

DOI: <https://doi.org/10.22201/iifs.18704905e.2026.1788>

SOCIAL NORMS IN BONOBO SOCIETIES: APPLYING THE NORMATIVE PLURALISM FRAMEWORK TO BEHAVIORAL EVIDENCE

MATEO ARIAS-VÉLEZ

Universidad Nacional Autónoma de México
Instituto de Investigaciones Filosóficas
México

mateoariasvelez@filosoficas.unam.mx
<https://orcid.org/0000-0001-7637-4904>

SUMMARY: According to the normative pluralistic approach (Westra and Andrews 2022; Westra et al. 2024), social norms are understood as normative regularities defined by two components: patterns of behavioral conformity and forms of social maintenance. I argue that bonobos exhibit social norms in at least three domains: inequity aversion, reactions to interruptions of social activities, and female coalition formation. For each domain, I identify both components of normative regularities. I conclude that current evidence supports the view that bonobos display genuine forms of social normativity that structure and regulate their societies.

KEYWORDS: animal normativity, normative regularities, moral psychology, animal mind, animal cognition

RESUMEN: Según el enfoque del pluralismo normativo (Westra y Andrews 2022; Westra et al. 2024), las normas sociales se entienden como regularidades normativas definidas por dos componentes: patrones de conformidad conductual y formas de mantenimiento social. Sostengo que los bonobos manifiestan normas sociales en al menos tres dominios: la aversión a la inequidad, las reacciones frente a la interrupción de actividades sociales y la formación de coaliciones femeninas. En cada caso, identifico ambos componentes de la regularidad normativa. Concluyo que la evidencia disponible respalda la idea de que los bonobos muestran formas genuinas de normatividad social que estructuran y regulan sus sociedades.

PALABRAS CLAVE: normatividad animal, regularidades normativas, psicología moral, mente animal, cognición animal

1. *Introduction*

The aim of this article is to argue that bonobo societies exhibit social norms in the form of socially maintained normative regularities. To this end, I propose to apply the normative pluralism framework (Westra and Andrews 2022; Westra et al. 2024) to the case of

bonobos. This framework allows normativity to be analyzed without presupposing a single cognitive architecture or a strict definition of mental capacities, which makes it particularly suitable for studying non-human species.

The central argument I defend in this article is that if bonobos exhibit socially maintained patterns of behavioral conformity, then they display social norms. According to the normative pluralism framework, a behavior qualifies as a normative regularity when it constitutes a socially maintained pattern of behavioral conformity (Westra and Andrews 2022; Westra et al. 2024). I argue that bonobos exhibit such normative regularities in certain social behaviors. I focus on three of these: first, inequity aversion. In cooperative contexts, this can be interpreted as a social response that reinforces a norm of equitable distribution. Second, reactions to interruptions of social activities. During activities such as grooming or play, bonobos tend to maintain social activities until a clear disengagement signal is given, and they use gestures to reestablish the interaction if it is interrupted. Third, female coalition formations. I argue that these coalitions operate as a form of third-party punishment aimed at protecting females and preserving group cohesion. Across these three behaviors, normative regularities can be observed, which supports the conclusion that bonobos manifest social norms within their societies.

Recognizing social norms in bonobos has implications for a philosophical debate within the field of moral psychology about what social norms are and whether they are unique to humans. In the literature on moral psychology, social norms are typically regarded as exclusively human (Westra et al. 2024). Most theoretical proposals assume that social norms arise from forms of cognition and representation that only humans possess (Bicchieri 2006; 2017). Some have argued that social norms are possible thanks to “ought-thoughts” as cognitive representations that only humans can form (Nichols 2004), to the human form of self-consciousness (Rochat 2015), to unique human capacities for shared intentionality (Tomasello 2016; 2019), to gene–culture coevolution in human history (Richerson and Boyd 2005; Henrich 2015; Kumar and Campbell 2022), or to specialized cognitive mechanisms for tool-making (Birch 2021; Sterelny 2021). All of these positions assume that social norms constitute a relatively unified set of cognitive mechanisms unique to humans. However, there is no consensus in moral psychology about what this unified cognitive architecture underlying the human sense of normativity actually is (O’Neill and Machery 2018).

For instance, one of the most influential approaches in moral psychology is that of Cristina Bicchieri (2006; 2017), who defines social norms as rules of behavior to which individuals have a conditional preference to conform. That is, individuals follow such rules only if (a) they believe that most other members of their group conform to the norm (empirical expectation), and (b) they believe that most members of their group believe they ought to conform to the norm as well (normative expectation) (Bicchieri 2017, p. 35). The motivation to conform to a norm is framed in terms of desires, such as the desire to avoid sanctions, to gain approval, to please others, etc. (Bicchieri 2006, p. 24). Consequently, Bicchieri's approach conceives social norms as a social construct whose building blocks are mental states such as beliefs and desires, which are instantiated through expectations and rational preferences (2006, p. 11).

Bicchieri's definition of social norms is problematic when applied to non-human primates, such as bonobos, insofar as it presupposes advanced forms of mentalization, including the attribution of propositional attitudes or mental states—specifically, the capacity to hold beliefs about what others believe. Such capacities are controversial in non-human animals, and there is no clear consensus regarding when and how they emerge in humans (Andrews et al. 2024). As a result, Bicchieri's approach becomes strongly mentalistic with respect to the psychology of norms (Westra and Andrews 2022) and may over-intellectualize both human and non-human conformity to norms (Andrews et al. 2024). In this vein, Bicchieri's approach and other similar explanations of norms mentioned above presuppose psychological requirements—such as a homogeneous cognitive mechanism for attributing propositional attitudes like beliefs—that only humans could satisfy (Westra et al. 2024).

