Parochial altruism: What it is and why it varies

Anne C. Pisor^{1,2,*} and Cody T. Ross²

¹ Department of Anthropology, Washington State University, Pullman, WA 99164-4910, USA.

² Max Planck Institute for Evolutionary Anthropology, Dept. of Human Behavior, Ecology and Culture, Germany.

*Correspondence: anne_pisor@eva.mpg.de

ABSTRACT

Parochial altruism (PA), or in-group favoritism paired with out-group hostility, is sometimes treated as a synonym for human intergroup relations. However, empirical data suggest that PA is highly variable—across individuals, across situations, and across groups. Here, we review theory and data on PA to explore the candidate sources for this variability. Along the way, we unpack assumptions (e.g., what constitutes a group?), identify precursors to PA behavior (e.g., context and internal states), and review evidence for the pairing of in-group favoritism with out-group hostility. We discuss phenomena with measurable impact on downstream behavior, including resource access and cultural institutions, but also flag how researcher expectations and methodological design impact reported variability in PA. We close by making recommendations for how researchers can reduce noise in the study of PA by checking assumptions and being deliberate in research design; this is key, as the PA literature is part of sensitive public discourse.

Key words. cooperation, intergroup conflict, intergroup relations, parochialism, parochial altruism, sociality

Word counts: Abstract: 153. **Total:** 9103 (excluding references).

1. Introduction

Parochial altruism (PA), or in-group favoritism paired with out-group hostility (Choi & Bowles 2007), is assumed to be a central feature of human behavior—and is sometimes even treated as a synonym for human intergroup relations (Böhm et al. 2020). However, empirical evidence for PA has been mixed (Rusch 2014). What might explain this variability? On the one hand, we should expect the magnitude of PA to vary, sometimes substantially, as a function of the net benefits of in-group versus out-group cooperation (Pisor & Surbeck 2019; Aldering & Böhm 2020). These net benefits can be modulated by everything from resource competition between groups (Bell & Moya 2021; Ross & Pisor 2021; De Dreu et al. 2020), to cultural institutions that encourage (Fearon & Laitin 1996) or hinder (Phelan & Hunt 1998) social relationships with out-group members, to an individual's *perceptions* of the relevant costs and benefits of intergroup cooperation (Barth 1998; Riek et al. 2006; Brewer 2010). Such variability is consistent with a universal cognitive architecture that—at minimum—is prepared for group living and tracks the potential advantages of within and between group interactions (De Dreu et al. 2020; Tooby et al. 2006; Brewer & Caporael 2006).

On the other hand, some variation in PA may not reflect varied outputs of human cognition at all. Instead, some of this variation may be noise—e.g., generated by researcher assumptions about intergroup relationships, or by the subtleties of variation in methodological design. For example, by assuming that PA structures human social relationships, researchers may fail to examine: (i) the extent to which group membership actually constrains social relationships (Pisor & Ross 2022; Pisor & Surbeck 2019), (ii) whether what looks like in-group favoritism might be kin favoritism (Rusch 2014; Pievani 2011) or group defense (Delton & Krasnow 2017; De Dreu et al. 2020), or (iii) what even constitutes a ‘group’ in the context of the PA hypothesis (Yamagishi & Mifune 2016). Further, subtle differences in methodological design can have large impacts on empirical findings (Lightner et al. 2017), and many studies of PA do not incorporate measures of out-group hostility—which is half of the PA hypothesis (Rusch 2014; Yamagishi & Mifune 2016). In short, our understanding of PA as a feature of human sociality may benefit from “looking more carefully at the scope of human phenomena we seek to understand” (Barrett 2020).

Here, we conduct an interdisciplinary review of the empirics of PA. We begin by reviewing the history of the concept, and candidate explanations for the evolutionary history and developmental trajectory of PA in humans. We then unpack some of the considerations that we believe underlie the study of PA, including debates about what constitutes a group, the role of different precursors of PA behavior (like context and individual characteristics), and the assumption that in-group cooperation and between-group conflict are tightly linked. We first discuss how variation in precursors to PA behavior—including variation in resource access and cultural institutions—may produce variability in PA, and then turn to the role that variation in researcher expectations and methodological design may play in driving purported variation in PA. Key here is consideration of factors like sample selection, the relevance of particular economic games to measurement of PA, and the triangulation of findings across different data sources. We close by making recommendations for how researchers can reduce noise in the study of PA by checking their assumptions and being deliberate in their research design. Reducing noise, and thus improving our understanding of this feature of human sociality, is especially pressing given the influence of the PA hypothesis and related ideas—like the costs and benefits of diversity (Alesina & La Ferrara 2005)—in the policy sphere and public discourse.

2. The what and why of parochial altruism

Intergroup conflict in humans has long been a focus of research in the social sciences (e.g., Sumner 1906). However, authors disagree as to its nature and origins, and even its definition. In psychology alone, for example, some hold that in-group favoritism and out-group hostility are inseparable, while others argue that even in the presence of in-group favoritism, the ways in which individuals think about out-group members can vary from negative to positive (Sherif 1966; Levine & Campbell 1971; Buttelmann & Böhm 2014). In anthropology, debate about the origins of out-group hostility is often couched in larger conversations about warfare (Zefferman & Mathew 2015); scholars continue to debate whether out-group hostility was present in our last common ancestor with chimpanzees and bonobos, or whether it appeared more recently—perhaps as a product of sedentism or cultural transmission (Otterbein 1999; Wrangham & Glowacki 2012; Fry 2018; Lemoine et al. 2022; Glowacki 2022). Across these disciplines, definitions of PA can differ too. For example, while some authors specifically refer to in-group cooperation, others refer only to in-group favoritism (e.g., Rusch 2014); though the latter term often implies in-group generosity, the term is broad enough to include situations in which cooperation is costless (Bernhard et al. 2006). Given our goal of understanding variance in PA, we wish to be inclusive of the larger literature, and we thus refer to PA as in-group favoritism paired with out-group hostility—which can include aggression, competition, conflict, devaluation, ostracism, punishment, and xenophobia (Bowles & Gintis 2004; Bernhard et al. 2006; Hruschka & Henrich 2013; Yamagishi & Mifune 2016).

Within larger conversations about the nature of intergroup relations, a particular hypothesis emerged: that of parochial altruism (see de Dreu et al. 2014; De Dreu et al. 2022, for useful reviews). Research on PA was propelled in large part by theoretical publications by economist Sam Bowles and colleagues (Bowles & Gintis 2003, 2004; Choi & Bowles 2007), which aimed to explain the evolution of wide-spread cooperation among unrelated humans. According to this work, PA likely emerged as a product of group selection: the ancestors of contemporary *Homo sapiens* relied on

within-community cooperation—that is, cooperation among individuals who regularly live in proximity to one another (Rodseth et al. 1991)—to: (i) buffer the risk inherent in food procurement, and (ii) exclude other groups from accessing resources, especially where resources occurred in patches across the landscape (Choi & Bowles 2007). They argue that although in-group cooperation may have been costly to inclusive fitness, as it often benefited non-kin, it may have generated group-level benefits—namely, resource access and resource defense—sufficient to offset these costs (Choi & Bowles 2007). The combination of in-group cooperation and intergroup competition would have made groups containers for cooperation (see Boyd & Richerson 1985; Yamagishi & Kiyonari 2000) and potentially made individuals socially vigilant against out-group favoritism, as it could undermine in-group success (Tooby et al. 2006). That said, Choi & Bowles (2007) predict that the degree to which PA is expressed should reflect the local costs and benefits of intergroup connections—a distinction often absent in the citing literature. Bowles & Gintis (2004), for instance, demonstrate that groups can both have adaptations for parochial altruism and rely on intergroup trade relationships.

Today, the PA hypothesis is sometimes treated as a unifying explanation for the prevalence of intergroup conflict in humans. It has influenced a wide range of research on intergroup relations in the last two decades, to the point where some authors treat intergroup relations and PA as synonymous (Böhm et al. 2020). The inclusion of the tenets of PA in popular books (Seabright 2004; Greene 2013) and policy recommendations (Waring et al. 2015; Choi et al. 2019) has further broadened the scope of their influence. However, many central assumptions of the PA hypothesis remain implicit, and important questions remain. For example: is it reasonable to assume that there are psychological predispositions for PA, or is PA an emergent phenomenon, resulting from learning, enculturation, and other processes that highlight certain group identities? Which groups count as groups for the purposes of PA—families, kin groups, ethnic groups, religious groups, political groups, sport groups? When should we expect intergroup hostility versus intergroup tolerance versus intergroup cooperation? If people are members of multiple groups, how are joint allegiances managed?

2.1. The evolutionary history of parochial altruism

To address these questions, it helps to consider the phylogenetic context and potential evolutionary history of PA. In many social non-human primate species, in-group cooperation is associated with intergroup conflict. Conflict is often preceded or followed by grooming between group members, interpreted as in-group cooperation (see Lemoine et al. 2022, for a review). During intergroup conflict, individuals may participate in alliances, especially those structured by kinship or rank, to defend resources or females (Kitchen & Beehner 2007). In other words, in many non-human primate species, kin-selected behavior undergirds out-group hostility.

That said, evidence suggests PA involving non-kin and distant relatives in chimpanzees (Kitchen & Beehner 2007). Assuming that chimpanzees and bonobos offer an analogy for the last common ancestor shared by humans and the genus *Pan*—chimpanzees and bonobos—the presence of PA in chimpanzees and (to a lesser degree) in bonobos may suggest that PA has been part of the hominin lineage since its beginnings (Lemoine et al. 2022, though cf. Wrangham & Glowacki 2012). As in humans, however, the intensity of PA in chimpanzees and bonobos appears to be flexible, reflecting variation in the costs and benefits of intergroup aggression—for example, reduced resource competition may lead to less PA when resources are less patchy (Glowacki et al. 2020) and population density is lower (Lemoine et al. 2022).

