BIOLOGICAL REVIEWS
Cambridge Philosophical Society

Biol. Rev. (2024), pp. 000–000.
doi: 10.1111/brv.13086

The forgotten adaptive social benefits of social learning in animals

Rachel A. Harrison[1,2†,*], Pooja Dongre[1†], Carel P. van Schaik[3,4] and Erica van de Waal[1,2]

[1] *Department of Ecology and Evolution, University of Lausanne, Le Biophore, Lausanne CH-1015, Switzerland*
[2] *The Sense Innovation and Research Center, Avenue de Provence 82, Lausanne CH-1007, Switzerland*
[3] *Department of Evolutionary Anthropology, University of Zurich, Winterthurerstrasse 190, Zürich CH-8057, Switzerland*
[4] *Center for the Interdisciplinary Study of Language Evolution (ISLE), University of Zurich, Affolternstrasse 56, Zurich CH-8050, Switzerland*

ABSTRACT

Theoretical and empirical scholars of cultural evolution have traditionally studied social learning strategies, such as conformity, as adaptive strategies to obtain accurate information about the environment, whereas within social psychology there has been a greater focus upon the social consequences of such strategies. Although these two approaches are often used in concert when studying human social learning, we believe the potential social benefits of conformity, and of social learning more broadly, have been overlooked in studies of non-humans. We review evidence from studies of homophily, imitation, and rapid facial mimicry that suggests that behaving like others affords social benefits to non-human animals and that behaviour matching may be deployed strategically to increase affiliation. Furthermore, we review studies of conformity in dispersers, and suggest that forgoing personal information or preferences in favour of those of the new group during immigration may be a strategy to facilitate social integration. We therefore propose that the informational and social functions of conformity apply to humans and animals alike. We use this perspective to generate several interesting research questions to inspire work in this field. For example, under what conditions do animals use informational or social conformity and what role does uncertainty play in social learning in immigrant individuals?

Key words: conformity, social transmission, non-human primates, cultural evolution, dispersal.

CONTENTS

I. INTRODUCTION

In recent decades, the study of social learning and animal cultures has been a fruitful area of research, greatly increasing our understanding of the strategies driving social learning in both humans and non-human animals (Kendal *et al*., 2018). Social learning has been studied from two main perspectives: cultural evolution, and social psychology. Cultural

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[*] Author for correspondence (Tel.: +41(0)21 692 42 70; E-mail: rachel.a.harrison1@gmail.com).
[†] Authors contributed equally to this work.

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evolutionary theory (Boyd & Richerson, 2005; Mesoudi, 2009; Mesoudi, Whiten & Laland, 2006) predicts that individuals should be selective in terms of when they learn, what they learn, and who they learn from; the heuristics or biases guiding this are called 'social learning strategies' (Laland, 2004). The adaptive value of the information transmitted during social learning has been a major focus of this work (Henrich & McElreath, 2003; Rendell *et al.*, 2010). Research on social learning strategies has thus explored questions such as how individual uncertainty impacts the likelihood of learning socially (e.g. Kendal *et al.*, 2015; Williamson & Meltzoff, 2011) or whether individuals are more likely to copy older group members who may have more knowledge to transmit (e.g. Wood, Kendal & Flynn, 2012). This approach assumes that the most important function of social learning is the adaptive value of the information transmitted to naive individuals who may acquire knowledge regarding foraging opportunities, predators, and other environmental factors, including the social environment, without incurring costs in terms of the effort and time of individual asocial learning (Giraldeau, Valone & Templeton, 2002; Laland, 2004).

Social psychology has equally focused on social learning processes, though from a different perspective. Bandura (1977) argued for the importance of social learning in human behaviour, and conducted a series of classic studies on when and from whom children learn (e.g. Bandura, Ross & Ross, 1961, 1963). Social psychology, perhaps more so than cultural evolutionary approaches, has also explored how social learning impacts inter-individual relationships in ways that may benefit the individual on both the short and long term (Deutsch & Gerard, 1955; Uzgiris, 1981). Moreover, psychologists have traditionally been more interested in identifying the detailed mechanisms involved in social learning than have those using the cultural evolution approach. However, social psychology has tended not to focus on long-term, multi-transmission or multi-generational (i.e. cultural) effects of social learning, including, most importantly, fitness consequences.

We are not the first to suggest that the two fields could work in concert more effectively to study social learning [Over & Carpenter (2013); see also Mesoudi (2009) for a review of the contrasts and connections between social psychology and cultural evolution approaches]. However, while both cultural evolution and social psychology have been applied to questions related to social learning in humans, we argue that an approach influenced by social psychology is largely missing in the non-human literature on social learning. Studies of social learning in non-humans most often follow a cultural evolutionary approach, placing emphasis on informational benefits of social learning, which has led to a neglect of the possible positive social consequences of social learning such as increased social integration or strengthened social bonds, while studies in humans from a social psychological perspective have tended not to measure whether changes in inter-individual relationships following social learning are adaptive and under selection. In this review, we argue that rather than only being short term or incidental, these social consequences may be equally fitness-relevant. In terms of whether non-human research might benefit from blending these dichotomous approaches, we focus on one social learning strategy in particular: conformity.

