHLEY and K. BAYERTZ), pp. 65–82. Oxford University Press, New York.
- KAWAI, M. (1965). Newly-acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima islet. *Primates* 6, 1–30.
- KELLY, D. & DAVIS, T. (2018). Social norms and human normative psychology. Social Philosophy and Policy 35, 54–76.
- KELLY, D. & DE BLOCK, A. (2022). Culture and cognitive science. In The Stanford Encyclopedia of Philosophy Summer 2022 Edition, (ed. E. N. ZALTA). The Metaphysics Research Lab, Philosophy Department, Stanford University, Stanford, CA. Electronic file available at https://plato.stanford.edu/archives/sum2022/entries/ culture-cogsci/.
- KELLY, D. & SETMAN, S. (2020). The psychology of normative cognition. In The Stanford Encyclopedia of Philosophy Summer 2022 Edition, (ed. E. N. Zalta). The Metaphysics Research Lab, Philosophy Department, Stanford University, Stanford, CA. Electronic file available at https://plato.stanford.edu/archives/ spr2021/entrics/psychology-normative-cognition/.
- KENDAL, R. L. (2008). Animal 'culture wars': evidence from the wild? The Psychologist 21, 312–315.
- KENDAL, R. L., BOOGERT, N. J., RENDELL, L., LALAND, K. N., WEBSTER, M. & JONES, P. L. (2018). Social learning strategies: bridge-building between fields. Trends in Cognitive Sciences 22(7), 651–665.
- KENDAL, R. L., GALEF, B. G. & VAN SCHAIK, C. P. (2010). Social learning research outside the laboratory: how and why? *Learning & Behavior* 38, 187–194.
- KENWARD, B., KARLSSON, M. & PERSSON, J. (2011). Over-imitation is better explained by norm learning than by distorted causal learning. Proceedings of the Royal Society B: Biological Sciences 278(1709), 1239–1246.

KEUPP, S., BEHNE, T. & RAKOCZY, H. (2013). Why do children overimitate? Normativity is crucial. Journal of Experimental Child Psychology 116(2), 392–406.

- KITCHER, P. (2011). The Ethical Project. Harvard University Press, Cambridge.
- KOOPS, K., SCHÖNING, C., ISAJI, M. & HASHIMOTO, C. (2015). Cultural differences in ant-dipping tool length between neighbouring chimpanzee communities at Kalinzu, Uganda. Scientific Reports 5(1), 1.
- KRACHUN, C., CARPENTER, M., CALL, J. & TOMASELLO, M. (2009). A competitive nonverbal false belief task for children and apes. *Developmental Science* 12(4), 521–535.
- KRÜGER, M., BARTELS, W. & KRIST, H. (2020). Illuminating the dark ages: pupil dilation as a measure of expectancy violation across the life span. *Child Development* 91(6), 2221–2236.
- KRUPENYE, C. & HARE, B. (2018). Bonobos prefer individuals that hinder others over those that help. Current Biology 28(2), 280–286.e5.
- KRUPENYE, C., KANO, F., HIRATA, S., CALL, J. & TOMASELLO, M. (2016). Great apes anticipate that other individuals will act according to false beliefs. *Science* 354(6308), 110–114.
- KRUPENYE, C., KÖSTER, M. & CLAY, Z. (2021). Bonobos' (Pan paniscus) and chimpanzees' (Pan troglodytes) understanding of, and pupillary responses to, others' needs. Proceedings of the Annual Meeting of the Cognitive Science Society 43, Electronic file available at https://escholarship.org/uc/item/2dm9h016.
- KUMAR, V. & CAMPBELL, R. (2022). A Better Ape: The Evolution of the Moral Mind and how it Made us Human. Oxford University Press, New York.
- LALAND, K. N., ATTON, N. & WEBSTER, M. M. (2011). From fish to fashion: experimental and theoretical insights into the evolution of culture. *Philosophical Transactions of the Royal Society of London B: Biological sciences* 366(1567), 958–968.