For humans, dense living became more common at the end of the Pleistocene, perhaps as early as 130,000 years ago, and was often centered around patchy resources (Sterelny 2016a; Singh & Glowacki 2021). On the one hand, this may have increased the opportunity for intergroup conflict over resource access, perhaps increasing selection pressures favoring PA (Choi & Bowles 2007; Singh & Glowacki 2021). On the other hand, dense living likely created more opportunities for economies of scale in trade and production, simultaneously raising the costs of miscoordination between people with different norms (Singh & Glowacki 2021; see also Boyd & Richerson 2022; Glowacki 2022). In other words, tradeoffs between resource competition, gains to trade, and the cost of conflict may have modulated the intensity of PA, then as now (Barth 1998; Choi & Bowles 2007; Pisor & Surbeck 2019; Bell & Moya 2021). Use of ethnic markers may have proliferated in the late Pleistocene (Sterelny 2016a), supporting economies of scale in trade and production, helping learners identify from whom to learn cultural information, and reducing the costs of coordination (Barth 1998; McElreath et al. 2003; Smaldino 2019; Moya 2022; Derex & Mesoudi 2020; Dunbar 2008). The proliferation of ethnic markers may or may not have altered *Homo sapiens*' evolved psychology: if we were already skilled at identifying and reasoning about groups (Pietraszewski 2022), ethnic markers like linguistic cues and dress may have simply scaffolded our recognition of different groups (Moya 2022). In short, whether or not late-Pleistocene increases in population density and the abundance of demarcated groups changed selection pressures favoring PA (e.g., Choi & Bowles 2007) is an open question; flexible PA may have long predated the late Pleistocene (see Glowacki 2022; Singh & Glowacki 2021).

2.2. The developmental trajectory of parochial altruism

Limited evidence from educated, industrialized populations (in the sense of Henrich et al. 2010) suggests that PA may have a developmental trajectory similar to society-specific norms for sharing (e.g., House et al. 2013). Most of

these studies are based on the Dictator Game or similar experiments, where a decider makes an offer of something valued, like stickers or candy, and the recipient has no choice but to accept the offer. Recipients are identified by their group membership—for example, their classroom, or their minimal group (i.e., an experimental group identified by a sticker color)—and children can allocate the valued resource to in-group and/or out-group recipients. These studies reveal that older children tend to be more in-group favoring than younger children—that is, if they are given the choice between allocating to in-group versus out-group members, older children pick in-group members at higher rates (Benozio & Diesendruck 2015; Chiang & Wu 2015; Majolo & Maréchal 2017; Fehr et al. 2008). This may indicate convergence on society-specific norms, as adults in some of the societies studied (e.g., the United Kingdom and Taiwan; Chiang & Wu 2015; Majolo & Maréchal 2017) also exhibit in-group favoritism (e.g., toward co-nationals Romano et al. 2017). However, whether due to the design of these tasks, or to a lack of pronounced in-group favoritism in young children, the effect sizes are usually small (Fehr et al. 2008). Further, the degree of in-group favoritism appears sensitive to: (i) cues of intergroup competition (e.g., a tournament), which can amplify PA (Majolo & Maréchal 2017), (ii) amounts given by other in-group members to out-group members (invoking ideas around conformity and reputation management) (Chiang & Wu 2015), (iii) the framing of resources as “yours” versus “ours”, and (iv) child gender (Benozio & Diesendruck 2015).

In short, the limited evidence we have from educated, industrialized populations cannot clearly disambiguate between a universal tendency for children to exhibit more in-group favoritism with age and a convergence on local adult norms for cooperative behavior. What is clear is that in-group favoritism is often not pronounced and, when present, is flexible—i.e., sensitive to a variety of inputs.

2.3. What is a group?

In our overview thus far, we have reviewed PA among a variety of groups, including human and non-human primate communities, classrooms, and minimal groups created solely for experimental purposes. What counts as a group under the tenets of PA? In the evolutionary sciences, a “group” is frequently defined as a collection of individuals among whom fitness interests overlap (Tooby et al. 2006; Pisor & Surbeck 2019) or whose outcomes are otherwise interdependent (Böhm et al. 2020). Pietraszewski (2022) gives an in-depth discussion of the term. Although groups of any size can have overlapping fitness interests (Richerson & Boyd 2008), ethnic groups are often treated as the default group in the PA literature from anthropology and adjacent fields (e.g., Choi & Bowles 2007). “Ethnicity” in this context refers to people who identify as members of a group with shared cultural institutions¹ (Barth 1956, 1998; McElreath et al. 2003; Moya & Boyd 2015; Moya 2022)—i.e., norms, rules, or laws that help individuals coordinate for mutual benefit (Glowacki 2020; North 1991). Shared cultural institutions, in turn, can generate or amplify overlapping fitness interests (Richerson et al. 2016), which can attract more group members (De Dreu et al. 2020). That said, ethnic phenomena, including group markers and shared cultural institutions, are also present in non-ethnic groups (Moya 2022); the preoccupation with ethnic groups in the literature may reflect an anthropological preoccupation with culture (Rodseth & Wrangham 2004).

Indeed, focusing too narrowly on how groups like ethnic groups structure in-group favoritism and out-group hostility can impact our ability to address broader questions, such as whether groups of all kinds structure PA (Moya 2022; Brewer & Campbell 1976; Bell & Moya 2021; Kurzban et al. 2001; Böhm et al. 2020; Rodseth & Wrangham 2004). Indeed, PA has been observed among everything from minimal groups (Yamagishi & Mifune 2016) to world religions (Purzycki et al. 2016) and nation states (Greene 2013; Romano et al. 2021). However, not all groups lend themselves to groupish, in-group-favoring behavior (Moya 2022). For example, though some authors treat bands as groups among mobile foragers (Bowles & Gintis 2003; Brewer & Caporael 2006; Glowacki 2022), rates of PA in these contexts appear to be low, as tensions are often diffused when individuals move between bands (Knauff 1991; Rodseth & Wrangham 2004; Layton et al. 2012). Even in groups that lend themselves to in-group favoritism, however, group identity alone is typically insufficient to generate PA (e.g., Brewer & Caporael 2006); other factors—such as incentives for intergroup competition, institutions promoting intergroup hostility, and cycles of retribution—are frequently implicated.

2.4. Internal states or behavior?

When discussing the PA hypothesis, researchers at times fail to separate internal states from behavior, though distinguishing the two can be important—for both theory and policy. Depending on the discipline and intellectual tradition, internal states may be called “motivations,” “preferences,” “beliefs,” “attitudes,” “dispositions,” or “sentiments;” these terms often appear in the literature on the evolution of cooperation (e.g., “other-regarding preferences”, “prosocial preferences”, “prosocial motivations;” Kappeler & Silk 2010). Internal states are generally assumed to guide behavior, as shown in Figure 1 by the path labeled *E* (Strauss 1992; Gervais & Fessler 2017; Guala 2019; Tooby et al. 2006). Behavior is not just the direct output of internal states, however, but is also affected directly and indirectly by individual

¹ This definition of ethnicity is limited, of course, not reflecting the usage of the word in other literatures or outside of academia; see Jenkins (1994) for a discussion.

Fig. 1: A simplified model of precursors to PA behavior, per our review of the literature. For other discussions urging distinction between different components of this system, see [de Dreu \(2010\)](#); [Pisor et al. \(2020\)](#). Note that the resemblance between our schematic and the Situation Construal Model ([Funder 2016](#)) is coincidence, though some of the ideas are similar.

characteristics—such as features of personality, or an individual’s past experiences—that some authors call “chronic individual differences” ([de Dreu 2010](#)) (see Figure 1, paths F, C-E, A-D, and A-B-E). Further, context or “structure” ([De Dreu & Gross 2019](#))—such as local cultural institutions and features of the local ecology—can impact behavior directly (Figure 1, path D) or indirectly (Figure 1, paths B-E, A-C-E, or A-F).

Context, individual characteristics, internal states, and behavior all often appear in discussions of PA, whether explicitly or implicitly. For example, cultural institutions may preclude PA behavior by: (i) removing opportunities for its expression (Figure 1, D), or (ii) by changing an individual’s beliefs about the punishment they will incur if they either engage in PA behavior or, alternatively, do *not* engage in it (Figure 1, B-E; [Fearon & Laitin 1996](#); [Abbink et al. 2012](#)). Individual characteristics may impact PA behavior directly—e.g., if low income affects an individual’s ability to reciprocate generosity, or invest in hostility (Figure 1, F; e.g., [Pisor et al. 2020](#))—or indirectly, by changing individuals’ context-dependent beliefs—e.g., about the intentions of out-group members in contexts of competition (Figure 1, A-B-E; [Thielmann et al. 2020](#); [De Dreu et al. 2020](#)). Importantly, economic experiments, which we will explore below, are usually designed to isolate and measure internal states, though they do so through the proxy of behavior ([Guala 2008](#); [Guala & Mittone 2010](#); [Thielmann et al. 2021](#)); likewise, social value orientation and welfare trade-off ratios rely on behavior to infer internal states, as they are the presumed to be the product of individual characteristics and context ([Delton et al. 2023](#); [Murphy et al. 2011](#)). On the other hand, observational data are often better measures of behavior—and survey data of reported behavior—in and of itself ([Pisor et al. 2020](#)).

With respect to internal states, researchers often treat PA as the human default, such that tolerance of or even cooperation with out-group members results only from an override of internal states favoring PA (e.g., [Clark et al. 2019](#)); in other words, researchers often treat internal states as relatively invariant to inputs from context and individual characteristics (Figure 1). Whether an override is what generates variability in PA, however, is an open question ([Levine & Campbell 1971](#)). The wide range of variability in PA uncovered in archaeological ([Sterelny 2016b](#)), ethnographic ([Pisor & Ross 2022](#); [Cashdan 2001](#)), genetic ([Dyble 2021](#)), experimental ([Yamagishi & Mifune 2016](#); [Columbus et al. 2023](#); [De Dreu et al. 2020](#)), and survey data ([Brewer & Campbell 1976](#)) problematizes the concept of a default hostility towards out-groups. Additional research is needed to identify whether internal states favoring PA are a human default; further developmental studies outside of industrialized and educated contexts will be key.