In contrast, the normative pluralism framework has been proposed as a methodological and conceptual approach for understanding social norms as the product of a diverse set of underlying cognitive, affective, and ecological processes of varying degrees of complexity, which makes it possible to identify social norms beyond the human dimension (Westra and Andrews 2022; Westra et al. 2024). In this sense, this perspective seeks to advance previous debates on animal normativity (such as those of Lorini 2018; Danón 2019; Andrews 2020). This approach is pluralistic insofar as it accepts that the cognitive processes involved in normative psychology can be highly diverse. Instead of treating social norms as a homogeneous category of mental representations, the normative pluralism framework suggests that the mechanisms of normative cognition may be quite heterogeneous, and

therefore there is no single set of cognitive mechanisms responsible for normative cognition. In this sense, since social norms are likely produced by a broad range of cognitive mechanisms, many of these mechanisms must be shared with non-human animals. Identifying a normative dimension in the social practices of bonobos supports this framework and extends its empirical scope, demonstrating its applicability beyond human beings.

Although similar approaches have been applied to chimpanzees (Fitzpatrick 2020; Danón 2024), this framework has not yet been directly applied to bonobos. While the empirical evidence on the social behaviors of bonobos—both in the wild and in captivity—remains more limited than that available for chimpanzees (Hare and Yamamoto 2017), I argue that the existing data support the claim that some of their social behaviors can be analyzed from a normative perspective.

The article is organized as follows: in section 1, I present the normative pluralism framework and the definition of normative regularity, which is based on two key elements: (1) the existence of a pattern of behavioral conformity and (2) the presence of social maintenance mechanisms. In section 2, I analyze how these two components are expressed in the inequity aversion observed in bonobos. Section 3 focuses on social activities such as grooming and play, which are likewise interpreted through the notion of normative regularity. Finally, in section 4, I examine female coalition formations, highlighting how these alliances can act as forms of social sanction.

2. The Normative Pluralism Framework

The normative pluralism framework proposes understanding social norms as normative regularities. According to this approach, rather than grounding social norms in discrete cognitive mechanisms, we should focus on identifiable behavioral patterns. This makes it possible to recognize that the psychology of social norms can emerge from multiple distinct processes. What these processes share is not a common cognitive architecture but a causal role: they act as forces that stabilize and maintain such normative regularities. In this sense, a social norm is not something separate from a normative regularity; they are, in fact, the same thing.

The normative pluralism framework defines normative regularities as “a socially maintained pattern of behavioral conformity within a community” (Westra and Andrews 2022, p. 9). This definition

is structured around three main components. The first is the concept of patterns of behavioral conformity. These describe observable regularities in the behavior of members of a community. One of the central motivations underlying this definition of social norms is that many standard accounts in moral psychology overlook the fact that social norms are identifiable behavioral phenomena. A key feature of this approach is that such patterns are aspects of the social world that can be recognized without needing to know the underlying psychological mechanisms that produce them. This idea aligns with Dennett's (1991) concept of real patterns, according to which certain phenomena can be considered real if they are stable, identifiable, and have predictive power, even if their internal mechanisms are unknown or diverse. This motivation makes it possible to define social norms in primarily behavioral terms before advancing claims about the kinds of psychological processes that might give rise to such norms. This point is precisely what enables a pluralistic account of the underlying psychological processes. Once social norms are identified as social and behavioral phenomena, then it becomes clear why one must allow for the possibility that a plurality of distinct psychological processes may underlie and sustain social norms across different species.

Therefore, we do not need to assume a single psychological architecture underpinning social norms. It is enough to recognize that certain behavioral recurrences within a community work as social norms because they help predict actions, explain interactions, and coordinate expectations. Thus, the existence of a social norm does not depend on all agents sharing the same cognitive representation of the norm, but rather on the presence of a stable and effective behavioral pattern. Once this pattern is detected, the pattern is the norm: no deeper psychological grounding is required to justify its status.

The second key component of the definition is social maintenance. Not every behavioral pattern constitutes a normative regularity; for it to operate as a social norm, it must be sustained by some form of social pressure that promotes conformity. A pattern is considered socially maintained when individual adherence to it can be explained by the social reactions that instances of conformity and non-conformity elicit. In other words, social maintenance refers to social responses or behaviors through which a community incentivizes conformity to the norm and discourages non-conformity (Westra and Andrews 2022). More specifically, the normative pluralism framework distinguishes between two broad types of social maintenance mechanisms: negative and positive. Negative social maintenance comprises

two forms of punishment: second-party and third-party punishment. Second-party punishment consists in negative responses by individuals who are directly affected or harmed by a violation of a social norm, whereas third-party punishment refers to negative responses by observers who are not directly affected by, or involved in, the transgression of the norm (Westra and Andrews 2022; Andrews et al. 2024). Third-party punishment is generally regarded as a strong empirical marker of the presence of a social norm (Westra et al. 2024). Examples of negative social maintenance include physical retaliation, signals of disapproval, protest, negative affective responses, withdrawal from the violator, and related behaviors (Andrews et al. 2024). Positive social maintenance mechanisms, by contrast, refer to social incentives aimed at promoting conformity to the norm. Examples include social inclusion in group activities, gains in social status, explicit verbal praise (in human cases), differential treatment and pedagogical practices such as teaching and facilitating social learning (Westra and Andrews 2022; Andrews et al. 2024). This means that community members not only observe and reproduce the behavior but also actively reinforce it, whether through approval, disapproval, reward, or punishment. In this way, social maintenance distinguishes normative regularities from mere customs or collective habits by highlighting their normative role within the social fabric.

The third and final component of the definition is the concept of community. This term refers to the set of relevant individuals who exhibit the pattern of behavioral conformity and participate in its social maintenance. In this sense, a social norm does not exist in the abstract but always within a specific group whose members share such regular behavior. This group can be all members of a population, a dyad, a subgroup, all members of the same species, or even members of different species. The specification of the community depends on the behavioral pattern under study. It is important to emphasize that the same individual can simultaneously belong to multiple normative communities and, therefore, conform to different norms depending on the context. This reinforces the idea that social norms do not depend exclusively on stable internal dispositions but are sensitive to the specific dynamics of the communities in which they operate. Recognizing the role of the community thus underscores the situated and plural nature of normative regularities.