II. APPROACHES TO THE STUDY OF CONFORMITY

The study of conformity has its roots in social psychology, with perhaps one of the most influential studies being seminal work in which undergraduate students tasked with matching images of lines to a target were significantly more likely to make an error if faced with a unanimous group of peers who gave the incorrect answer (Asch, 1956). Conformity has since been defined in a variety of ways within the cultural evolution literature [see Whiten (2019) for a review], with perhaps the simplest being 'copy the majority' (Laland, 2004) (also termed 'linear conformity' by Claidière & Whiten, 2012), while other definitions refer to disproportionate copying of majority behaviours ('conformist transmission'; Boyd & Richerson, 1988). These definitions are verbal descriptions of formal models, which make specific predictions regarding the population-level effects of such a learning strategy and are often not explicitly tested in social psychology approaches to conformity (Mesoudi, 2009). Drawing more on social psychology, some definitions have also included the overriding of personal knowledge in deference to group behaviour (also termed 'strong conformity'; Haun & Tomasello, 2011). Studies of conformity in humans have additionally often delineated two types of conformity, defined by the underlying proximate motivation: 'informational' conformity, employed to access the best information available about reality, and 'normative' conformity, which is used to manage social interactions (Claidière & Whiten, 2012; Deutsch & Gerard, 1955). We will refer to both 'informational' and 'normative' conformity throughout this review, following the existing literature on conformity, but note that both types involve the acquisition of information in a strict sense: 'informational' conformity generally implies gathering information about the physical environment, while 'normative' conformity implies acquiring information about the beliefs and attitudes of others, indicating how best to behave within the social environment. Experimentally, normative conformity is usually identified by a control condition allowing participants to make their choice in private (arguably thus removing any social pressure to conform). If conformity to the group's behaviour is reduced in private, it can be argued that any observed conformity in a group context is motivated by social integration rather than accessing information about the physical environment. In humans, this method has demonstrated that, at least for perceptual tasks in the style of Asch (1956), conformity appears to be normatively motivated, with participants conforming to the group opinion more often if they make their answer publicly rather than privately (Haun & Tomasello, 2011; Sibilsky *et al.*, 2021; Zhang *et al.*, 2017). Both

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'informational' and 'normative' conformity are proximate definitions, built upon the supposed motivations of actors rather than the ultimate function of conformist behaviour.

It has been argued that normativity evolved uniquely in the human lineage (e.g. Schmidt & Rakoczy, 2019), and generally definitions of normativity require the imposition of sanctions for transgressions against group norms [e.g. Schlingloff & Moore (2017), although see also Westra & Andrews (2022)]. Evidence of these kinds of sanctions, particularly by third-party bystanders, is limited in non-humans (Riedl *et al.*, 2012; Rudolf von Rohr, Burkart & van Schaik, 2011), although it has been argued that non-humans may show evidence of precursors to social norms, evidenced by bystander reactions to violations, such as chimpanzees (*Pan troglodytes*) paying greater attention to videos of infanticide than to videos of aggression between adults or colobus hunting (von Rohr *et al.*, 2015). While some authors have suggested that experimental observations of apparently conformist behaviour in non-humans may be consistent with normative motivations [Hopper *et al.* (2011) although see van Leeuwen & Haun (2013) for an alternative interpretation], we suggest for clarity instead distinguishing normative conformity (conforming to behaviours when there may be sanctions against non-conformity) from social conformity as defined in van de Waal, van Schaik & Whiten (2017, p. 9): 'by social conformity we mean that individuals act like others not to acquire an informational, but instead a social benefit that derives from simply "being like others"'. These 'social benefits' would be fitness-related benefits derived from increased integration or status within a group as a result of conformist behaviour (see Fig. 1). Both normative and social conformity explicitly relate to social rather than informational functions. We believe it is important to distinguish the functions of conformity from the proximate mechanisms, and that it is possible that multiple mechanisms are compatible with informational, social, and normative functions of conformity.

Herein, we argue that an adaptive social function of conformity plays a larger role in non-human animals than previously thought, and that incorporating approaches from the social psychology literature could prove useful in exploring this. We will also consider mechanisms related to conformity, and whether these might serve both informational and social functions. Studies across taxa, including in humans, have demonstrated that social integration impacts survival and reproductive success [Archie *et al.*, 2014; Gerber *et al.*, 2022; Kajokaite *et al.*, 2022; Yang *et al.*, 2016; see Snyder-Mackler *et al.* (2020) for a review], indicating a selective pressure favouring the emergence of strategies to increase integration. While the mechanisms underlying the relationship between social integration and fitness are still subject to debate (Ostner & Schülke, 2018; Thompson, 2019), social integration may aid in, amongst others, predator avoidance (Josephs *et al.*, 2016) and thermoregulation (McFarland *et al.*, 2015). Studies linking social integration and fitness, while as yet correlational, strongly suggest that affiliation with others provides fitness benefits. In addition to this, for conformity to have plausibly evolved for a social function, then (*i*) physical and behavioural similarity should promote affiliation and (*ii*) the likelihood of learning socially should increase during periods when an individual is integrating into a new social group or forming new social relationships. To explore whether these two criteria are met, we will use examples from both the human and non-human literature.

III. HOMOPHILIC ASSORTMENT

Plentiful evidence shows that physical and behavioural similarity promotes affiliation. Homophily – the widespread phenomenon whereby similar individuals associate preferentially

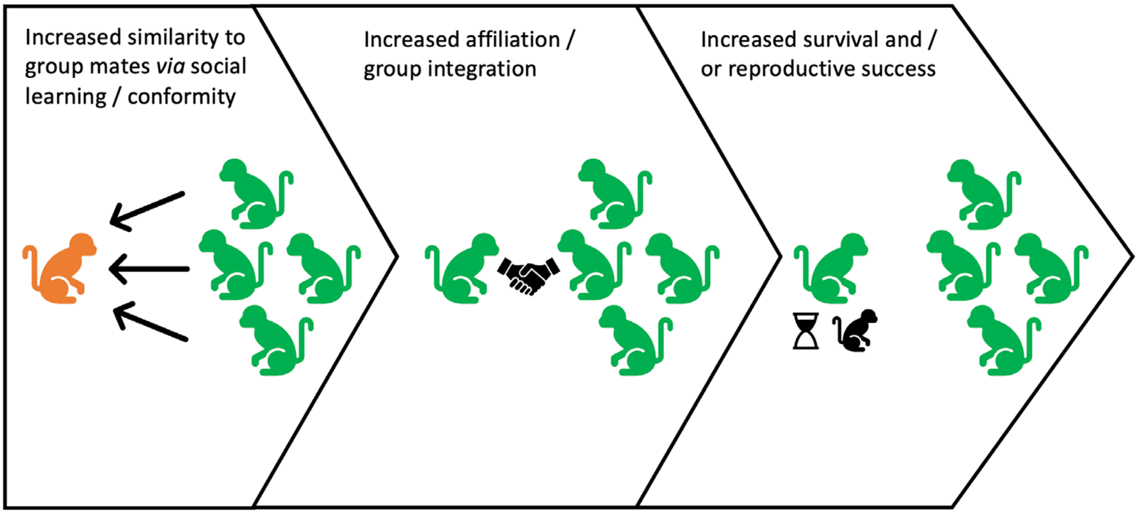

Fig. 1. Proposed causal link between social learning, increased affiliation, and fitness benefits. Traditional social learning studies in non-human animals have tended to overlook the influence of social learning upon group integration and affiliation, whilst traditional social psychology approaches in humans have generally not addressed potential fitness implications.