- LALAND, K. N. & GALEF, B. G. (cds) (2009). The Question of Animal Culture. Harvard University Press, Cambridge.
- LALAND, K. N. & JANIK, V. M. (2006). The animal cultures debate. Trends in Ecology & Evolution 21(10), 542–547.
- LALAND, K. N. & WILLIAMS, K. (1998). Social transmission of maladaptive information in the guppy. *Behavioral Ecology* 9(5), 493–499.
- LEWIS, L. S. & KRUPENYE, C. (2022). Eye-tracking as a window into primate social cognition. American Journal of Primatology 84, e23393 (doi: 10.1002/ajp.23393).
- LORINI, G. (2018). Animal norms: an investigation of normativity in the non-human social world. Law. Culture and the Humanities 18(3), 652–673.
- LUCAS, A. J., KINGS, M., WHITTLE, D., DAVEY, E., HAPPÉ, F., CALDWELL, C. A. & THORNTON, A. (2020). The value of teaching increases with tool complexity in cumulative cultural evolution. *Proceedings of the Royal Society B: Biological Sciences* 287(1939), 20201885.
- LUNCZ, L. V. & BOESCH, C. (2014). Tradition over trend: neighboring chimpanzee communities maintain differences in cultural behavior despite frequent immigration of adult females. *American Journal of Primatology* 76, 649–657.
- LUNCZ, L. V., SIRIANNI, G., MUNDRY, R. & BOESCH, C. (2018). Costly culture: differences in nut-cracking efficiency between wild chimpanzee groups. *Animal Behaviour* 137, 63–73.
- LUNCZ, L. V. & VAN DE WAAL, E. (2021). Cultural transmission in dispersing primates. In Chimpanzees in Context: A Comparative Perspective on Chimpanzee Behavior, Cognition, Conservation, and Welfare (eds L. M. HOPPER and S. R. Ross), pp. 410–427. University of Chicago Press, Chicago.
- LUNCZ, L. V., WITTIG, R. M. & BOESCH, C. (2015). Primate archaeology reveals cultural transmission in wild chimpanzees (Pan troglodytes verus). Philosophical Transactions of the Royal Society B: Biological Sciences 370(1682), 20140348.
- Lurz, R. W., Krachun, C., Mareno, M. C. & Hopkins, W. D. (2022). Do chimpanzees predict others' behavior by simulating their beliefs? *Animal Behavior and Cognition* 9(2), 153–175.
- Lyn, H., Franks, B. & Savage-Rumbaugh, E. S. (2008). Precursors of morality in the use of the symbols "good" and "bad" in two bonobos (*Pan paniscus*) and a chimpanzee (*Pan troglodytes*). *Language & Communication* **28**, 213–224.
- MATHEW, S. (2017). How the second-order free rider problem is solved in a small-scale society. American Economic Review 107(5), 578–581.
- MATHEW, S., BOYD, R. & VAN VEELEN, M. (2013). Human cooperation among kin and close associates may require enforcement of norms by third parties. In *Cultural Evolution: Society, Technology, Llanguage, and Religion* (eds P. J. RICHERSON and M. CHRISTIANSEN), pp. 45–60. MIT Press, Cambridge.
- MATSUZAWA, T. (2009). Symbolic representation of number in chimpanzees. Current Opinion in Neurobiology 19(1), 92–98.
- MATSUZAWA, T. & YAMAKOSHI, G. (1996). Comparison of chimpanzee material culture between Bossou and Nimba, West Africa. In *Reaching into Thought: The Minds of the Great Apes* (eds A. Russon, K. Bard and S. Parker), pp. 211–232. Cambridge University Press, Cambridge.
- McGrew, W. C. (2003). Ten dispatches from the chimpanzee culture wars. In Animal Social Complexity: Intelligence, Culture, and Individualized Societies (eds F. B. DE WAAL and P. L. TYACK), pp. 419–439. Harvard University Press, Cambridge, MA.