It is worth noting that normative regularities may have a cultural component, a phenomenon that Westra et al. (2024) describe as communal normative regularities. Certain behaviors understood

as cultural variations—namely, community-specific traits transmitted through social learning—might be regulated by social norms. These communal social norms are defined as “suites of normative regularities that serve to distinguish different animal communities behaviourally within a given species” (Westra et al. 2024, p. 1069). As such, communal normative regularities enable the characterization of communities in terms of culturally distinctive normative patterns. This cultural dimension of social norms is closely connected to group identity as a normative phenomenon, often taking the form of implicit principles such as “What we do around here” (Andrews et al. 2024). Evidence from bonobos, as with other great apes, supports the existence of community-specific cultural variation across both material and immaterial domains (van Leeuwen et al. 2020), both in captive and wild populations. Approximately fourteen such behaviors have been identified, some shared with chimpanzees and nine unique to bonobos (Hohmann and Fruth 2003). Cultural variation in captive bonobos has been documented in grooming, play, and group-specific sociability (Tokuyama et al. 2019; van Leeuwen et al. 2024), as well as in emotional expressions such as consolation, which vary across communities (Brooker et al. 2025). Moreover, wild bonobo groups display distinct hunting preferences despite sharing the same geographical space, a pattern plausibly explained by conformity to group-specific social norms (Samuni et al. 2020; Whiten 2020).

Therefore, an investigation into normative regularities must clearly determine these three components: it should begin with the identification of (1) patterns of behavioral conformity and specify whether such patterns are subject to (2) forms of social maintenance within a (3) specific community (Westra et al. 2024). In other words, it is not enough to observe a regularity; it is necessary to establish that this regularity is sustained through social mechanisms that incentivize conformity and discourage non-conformity. Regarding the third component of the definition, this article focuses on the case of bonobo communities, whether in captivity or in the wild. Therefore, the emphasis lies on identifying the two remaining components of the definition. I proceed to argue that these two fundamental aspects manifest in three domains of bonobo social behavior: inequity aversion, reactions to interruptions of social activities, and female coalition formation, which constitute examples of normative regularities.

3. *Inequity Aversion in Bonobo Societies*

In this section, I argue that responses to inequity aversion in bonobos constitute forms of social maintenance. Such responses should not be understood merely as affective or instrumental reactions to unfavorable distributions, but rather as indicators of an underlying behavioral pattern. Specifically, responses to inequity can be conceived as forms of social maintenance that reveal the presence of an implicit norm regarding the equitable distribution of resources. This norm should not be understood as an explicitly formulated or reflexively internalized rule, but rather as a behavioral pattern that guides and structures cooperative interaction between partners, especially in contexts where benefits must be distributed proportionally to effort.

Inequity aversion can be defined as the manifestation of negative reactions to the unequal distribution of rewards among individuals who have performed similar tasks (Ritov et al. 2024; Radovanović et al. 2025). These responses can take various forms, one of the most common being the refusal to continue participating in the activity. In such cases, the subject chooses to withdraw upon observing that their partner has received a more valuable reward for the same effort (Brosnan and de Waal 2003). Two modalities of inequity aversion are distinguished: advantageous and disadvantageous. Advantageous inequity aversion refers to situations in which the agent receives more than their partners. Conversely, disadvantageous inequity aversion refers to situations where the agent receives less than their partners for the same effort (Brosnan 2006).

Cooperative dyadic interactions are commonly used to experimentally evaluate responses to inequity. These involve two individuals collaborating on the same task. In this type of experimental setup, a token exchange task is employed. This task requires participants to hand over a token to an experimenter in exchange for a reward. This allows for a comparative examination of individuals' responses to different distributions of benefits.

Although studies on inequity aversion in bonobos remain limited, two recent investigations have addressed this issue (Verspeek and Stevens 2022; Radovanović et al. 2025). Both studies focused on analyzing bonobos' responses to disadvantageous inequity situations, using the token exchange task paradigm mentioned earlier. To date, no empirical evidence has been found supporting the presence of advantageous inequity aversion in this species (Verspeek and Stevens 2022). In these experiments, cooperative interactions among bonobos were structured based on significant social bonds, predominantly

mother–offspring relationships as well as relationships among adult females.

3.1. Patterns of Behavioral Conformity in Bonobos' Inequity Aversion

I suggest that the social norm observed behind responses to inequity can be formulated as follows: “Two individuals performing the same task should receive the same reward”, or more concisely, “Equal reward for equal effort”. Within the context of cooperative work, such as the token exchange task, it is evident that individuals manifest a stable expectation of receiving equitable compensation for their efforts. This repeated and recognizable expectation allows the behavior to be characterized as an identifiable regularity: whenever a cooperative activity takes place, an equitable distribution of benefits is expected.

The behavioral pattern of “Equal reward for equal effort” can be interpreted as a normative regularity, rather than a mere emotional response to frustration. Some authors have argued that rejection responses to inequity could be explained by frustration generated when individuals shift from receiving a high-value reward to a lower-value one, without genuine social comparison mediating this change (Roma et al. 2006; Silberberg et al. 2009). From this perspective, the rejection behaviors observed in bonobos could be understood as a disappointment reaction to the loss of a more valuable reward, rather than an evaluation of equitable distribution among individuals (Ritov et al. 2024).¹ According to this view, bonobos would not be responding to inequality per se, but to the dissatisfaction of prior expectations.

¹ There is ongoing debate regarding how to interpret studies of inequity aversion in non-human animals. Within this literature, two main explanatory hypotheses have been proposed. The first is the inequity aversion hypothesis. According to this view, responses to unequal outcome distributions result from social comparison between individuals engaged in a shared activity (Brosnan and de Waal 2003; Radovanović et al. 2025). The second is the disappointment hypothesis, which holds that the observed behaviors do not reflect social comparison but rather individual frustration arising from not receiving a more valuable reward. On this account, subjects respond to the discrepancy between expected and obtained rewards, rather than to the relative outcomes of their partners. Thus, participants' attention is directed toward the higher-value reward itself, rather than toward their partners (Ritov et al. 2024). A related variant of the disappointment hypothesis allows for a social dimension, suggesting that primates' responses to unequal reward distributions express social disappointment toward the human experimenter for failing to provide an adequate reward, rather than any concern for equity (Engelmann et al. 2017). However, some researchers have argued that neither the individual nor the social version of the disappointment hypothesis can adequately account for the available experimental

Nonetheless, interpreting these behaviors as indicators of an implicit social norm highlights that these responses are not limited to an individual emotional state but form part of a behavioral pattern. From this perspective, it is unnecessary to assume in advance whether, at the cognitive level, there exists a conscious social comparison or merely an affective response. It is enough to recognize a consistent regularity: whenever an unequal distribution occurs following cooperative activity, a rejection response arises. This means that inequity aversion responses might be subject to a pattern of behavioral conformity within bonobo societies.