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(Fu *et al.*, 2012; Haun & Over, 2015; McPherson, Smith-Lovin & Cook, 2001) – is an important proximate mechanism underlying group formation, coordination and cooperation (Franz, Schülke & Ostner, 2013). Within groups, social interactions are rarely random, and across diverse taxa, patterns of interaction and association are often shaped by homophily according to physical traits such as sex (Dey & Quinn, 2014; Hirsch, Stanton & Maldonado, 2012; Lusseau & Newman, 2004; Weiss *et al.*, 2021), age (Bouskila *et al.*, 2015; Lusseau & Newman, 2004; Ozella *et al.*, 2020; van den Bos & de Vries, 1996; Weiss *et al.*, 2021) and size (Croft *et al.*, 2005; Eifler *et al.*, 2016; for review of fish shoals, see Krause *et al.*, 2000). Physical traits such as these are likely to reflect similar underlying physiological states and therefore energetic demands (Ruckstuhl, 1999), demonstrating a role of homophily in reducing the costs of group coordination.

In addition to physical traits, and with greater relevance to the role of social learning in promoting affiliation, homophily shapes social networks of diverse taxa according to repeatable behavioural tendencies (Kovacs, Perrtree & Cox, 2017) or personality traits (Briard, Dorn & Petit, 2015; Croft *et al.*, 2005, 2009; Ebenau *et al.*, 2019; Massen & Koski, 2014; Morton *et al.*, 2015), which may provide increased opportunities to affiliate between the most behaviourally similar individuals. Notably, when homophily is based on personality, traits related to sociality are often involved, and importantly, homophily according to sociable traits occurs across the whole spectrum of sociability, not only in highly sociable individuals (Ebenau *et al.*, 2019; Massen & Koski, 2014; Morton *et al.*, 2015). Whilst this could be related to energetic budget allocation, as with the physical traits above, social tendencies may also be an honest signal of cooperation to maintain group cohesion. Furthermore, for species that live in stable groups and form differentiated, long-lasting social bonds with group members, forming and maintaining bonds requires investment of time and energy, and partners that seem predictable or likely to reciprocate in interactions might therefore be preferred (Massen & Koski, 2014). Likewise, other observable behavioural similarities could reflect honest signals of synergetic potential, thereby facilitating homophilic social bonding. Machado *et al.* (2019) demonstrated that bottlenose dolphins (*Tursiops truncatus gephyreus*) that perform a specialised foraging technique involving coordination with human fishermen are more likely to associate, including outside of the foraging context. Similarly, bottlenose dolphins using marine sponges in foraging preferentially associate with others who perform the same foraging behaviour (Bizzozzero *et al.*, 2019; Mann *et al.*, 2012). In humans, homophily is well documented according to a wide range of factors, from demographic traits such as sex, age, and ethnicity, to behaviour and personality, and even attitudes and beliefs (DellaPosta, Shi & Macy, 2015; Haun & Over, 2015; McPherson *et al.*, 2001). Human infants less than a year old already demonstrate an affinity for others that share their preferences (Mahajan & Wynn, 2012), and 14-month-old infants expect that others with shared preferences affiliate with one another (Liberman, Kinzler & Woodward, 2021). While it is unclear from purely observational studies in which direction the causal relationship operates (i.e. do individuals who behave similarly then associate more, do individuals become more similar due to frequent association, or is there reciprocal influence?), these studies of homophily in both humans and non-human animals demonstrate that behavioural similarity and affiliation are linked. One means of elucidating the potential causal relationship is to examine how social learning mechanisms operating to increase behavioural similarity between individuals influence affiliation.

IV. IMITATION, MIMICRY, AND SOCIAL AFFILIATION

For conformity to have evolved for primarily social purposes, learning socially from others should increase affiliation with them, and this should be a strategy used when trying to integrate socially. There are benefits to group membership that may be attained by behaving like others in order to solve a coordination problem [e.g. emerging from a sleeping den at the same time as group members (Thornton, Samson & Clutton-Brock, 2010), roosting in the same location as conspecifics (Teng *et al.*, 2012), for review see Stephens & Heinen (2018)]. However, the potential benefit of matching the behaviour of others may extend beyond this if it modulates the quality of an individual's social relationships. In both human and non-human primates, imitation has been shown to have an impact upon social affiliation. Capuchin monkeys (*Cebus apella*) preferred to look at humans who imitated their manipulations of a plastic ball, rather than humans who performed contingent, non-imitative, actions. Beyond this, the capuchins also preferentially spent time in proximity to, and were more likely to engage in token exchange with, the imitator rather than the non-imitator (Paukner *et al.*, 2009). In juvenile rhesus macaques (*Macaca mulatta*), individuals who more frequently 'mimicked' group members (interacting with the same object, foraging in the same location, or moving in the same direction as a group member) received more play overtures than those who mimicked less often (Anderson & Kinnally, 2021). These affiliative responses to imitators appear to emerge early in ontogeny, with infant rhesus macaques showing increased visual attention and affiliative gestures towards a human experimenter who mimicked their facial expressions (Sclafani *et al.*, 2015). These studies demonstrate that in non-human primates, imitation of behaviours, or similarity in behaviour likely driven by local enhancement, has the potential to increase affiliative behaviours between individuals.

In humans, it has already been suggested that imitation serves an affiliative function, with Uzgiris (1981) arguing that alongside an informational function, imitation in infants serves to communicate 'mutuality' (the connection between individuals). Experimental studies support this view: young infants (~4.5 months) preferentially attend to imitators, and

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older infants (∼12 months) preferentially reach for imitators rather than non-imitators, after observing third-party interactions (Powell & Spelke, 2018). This indicates that a preference for imitators emerges early in development in humans and extends beyond a preference for individuals who imitate *us* to a preference for those who imitate *others*. A preference for imitators could therefore have effects on affiliation outside of the dyadic interaction in which imitation occurred, with bystanders also choosing to affiliate with an imitative individual. Together, these studies suggest that imitative interactions carry social meaning for both human and non-human primates and thus can impact affiliation.