2.5. Strong PA, weak PA, and intergroup tolerance

Though the PA hypothesis suggests that in-group favoritism and out-group hostility are likely to occur together, they are often decoupled in empirical contexts. Compelling data indicate that high levels of in-group favoritism occur even in the absence of out-group hostility (e.g., [Purzycki & Lang 2019](#); [Hruschka & Henrich 2013](#); [Yamagishi & Mifune 2016](#); [Brewer & Caporael 2006](#); [Schaub 2017](#); [Cashdan 2001](#); [Rusch 2014](#); [de Dreu et al. 2014](#); [Böhm et al. 2020](#); [Balliet et al. 2014](#); [Abbink et al. 2012](#); [De Dreu et al. 2020](#); [Columbus et al. 2023](#)). Indeed, while intergroup competition can certainly stabilize within-group cooperation ([Choi & Bowles 2007](#)), some suggest that the conditions under which these two phenomena become linked may be narrow² ([Dyble 2021](#)). This largely reflects the conclusions of those who research coalitional psychology: coalitional identity undergirds within-coalition cooperation in humans ([Redhead & von Rueden 2021](#); [Pietraszewski 2022](#); [Tooby et al. 2006](#)), but coalitions can change across circumstances. Between-coalition conflict can strengthen within-coalition cooperation, but when and whether coalitions mobilize against one another is a separate question ([Tooby et al. 2006](#); [Leech & Cronk 2017](#)).

² Note that in their influential simulation, [Choi & Bowles \(2007\)](#) allowed parochialism and in-group altruism to evolve independently, never suggesting they *had* to be coupled. Rather, they show that specific selective processes can lead to the two becoming linked. They underscore, however, that this linkage should be assessed with empirical data—and it is the empirical data which suggest that in-group favoritism and out-group hostility are often not linked.

As such, to discuss the when and why of PA, we must distinguish “weak” from “strong” PA—and thus intergroup tolerance from intergroup hostility. When in-group favoritism occurs in the absence of out-group hostility, we may refer to it as “weak PA” (Böhm et al. 2020) or not refer to it as PA at all, as in-group favoritism is so common. “Weak PA” implies intergroup tolerance—for example, when human or non-human primate groups come into contact and effectively ignore each other (Pisor & Surbeck 2019), or when peace systems (Glowacki 2022; Fearon & Laitin 1996) or complementarities (e.g., via trade and markets; Jha 2013; Schaub 2017) promote tolerance in humans. Intergroup tolerance can provide a basis for intergroup relationships in turn, especially if interactions with out-group members generate net benefits for both parties (Pisor & Surbeck 2019; Columbus et al. 2023). Unlike “weak PA,” “strong PA” involves the explicit coupling of in-group favoritism and out-group hostility; the literature reviewed above suggests that strong PA is less common than weak PA (Böhm et al. 2020).

3. What can explain the variability in parochial altruism?

Scholars largely agree that PA varies in humans (Rusch 2014; Baldassarri & Abascal 2020) due to variation in the relevant costs and benefits to intergroup hostility across contexts (e.g., Romano et al. 2017; Lang et al. 2019; Pisor & Ross 2022) and across individuals (e.g., Bogaert et al. 2008; Thielmann et al. 2020). However, our literature review suggests that some of the purported variation in PA may be a product of variation in researcher expectations and methodological practices. Here, we expand on how variation in the affordances of PA, researcher expectations, and methodology can each impact our understanding of PA—and, in turn, our characterizations of human sociality more broadly.

3.1. Variation in the affordances of parochial altruism

There are three common explanations for variation in the relative costs and benefits of PA³. All of these focus on out-group hostility, as in-group favoritism is often present even in the absence of out-group hostility (see our review above and Böhm et al. 2020). The first two explanations pertain to context and the third to individual characteristics (per Figure 1):

1. *Variation in incentives for intergroup competition over something limited, like resource access.* As argued by Bowles and colleagues, competition over resource access in the human evolutionary past may have selected for internal states that are precursors to PA behavior (Choi & Bowles 2007; Bowles 2008). The literatures on intergroup threat and intergroup conflict in psychology likewise find a relationship between defensible, limited resources and intergroup competition (Böhm et al. 2020; Brewer 2010; Riek et al. 2006). Of course, not all human ecologies feature defensible resources or high demand for limited resources; this means that there should be geographic variation in the affordances of PA (Bell & Moya 2021). However, when competition over limited resources is in play, a group’s size, competitive ability, and power become relevant to its success in competition over resources (Ellemers et al. 1999; Fiske et al. 2016; Richerson et al. 2016). Success changes a group’s status relative to other groups, influencing the desirability of group membership (Waring 2012; Waring & Bell 2013; De Dreu et al. 2020; Richerson et al. 2016). Groups that attract more members require more resources; this means that even fewer resources will be available to out-group members, which can stimulate further competition (De Dreu et al. 2020). That said, when the status gap between groups grows, it can impact behavior in unexpected ways; for example, it is sometimes found that if members of a high-status group do not perceive members of a low-status group to be competitors, they may be magnanimous toward them (Hewstone et al. 2002).
2. *Cultural institutions, or their absence.* When individuals share the same norms for proper behavior (e.g., in markets or collective actions), the costs of coordination are reduced (Barth 1998; McElreath et al. 2003; Bunce & McElreath 2018; Moya & Boyd 2015; Ensminger 1997; Bell & Moya 2021; Moya 2022). These norms often emerge endogenously—for example, when between-group mobility is low, a high likelihood of repeated interactions with in-group members may mean that individuals pay more attention to in-group generosity, which may make in-group favoritism normative (Roberts 2007; Yamagishi & Kiyonari 2000). Cultural institutions can enforce and spread shared norms (e.g., McElreath et al. 2003), and such institutions may be maintained by the individual-level benefits of improved coordination⁴ (Habyarimana et al. 2007; Mantilla et al. 2021). However, if there are net benefits to be gained by avoiding conflict (intergroup tolerance), or even by coordinating across group boundaries (intergroup relationships): (i) institutions may emerge that punish individuals who generate costs for out-group members (Fearon & Laitin 1996; Fry 2018; Pisor & Surbeck 2019), (ii) individuals might seek competency in the norms of other groups in order to lower the costs of coordination (Ruben 1989; Bunce 2020), and (iii) institutions may emerge that support connections across group boundaries, such as through marriage, trade, and ritualized relationships (Bollig 2010; Jackson 1983; Jha 2013).

³ Importantly, this list is not exhaustive. For some additional examples, see De Dreu et al. (2022)

⁴ Note that researchers disagree over whether norms and institutions appear, persist, and spread because they generate individual-level or group-level benefits, or both (see Purzycki 2020, for discussion).

3. *Positively-valenced exposure to out-groups can expand loyalties; negatively-valenced exposure can enhance parochial altruism.* When individuals are exposed to out-group members—either directly, through face-to-face interactions, or indirectly, via information transmission from others—they may develop additional loyalties and become less willing to favor individuals of their own group. This is assuming, however, that exposure to out-group members is positively valenced or generates net benefits for the individual. There are various explanations for how positively-valenced exposure translates into expanded loyalties, from identity fusion to the strategic building of social capital (Brewer & Campbell 1976; Beck 2006; Buchan et al. 2009; Fukuyama 2001; Hruschka & Henrich 2013; Mau et al. 2008; Singer 1981). These explanations imply that positively-valenced exposure increases the value individuals place on out-group members, either as beings (Singer 1981) or, more specifically, as potential social partners (Pisor & Gurven 2015). On the other hand, when exposure to an out-group is negatively valenced—for example, when individuals have experienced civil war (Schaub 2017) or discrimination (Waring & Bell 2013; Pisor & Gurven 2018)—individuals may update their beliefs about the potential net benefits of interacting with out-group members; in other words, a change in their individual characteristics may change their internal state. In such contexts, internal states that promote in-group favoritism may increase an individual’s chance of obtaining net benefits (Yamagishi & Kiyonari 2000).

These three explanations—competition, institutions, and exposure—are not mutually exclusive. For example, differences in pro-self and pro-social behavior as measured by social value orientation (Messick & McClintock 1968) may reflect internal states (though cf. de Dreu 2010), which integrate context and individual characteristics (Figure 1). Indeed, a person’s social value orientation appears to be a product of gene expression plus past experiences (Bogaert et al. 2008), incentives for competition (e.g., degree of capitalism), and enculturation to local norms (Shahrier et al. 2016). Social value orientation is sometimes predictive of favoritism, especially in-group favoritism, although not out-group hostility (Romano et al. 2017; de Dreu 2010; Columbus et al. 2023).

In short, competition, institutions, and exposure all generate variation in the benefits and costs of intergroup competition and intergroup relationships—namely, by affecting whether the expected affordances of within-group interactions are greater than those of between-group interactions. We should expect that the minds of *Homo sapiens* attend to the pros and cons of various social relationships; between-group connections are no exception (Brewer & Campbell 1976; Waring & Bell 2013; Pisor & Gurven 2018). However, few researchers explicitly address whether any of the explanations above are alone sufficient to account for observed variation in PA (for examples of those that do, see: Hruschka & Henrich 2013; Vardy & Atkinson 2019; Levine & Campbell 1971).