3.2. Social Maintenance within Norms of Inequity Aversion

Responses to inequity can be understood as forms of social maintenance for a social norm. In this sense, the identified normative regularity—according to which an equitable distribution of rewards is expected in response to equivalent effort—not only manifests in repeated behavior but is also sustained through responses to its violation. In the case of bonobos, negative responses such as rejecting the offered reward, ceasing the token exchange, and leaving the experimental area are exhibited (Verspeek and Stevens 2022; Radovanović et al. 2025). I propose that these behaviors should not be understood as mere individual reactions but as expressions of a form of normative regulation within the social life of the group.

Responses to inequity serve as typical mechanisms of social maintenance for a norm. In this context, such responses can be interpreted as signals that a normative regularity has been violated and must be restored. In other words, through these responses, individuals implicitly sanction violations of the behavioral pattern, thereby contributing to its preservation. Reluctance to continue participating in the cooperative activity can thus be understood as a form of normative pressure aimed at encouraging conformity to the norm. This norm is sustained through these negative responses, which, besides expressing dissatisfaction, also modulate future social interactions. It has been noted that recognizing disadvantageous inequity and the corresponding aversion can lead the disadvantaged individual to punish the unfair partner, prefer more equitable collaborators in subsequent activities, and, in some cases, exclude the unfair individual (Radovanović et al. 2025). This reinforces the normative dimension of responses to inequity since through punishment and rejection, unfair individuals

findings (Radovanović et al. 2025). As a result, there is currently no clear consensus as to which hypothesis offers the best explanation of inequity aversion experiments.

are incentivized to conform to the shared behavioral pattern. Thus, these responses go beyond mere emotional expression; they constitute a social maintenance mechanism that preserves a behavioral pattern within bonobo societies.

The flexible nature of the forms of social maintenance observed in bonobos reinforces the normative interpretation of these behaviors. Unlike rigid, biologically fixed behavioral patterns—which do not allow for exceptions—responses to inequity in bonobos appear to be modulated by the social context, which indicates a degree of normative sensitivity. In particular, it has been observed that bonobos may tolerate an unequal distribution of rewards when it benefits an individual with whom they have a significant bond, such as a family member or a close social partner (Verspeek and Stevens 2022; Radovanović et al. 2025). This selective tolerance suggests that the “Equal reward for equal effort” norm does not operate inflexibly but can be modulated according to relational or contextual considerations. However, this tolerance does not extend to relationships with unfamiliar or socially distant individuals, where negative responses to inequity tend to reappear (Radovanović et al. 2025).

In sum, the aversion to inequality observed in bonobos can be understood as a form of social maintenance aimed at promoting conformity to a norm of equitable distribution. In this sense, responses to inequity reveal the existence of a foundational social norm—namely, a shared expectation of equity in resource distribution when there is equivalent effort. This norm, socially sustained and contextualized, allows us to understand bonobo behavior not only as the result of fixed emotional responses but also as an expression of forms of social normativity. Therefore, inequity aversion behaviors in bonobos are framed within a normative regularity.

4. Reactions to Interruptions of Social Activities in Bonobo Societies

In this section, I argue that bonobos’ reactions to interruptions of social activities, such as grooming and social play,² manifest normative regularities. In particular, I propose that these primates follow social

²The scientific literature typically describes these behaviors in terms of joint action and joint commitment. However, there is ongoing debate regarding the attribution of such capacities to non-human animals. Research on joint action originally focused on human children and was later extended to comparative studies involving humans and chimpanzees. Within the literature on humans, it has been argued that there are different types of joint actions and joint commitments that emerge across distinct developmental stages, and that not all joint actions involve a sense of mutual

norms that regulate both the initiation and termination of social activities. Moreover, the use of communicative gestures to encourage the continuation of an interrupted interaction constitutes a form of social maintenance. Thus, the fact that bonobos actively prompt their partners to resume social activities through specific signals (Pika and Zuberbühler 2008; Heesen et al. 2020, 2021a, 2021b; Bangerter et al. 2022) indicates the existence of an implicit norm that reinforces the obligation to complete the initiated activity.

A social activity can be defined as a cooperative action between at least two individuals who coordinate their individual efforts with the aim of achieving a common goal (Heesen et al. 2021a, 2021b). Reactions to interruption refer to the behavioral and communicative responses that arise when an ongoing social activity is disrupted. Such responses do not occur automatically but are mediated by communicative signals exchanged between participants, which encourage the continuation or restoration of the activity (Bangerter et al. 2022).

Social activities are structurally marked by entry and exit phases. These phases are characterized by the production of communicative signals that indicate the initiation or termination of the cooperative interaction. Such signals may include mutual gaze, physical contact, and vocalizations. In particular, mutual gaze recurrently marks the beginning and end of the social activity. Similarly, the termination of the action tends not to be abrupt but is also preceded by closing signals (Heesen et al. 2021a).

In bonobos, reactions to interruptions have been studied in the context of two types of social activities: social play and grooming; in the case of social play, bonobos engaged in various playful activities with both conspecifics and humans. These interactions involved an object and required both participants to perform alternating turn-taking sequences, as well as to coordinate their attention toward the task, the object, and the other agent (Pika and Zuberbühler 2008). Grooming, on the other hand, is a social behavior characteristic of primates that involves cleaning a partner's fur by removing parasites, dirt, or other impurities, and likewise requires active coordination between two individuals. Therefore, it is considered a relevant type of social activity for analyzing reactions to interruptions.

obligation between participants. Given the conceptual and psychological complexity of these phenomena, some authors have criticized their attribution to other animal species. To avoid entering this debate, and given that the normative pluralistic framework adopted here does not require positing specific underlying mental states, I use the terms “reactions to interruption” and “social activities” to refer to these behaviors.