Crucially, many of these studies demonstrate a causal relationship between imitation and affiliation with imitation increasing affiliation, rather than close associates happening to learn more from one another. While the studies discussed here largely focus on imitation (high-fidelity action copying), we suggest that any form of social learning which leads to behavioural matching between two individuals would have the same effect (i.e. the important aspect is the resulting similarity in behaviour, not the social learning mechanism it results from). Studies of human infants (e.g. Mahajan & Wynn, 2012) show that partner preference can be influenced by behavioural similarities as simple as a shared food preference. Such behavioural similarity could be driven by social learning mechanisms much simpler than imitation (in the case of food selection, by stimulus or local enhancement). Therefore, even if, as has been suggested, non-human species do not engage in high-fidelity action copying (Tennie, Call & Tomasello, 2009, 2012), other social learning mechanisms that result in behavioural matching between individuals would be sufficient to drive increased affiliation. Imitation recognition (the ability to recognise when one is being imitated) has been demonstrated throughout the primate lineage, in both monkeys and great apes (Haun & Call, 2008; Paukner *et al*., 2005, 2009). Therefore, it is possible that sensitivity to behavioural matching by others pre-dates the ability to engage in high-fidelity copying.

Imitation is also used by humans as a strategy to mitigate ostracism. Over & Carpenter (2009) found that children primed with ostracism copied more components of a series of demonstrated unnecessary actions than those in a control group. Increased social learning following ostracism has been found repeatedly, both in cases of direct (Hopkins & Branigan, 2020; Watson-Jones, Whitehouse & Legare, 2016) and third-party (Watson-Jones *et al*., 2014) ostracism, and has been shown in adults as well as children [Williams, Cheung & Choi, 2000, although see Stengelin *et al*., 2021]. Williams *et al*. (2000) found adults primed with ostracism in an online game were more likely to conform to incorrect answers given by confederates in an Asch-style perceptual judgement task. Children also explicitly identify conformity as a potential strategy to achieve social integration. Cordonier, Nettles & Rochat (2018) showed children a group of puppets, which looked inside a box and whispered to the child what they each saw, the last puppet giving a different answer to the others. When asked what the last puppet should do to make friends, five-year-old children (but not three-year-olds) stated that the puppet should conform to the majority opinion, contrary to its own, thus showing strong conformity. The authors link this understanding of strategic strong conformity to children's development of theory of mind, and indeed, making this judgement about third-party interactions indicates an understanding that others are engaged in social image management. Taken together, these studies indicate that in human adults and children, social learning, including strong conformity, is used consciously or subconsciously to increase affiliation with others following direct or even indirect experience of ostracism.

It has been suggested that, in the studies cited above, individuals who experienced ostracism may have been simply more likely to attend to and reproduce *any* behaviours (not only social information, but also information presented asocially in a proposed 'ghost' control; Heyes, 2017). There is, however, evidence suggesting that ostracism primes humans to attend specifically to *social* information. Gardner, Pickett & Brewer (2000) found that after experiencing ostracism in a simulated chat room, participants showed selective memory for social events rather than individual events. The valence of the events had no effect – both positive and negative interpersonal events were recalled more than individual events. This finding hints at a deeper mechanism: not only are we more likely to learn socially when trying to gain social acceptance, but we are biased towards encoding social information, potentially better allowing us to learn socially.

Research into rapid behavioural mimicry also points towards social payoffs driving social learning. This unconscious form of mimicry (also referred to as 'automatic imitation' and 'simple imitation'; Heyes, 2012) is observed in both human and non-human primates (Davila Ross, Menzler & Zimmermann, 2008; Davila-Ross *et al*., 2011; Mancini, Ferrari & Palagi, 2013*b*) as well as non-primate mammals (Palagi, Nicotra & Cordoni, 2015; Palagi *et al*., 2019; Taylor *et al*., 2019). This process is often not discussed in the context of social learning, as novel behaviours are generally not learned this way (Heyes, 2012) and mimicking results in action-only copying (as opposed to action+goal or action+goal+result copying; Carpenter & Call, 2002), making mimicry of limited interest to those focused on cultural evolution as a process of information transfer. Nonetheless, this simple automatic behaviour can give us a critical insight into the function of social learning if both are considered as mechanisms leading to behavioural matching between individuals. Mimicry is used by humans to increase affiliation, both when affiliation is a conscious goal and when it is primed unconsciously (Lakin & Chartrand, 2003). As with instrumental imitation, discussed above, increased rates of behavioural mimicry are observed in humans following ostracism (Lakin, Chartrand & Arkin, 2008). Rapid facial mimicry has been shown to be linked to longer play bouts in multiple primate and non-primate species (Mancini, Ferrari & Palagi, 2013*a*; Palagi *et al*., 2019; Scopa & Palagi, 2016), and while the causal direction of this relationship has not yet been elucidated, it is possible that engaging in

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rapid facial mimicry leads to increased affiliation within play dyads. Unlike instrumental imitation or conformity, which may be at least partially consciously controlled in humans, mimicry is spontaneous and generally not thought to be under conscious control, with evidence that automatic imitation occurs even when participants are incentivised not to copy (Belot, Crawford & Heyes, 2013). Its use as a response to ostracism therefore points towards this being a deep-rooted impulse rather than a conscious strategy. Interestingly, some of the most compelling evidence for a capacity for high-fidelity imitation in non-human primates comes from 'do-as-I-do' paradigms, in which subjects imitate the posture or gestures of human experimenters following training (Custance, Bard & Whiten, 1995; Hribar, Sonesson & Call, 2014), and from observations of individuals performing unusual and arbitrary body movements or manipulations (e.g. Goldsborough *et al.*, 2021; van Leeuwen, Cronin & Haun, 2014). If social learning serves a social function, it is possible that this is why non-human animals appear to apply social learning more readily when matching postures or arbitrary behaviours in the social domain in comparison to ecological problem solving.

V. CONFORMITY DURING SOCIAL INTEGRATION

We have presented evidence, from animals and humans, that behaving similarly to others may have important social consequences, and that, due to the proven relationship between social integration and fitness, these may extend to long-term adaptive fitness benefits. At the most basic level, behavioural similarity can facilitate group coordination, and at least in some cases, can lead to increased affiliation. Based on this, we propose that socially motivated conformity may be more common in animals than previously acknowledged and may play a role in social integration.