3.2. Researcher expectations about parochial altruism

While competition, institutions, and exposure are common explanations for why the intensity of PA may vary, researcher expectations may also impact reported levels of PA. For example, researchers may:

1. *Select study sites in areas where intergroup relations are characterized by conflict.* Fearon & Laitin (1996) note that much of the research on intergroup relations focuses on cases of between-group conflict, essentially selecting on the dependent variable and making such conflict seem ubiquitous: “violence is assumed to follow ethnic tensions as night follows day” [p. 716]. “The salience and extremity of intergroup hostility” to researchers can thus lead to a literature in which “the study of intergroup relations is equivalent to the study of intergroup conflict” (Brewer 2010, p. 535). Our point here is not that intergroup conflict is rare, but rather that human flexibility is not to be understated. At very least, while there are many instances of intergroup contact in humans, the fraction of these instances where conflict actually *occurs* is much smaller (Fearon & Laitin 1996). As such, we cannot gain an unbiased understanding of how and why PA varies in humans if the literature focuses only on a highly selective subset of humanity (Pisor & Surbeck 2019; Sherif 1966; Barrett 2020).
2. *Conflate generalized cooperation with cooperation targeted toward in-group members.* Silva & Mace (2014) argue that unless we assess which groups matter the most to participants, we may mean to measure in-group favoritism but instead capture a willingness to cooperate with most others—a “generalized” preference for cooperation sometimes associated with the concept of generalized trust (Nannestad 2008; Yamagishi 2011). As such, collecting social network data that include the group identities of each person, as well as their favoritism and hostility toward each other, can improve our understanding of how group identities structure cooperation (e.g., Moya 2022).
3. *Conflate PA with motivations to protect valued social partners, who are often in-group members.* According to this argument, because most social relationships are with members of the same group, “what may look on the surface like the selfless defense of in-group interests, may instead be the message ‘don’t tread on me and mine’” (Delton & Krasnow 2017, p. 741).
4. *Accidentally label variation in some other feature of human sociality as variation in PA.* For example, both PA and nepotism entail favoritism toward certain individuals—in-group members or kin (Rusch 2014; Pievani 2011). If there are enough kin in one’s in-group, then behaviors that benefit kin—like not closely monitoring who did what for whom (Sahlins 1972)—could benefit in-group members as a byproduct (Rusch 2014). Or, taking another example from our own work (Pisor & Ross 2022), if different groups live in different ecological areas, then preferences

for long-distance relationships that span ecozones could look like preferences for intergroup relationships—even if the fact that such relationships span group boundaries is causally immaterial (e.g., Barth 1956; Pisor & Ross 2022).

Of course, not all work on PA is affected by the researcher expectations outlined above—these are merely generalized critiques voiced by researchers of intergroup relations. That said, expectations can certainly guide what research questions are asked and how researchers interpret their data (Barrett 2020). If we expect PA to be a defining feature of human sociality, we may interpret a variety of data as evidence for or against PA, rather than considering other, sometimes more parsimonious, explanations.

3.3. *Measuring parochial altruism*

Depending on a given researcher's inferential objectives, PA may be measured in a variety of ways. In some cases, researchers use self-report data, experimental economic games, social discounting tasks, and social network data to measure PA. In other cases, researchers infer PA from patterns in aggregate, ecological-level data. As mentioned before with respect to researcher expectations, variation in methodological design can have noteworthy impacts on inferences about PA and related phenomena.

3.3.1. Economic games

Experimental economic games are perhaps the most commonly used tool for assessing PA, and researchers usually consider such games to be a measure of internal states (e.g., Guala 2008; Guala & Mittone 2010; Thielmann et al. 2021). In economic games, participants make decisions that affect the amount of currency received by other individuals—referred to variously as alters or recipients, and who are usually anonymous. For example, in a classic game called the Dictator Game, the decider makes an offer and the alter has no choice but to accept it, while in the Prisoner's Dilemma, a decider and an alter each have to independently choose whether to cooperate or defect, and their decisions jointly determine the payouts they each receive. Although classic games like the Dictator Game and Prisoner's Dilemma have been frequently used to study PA, unless their designs are substantially modified, they do not allow researchers to measure the coupling of in-group favoritism and out-group hostility as predicted by strong PA (Rusch 2014; Yamagishi & Mifune 2016). As discussed in Section 2.2, they more readily measure in-group or out-group favoritism—that is, weak PA. We review these classic games, and other methods that do not measure out-group hostility, in the first six rows of Table 1.

Game designs that either compare in-group favoritism with out-group hostility, or make it such that in-group favoritism generates out-group hostility as a byproduct, are better suited to measure strong PA. One important game in the literature is the intergroup prisoner's dilemma—maximizing difference (IPD-MD) game (e.g., Böhm et al. 2022; Columbus et al. 2023; de Dreu 2010). The IPD-MD allows weak PA to be decoupled from strong PA, such that participants can favor in-group members with or without expressing hostility toward out-group members. The intergroup parochial and universal cooperation (IPUC) game is a nested dilemma that extends the IPD-MD, allowing individuals to engage in ingroup favoritism (weak PA), ingroup favoritism paired with outgroup hostility (strong PA), or favoritism toward both ingroup and outgroup (universal cooperation) (Aaldering & Böhm 2020; De Dreu et al. 2020), addressing concerns that what looks like in-group favoritism may be universal cooperation in some cases (Silva & Mace 2014).

A particular strength of economic games is that they can offer high internal validity and allow for experimental manipulations (Pisor et al. 2020). A researcher can, for example, manipulate relevant group identities by changing the composition of an experimental group (e.g., Silva & Mace 2014) or by changing or obscuring the group identity of a potential recipient (e.g., Romano et al. 2017). This allows researchers to test for differences in favoritism or hostility as a function of the manipulated variable. However, the external and ecological validity of experimental games has been called into question, with experimental behavior in games often having little association with relevant behavior in the “real world” (e.g., Gurven & Winking 2008; Winking & Mizer 2013; Galizzi & Navarro-Martinez 2019; Naar 2020). Similarly, test-retest reliability in games is often low (Chuang & Schechter 2015), behavior is often not consistent across games that should tap similar constructs (Lönngqvist et al. 2015; Naar 2020) unless all games are framed as being about the same thing (Yamagishi et al. 2013; Lightner et al. 2017), and respondents, especially non-numerate ones, might be confused by peculiar or complicated game rules (Dave et al. 2010; Cook 2015). Taken together, these observations underscore the sensitivity of experimental findings to minute features of design (Hagen & Hammerstein 2006). Moreover, by generally focusing on the effect of only a single variable (e.g., the group identity of a potential recipient), experimental approaches often fail to account for how people—in real-world scenarios—weight behavior in light of a plethora of competing heuristics, some of which are highlighted in Figure 1 (e.g., Gurven & Winking 2008; Winking & Mizer 2013; Naar 2020). For example, an individual's internal state might motivate them to favor both in-group individuals and individuals who are most in need (e.g., Hewstone et al. 2002). The latter consideration might overwhelm the former in some contexts, and so—if out-group members happen to be more in-need—economic game play might suggest internal states consistent with PA, while real-world behavior (in the same set of individuals) might suggest no PA, or even elevated cooperation directed to out-group members (Pisor et al. 2020).

Table 1: A summary of tools used to study parochial altruism and its causes and consequences. The first section of the table focuses on approaches in which researchers can select the group identity of the alter(s). The second section focuses on tools that measure the relationship between context and PA behavior outside of the laboratory. The third section focuses on network-based tools that attempt to bridge the gap between the control of the laboratory and the ecological validity of studies of real-world behavior. For other helpful summaries of existing economic experiments, see [Thielmann et al. \(2021\)](#) for a general overview, and [Böhm et al. \(2020\)](#) for one specific to intergroup relations.

Method	Design	Pros	Cons	Citation
Dictator Game (DG)	Of endowment X, decider chooses to offer Y to alter; alter cannot respond	Potential proxy for favoritism toward a single target, whether ingroup or outgroup	Does not measure hostility (i.e., cannot measure strong PA); may better measure fairness than favoritism	(Guala & Mittone 2010)
Ultimatum Game (UG)	Of endowment X, decider chooses to offer Y to alter; alter can accept, with decider getting X-Y and alter getting Y, or reject with both getting nothing	Potential proxy for favoritism toward a single target, whether ingroup or outgroup	Does not measure hostility; does not distinguish between preferences and strategy (i.e., internal states and context)	(Gil-White 2004)
Prisoner's Dilemma (PD)	Two parties simultaneously decide whether to cooperate or defect, with payouts $DC > CC > DD > CD$	Potential proxy for favoritism toward a single target, whether ingroup or outgroup	Does not measure hostility; does not distinguish between preferences and strategy (i.e., internal states and context)	(Romano et al. 2021)
Public Goods Game (PGG)	In experimental groups of 3+ participants, deciders decide how much to contribute to a common pool, which is multiplied and redistributed; when used to study PA, experimental group composition is typically manipulated	Potential proxy for favoritism toward in-group and/or out-group targets	Does not measure hostility; does not distinguish between preferences and strategy (i.e., internal states and context)	(Schaub 2017)
Social Value Orientation (SVO) Slider Measure	Decider makes decisions about how much money they would like for self and anonymous other (in-group, out-group, or unspecified); decisions triangulate decider's social orientation type	Can measure pro-social orientation toward both in-group and out-group alters	Does not measure hostility	(Columbus et al. 2023)
Resource Allocation Game (RAG)	Decider makes series of die rolls and, given how die lands, is to put coins in cups for the self or an in-group or out-group recipient; deviations from fair divisions at population level are interpreted as favoritism	Measures deciders' willingness to be fair and avoid in-group favoritism and/or selfishness	Does not measure hostility; difficult to make individual-level inferences about internal states	(Lang et al. 2019)
Intergroup Prisoner's Dilemma—Maximizing Difference (IPD-MD)	Decider can give to one of two pools—in-group benefitting and in-group benefitting at outgroup cost—and/or keep money	Differentiates in-group favoritism from ingroup favoritism paired with outgroup hostility (that is, weak PA from strong PA)	Does not measure out-group favoritism	(Halevy et al. 2008)
Intergroup Parochial and Universal Cooperation Game (IPUC)	Decider can contribute to three pools—in-group benefitting, in-group benefitting at outgroup cost, and in-group and out-group benefitting—and/or keep money	Differentiates in-group favoritism from in-group favoritism paired with outgroup hostility from “universal cooperation”	The ecological validity of this method, like all experimental measures above, is questionable	(Aaldering & Böhm 2020)
Ethnolinguistic fractionalization (ELF)	Measures the extent of ethnic (or other type of group identity) diversity at a specific level of resolution (e.g., county) and associates it with other aggregate variables, like rates of public goods contributions or rates of between group violence	Measures ecologically valid behavior outside of an experimental context and links it to diversity in group composition at some aggregate level of resolution	Does not reveal much about individual-level internal states; lacks experimental control; analyses are sensitive to confounding and the ecological regression fallacy	(Alesina et al. 2003)
Indices of ethnic competition (ECI) and demographic disadvantage (DDI)	Measures the extent of scope for ethnic (or other type of group identity) competition at a specific level of resolution (e.g., county) and associates it with other aggregate variables, like rates of public goods contributions or rates of between group violence	Measures ecologically valid behavior outside of an experimental context and links its to demographic indices that are purported precursors of PA	Does not reveal much about individual-level, internal states; lacks experimental control; analyses are sensitive to confounding and the ecological regression fallacy	(Slack & Doyon 2001)
Social Network Analysis (SNA)	Uses measured characteristics of individuals combined with reports of positive or negative ties to analyze how individual, dyadic, and network characteristics predict behavior	Measures reported or observed behavior outside of the experimental context	Time-consuming to collect; may or may not reveal internal states; sensitive to typical biases affecting any self-reported data	(Pisor et al. 2020)
Recipient Identity-Conditioned Games (RICH)	Respondents are presented with photos of known alters and complete three tasks: allocating coins to alters, removing coins from alters, and paying to punish alters	Proxies internal states given context and individual characteristics of decider and alter	Does not involve experimental manipulation of group identity variables, so the causal effect of group identity can only be recovered if appropriate controls are included	(Gervais 2017)