Experimental studies designed to evaluate reactions to interruptions in bonobos consisted of artificially interrupting these social activities and observing subsequent behavior. Interruptions occurred in two ways: in some cases, one of the participants voluntarily withdrew from the interaction; in others, the interruption was caused by external factors. The aim of these designs was to examine whether bonobos would resume the same activity with their original partner, whether they attempted to encourage the participation of the partner who withdrew, or whether, on the contrary, they initiated a new interaction with a third party. The results indicate that, following an interruption, bonobos tend to resume social activity with their original partner, rather than with just any individual. Moreover, they do not resume the actions arbitrarily but accurately reproduce prior roles, spatial positions, and specific behaviors (Heesen et al. 2021a). For example, during grooming, they continue attending the same areas of the body as before the interruption. In general, it was observed that bonobos are more likely to resume social activities than interrupted individual activities. Additionally, bonobos who interrupt a social activity tend to produce communicative signals to restore the interaction. Rather than unilaterally abandoning the interaction, bonobos clearly mark the entry and exit phases of social activities through mutual gaze and physical contact (Heesen et al. 2021a, 2021b). Significantly, individuals encouraged their reluctant partners to resume their role in social interaction through communicative gestures (Pika and Zuberbühler 2008).

4.1. Patterns of Behavioral Conformity in Bonobos' Reactions to Interruptions of Social Activities

The underlying pattern of behavioral conformity related to reactions to interruptions of social activities in bonobos can be formulated as an implicit norm such as: “You should not abandon a social activity before completing it”, or “A cooperative activity should be continued until its completion or until a closing signal is produced”, or “You should not withdraw until the social activity has concluded”. Empirical evidence shows that when social activities were experimentally interrupted, bonobos tended to resume them with their original partners, regardless of the experimental condition or the nature of the social bond (Heesen et al. 2020). Whenever a social activity is interrupted, bonobos attempt to resume it. This recurrence suggests that social activities constitute a stable behavioral pattern within bonobo societies.

Furthermore, the fact that bonobos do not resume grooming with just any other individual present, nor do they randomly select new body parts to continue the task (Heesen et al. 2020), reinforces the thesis that these behaviors are normatively structured. The persistence in completing the activity with the same partner and resuming it under the same conditions as before the interruption—same role, same body location, same turn-taking order—suggests the existence of a tacit norm that “The social activity must be completed until a consensual closing signal is given”.

There is evidence indicating that bonobos are aware that violating a norm can entail social consequences. This reinforces the normative dimension of the phenomenon. It has been proposed that individuals might view the interruption of a social activity for individually motivated reasons (e.g., pursuing a food reward) as more inappropriate than interruptions motivated by events relevant to the group (Heesen et al. 2020). This distinction suggests that breaking the structure of the activity is not judged solely in instrumental terms but according to socially shared normative criteria about what constitutes a valid justification for abandoning a social activity. This, in turn, indicates that the behavior does not simply respond to individual motivations but is embedded within a normative pattern that regulates cooperation among individuals.

It could be argued that the motivation to resume social activities in bonobos simply reflects the desire to complete an unfinished task. However, empirical evidence suggests that this motivation goes beyond mere instrumental impulse. In particular, bonobos are less likely to resume an interrupted activity when it is solitary than when it is social, a pattern that is difficult to explain in purely instrumental terms. Rather, this behavior reveals a sense of obligation both to the partner and to the cooperative activity itself (Heesen et al. 2020). In this sense, such obligation can be understood as the result of recognizing a behavioral pattern, that is, following an implicit norm that holds social relevance for the individuals involved.

Understanding reactions to interruptions of social activities as governed by social norms helps explain why it appears to be independent of social rank and the quality of social bonds. Studies have shown that the likelihood of resuming and completing social activities does not depend on the quality of the social bond between participants, nor on their position in the hierarchy or kinship. In other words, the evidence shows that regardless of rank or kinship, bonobos seem to invest communicative efforts to ensure the social activity is resumed

and fully carried out (Heesen et al. 2021a). This independence from social status reinforces the idea that bonobos act not merely out of affinity or familiarity but are guided by a shared social norm. The tendency to resume cooperative activity with the same partner, even in the absence of strong affective bonds, can be interpreted as a form of responding to the implicit norm. Under this interpretation, reactions to interruptions of social activities are ruled by a social norm whose validity does not derive from individual ties with a specific participant, but from the norm itself. In sum, this behavior reveals not only an empirical recurrence but a normative behavioral pattern.

4.2. Social Maintenance within the Norms of Reactions to Interruptions of Social Activities

In this context, I propose that the persistent use of communicative gestures by bonobos toward deserters to restore interaction (Pika and Zuberbühler 2008; Heesen et al. 2020; 2021a; 2021b; Bangerter et al. 2022) can be understood as a form of social maintenance that sustains the norm and incentivizes non-conformers. To be more precise, these signals operate as normative instruments to socially pressure the reluctant partner to conform to the norm—that is, to resume their participation until the activity is completed, and a consensual closing signal is emitted.

Empirical evidence supports this interpretation. In cases of social play, it was observed that an individual takes their partner's hand to guide them back to the social activity (Pika and Zuberbühler 2008). In grooming scenarios, bonobos tended to expose the part of the body that was being groomed before the interruption, as a way of explicitly inviting the continuation of the task (Heesen et al. 2020). Bonobos become insistent when they notice that their partner is reluctant to resume the activity (Heesen et al. 2021a). In this sense, communicative signals operate as forms of positive social maintenance of the norm—that is, as strategies to encourage conformity without resorting to punishment, but through repeated invitations to conform to the behavioral pattern. Consequently, the use of communicative gestures to maintain social activities reveals a normatively organized structure of this phenomenon, in which individuals not only act together but also know that they must continue until the appropriate normative criteria for closure are met.