Evidence from humans shows that we not only associate with similar others, but also learn new preferences from similar others (DellaPosta *et al.*, 2015), which increases similarity between individuals within networks, which in turn may further increase affiliation between associates. Research suggests that a similar process involving homophily and conformity occurs during vocalisation pattern (coda) learning by sperm whales (*Physeter macrocephalus*) (Cantor *et al.*, 2015). Individuals appear, first, to associate preferentially with others with similar codas, and subsequently, to modify their codas to be more like those most frequently encountered among their associates. Importantly, this demonstrates that a bidirectional process, whereby individuals associate with similar others *and* modify their behaviour to be more like that of their associates, is not unique to humans. Becoming more similar to others might be important when individuals have limited control over with whom they associate, to promote social cohesion, and behaving like others might facilitate the formation of new social ties when needed. For example, when experimentally grouped together, individuals of several other species have been found to modify various aspects of their own behaviour to be more similar to their new group mates (Herbert-Read *et al.*, 2013; King, Williams & Mettke-Hofmann, 2015; Schuett & Dall, 2009; Zürcher, Willems & Burkart, 2019). Furthermore, vocal convergence occurs in humans and other primates, in both the short and the long term (reviewed in Ruch, Zürcher & Burkart, 2018). In most cases, individuals introduced into a group modify their vocalisations to be more similar to the group that they have joined, with modifications made following a change in social context termed 'vocal accommodation' by Ruch *et al.* (2018). This suggests that when socially integrating or establishing connections with others is important, there may be evolutionarily conserved social drives to behave more similarly to others.

One field study hinted at a social motivation for conformity in wild non-human animals (van de Waal *et al.*, 2017). This work was based on long-term observation of wild vervet monkeys (*Chlorocebus pygerythrus*) following an experiment (van de Waal, Borgeaud & Whiten, 2013) that found conformity to food choices in dispersing males. In van de Waal *et al.* (2013), groups of monkeys acquired a preference for one colour of dyed maize (blue or pink) *via* training sessions in which one colour was rendered unpalatable. Following these training sessions, the maize was presented repeatedly, but without any bitter taste. Low-ranking females tended to eat both the groups' preferred (trained) colour and the previously unpalatable colour due to monopolisation of the former by more dominant group members (van de Waal *et al.*, 2017). Later, group fissions occurred, with six of these low-ranking females permanently leaving their home groups to form new groups. They were tested again in their new fission groups, and under these conditions universally returned to their originally trained group preference colour. This was despite direct individual experience that both colours of maize were equally palatable, and the fact that only one of the six adult females tested had ever directly tasted the maize when it was unpalatable (van de Waal *et al.*, 2017). This loyalty to the trained group preference therefore does not seem explicable *via* purely informational motivations, as individuals had already personally sampled information about the food (i.e. that both colours were equally palatable), and were tested within a familiar environment, as the fission groups occupied territory overlapping that of their original group. Rather, this finding suggests an ongoing social motivation to behave like the parent group (or perhaps like high-ranking members of the parent group). An alternative explanation could be the maladaptive application of informational conformity, although this would seem unusual in a context in which the vervets had little reason to be uncertain about the palatability of the foods.

When examining the possibility of an adaptive social function of conformity, it is important that our tests are capable of eliciting that motivation. Studies in the wild are ideal for this, as the pressures that would have shaped these phenomena should be present. Studies in the wild are increasingly

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revealing conformist behaviour in dispersing individuals, who have been found to match the foraging strategy, tool-material preference, and food preferences of their new groups (Aplin *et al.*, 2015; Luncz, Wittig & Boesch, 2015; Luncz *et al.*, 2018; Luncz & Boesch, 2014; van de Waal *et al.*, 2013). In these examples, individuals either had prior knowledge of alternative behaviours with equal or even higher value, which implies that the motivation to conform was not informational, or the adopted behaviour was highly arbitrary with no intrinsic functional value. However, none of these studies formally assessed a link between conformity to group preferences and social integration. So far, we only have two anecdotal cases. First, van de Waal *et al.* (2013) report anecdotally that the single male vervet monkey that did not change his food preference to match his new group after immigrating was aggressively forced out of the group soon after. This anecdote is to be treated with some caution, as there are no data provided on the integration success of the conforming males. It may be that the male's failure to conform in terms of food choice was symptomatic of a failure to conform to other group-typical behaviours (i.e. patterns of sociality and grooming reciprocity, Kerjean, van de Waal & Canteloup, 2024), leading to his expulsion, but of course it is possible that his failure to integrate successfully into the group was unrelated to his food choice. The second anecdotal study, in captive chimpanzees, links behaviour matching more clearly to social integration (Goldsborough *et al.*, 2021). Two female chimpanzees were introduced into a group that traditionally performed an apparently arbitrary behaviour – the 'cross-arm walk'. The authors report that one immigrant female immediately performed the cross-arm walk upon immigration, and the other did not (Goldsborough *et al.*, 2021). Subsequent analyses revealed that the immigrant who performed the behaviour became better socially integrated into the network of the group than did the other individual.

Experimental studies in captivity have also explored whether non-human primates conform to others, and whether such conformity may be socially motivated (Haun, Rekers & Tomasello, 2012, 2014; Vale *et al.*, 2017). Haun *et al.* (2012) found majority-biased transmission of a new behaviour in chimpanzees and children, but not orangutans (*Pongo pygmaeus*), while Haun *et al.* (2014) found conformity, involving switching from a previously learned behaviour to an alternative ('strong conformity'), in children, but not chimpanzees or orangutans. This led the authors to conclude that strong conformity is restricted to humans. Whilst these studies were carefully designed to target specific social learning strategies, Haun *et al.* (2014) may have failed to elicit underlying social motivations for strong conformity in the chimpanzees. Importantly, this experiment did not involve any overt social pressure on individuals to conform, as the participants were already members of the group. Because humans can participate in many different and diverse social groups, we may respond to social (or normative) pressure more readily and in more diverse situations than non-human primates. By contrast, social pressure may be more situationally constrained in animals, such as when immigrating into a new group, a situation when forming new social bonds is necessary. Therefore, similar experiments involving individuals that are new to a group are required to test for social conformity in non-humans. Vale *et al.* (2017) exploited the reorganisation of several groups of captive chimpanzees to test for conformity to food preferences, following van de Waal *et al.* (2013). This study did not find conformity of immigrants to the resident majorities' food preferences, but rather that both residents and immigrants sampled the food that they previously learned to dislike after observing their new group mates eat it (before reverting to their original preferences; Vale *et al.*, 2017). Here, too, a variety of factors which may promote conformity in wild dispersers were lacking, due to small group sizes and the age and sex of some immigrant individuals. In general, whilst controlled captive experiments have many benefits, it can be extremely hard to replicate the evolutionary pressures that may influence the behaviour of wild animals (for review, see Harrison & van de Waal, 2022).