3.3.2. Aggregate-level studies

If PA has appreciable effects on real-world behavior, the consequences of PA should be detectable in aggregate-level (e.g., county-level) indices of in-group favoritism (i.e., in rates of public goods provisioning) and out-group hostility (e.g., in rates of inter-ethnic violence). Thus, in an effort to test if laboratory findings generalize more widely, researchers have studied aggregate-level outcomes to infer the presence, causes, and consequences of PA (see Table 1, second section). Many of these studies focus on the role of context, especially on variation in incentives for intergroup competition over limited resources—often exacerbated when group size is increasing and groups see one another as competitors (e.g., [De Dreu et al. 2020](#); [Hewstone et al. 2002](#)) [Alesina et al. \(1999\)](#), for example, used aggregate demographic data to show that, at a community level, white Americans appeared to decrease investment in public programs on average as ethnic diversity increased. Similarly, [Slack & Doyon \(2001\)](#) applied event history analysis to war crimes data from the former Yugoslavia (1990-1993) and found that civilian-involved acts of violence—mostly Bosnian Serbs harming Bosniak Muslims—were more likely to occur in areas with higher “indices of ethnic competition”—that is, in areas where Serbs and Muslims had similar population sizes—and in areas where the Muslim population was experiencing higher growth relative to the Serb population. Using similar methods, other empirical work has since explored the effects of inequality across ethnic groups on outcomes potentially indicative of in-group favoritism and out-group hostility, such as public goods provisioning, economic performance, and conflict rates (e.g., [Alesina et al. 2016](#)).

A strength of these empirical studies is that they explore the potential real-world consequences of PA, testing both whether group identity structures behavior and how the intensity of in-group cooperation and out-group hostility vary as a function of differences in context. However, weaknesses of these aggregate-level methods is that they lack experimental control and are thus highly sensitive to both confounding variables and the ecological regression fallacy. For example, they may assume ethnic groups are the most relevant and salient to intergroup relations (Section 2.3); focus on areas with recent conflict, selecting on the dependent variable (Section 3.2); and aggregate across higher-order units, such as villages, regions, or nations, such the associations that are observed *across* units may not reflect causal relationships that occur *within* units (see [Freedman 1999](#)).

3.3.3. Integrative, network-based methods

All methods come with trade-offs between internal and external validity. Economic games applied to the topic of PA are thought to afford high internal validity by permitting experimental manipulation of group membership ([Yamagishi & Kiyonari 2000](#); [Waring & Bell 2013](#); [Yamagishi & Mifune 2016](#); [Silva & Mace 2014](#); [Espín et al. 2022](#)), while observational studies of PA behavior are thought to afford high external validity by permitting researchers to study if and when laboratory findings generalize to behavioral patterns in the real world ([McElreath et al. 2008](#)). As reviewed above, each approach has its limitations. Accordingly, the generalizability and reliability of research on PA may be improved by triangulating results using multiple methods, and replication—using consistent protocols across variable contexts. We advocate consideration of additional methods that: (i) capture between-individual variability in PA as a function of context and individual characteristics, including characteristics of the alter and the dyad of which the individual and alter are a part; and (ii) can be deployed with multiple samples, including outside of educated, industrialized contexts, to improve comparability. One approach that we find particularly promising is the joint deployment of social network analysis paired with Recipient Identity-Conditioned Heuristic (RICH) economic games ([Gervais 2017](#)). In [Ross & Pisor \(2023\)](#), we provide a detailed analysis of social network and RICH data from two multi-ethnic communities on the Pacific coast of Colombia; the data illustrate important between-individual, between-dyad, and between-site differences in PA. Here, we outline the potential of such a networks-based approach to address some of the limitations of other methods.

Social network questionnaires can be designed to measure both positive ties (e.g., nominations of friendships or food/money transfers) and negative ties (e.g., nominations of alters who people fear, shun, or have conflicts with) and study patterns in such ties as a function of group identity. Importantly, social network data can measure real-world behavior concerning both in-group favoritism and out-group hostility, while avoiding the ecological inference fallacy that problematizes interpretation of aggregate-level empirical data.

RICH economic games involve tasks in which deciders have a chance to: (i) allocate money to, (ii) take money from, and (iii) at a cost to themselves, reduce the payouts of a set of known alters. In these games, a photograph roster is used to allow each decider to make economic decisions with respect to each other person in the study (see [Ross & Redhead 2021](#), for details and software tools). These games thus: (i) measure generosity, exploitation, and hostility toward in-group and out-group alters that each participant knows, and (ii) permit researchers to study how group membership affects internal states (e.g., sentiments toward alters) while statistically controlling for potential confounds using standard tools from social network analysis (e.g., using the social relations model, or its generalizations; [Kenny & La Voie 1984](#); [Koster & Leckie 2014](#)). In contrast to other economic games not played on networks, RICH games permit researchers to study how game decisions are influenced by multiple individual-level and dyad-level variables, and thus possibly competing heuristics—e.g., the relative effects of group identity and economic need can be studied via network-based multiple regression ([Pisor et al. 2020](#)).

4. Conclusions and future directions

In a recent paper provocatively titled “Tribalism is human nature,” [Clark et al. \(2019\)](#) write that in-group favoritism is “natural” and “nearly ineradicable.” Such characterizations can have wide-reaching effects on how researchers and policymakers think about intergroup relations. Although parochial altruism (PA), or in-group favoritism paired with out-group hostility, is commonly treated as the default for human intergroup relations ([Böhm et al. 2020](#); [Brewer 2010](#); [Fearon & Laitin 1996](#)), empirically measured levels of PA actually vary substantially across individuals, across contexts, and across groups ([Rusch 2014](#))—it is far from “nearly ineradicable,” but treating it as such can create a self-fulfilling prophecy ([Böhm et al. 2022](#)). As we have outlined here, variability in measured PA can reflect variation in what is measured (e.g., internal states versus behavior; Figure 1) and how context varies (e.g., due to changes in the net benefits of intergroup competition). However, researchers’ expectations and methods matter too. There is evidence that researchers’ expectations have influenced where PA is studied, how PA is studied, and how results are interpreted ([Fearon & Laitin 1996](#)). If we expect to see a social world shaped by a given phenomenon, we may mischaracterize human sociality ([Barrett 2020](#)). Such mischaracterizations have policy implications—including, for example, how we expect individuals to respond to conflicts (cf. [Schaub 2017](#)).