- Melis, A. P., Call, J. & Tomasello, M. (2006a). Chimpanzees (Pan troglodytes) conceal visual and auditory information from others. Journal of Comparative Psychology 120(2), 154–162.

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- Melis, A. P., Hare, B. & Tomasello, M. (2006b). Chimpanzees recruit the best collaborators. Science 311(5765), 1297–1300.
- MENDES, N., STEINBEIS, N., BUENO-GUERRA, N., CALL, J. & SINGER, T. (2018).
 Preschool children and chimpanzees incur costs to watch punishment of antisocial others. Nature Human Behaviour 2(1), 45–51.
- Mesoudi, A. (2011). Cultural Evolution: How Darwinian Theory Can Explain Human Culture and Synthesize the Social Sciences. University of Chicago Press, Chicago.
- MONTES-LOURIDO, P., KAR, M., KUMBAM, I. & SADAGOPAN, S. (2021). Pupillometry as a reliable metric of auditory detection and discrimination across diverse stimulus paradigms in animal models. *Scientific Reports* 11(1), 3108.
- MONTREY, M. & SHULTZ, T. R. (2020). The evolution of high-fidelity social learning. Proceedings of the Royal Society B: Biological Sciences 287(1928), 20200090.
- MORRIS, A. & CUSHMAN, F. (2018). A common framework for theories of norm compliance. Social Philosophy and Policy 35(1), 101–127.
- NICHOLS, S. (2021). Rational Rules: Towards a Theory of Moral Learning. Oxford University Press, Oxford.
- NISHIDA, T., HOSAKAM, K., NAKAMURA, M. & HAMAI, M. (1995). A within-group gang attack on a young adult male chimpanzee: ostracism of an ill-mannered member? *Primates* 36, 207–211.
- O'NEILL, E. & MACHERY, E. (2018). The normative sense: what is universal? What varies? In *The Routledge Handbook of Moral Epistemology* (eds A. ZIMMERMAN, K. JONES and M. TIMMONS), pp. 38–56. Routledge, New York.
- Pepperberg, I. M. & Carey, S. (2012). Grey parrot number acquisition: the inference of cardinal value from ordinal position on the numeral list. *Cognition* 125(2), 219–232.
- POWELL, R. (2023). Social norms and superorganisms. Biology and Philosophy 38(21), 21.
 RAIHANI, N. J., GRUTTER, A. S. & BSHARY, R. (2010). Punishers benefit from third-party punishment in fish. Science 327, 171.
- RICHERSON, P. J. & BOYD, R. (2005). Not by Genes Alone: How Culture Transformed Human Evolution. University of Chicago Press, Chicago.
- RIEDL, K., JENSEN, K., CALL, J. & TOMASELLO, M. (2012). No third-party punishment in chimpanzees. Proceedings of the National Academy of Sciences 109(37), 14824—14829.
- ROCHAT, P. (2015). Self-conscious roots of human normativity. Phenomenology and the Cognitive Sciences 14(4), 741–753.
- ROUGHLEY, N. & BAYERTZ, K. (eds) (2019). The Normative Animal? On the Anthropological Significance of Social, Moral, and Linguistic Norms. Oxford University Press, New York.
- Rudolf von Rohr, C., Burkart, J. & Schaik, C. (2011). Evolutionary precursors of social norms in chimpanzees: a new approach. *Biology and Philosophy* 26, 1–30.
- RUDOLF VON ROHR, C., KOSKI, S. E., BURKART, J. M., CAWS, C., FRASER, O. N., ZILTENER, A. & VAN SCHAIK, C. P. (2012). Impartial third-party interventions in captive chimpanzees: a reflection of community concern. *PLoS One* **7**(3), e32494.