Aside from dispersal, another life period in which individuals may rely on conformist transmission to acquire group-typical behaviour is juvenility. Studies of vocalisations in birds demonstrate that individuals show conformist tendencies when learning songs (Lachlan, Ratmann & Nowicki, 2018; Nelson & Poesel, 2014). Outside of the juvenile period, some cetaceans also demonstrate conformity in song; humpback whales (*Megaptera novaeangliae*) demonstrate a pattern of song revolutions, in which a population's song is rapidly replaced with a novel one, transmitted from neighbouring populations (Garland *et al.*, 2011). Critically, at any given time, males within a population conform to the same song pattern (Garland & McGregor, 2020). Unlike foraging techniques or food choice, vocalisations are inherently social signals, and thus their transmission has been studied more often with social functions in mind. In many cases, their function is argued to follow a different pathway than that proposed for conformist learning herein: songs are often subject to sexual selection, therefore having direct fitness implications, rather than impacting fitness indirectly *via* an individual's level of social integration (Williams *et al.*, 2022). While the cause of song change over time in humpback whales has been proposed to be sexual selection, with a preference for novel songs (Garland, Garrigue & Noad, 2021; Herman, 2017; McLoughlin *et al.*, 2018), the function of the apparent conformist bias in humpback song learning remains unclear (with the combination of a novelty bias with conformity to the current song termed 'constrained novelty'; Garland *et al.*, 2021). It has been suggested that song might serve to attract females to groups of males in a 'lekking' system, as well as attracting colonists to wintering grounds (Herman, 2017). In such cases, one might imagine that a conformist group chorus might be more functional than divergent individual songs. In birds, songs also serve as markers of group identity (Briefer *et al.*, 2008), facilitating territory defence, and, more closely linked to the argument put forward herein, shared songs may increase affiliation between individuals (Brown & Farabaugh, 1997).

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Whether apparent conformity in the wild actually relies on frequencies of behaviours in a group sampled by the learner is yet to be determined. This question has been subject to extensive debate (van Leeuwen *et al*., 2016; van Leeuwen & Haun, 2014; Whiten & van de Waal, 2016), which is heavily influenced by a cultural evolutionist view of conformity. It is based upon models that generally assume animals have access to complete information about the behaviour of their group with which to ascertain which behaviours are exhibited by a majority of group members [see Morgan, Acerbi & van Leeuwen (2019) and Nöbel *et al*. (2022) for further discussion]. The debate focuses largely upon the value of conformity in terms of accessing information about the environment. It is possible that individuals produce behaviours that are typical to the group after observing just a few individuals (Goldsborough *et al*., 2021; Watson *et al*., 2018*a*). This could appear to be a majority bias (Acerbi *et al*., 2016), and nonetheless result in positive social consequences such as increased affiliation from many group members, thus facilitating social integration. As Morgan *et al*. (2019) point out, individuals in social groups are not equally likely to be observed, with well-connected individuals being disproportionately influential, potentially causing a 'majority illusion' (Lerman, Yan & Wu, 2016), in which the behaviour of well-connected individuals is assumed to be the typical behaviour in a group. In terms of a social function of conformity, however, the effect of this majority illusion would potentially be beneficial, as behaving like well-connected individuals would increase an individual's chance of positive affiliative interactions with these core group members.

It is much harder in the wild to test the degree to which an individual attends to a majority, a single influential individual or simply the first individual observed (e.g. Goldsborough *et al*., 2021) before modifying their behaviour. Indeed, mechanisms such as imitation and rapid facial mimicry, as discussed above, do work at the dyadic level, so it may appear that dyadic-level processes are sufficient to result in 'conformity' (see Table 1). However, in several species, evidence does suggest that individuals frequently make decisions regarding where and when to move, and modify their behaviour, potentially in conflict with their individual needs, in accordance with the behaviour of a decisive majority (e.g. Lee & Teichroeb, 2016; Strandburg-Peshkin *et al*., 2015; Sueur, Deneubourg & Petit, 2010; Walker *et al*., 2017; see Conradt & Roper, 2003). Processes such as quorum sensing (Sumpter & Pratt, 2008) have been studied primarily as a mechanism allowing consensus in the context of group movement (Sueur, Petit & Deneubourg, 2009; Sueur *et al*., 2010), but may also allow individuals to identify and follow majority behaviours in social groups (Watson *et al*., 2018*a*; see Table 1). The cognitive mechanisms involved in coordinating movement and learning (socially) a new behaviour may differ (although see Heyes & Pearce, 2015), and it may be simpler visually to track group movements as opposed to attending to subtler variations in behaviour, which in the case of conformist learning of behaviours may involve sequential sampling of infrequent behaviours and recalling the individual identity of actors in order to assess the frequency of a behaviour within a social group. Studies of group movement and quorum sensing do, however, suggest that animals attend to and track the behaviour of multiple group mates, and respond to majority influences during day-to-day behaviours, with inherently social motivations related to being part of a group.

These mechanistic questions are crucial to our understanding of the population-level effects of conformist social transmission but a focus on them rather than the social

Table 1. Proposed social learning functions and mechanisms in non-human animals.