In our review of the PA literature, we have highlighted areas of PA research that we believe would be well-served by more researcher reflection and caution—and these critiques apply with equal force to research on intergroup relations and group psychology more broadly. Areas that could be well-served by more reflection and caution include:

1. *Examining assumptions about PA in humans.* The PA hypothesis refers to just a subset of intergroup relations in which in-group favoritism and out-group hostility are directly related—perhaps due to selection linking the two ([Choi & Bowles 2007](#)). Intergroup relations take many more forms ([Böhm et al. 2020](#); [Brewer 2010](#)) and range from hostile to peaceful ([Glowacki 2022](#)). If our expectation is that human intergroup relations are defined by PA, we may design studies that reflect this assumption ([Pisor & Ross 2022](#)) and/or preferentially conduct research in locations where levels of out-group hostility are atypically high ([Fearon & Laitin 1996](#); [Pisor & Surbeck 2019](#)). The flexibility of human sociality is not to be underestimated.
2. *Differentiating weak from strong PA.* As reviewed above, many studies aiming to study PA focus instead on just favoritism—in-group favoritism by itself, or in-group versus out-group favoritism. This is true, for example, in much of the literature on PA in children. The IPUC, IPD-MD, and RICH games offer methods for measuring both in-group favoritism and out-group hostility—with the IPUC and IPD-MD designed with internal states in mind, and RICH games designed to measure behavior given context, individual characteristics, and internal states ([Aaldering & Böhm 2020](#); [Halevy et al. 2008](#); [Gervais 2017](#)).
3. *Engaging in specific study of different components of PA.* Indeed, the precursors to PA behavior (Figure 1)—which appear both implicitly and explicitly in the PA literature—can each be studied, allowing us to better understand how upstream changes create variability in internal states and behavior across individuals, across situations, and across groups (e.g., [Thielmann et al. 2021](#)). Work by [Thielmann et al. \(2020\)](#), [de Dreu \(2010\)](#), [Columbus et al. \(2023\)](#), and others has begun to unpack how structural vs “chronic individual differences” ([de Dreu 2010](#)) contribute to internal states and/or behavior pertinent to PA.
4. *Designing methods that match research questions.* Whether studying PA or another aspect of human sociality, we suggest that researchers ensure that the methods they choose match the questions they wish to answer ([Barrett 2020](#)). We have had issues with this ourselves ([Pisor & Ross 2022](#)) and, in [Pisor et al. \(2020\)](#), offer pointers for how to improve the match between hypotheses and design of economic games.
5. *Considering both internal and external validity, especially before generalizing.* Experimental, laboratory-based studies of PA are popular, especially because they serve as proxies for internal states with experimental controls ([Thielmann et al. 2021](#)). There is a tendency for authors to generalize from these findings to humanity generally. However, concerns have been raised about the internal, external, and ecological validity of economic games (e.g., [Naar 2020](#); [Galizzi & Navarro-Martinez 2019](#); [Chuang & Schechter 2015](#)). For claims of generalizability to be defensible, the phenomenon under study should appear consistently across studies, samples, and methods ([Tiokhin et al. 2019](#)). Thus, we need to triangulate findings across methods, and consider deploying methods with high ecological validity (such as network-based games) across diverse contexts to complement and cross-validate findings derived from laboratory methods with tighter experimental control—but possibly less relevance to real-world behavior.
6. *Drawing on existing data to formulate explicit hypotheses.* Though there is still much we do not know about PA (e.g., [Böhm et al. 2020](#); [Yamagishi & Mifune 2016](#)), existing data of all kinds, from archaeological to experimental, can inform more explicit hypotheses and hypothesis testing going forward. For example, it can be difficult to elicit intergroup hostility; however, modeling and experimental data offer suggestions about when and why it might emerge—surprisingly, not in all situations of high resource density, but perhaps when population pressure is high or groups are caught in cycles of retribution ([Bell & Moya 2021](#); [Columbus et al. 2023](#)). These findings make testable predictions that can be studied empirically, e.g., combining ethnography, social network data, and field experiments.

Barrett (2020) also provides detailed discussion and recommendations pertinent to each of the above points.

In sum, one of the most characteristic features of humans is our flexibility (Potts 2012)—and flexibility in our social worlds is no exception (Pisor & Surbeck 2019). If researchers are deliberate in how we study intergroup relations, this may not only improve our characterizations of human sociality, but may change our expectations for how intergroup relations play out in the real world, affecting our approaches to policy and interventions in turn.

5. Acknowledgments

The authors thank the Max Planck Institute for Evolutionary Anthropology Department of Human Behavior Ecology and Culture (MPI-EVA HBEC), Michael Gurven, Dan Hruschka, Darcy Bird, Aaron Blackwell, Paul Bloom, Robert Böhm, Anne Degraeve, Zach Garfield, Monique Borgerhoff Mulder, Simon Columbus, Dan Fessler, Adam Kenny, Paul Seabright, Kris Smith, WSU's 2021 Evolution of Human Sociality seminar, Amsterdam Cooperation Lab's Cooperation Colloquia, and four anonymous reviewers for helpful feedback and discussion.

6. Funding

This work was supported by MPI-EVA HBEC.

7. Data availability

Not applicable.

8. Conflict of interest

None.

References

- Aaldering, H. & Böhm, R. (2020). Parochial versus universal cooperation: Introducing a novel economic game of within-and between-group interaction. *Social Psychological and Personality Science*, 11, 36–45.
- Abbink, K., Brandts, J., Herrmann, B. et al. (2012). Parochial altruism in inter-group conflicts. *Economics Letters*, 117, 45–48.
- Alesina, A., Baqir, R. & Easterly, W. (1999). Public goods and ethnic divisions. *The Quarterly journal of economics*, 114, 1243–1284.
- Alesina, A., Devleeschauwer, A., Easterly, W. et al. (2003). Fractionalization. *Journal of Economic growth*, 8, 155–194.
- Alesina, A. & La Ferrara, E. (2005). Ethnic diversity and economic performance. *Journal of economic literature*, 43, 762–800.
- Alesina, A., Michalopoulos, S. & Papaioannou, E. (2016). Ethnic inequality. *Journal of Political Economy*, 124, 428–488.
- Baldassarri, D. & Abascal, M. (2020). Diversity and prosocial behavior. *Science*, 369, 1183–1187.
- Balliet, D., Wu, J. & De Dreu, C. (2014). Ingroup Favoritism in Cooperation. *Psychological Bulletin*, 140, 1556–1581.
- Barrett, H. C. (2020). Deciding what to observe: Thoughts for a post-WEIRD generation. *Evolution and Human Behavior*, 41, 445–453.
- Barth, F. (1956). Ecologic relationships of ethnic groups in Swat, North Pakistan. *American Anthropologist*, 58, 1079–1089.
- Barth, F. (1998). *Ethnic groups and boundaries*. Waveland Press.
- Beck, U. (2006). *Cosmopolitan vision*. Polity.
- Bell, A. & Moya, C. (2021). *Evolution of outgroup aversion within and across territories*. Working paper.
- Benozio, A. & Diesendruck, G. (2015). Parochialism in preschool boys' resource allocation. *Evolution and Human Behavior*, 36, 256–264.
- Bernhard, H., Fischbacher, U. & Fehr, E. (2006). Parochial altruism in humans. *Nature*, 442, 912–915.
- Bogaert, S., Boone, C. & Declerck, C. (2008). Social value orientation and cooperation in social dilemmas: A review and conceptual model. *British Journal of Social Psychology*, 47, 453–480.
- Böhm, R., Rusch, H. & Baron, J. (2020). The psychology of intergroup conflict. *Journal of Economic Behavior and Organization*, 178, 947–962.
- Bollig, M. (2010). *Risk management in a hazardous environment* volume 2. Springer Science & Business Media.
- Bowles, S. (2008). Conflict: Altruism's midwife. *Nature*, 456, 326–327.
- Bowles, S. & Gintis, H. (2003). Origins of human cooperation. In P. Hammerstein (Ed.), *Genetic and cultural evolution of cooperation* (pp. 429–442). MIT press.
- Bowles, S. & Gintis, H. (2004). Persistent parochialism. *Journal of Economic Behavior & Organization*, 55, 1–23.
- Boyd, R. & Richerson, P. J. (1985). *Culture and the evolutionary process*. Chicago: University of Chicago Press.
- Boyd, R. & Richerson, P. J. (2022). Large-scale cooperation in small-scale foraging societies. *Evolutionary Anthropology: Issues, News, and Reviews*, 31, 175–198. _eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1002/evan.21944>.
- Brewer, M. B. (2010). Intergroup Relations. In R. F. Baumeister, & E. J. Finkel (Eds.), *Advanced Social Psychology* (pp. 535–571). Oxford: Oxford University Press.
- Brewer, M. B. & Campbell, D. T. (1976). *Ethnocentrism and intergroup attitudes*. Oxford: Sage.
- Brewer, M. B. & Caporael, L. R. (2006). An evolutionary perspective on social identity. *Evolution and Social Psychology*, 143, 161.
- Buchan, N. R., Grimalda, G., Wilson, R. et al. (2009). Globalization and human cooperation. *Proceedings of the National Academy of Sciences*, 106, 4138–4142.
- Bunce, J. (2020). Sustaining cultural diversity through cross-cultural competence. *SocArXiv*, .
- Bunce, J. A. & McElreath, R. (2018). Sustainability of minority culture when inter-ethnic interaction is profitable. *Nature Human Behaviour*, 2, 205–212.
- Buttelmann, D. & Böhm, R. (2014). The ontogeny of the motivation that underlies in-group bias. *Psychological Science*, 25, 921–927.
- Böhm, R., Halevy, N. & Kugler, T. (2022). The power of defaults in intergroup conflict. *Organizational Behavior and Human Decision Processes*, 168, 104105.
- Cashdan, E. (2001). Ethnocentrism and xenophobia. *Current Anthropology*, 42, 760–764.
- Chiang, Y.-S. & Wu, C.-I. (2015). Social influence and the adaptation of parochial altruism: a dictator-game experiment on children and adolescents under peer influence. *Evolution and Human Behavior*, 36, 430–437.