In summary, I have suggested that bonobos possess social norms that regulate reactions to interruptions of social activities. These implicit norms can be understood as patterns of behavioral conformity

according to which a cooperative action should not be interrupted until its consensual completion. Such norms appear to structure the expectation that participants will maintain their involvement until a closing signal recognized by all parties is produced. When this norm is violated—that is, when one individual withdraws from the social activity before it concludes and without producing the corresponding exit gesture—the other participants tend to emit communicative signals aimed at promoting their return and the resumption of the activity. These communicative efforts to restore the behavioral pattern can be interpreted as forms of social maintenance of the norm. All of this suggests that reactions to interruptions of social activities are governed by a socially maintained behavioral pattern that is important for bonobo communities.

5. Female Coalitions in Bonobo Societies

In this section, I argue that female coalition formation in bonobos can be interpreted as a form of social maintenance that reveals the existence of an underlying norm. In particular, these coalitions operate as a third-party punishment mechanism: their formation follows a consistent pattern in which, whenever a male exhibits aggressive behavior toward females or offspring, a collective response arises to sanction him. This suggests that these alliances are guided by a normative regularity aimed at protecting group cohesion and ensuring the well-being of its most vulnerable members.

Female coalitions consist of strategic alliances between two or more females aimed at targeting a conspecific, typically a male within the group (Tokuyama and Furuichi 2016). It has been documented in both captive and wild bonobos that females frequently form coalitions, which may be dyadic or involve more than two individuals, including unrelated females (Surbeck et al. 2025). These coalitions are neither random nor reactive in a merely individual sense; rather, they tend to be activated in response to prior aggressive behaviors by males toward females and offspring (Tokuyama and Furuichi 2016). In a recent observation, researchers documented an adult male bonobo being repeatedly attacked by a coalition of several adult females. The authors hypothesized that the incident was likely triggered by the male's aggression toward an offspring two days prior (Pashchevskaya et al. 2025).

It has been observed that these coalitions are not limited to the intragroup context. In encounters between different groups, females

may form alliances with females from other groups to collectively respond to male threats or aggression (Tokuyama et al. 2019). Furthermore, coalitions exhibit a hierarchical structure, with older females tending to support younger ones. Recently, it has been proposed that female coalitions also constitute a behavioral strategy aimed at increasing female power relative to males, thereby reconfiguring the group's hierarchical dynamics (Surbeck et al. 2025).

5.1. Patterns of Behavioral Conformity in Bonobos' Female Coalitions

The pattern of behavioral conformity underlying female coalition formation can be formulated as an implicit social norm such as: "Females and offspring should not be disturbed." Given that females in bonobo societies occupy privileged positions in the hierarchy—including priority access to resources such as food (Tokuyama and Furuichi 2016)—it is consistent that there are social norms aimed at protecting their physical and social integrity. Violating this integrity can have destabilizing implications for the cohesion of the group as a whole.

Bonobo societies are distinguished by their peaceful character and high level of tolerance. It is likely that bonobos perceive the general tranquility of the group as appropriate and desirable, and therefore as a habitual state that should be preserved and collectively restored when disrupted. Thus, the social norm behind female coalition formation aims to preserve group harmony and maintain the stability of its hierarchy. In this way, disruptive behavior not only breaks collective tranquility but becomes more serious when directed at individuals considered fundamental to the cohesion and stability of the community, such as females and offspring.

Empirical evidence supports this interpretation. Female coalitions in bonobos do not occur arbitrarily but are specifically activated when males display aggressive behaviors toward females or offspring (Tokuyama and Furuichi 2016). Whenever an episode of harassment, aggression, or disturbance by a male occurs, a coalition response by females tends to emerge (Vervaecke et al. 2000). This stable and identifiable recurrence reveals the presence of a normative behavioral pattern within bonobo groups.

5.2. Social Maintenance within the Norms Governing Female Coalitions

I argue that female coalition formation in bonobos constitutes a form of social maintenance for a behavioral pattern. The purpose of these coalitions lies in applying third-party punishment against males who do not conform to the implicit norm of not harming females and offspring. Third-party punishment is a type of negative response that refers to the sanction imposed on non-conformers by observers who are not directly affected by or involved in the transgression (Andrews et al. 2024). In the case of bonobos, the females who participate in the coalition are not always direct victims of the disruptive behavior; rather, they intervene in solidarity with the purpose of correcting or deterring non-conformers who threaten the group's cohesion. In this sense, these coalitions constitute social maintenance mechanisms that sanction violations of an underlying behavioral pattern aimed at protecting the integrity of females and offspring and the overall stability of the group. The recurrence and consistency of these responses make it possible to interpret them not as mere emotional reactions but as a form of social maintenance of a norm within the social fabric of bonobo communities.

The fact that coalition formation maintains a consistent structure regarding the rank of its members reinforces this interpretation. Evidence suggests that the most frequent coalitions are those formed by older females supporting younger females. Rather than being a case of reciprocal agonistic support among females, observational evidence from wild bonobos indicates that this is a unidirectional pattern (Tokuyama and Furuichi 2016). Older females appear to hold higher rank within bonobo societies, and these coalitions seem to be part of the mechanisms through which an implicit norm is socially maintained. The unidirectional support of adult females toward younger females suggests that the motivations for coalitions are strictly social and aimed at maintaining norms for the general welfare of the group. In this sense, the older females within these coalitions play a group control role over aggressive and harassing males.

Overall, the evidence can be interpreted to suggest that coalitions play a role in maintaining social order. These coalitions help suppress disruptive behaviors within the group. This is why individuals who challenge the hierarchical order of females through aggression or harassment are those most frequently targeted (Vervaecke et al. 2000). This indicates that coalitions act as mechanisms of social regulation

and group control intended to sustain the hierarchy, since failing to do so would put the stability of the social structure at risk.

Additionally, it has been noted that female coalitions not only help preserve females' privileged positions within the social structure but also enhance them. In bonobo societies, female coalitions appear to be aimed at controlling males, thereby serving to gain power over them and to maintain social order and well-being (Surbeck et al. 2025). In other words, female coalitions are fundamental strategies for maintaining power and sustaining the structure of bonobo societies. Female coalitions operate as forms of social norm maintenance within their societies—norms related to peace and the protection of females and their offspring.