Enhanced fitness *via*:	Context	Level	Means	Mechanisms
Environmental information[1]	Ignorance[2], uncertainty[3]	Dyad	Homophily[4] or attention at a distance	Context-, content-, or frequency-dependent selection of model(s) and various social-learning mechanisms (from enhancement to emulation and imitation)
		Group	Conformity[5] – *informational*	Quorum sensing (or dyadic shortcut?)
Social integration	Immigration, maturational status change	Dyad	Homophily[4]	Behaviour matching through mimicry, rapid facial imitation[6] and prosocial acts
		Group	Conformity[5] – *social*	Quorum sensing (or dyadic shortcut?)
Normative uniformity	Cohesive groups with vital group-level tasks	Group	Conformity[5] – *normative*	Quorum sensing (or dyadic shortcut?) and sensitivity to risk of sanctioning by (other) group members

[1] Ecological: predation, parasites, food finding, coordination of movement.
[2] Usually immatures without learned skills.
[3] Usually adults in novel situations (e.g. after dispersal).
[4] Similarity-based association.
[5] Aligning behaviour with that of a group's majority, sometimes against previous preference.
[6] Homophily and behaviour matching may show bidirectional causality; both partners may show either or both, rather than learner towards model only.

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function of conformity to group-typical behaviours may leave us with an incomplete picture. Considering that potential social functions may provide insights regarding mechanism, alternative frameworks such as affective social learning [which proposes that learners assess the social relevance and value of behaviours by observing the affective expressions of others (Clément & Dukes, 2022; Gruber *et al.*, 2021; Gruber & Sievers, 2019)] may be usefully applied in concert with this approach. Equally, a focus on social functions could change our perspective on group behaviours. Consider the following sequence of events: group members are all feeding in the same patch, and new arrivals join them purely to remain with the group. These new arrivals then acquire information socially thanks to their proximity to group members. Both their choice of food patch and potential information acquisition could be interpreted as 'conforming' but would in fact arise as a by-product of other social behaviour.

VI. DIRECTIONS FOR FUTURE RESEARCH

We believe that exploration of the potential social benefits of conformity, and social learning more broadly, opens up multiple avenues of research in non-human animals. We propose that future studies should examine the extent to which conformity, and social learning more broadly, serves social or informational functions in non-humans (see Table 1). A key area in which evidence is lacking is studies directly linking behavioural conformity to increased fitness, *via* increased social integration. While we have presented evidence in this review that social learning that increases inter-individual similarity can promote affiliation (e.g. Paukner *et al.*, 2009), that inter-individual similarity promotes affiliation (e.g. Machado *et al.*, 2019), and that social integration has fitness benefits (e.g. Snyder-Mackler *et al.*, 2020), there is as yet no study empirically demonstrating this chain of causal effects. Individuals are likely to differ in their propensity for social information use (Watson *et al.*, 2018*b*), and therefore within a population some may benefit from social learning-facilitated integration to a greater extent than others. It is likely that the only context in which this could be demonstrated is *via* long-term field studies, potentially following individuals from dispersal (in order to examine the impact of social learning upon integration) and measuring their lifetime fitness in order to link social learning, integration, and fitness.

Further research should also explore whether informational and social motivations drive social learning in different contexts. What is the contribution of uncertainty to social learning in dispersing individuals? If social learning from, or conformity to, the new group is primarily socially motivated, any uncertainty about the ecological payoff of specific behaviours in the environment should have little impact – the potential social benefit will promote social learning even if the individual is highly certain that their existing knowledge is functional. Conversely, if informational motivations power social learning when integrating into a new group, relative uncertainty regarding payoff should influence the likelihood of social learning. Experiments could provide dispersing individuals with opportunities to learn socially from new group members and subsequently track their social integration. One could test immigrants' proclivity to conform in home-range overlaps with their previous group *versus* non-overlapping areas to manipulate their uncertainty (Fig. 2). Furthermore, detailed studies of splinter groups could identify to what extent they maintain behaviours from the parent group in a new territory where alternative behaviours might be more effective.

Additionally, researchers should consider the extent to which apparent conformity is majority-biased. Do dyadic social learning processes give rise to what appears as conformity; and, if learned behaviours are already typical in a group, will there be any detectable difference in (*i*) the speed of transmission, and (*ii*) affiliative outcomes? Careful planning of field, captive and modelling studies can target specific mechanisms of social learning and conformity.

Conformity (and social learning more broadly) serving a social function (increasing fitness *via* increased social integration) rather than an informational function (increased fitness *via* more accurate information about the ecological environment) may be most easily identifiable in species that demonstrate group-specific social customs. One example would be handclasp grooming (HCG) in chimpanzees (McGrew & Tutin, 1978), in which individuals raise one arm overhead and clasp their partner's hand, wrist or arm while grooming. Communities have been shown to differ in their preference for the specific style of HCG performed (McGrew *et al.*, 2001; van Leeuwen *et al.*, 2012, 2017), and recent research has shown that after performing a wider variety of styles when young, chimpanzees converge upon the existing preference of their group as they mature (van Leeuwen & Hoppitt, 2023) in a manner that is consistent with conformist learning. Beyond easily visible social customs such as HCG, it is possible that group-specific social dynamics [e.g. social tolerance (Cronin *et al.*, 2014), levels of grooming reciprocity (Kerjean *et al.*, 2024)] are acquired by immigrants after dispersal. Only long-term observational studies incorporating multiple groups will be able both to identify such group-specific social dynamics and to confirm whether immigrants who adopt them are able to become better integrated into the group in a manner which impacts their fitness.

While conformity with a social function may be most easily identifiable within the domain of social behaviour, it is also possible that conformity (and social learning more broadly) carries social benefits only in certain domains, with social behaviour being the most obvious. Within other behavioural domains, such as foraging, innovation, rather than social learning, may confer social benefits such as increased affiliation [as demonstrated by Kulahci, Ghazanfar & Rubenstein (2018), in which ring-tailed lemurs (*Lemur catta*) that solved an artifical foraging task received more affiliation from groupmates]. In humans, U.S. adults judged children who showed