- Choi, D. D., Poertner, M. & Sambanis, N. (2019). Parochialism, social norms, and discrimination against immigrants. *Proceedings of the National Academy of Sciences*, 116, 16274–16279.
- Choi, J.-K. & Bowles, S. (2007). The coevolution of parochial altruism and war. *Science*, 318, 636–640.
- Chuang, Y. & Schechter, L. (2015). Stability of experimental and survey measures of risk, time, and social preferences. *Journal of Development Economics*, 117, 151–170.
- Clark, C. J., Liu, B. S., Winegard, B. M. et al. (2019). Tribalism is human nature. *Current Directions in Psychological Science*, 28, 587–592.
- Columbus, S., Thielmann, I., Zettler, I. et al. (2023). Parochial reciprocity. *Evolution and Human Behavior*, .
- Cook, J. H. (2015). Confusion in risk aversion experiments in low-income countries. Available at SSRN 2617701, .
- Dave, C., Eckel, C. C., Johnson, C. A. et al. (2010). Eliciting risk preferences. *Journal of Risk and Uncertainty*, 41, 219–243.
- De Dreu, C. K., Gross, J., Fariña, A. et al. (2020). Group cooperation, carrying-capacity stress, and intergroup conflict. *Trends in Cognitive Sciences*, 24, 760–776.
- De Dreu, C. K. W., Fariña, A., Gross, J. et al. (2022). Prosociality as a foundation for intergroup conflict. *Current Opinion in Psychology*, 44, 112–116.
- De Dreu, C. K. W. & Gross, J. (2019). Revisiting the form and function of conflict: Neurobiological, psychological, and cultural mechanisms for attack and defense within and between groups. *Behavioral and Brain Sciences*, 42, e116.
- Delton, A. W., Jaeggi, A. V., Lim, J. et al. (2023). Cognitive foundations for helping and harming others: Making welfare tradeoffs in industrialized and small-scale societies. *Evolution and Human Behavior*, .
- Delton, A. W. & Krasnow, M. M. (2017). The psychology of deterrence explains why group membership matters for third-party punishment. *Evolution and Human Behavior*, 38, 734–743.
- Dereux, M. & Mesoudi, A. (2020). Cumulative cultural evolution within evolving population structures. *Trends in Cognitive Sciences*, . Publisher: Elsevier.
- de Dreu, C. K. (2010). Social value orientation moderates ingroup love but not outgroup hate in competitive intergroup conflict. *Group Processes & Intergroup Relations*, 13, 701–713. Publisher: SAGE Publications Ltd.
- de Dreu, C. K., Balliet, D. & Halevy, N. (2014). Parochial cooperation in humans. In *Advances in Motivation Science* (pp. 1–47). Elsevier volume 1.
- Dunbar, R. I. M. (2008). Cognitive constraints on the structure and dynamics of social networks. *Group Dynamics: Theory, Research, and Practice*, 12, 7–16.
- Dyble, M. (2021). The evolution of altruism through war is highly sensitive to population structure and to civilian and fighter mortality. *Proceeding of the National Academies of Sciences*, 118, e2011142118.
- Ellemers, N., Kortekaas, P. & Ouwerkerk, J. (1999). Self categorization, commitment to the group and social self esteem as related but distinct aspects of social identity. *European Journal of Social Psychology*, 28, 371–398.
- Ensminger, J. (1997). Transaction costs and Islam. *Journal of Institutional and Theoretical Economics*, (pp. 4–29).
- Espín, A. M., Brañas-Garza, P., Gamella, J. F. et al. (2022). Culture and group-functional punishment behaviour. *Evolutionary Human Sciences*, 4, e35.
- Fearon, J. D. & Laitin, D. D. (1996). Explaining interethnic cooperation. *American Political Science Review*, 90, 715–735.
- Fehr, E., Bernhard, H. & Rockenbach, B. (2008). Egalitarianism in young children. *Nature*, 454, 1079–1083. Number: 7208 Publisher: Nature Publishing Group.
- Fiske, S. T., Dupree, C. H., Nicolas, G. et al. (2016). Status, power, and intergroup relations. *Current Opinion in Psychology*, 11, 44–48.
- Freedman, D. A. (1999). Ecological inference and the ecological fallacy. *International Encyclopedia of the social & Behavioral sciences*, 6, 1–7.
- Fry, D. P. (2018). The evolutionary logic of human peaceful behavior. *Peace Ethology*, (pp. 249–265).
- Fukuyama, F. (2001). Social capital, civil society and development. *Third World Quarterly*, 22, 7–20.
- Funder, D. C. (2016). Taking situations seriously: The Situation Construal Model and the Riverside Situational Q-Sort. *Current Directions in Psychological Science*, 25.
- Galizzi, M. M. & Navarro-Martinez, D. (2019). On the external validity of social preference games. *Management Science*, 65, 976–1002.
- Gervais, M. M. (2017). RICH economic games for networked relationships and communities. *Field Methods*, 29, 113–129.
- Gervais, M. M. & Fessler, D. M. (2017). On the deep structure of social affect. *Behavioral and Brain Sciences*, 40.
- Gil-White, F. J. (2004). Ultimatum game with an ethnicity manipulation: Results from Khovdiin Bulgan Sum, Mongolia. In *Foundations of Human Sociality: Ethnography and Experiments in 15 Small-Scale Societies* (pp. 260–304). Oxford: Oxford University Press.
- Glowacki, L. (2020). The emergence of locally adaptive institutions. *Biosystems*, 198, 104257.
- Glowacki, L. (2022). The evolution of peace. *Behavioral and Brain Sciences*, (pp. 1–100).
- Glowacki, L., Wilson, M. L. & Wrangham, R. W. (2020). The evolutionary anthropology of war. *Journal of Economic Behavior & Organization*, 178, 963–982.
- Greene, J. D. (2013). *Moral tribes*. Penguin.
- Guala, F. (2008). The Ultimatum Game from testing to measurement device. *Philosophy of Science*, 75, 658–669.
- Guala, F. (2019). Preferences: neither behavioural nor mental. *Economics & Philosophy*, 35, 383–401. Publisher: Cambridge University Press.
- Guala, F. & Mittone, L. (2010). The Dictator Game. *Journal of Socio-Economics*, 39, 578–584.
- Gurven, M. & Winking, J. (2008). Collective action in action. *American Anthropologist*, 110, 179–190.
- Habyarimana, J., Humphreys, M., Posner, D. N. et al. (2007). Why does ethnic diversity undermine public goods provision? *American Political Science Review*, 101, 709–725.
- Hagen, E. H. & Hammerstein, P. (2006). Game theory and human evolution. *Theoretical Population Biology*, 69, 339–348.
- Halevy, N., Bornstein, G. & Sagiv, L. (2008). “in-group love” and “out-group hate” as motives for individual participation in intergroup conflict: A new game paradigm. *Psychological science*, 19, 405–411.
- Henrich, J., Heine, S. J. & Norenzayan, A. (2010). The weirdest people in the world? *Behavioral and brain sciences*, 33, 61–83.
- Hewstone, M., Rubin, M. & Willis, H. (2002). Intergroup bias. *Annual Review in Psychology*, 53, 575–604.
- House, B. R., Silk, J. B., Henrich, J. et al. (2013). Ontogeny of prosocial behavior across diverse societies. *Proceedings of the National Academy of Sciences*, 110, 14586–14591. Publisher: Proceedings of the National Academy of Sciences.
- Hruschka, D. J. & Henrich, J. (2013). Economic and evolutionary hypotheses for cross-population variation in parochialism. *Frontiers in Human Neuroscience*, 7, 559.
- Jackson, J. E. (1983). *The Fish People*. Cambridge: Cambridge University Press.
- Jenkins, R. (1994). Rethinking ethnicity. *Ethnic and Racial Studies*, 17, 197–223.
- Jha, S. (2013). Trade, institutions, and ethnic tolerance: Evidence from south asia. *American political Science review*, 107, 806–832.
- Kappeler, P. M. & Silk, J. B. (Eds.) (2010). *Mind the gap: tracing the origins of human universals*. Heidelberg ; New York: Springer.
- Kenny, D. A. & La Voie, L. (1984). The social relations model. *Advances in Experimental Social Psychology*, 18, 142–182.
- Kitchen, D. & Beehner, J. (2007). Factors affecting individual participation in group-level aggression among non-human primates. *Behaviour*, 144, 1551–1581. ISBN: 0005-7959.