In sum, I have argued that female coalition formation in bonobos constitutes a form of third-party punishment that maintains a normative regularity concerning the integrity of females and offspring. These coalitions operate as collective mechanisms of social control in response to male aggression, seeking to preserve group well-being, protect its most vulnerable members, and sustain the hierarchical balance that benefits females. Therefore, rather than being mere defensive reactions, coalitions should be understood as forms of social maintenance for a norm that safeguards females—and, through them, the stability and organization of bonobo societies.

6. *Conclusion*

I have argued that bonobos exhibit behaviors that can be interpreted as social norms. To do so, I have followed the definition of social norms proposed by the normative pluralism framework, according to which social norms are normative regularities (Westra and Andrews 2022; Westra et al. 2024). I have pointed out that these social norms can be identified in at least three typical social behaviors found in bonobo societies: responses of inequity aversion, reactions to interruptions of social activities, and female coalition formation. In each of these, I have identified two fundamental components of normative regularities: (1) the pattern of behavioral conformity and (2) the forms of social maintenance that sustain it.

It can be concluded that the available evidence shows that bonobo societies possess implicit social norms in the form of normative regularities governing fundamental aspects of their society, such as equitable resource distribution, the completion of social activities, the protection of important members of their societies such as females and offspring, and the preservation of social structure.

Moreover, bonobo societies actively engage in the social maintenance of these normative regularities, whether through negative responses—such as protests against situations of inequity—or through positive responses, like the use of communicative gestures to encourage conspecifics to uphold their activities. All of this indicates that social norms are important to members of bonobo communities and that these norms play a significant role in their social interactions.

A potential objection to the present account is that the available evidence does not clearly establish the existence of social maintenance mechanisms in the three cases discussed, and that the behaviors in question are therefore over-interpreted as normative regularities. For example, it might be argued that evidence for inequity aversion is confined to token-exchange experiments, that bonobos do not exert social pressure to sustain joint activities in wild contexts, or that female coalitions do not function as forms of third-party punishment against male aggression. This concern can be addressed by noting that the objection rests on the assumption that a normative reading introduces explanatory commitments that go beyond the available evidence. However, the present account does not posit additional mechanisms or entities beyond those already required to describe the observed behavioral patterns and social responses. Rather, it offers a minimal normative interpretation of the same empirical regularities, one that captures their stability, their sensitivity to specific forms of deviation, and their socially mediated maintenance over time. Accordingly, it is sufficient, for the purposes of attributing a minimal and pluralistic form of normativity, to identify relatively stable behavioral patterns whose violation elicits social responses aimed at correction or restoration. On this view, experimental evidence of inequity aversion supports sensitivity to violated fairness expectations under conditions of equal effort; reactions to interruptions are evidenced by socially maintained regularities in social activities, where premature withdrawal prompts communicative repair; and female coalitions need only be systematically activated in response to specific forms of aggression, rather than functioning as punishment in all cases. The identification of implicit social norms in bonobo societies strengthens the normative pluralism framework and provides additional empirical evidence on animal normativity, complementing previous analyses in chimpanzees. This reinforces the thesis that certain behavioral regularities, sustained by social maintenance mechanisms, can be interpreted as social norms even in non-human species.

The possibility remains open that future research will identify new normative regularities in other areas of bonobo behavior. Advancing along this line will not only allow for a deeper understanding of the social dynamics of this species but also enable a more precise grasp of the structural complexity of social norms in animal communities, thereby facilitating meaningful comparisons with the normative dimension in humans.

Likewise, it would be pertinent to extend approaches inspired by normative pluralism to other species of great apes. This framework could enrich philosophical elaborations in the field of the psychology of norms by providing comparative evidence that supports discussions on the nature and origins of normativity within the primate lineage. Together, these advances would contribute to the development of more comprehensive, rigorous, and coherent theoretical frameworks aligned with an evolutionary perspective on social norms in both human and non-human communities.³

REFERENCES

- Andrews, Kristin, 2020, “Naïve Normativity: The Social Foundation of Moral Cognition”, *Journal of the American Philosophical Association*, vol. 6, no. 1, pp. 36–56. (<https://doi.org/10.1017/apa.2019.30>)
- Andrews, Kristin, Simon Fitzpatrick, and Evan Westra, 2024, “Human and Nonhuman Norms: A Dimensional Framework”, *Philosophical Transactions of the Royal Society B: Biological Sciences*, vol. 379, no. 1897, 20230026. (<https://doi.org/10.1098/rstb.2023.0026>).
- Bangerter, Adrian, Emilie Genty, Raphaela Heesen, Federico Rossano, and Klaus Zuberbühler, 2022, “Every Product Needs a Process: Unpacking Joint Commitment as a Process across Species”, *Philosophical Transactions of the Royal Society B: Biological Sciences*, vol. 377, no. 1859, 20210095. (<https://doi.org/10.1098/rstb.2021.0095>).
- Bicchieri, Cristina, 2017, *Norms in the Wild: How to Diagnose, Measure, and Change Social Norms*, Oxford University Press, New York.
- Bicchieri, Cristina, 2006, *The Grammar of Society*, Cambridge University Press, New York.

³ I would like to thank Kristin Andrews and Susana Monsó for their valuable feedback during the formulation of the core ideas in this article. I am also grateful to Mike Rotter, Carlos Gonzalez-Sierra, Marriah Alcantara and two anonymous reviewers for their helpful comments and suggestions on earlier drafts. Finally, I thank the Secretaría de Ciencia, Humanidades, Tecnología e Innovación (SECIHTI) for the doctoral research grant that supported the writing of this paper.