- RUDOLF VON ROHR, C., VAN SCHAIK, C. P., KISSLING, A. & BURKART, J. M. (2015). Chimpanzees' bystander reactions to infanticide. *Human Nature* **26**(2), 143–160.
- SASAKI, T. & BIRO, D. (2017). Cumulative culture can emerge from collective intelligence in animal groups. *Nature Communications* 8, 15049.
- SCHEL, A. M., MACHANDA, Z., TOWNSEND, S. W., ZUBERBÜHLER, K. & SLOCOMBE, K. E. (2013). Chimpanzee food calls are directed at specific individuals. *Animal Behaviour* 86(5), 955–965.
- SCHLINGLOFF, L. & MOORE, R. (2017). Do chimpanzees conform to social norms? In Routledge Handbook of Philosophy of Animal Minds (cds K. Andrews and J. Beck), pp. 381–389. Routledge, New York.
- SCHMIDT, M. F. H. & RAKOCZY, H. (2019). On the uniqueness of human normative attitudes. In *The Normative Animal? On the Anthropological Significance of Social, Moral, and Linguistic Norms* (eds N. ROUGHLEY and K. BAYERTZ), pp. 121–136. Oxford University Press, Oxford.
- SCHNEIDER, C., CALL, J. & LIEBAL, K. (2010). Do bonobos say NO by shaking their head? Primates 51, 199–202.
- SCHOFIELD, D. P., McGrew, W. C., Takahashi, A. & Hirata, S. (2018). Cumulative culture in nonhumans: overlooked findings from Japanese monkeys? *Primates* 59, 113–122.
- SCHUPPLI, C. & VAN SCHAIK, C. P. (2019). Animal cultures: how we've only seen the tip of the iceberg. Evolutionary Human Sciences 1, e2.
- SELLARS, W. (1949). Language, rules and behavior. In John Dewey: Philosopher of Science and Freedom (cd. S. HOOK), pp. 289–315. Dial Press, New York.
- SHETTLEWORTH, S. J. (2010). Clever animals and killjoy explanations in comparative psychology. Trends in Cognitive Science 14, 477–481.
- SINGH, M. & BOOMSMA, J. J. (2015). Policing and punishment across the domains of social evolution. Oikus 124, 971–982.

- SOSA, S., SUEUR, C. & PUGA-GONZALEZ, I. (2020). Network measures in animal social network analysis: their strengths, limits, interpretations and uses. *Methods in Ecology* and Evolution 12(1), 10–21.
- SRIPADA, C. & STICH, S. P. (2006). A framework for the psychology of norms. In *The Innate Mind Volume 3: Culture and Cognition* (eds P. CARRUTHERS, S. LAURENCE and S. STICH), pp. 280–301. Oxford University Press, Oxford.
- STERELNY, K. (2021). The Pleistocene Social Contract. Oxford University Press, Oxford.
- STRAUSS, E. D. & HOLEKAMP, K. E. (2019). Social alliances improve rank and fitness in convention-based societies. Proceedings of the National Academy of Sciences 116(18), 8919–8924.
- TENNIE, C. (2019). Could nonhuman great apes also have cultural evolutionary psychology? Behavioral and Brain Sciences 42, E184.
- Tennie, C., Bandini, E., van Schaik, C. P. & Hopper, L. M. (2020). The zone of latent solutions and its relevance to understanding ape cultures. *Biology and Philosophy* 35(5), 55.
- THERIAULT, J. E., YOUNG, L. & BARRETT, L. F. (2021). The sense of should: a biologically-based framework for modeling social pressure. *Physics of Life Reviews* **36**, 100–136.
- TOMASELLO, M. (2016a). A Natural History of Human Morality. Harvard University Press, Cambridge.
- Tomasello, M. (2016b). The ontogeny of cultural learning. Current Opinion in Psychology 8, 1–4.
- TOMASELLO, M. (2019). The moral psychology of obligation. Behavioral and Brain Sciences 43, E56.