- Knauff, B. M. (1991). Violence and sociality in human evolution [and comments and replies]. *Current Anthropology*, 32, 391–428.
- Koster, J. M. & Leckie, G. (2014). Food sharing networks in lowland Nicaragua: An application of the social relations model to count data. *Social Networks*, 38, 100–110.
- Kurzban, R., Tooby, J. & Cosmides, L. (2001). Can race be erased? . *Proceedings of the National Academy of Sciences*, 98, 15387–15392.
- Lang, M., Purzycki, B. G., Apicella, C. L. et al. (2019). Moralizing gods, impartiality and religious parochialism across 15 societies. *Proceedings of the Royal Society B*, 286, 20190202.
- Layton, R., O'Hara, S. & Bilsborough, A. (2012). Antiquity and social functions of multilevel social organization among human hunter-gatherers. *International Journal of Primatology*, 33, 1215–1245.
- Leech, B. L. & Cronk, L. (2017). Coordinated policy action and flexible coalitional psychology: How evolution made humans so good at politics. *Cognitive Systems Research*, 43, 89–99.
- Lemoine, S. R. T., Samuni, L., Crockford, C. et al. (2022). Parochial cooperation in wild chimpanzees: a model to explain the evolution of parochial altruism. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 377, 20210149. Publisher: Royal Society.
- Levine, R. A. & Campbell, D. T. (1971). *Ethnocentrism: Theories of Conflict, Ethnic Attitudes, and Group Behavior*. (First edition ed.). New York: John Wiley & Sons.
- Lightner, A. D., Barclay, P. & Hagen, E. H. (2017). Radical framing effects in the ultimatum game. *Royal Society Open Science*, 4, 170543.
- Lönnqvist, J.-E., Verkasalo, M., Walkowitz, G. et al. (2015). Measuring individual risk attitudes in the lab. *Journal of Economic Behavior & Organization*, 119, 254–266.
- Majolo, B. & Maréchal, L. (2017). Between-group competition elicits within-group cooperation in children. *Scientific Reports*, 7, 43277. Number: 1 Publisher: Nature Publishing Group.
- Mantilla, C., Zhou, L., Wang, C. et al. (2021). Favoring your in-group can harm both them and you: Ethnicity and public goods provision in China. *Journal of Economic Behavior & Organization*, 185, 211–233.
- Mau, S., Mewes, J. & Zimmermann, A. (2008). Cosmopolitan attitudes through transnational social practices? *Global Networks*, 8, 1–24.
- McElreath, R., Bell, A. V., Efferson, C. et al. (2008). Beyond existence and aiming outside the laboratory: estimating frequency-dependent and pay-off-biased social learning strategies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363, 3515–3528.
- McElreath, R., Boyd, R. & Richerson, P. (2003). Shared norms and the evolution of ethnic markers. *Current Anthropology*, 44, 122–130.
- Messick, D. M. & McClintock, C. G. (1968). Motivational bases of choice in experimental games. *Journal of Experimental Social Psychology*, 4, 1–25.
- Moya, C. (2022). What does it mean for humans to be groupish? *Philosophy Compass*, .
- Moya, C. & Boyd, R. (2015). Different selection pressures give rise to distinct ethnic phenomena. *Human Nature*, 26, 1–27.
- Murphy, R. O., Ackermann, K. A. & Handgraaf, M. J. J. (2011). Measuring Social Value Orientation. *Judgment and Decision Making*, 6, 771–781. Publisher: Cambridge University Press.
- Naar, N. (2020). Gaming anthropology. *American Anthropologist*, (pp. 1–15).
- Nannestad, P. (2008). What have we learned about generalized trust, if anything? *Annual Review of Political Science*, 11, 413–436.
- North, D. C. (1991). Institutions. *The Journal of Economic Perspectives*, 5, 97–112.
- Otterbein, K. F. (1999). A history of research on warfare in anthropology. *American Anthropologist*, 101, 794–805.
- Phelan, M. P. & Hunt, S. A. (1998). Prison gang members' tattoos as identity work. *Symbolic Interaction*, 21, 277–298.
- Pietraszewski, D. (2022). Toward a computational theory of social groups: A finite set of cognitive primitives for representing any and all social groups in the context of conflict. *Behavioral and Brain Sciences*, 45, e97. Publisher: Cambridge University Press.
- Pievani, T. (2011). Born to cooperate? In R. W. Sussman, & C. R. Cloninger (Eds.), *Origins of Altruism and Cooperation* (p. 41). New York, NY: Springer.
- Pisor, A. C., Gervais, M. M., Purzycki, B. et al. (2020). Preferences and constraints. *Royal Society Open Science*, 7, 192090.
- Pisor, A. C. & Gurven, M. (2015). Corruption and the other(s). *PloS one*, 10, e0144542.
- Pisor, A. C. & Gurven, M. (2018). When to diversify, and with whom? *Evolution and Human Behavior*, 39, 30–39.
- Pisor, A. C. & Ross, C. T. (2022). *Intergroup relationships and long-distance relationships serve different functions*. OSF Preprints.
- Pisor, A. C. & Surbeck, M. (2019). The evolution of intergroup tolerance in nonhuman primates and humans. *Evolutionary Anthropology*, 28, 210–223.
- Potts, R. (2012). Evolution and environmental change in early human prehistory. *Annual Review of Anthropology*, 41, 151–167.
- Purzycki, B. G. (2020). Institutions, natural selection (s), and religion. *Religion, Brain & Behavior*, 10, 77–84.
- Purzycki, B. G., Apicella, C., Atkinson, Q. D. et al. (2016). Moralistic gods, supernatural punishment and the expansion of human sociality. *Nature*, 530, 327.
- Purzycki, B. G. & Lang, M. (2019). Identity fusion, outgroup relations, and sacrifice. *Cognition*, 186, 1–6.
- Redhead, D. & von Rueden, C. R. (2021). Coalitions and conflict: A longitudinal analysis of men's politics. *Evolutionary Human Sciences*, 3, e31.
- Richerson, P., Baldini, R., Bell, A. V. et al. (2016). Cultural group selection plays an essential role in explaining human cooperation. *Behavioral and Brain Sciences*, 39.
- Richerson, P. J. & Boyd, R. (2008). *Not by genes alone*. Chicago: University of Chicago press.
- Riek, B. M., Mania, E. W. & Gaertner, S. L. (2006). Intergroup threat and outgroup attitudes. *Personality and Social Psychology Review*, 10, 336–353.
- Roberts, G. (2007). Evolution of direct and indirect reciprocity. *Proceedings of the Royal Society B: Biological Sciences*, 275, 173–179. Publisher: Royal Society.
- Rodseth, L. & Wrangham, R. (2004). Human kinship: A continuation of politics by other means. *Kinship and behavior in primates*, 389419.
- Rodseth, L., Wrangham, R. W., Harrigan, A. M. et al. (1991). The human community as a primate society. *Current Anthropology*, 32, 221–254.
- Romano, A., Balliet, D., Yamagishi, T. et al. (2017). Parochial trust and cooperation across 17 societies. *Proceedings of the National Academy of Sciences*, 114, 12702–12707. Publisher: Proceedings of the National Academy of Sciences.
- Romano, A., Sutter, M., Liu, J. H. et al. (2021). National parochialism is ubiquitous across 42 nations around the world. *Nature Communications*, 12, 1–8.
- Ross, C. T. & Pisor, A. C. (2021). *Parochialism can be modulated by inequality*. Working paper.
- Ross, C. T. & Pisor, A. C. (2023). Identity-group boundaries, perceived inequality, and variability in the expression of parochial altruism. *OSF Preprint*, (pp. 1–15).
- Ross, C. T. & Redhead, D. (2021). Dietyrin: An R package for data collection, automated data entry, and post-processing of network-structured economic games, social networks, and other roster-based dyadic data. *Behavior Research Methods*, (pp. 1–21).
- Ruben, B. D. (1989). The study of cross-cultural competence. *International Journal of Intercultural Relations*, 13, 229–240.
- Rusch, H. (2014). The evolutionary interplay of intergroup conflict and altruism in humans. *Proceedings of the Royal Society B*, 281.
- Sahlins, M. (1972). *Stone Age Economics*. New York, NY: Routledge Chapman Hall. ISSN: 00251496.
- Schaub, M. (2017). Threat and parochialism in intergroup relations. *Proceedings of the Royal Society B*, 284, 20171560.

- Seabright, P. (2004). *The Company of Strangers*. Princeton University Press.
- Shahrier, S., Kotani, K. & Kakinaka, M. (2016). Social value orientation and capitalism in societies. *PLOS ONE*, 11, e0165067. Publisher: Public Library of Science.
- Sherif, M. (1966). *In common predicament:: Social psychology of intergroup conflict and cooperation*. Houghton Mifflin.
- Silva, A. S. & Mace, R. (2014). Cooperation and conflict. *Proceedings of the Royal Society B*, 281, 20141435.
- Singer, P. (1981). *The expanding circle*. Princeton University Press.
- Singh, M. & Glowacki, L. (2021). Human social organization during the Late Pleistocene: Beyond the nomadic-egalitarian model. *EcoEvoRxiv preprint*, (pp. 1–21).
- Slack, J. A. & Doyon, R. R. (2001). Population dynamics and susceptibility for ethnic conflict: The case of bosnia and herzegovina. *Journal of Peace Research*, 38, 139–161.
- Smaldino, P. E. (2019). Social identity and cooperation in cultural evolution. *Behavioural Processes*, 161, 108–116.
- Sterelny, K. (2016a). Cooperation, culture, and conflict. *The British Journal for the Philosophy of Science*, 67, 31–58.
- Sterelny, K. (2016b). Cooperation, culture, and conflict. *The British Journal for the Philosophy of Science*, 67, 31–58.
- Strauss, C. (1992). Models and motives. In R. G. D'Andrade, & C. Strauss (Eds.), *Human Motives and Cultural Models* (p. 10). Cambridge University Press.
- Sumner, W. G. (1906). *Folkways: A Study of Mores, Manners, Customs and Morals*. New York: Cosimo Classics.
- Thielmann, I., Böhm, R., Ott, M. et al. (2021). Economic games: An introduction and guide for research. *Collabra: Psychology*, 7, 19004.
- Thielmann, I., Spadaro, G. & Balliet, D. (2020). Personality and prosocial behavior: A theoretical framework and meta-analysis. *Psychological Bulletin*, 146, 30–90.
- Tiokhin, L., Hackman, J., Munira, S. et al. (2019). Generalizability is not optional. *Royal Society open science*, 6, 181386.
- Tooby, J., Cosmides, L. & Price, M. E. (2006). Cognitive adaptations for n-person exchange: the evolutionary roots of organizational behavior. *Managerial and Decision Economics*, 27, 103–129.
- Vardy, T. & Atkinson, Q. D. (2019). Property damage and exposure to other people in distress differentially predict prosocial behavior after a natural disaster. *Psychological Science*, 30, 563–575.
- Waring, T. M. (2012). Cooperation dynamics in a multiethnic society. *Current Anthropology*, 53, 642–649.
- Waring, T. M. & Bell, A. V. (2013). Ethnic dominance damages cooperation more than ethnic diversity. *Evolution and Human Behavior*, 34, 398–404.
- Waring, T. M., Kline, M. A., Brooks, J. S. et al. (2015). A multilevel evolutionary framework for sustainability analysis. *Ecology and Society*, 20.
- Winking, J. & Mizer, N. (2013). Natural-field dictator game shows no altruistic giving. *Evolution and Human Behavior*, 34, 288–293.
- Wrangham, R. W. & Glowacki, L. (2012). Intergroup aggression in chimpanzees and war in nomadic hunter-gatherers. *Human Nature*, 23, 5–29.
- Yamagishi, T. (2011). *Trust*. Springer.
- Yamagishi, T. & Kiyonari, T. (2000). The group as the container of generalized reciprocity. *Social Psychology Research Quarterly*, 63, 116–132.
- Yamagishi, T. & Mifune, N. (2016). Parochial altruism. *Current Opinion in Psychology*, 7, 39–43.
- Yamagishi, T., Mifune, N., Li, Y. et al. (2013). Is behavioral pro-sociality game-specific? *Organizational Behavior and Human Decision Processes*, 120, 260–271.
- Zefferman, M. R. & Mathew, S. (2015). An evolutionary theory of large-scale human warfare. *Evolutionary Anthropology*, 24, 50–61.