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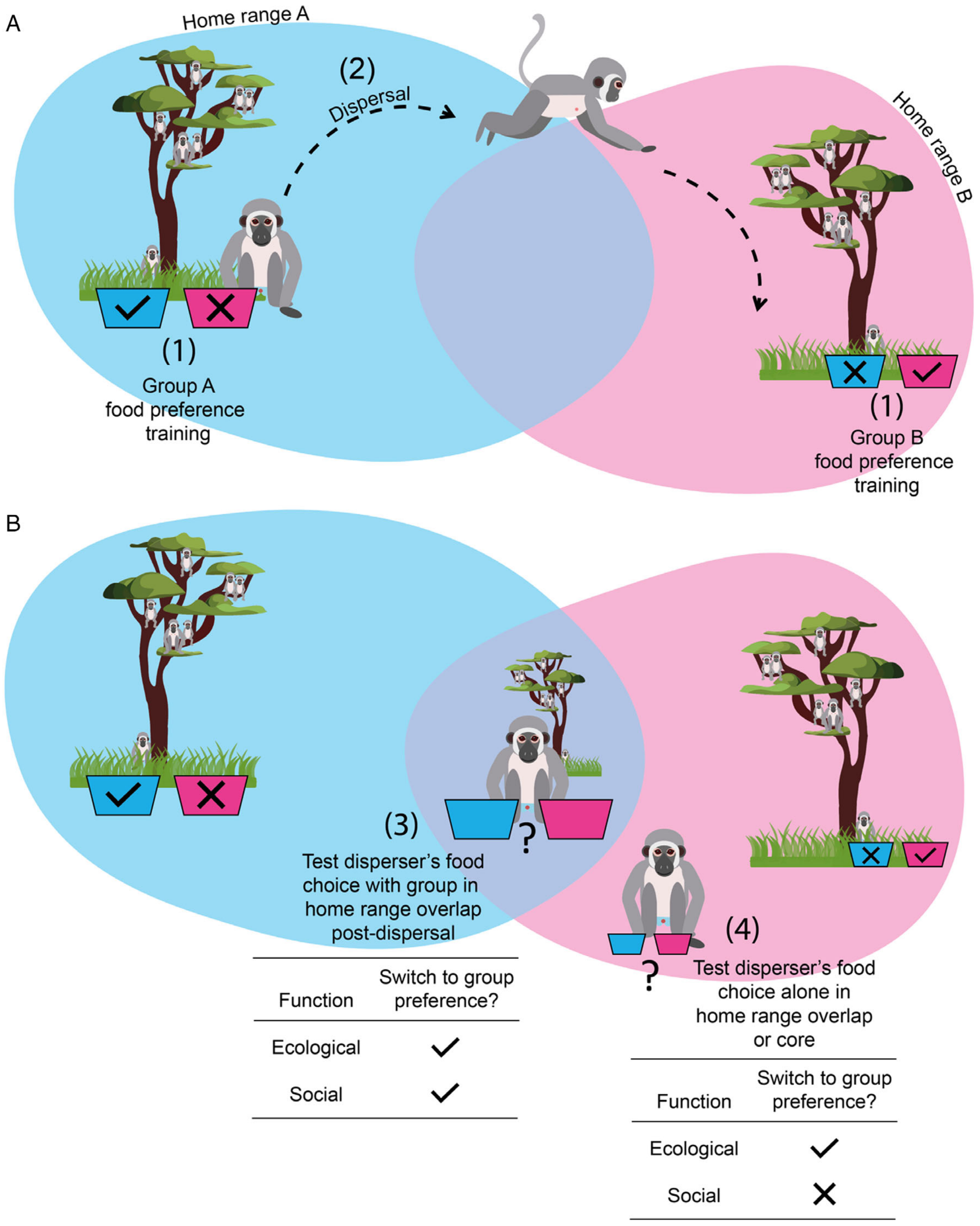

Function	Switch to group preference?
Ecological	✓
Social	✓

Function	Switch to group preference?
Ecological	✓
Social	✗

Fig. 2. A proposed experimental design to test for ecological *versus* social functions of conformity in dispersing primates, following van de Waal *et al.* (2013). An individual would be trained to hold one food preference in its natal group (A), before dispersing to a group with the opposite preference. After dispersal (B), the individual's food preference would be tested in a home range overlap area in the presence of its' new group, as well as being tested individually to test for the impact of an audience on its choice. Artwork courtesy of Chen Chi-Hsin.

low conformity to a demonstration when making a necklace as 'smarter' than children who showed high conformity (Clegg, Wen & Legare, 2017), suggesting that innovation may be rewarded more than conformist learning. However, this result varied culturally, with Ni-Vanuatu adults rating highly conformist children as more intelligent (Clegg *et al.*, 2017), and when children themselves were asked to rate peers, both Western (U.S.) and non-Western

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(Ni-Vanuatu) children rated conformist children as more intelligent (Wen, Clegg & Legare, 2019).

VII. CONCLUSIONS

(1) Evidence from both humans and non-human animals indicates that behaving similarly to others can have general social benefits, from facilitating group cohesion to social bonding, and new immigrants may use social learning to achieve behavioural similarity to others when forming new social bonds is important. Social learning may therefore serve both social and informational functions, and conformity is one mechanism that may allow animals to integrate into social groups. The distinction between informational and normative conformity arose within human psychology, with these alternatives seen as goals of the actor. This may have excluded serious consideration of possible alternative functions of conformity in non-human animals, resulting in assumptions regarding the adaptiveness of information. This may also have led evolutionary theorists to concentrate on majority-biased transmission as a central theme of conformity.

(2) Rather than taking a goal-oriented anthropocentric view of social learning, we propose to examine the informational or social functions of social learning *via* the potential benefits, including immediate social consequences as studied in the social psychology tradition. This offers more scope to pursue investigations into the potential social functions of not only conformity, but also of social learning more generally. Moreover, informational and social functions need not be mutually exclusive, and further research into the conditions that produce either will be beneficial.

(3) Finally, it remains unclear whether conformity that appears to be majority-biased social learning truly is majority-biased, or whether this appearance emerges through the copying of a few individuals that exhibit group-typical behaviour. Similar social benefits would arise in either situation. We propose that future research should probe the potential social functions of conformity, and social learning more broadly, in non-human animals. This topic will likely benefit from interdisciplinary approaches combining expertise from social psychologists, behavioural ecologists, and cultural evolutionists, in both theoretical and empirical research.

VIII. ACKNOWLEDGEMENTS

R. H., P. D., and E. v. d. W. were supported by the Swiss National Science Foundation (grant numbers PP03P3_170624 and PP00P3_198913) awarded to E. v. d. W. We are grateful to Chen Chi-Hsin for the vervet artwork featured in Figure 2. Open access funding provided by Universite de Lausanne.

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(*Received 9 May 2023; revised 5 April 2024; accepted 9 April 2024*)

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