- TOMASELLO, M. (2022). The Evolution of Agency: Behavioral Organization from Lizards to Humans. MIT Press, Cambridge, MA.
- Tomasello, M., Kruger, A. & Ratner, H. (1993). Cultural learning. Behavioral and Brain Sciences 16(3), 495–511.
- ULYAN, M. J., BURROWS, A. E., BUZZELL, C. A., RAGHANTI, M. A., MARCINKIEWICZ, J. L. & PHILLIPS, K. A. (2006). The effects of predictable and unpredictable feeding schedules on the behavior and physiology of captive brown capuchins (Cebus apella). Applied Animal Behaviour Science 101(1), 154–160.
- VAN DE WAAL, E., BORGEAUD, C. & WHITEN, A. (2013). Potent social learning and conformity shape a wild primate's foraging decisions. Science 340(6131), 483–485.
- VAN LEEUWEN, E. (2021). Temporal stability of chimpanzee social culture. Biology Letters 17(5), 20210031.
- VAN LEEUWEN, E. J., CRONIN, K. A. & HAUN, D. B. (2014). A group-specific arbitrary tradition in chimpanzees (Pan troglodytes). Animal Cognition 17(6), 1421–1425.
- VAN SCHAIK, C. P. (2012). Animal culture: chimpanzee conformity. Current Biology 22(10), R402–R404.
- VAN SCHAIK, C. P., ANCRENAZ, M., BORGEN, G., GALDIKAS, B., KNOTT, C. D., SINGLETON, I., SUZUKI, A., UTAMI, S. S. & MERRILL, M. (2003). Orangutan cultures and the evolution of material culture. *Science* **299**(5603), 102–105.
- VINCENT, S., RING, R. & ANDREWS, K. (2018). Normative practices of other animals. In *The Routledge Handbook of Moral Epistemology* (eds A. ZIMMERMAN, K. JONES and M. TIMMONS), pp. 57–83. Routledge, New York. Electronic file available at https://philarchive.org/rec/VINNPO.
- WATSON, S. K., TOWNSEND, S. W., SCHEL, A. M., WILKE, C., WALLACE, E. K., CHENG, L., WEST, V. & SLOCOMBE, K. E. (2015). Vocal learning in the functionally referential food grunts of chimpanzees. *Current Biology* 25(4), 495–499.
- WESTRA, E. & ANDREWS, K. (2021). If skill is normative, then norms are everywhere.

 Analyse & Kritik 43(1), 203–218.
- WESTRA, E. & ANDREWS, K. (2022). A pluralistic framework for the psychology of norms. Biology and Philosophy 37(40).
- WHITEHEAD, H. & RENDELL, L. (2015). The Cultural Lives of Whales and Dolphins. University of Chicago Press, Chicago.
- WHITEN, A. (2021). The burgeoning reach of animal culture. Science 372(6537), eabe6514.
- WHITEN, A., GOODALL, J., McGrew, W. C., NISHIDA, T., REYNOLDS, V., SUGIYAMA, Y., TUTIN, C. E. G., WRANGHAM, R. W. & BOESCH, C. (1999). Cultures in chimpanzees. *Nature* 399(6737), 682–685.
- WHITEN, A., HARRISON, R. A., McGUIGAN, N., VALE, G. L. & WATSON, S. K. (2021). Collective knowledge and the dynamics of culture in chimpanzees. Philosophical Transactions of the Royal Society B: Biological Sciences 377(1843), 20200321.
- WHITEN, A., HORNER, V. & DE WAAL, F. B. M. (2005). Conformity to cultural norms of tool use in chimpanzees. Nature 437, 737–740.
- WRANGHAM, R. (2019). Goodness Paradox: The Strange Relationship between Virtue and Violence in Human Evolution. Knopf Doubleday Publishing Group, New York.
- ZWIRNER, E. & THORNTON, A. (2015). Cognitive requirements of cumulative culture: teaching is useful but not essential. Scientific Reports 5, 16781.

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