- Birch, Jonathan, 2021, “Toolmaking and the Evolution of Normative Cognition”, *Biology and Philosophy*, vol. 36, no. 4. (<https://doi.org/10.1007/s10539-020-09777-9>)
- Brooker, Jake S., Christine E. Webb, Stephanie Kordon, Frans B.M. de Waal, and Zanna Clay, 2025, “Within-Species Variation Eclipses Between-Species Differences in Pan Consolation”, *Evolution and Human Behavior*, vol. 46, no. 1, 106682. (<https://doi.org/10.1016/j.evolhumbehav.2025.106682>)
- Brosnan, Sarah F., 2006, “Nonhuman Species Reactions to Inequity and Their Implications for Fairness”, *Social Justice Research*, vol. 19, pp. 153–185. (<https://doi.org/10.1007/PL00022136>)
- Brosnan, Sarah F., and Frans B.M. de Waal, 2003, “Monkeys Reject Unequal Pay”, *Nature*, vol. 425, pp. 297–299. (<https://doi.org/10.1038/nature01963>)
- Danón, Laura, 2024, “Normativity in Chimpanzees’ Tool Behavior”, *Topoi*. (<https://doi.org/10.1007/s11245-024-10137-5>)
- Danón, Laura, 2019, “Animal Normativity”, *Phenomenology and Mind*, no. 17, pp. 176–187. (<https://doi.org/10.13128/pam-8035>)
- Dennett, Daniel C., 1991, “Real Patterns”, *The Journal of Philosophy*, vol. 88, pp. 27–51.
- Engelmann, Jan M., Jeremy B. Clift, Esther Herrmann, and Michael Tomasello, 2017, “Social Disappointment Explains Chimpanzees’ Behaviour in the Inequity Aversion Task”, *Proceedings of the Royal Society B: Biological Sciences*, vol. 284, no. 1861, 20171502. (<https://doi.org/10.1098/rspb.2017.1502>)
- Fitzpatrick, Simon, 2020, “Chimpanzee Normativity: Evidence and Objections”, *Biology & Philosophy*, vol. 35, no. 45. (<https://doi.org/10.1007/s10539-020-09763-1>)
- Hare, Brian, and Shinya Yamamoto, 2017, *Bonobos: Unique in Mind, Brain, and Behavior*, Oxford University Press, Oxford.
- Heesen, Raphaela, Adrian Bangerter, Klaus Zuberbühler, Katia Iglesias, Christof Neumann, Aude Pajot, Laura Perrenoud, Jean-Pascal Guéry, Federico Rossano, and Emilie Genty, 2021a, “Assessing Joint Commitment as a Process in Great Apes”, *iScience*, vol. 24, no. 8, 102872. (<https://doi.org/10.1016/j.isci.2021.102872>)
- Heesen, Raphaela, Klaus Zuberbühler, Adrian Bangerter, Katia Iglesias, Federico Rossano, Aude Pajot, Jean-Pascal Guéry, and Emilie Genty, 2021b, “Evidence of Joint Commitment in Great Apes’ Natural Joint Actions”, *Royal Society Open Science*, vol. 8, no. 12, 211121. (<https://doi.org/10.1098/rsos.211121>)
- Heesen, Raphaela, Adrian Bangerter, Klaus Zuberbühler, Federico Rossano, Katia Iglesias, Jean-Pascal Guéry, and Emilie Genty, 2020, “Bonobos Engage in Joint Commitment”, *Science Advances*, vol. 6, no. 51, eabd1306. (<https://doi.org/10.1126/sciadv.abd1306>)

- Henrich, Joseph, 2015, *The Secret of Our Success: How Culture Is Driving Human Evolution, Domesticating Our Species, and Making Us Smarter*, Princeton University Press, Princeton, New Jersey.
- Hohmann, Gottfried, and Barbara Fruth, 2003, "Culture in Bonobos? Between-Species and Within-Species Variation in Behavior", *Current Anthropology*, vol. 44, no. 4, pp. 563–571. (<https://doi.org/10.1086/377649>)
- Kumar, Victor, and Richmond Campbell, 2022, *A Better Ape: The Evolution of the Moral Mind and How It Made Us Human*, Oxford University Press, New York.
- Lorini, Giuseppe, 2018, "Animal Norms: An Investigation of Normativity in the Non-Human Social World", *Law, Culture and the Humanities*, vol. 18, no. 3, pp. 1–22. (<https://doi.org/10.1177/1743872118800008>)
- Nichols, Shaun, 2004, *Sentimental Rules: On the Natural Foundations of Moral Judgment*, Oxford University Press, Oxford.
- O'Neill, Elizabeth, and Edouard Machery, 2018, "The Normative Sense: What Is Universal? What Varies?", in Aaron Zimmerman, Karen Jones, and Mark Timmons (eds.), *The Routledge Handbook of Moral Epistemology*, Routledge, New York, pp. 38–56.
- Pashchevskaya, Sonya, Barbara Fruth, Sofia Lunde Kjørland, Leonardo Berton, Linda Vigilant, and Gottfried Hohmann, 2025, "Coalitionary Intra-Group Aggression by Wild Female Bonobos", *Current Biology*, vol. 35, no. 19, pp. R912–R913. (<https://doi.org/10.1016/j.cub.2025.08.010>)
- Pika, Simone, and Klaus Zuberbühler, 2008, "Social Games between Bonobos and Humans: Evidence for Shared Intentionality?", *American Journal of Primatology*, vol. 70, no. 3, pp. 207–210. (<https://doi.org/10.1002/ajp.20469>)
- Radovanović, Kia, Anoek Lorskens, Sebastian Schütte, Juliane Bräuer, Josep Call, Daniel B.M. Haun, and Edwin J.C. van Leeuwen, 2025, "Bonobos Respond Aversively to Unequal Reward Distributions", *Proceedings of the Royal Society B: Biological Sciences*, vol. 292, no. 2045, 2873. (<https://doi.org/10.1098/rspb.2024.2873>)
- Richerson, Peter J., and Robert Boyd, 2005, *Not by Genes Alone: How Culture Transformed Human Evolution*, University of Chicago Press, Chicago.
- Ritov, Oded, Christoph J. Völter, Nichola J. Raihani, and Jan M. Engelmann, 2024, "No Evidence for Inequity Aversion in Non-Human Animals: A Meta-Analysis of Accept/Reject Paradigms", *Proceedings of the Royal Society B: Biological Sciences*, vol. 291, no. 2035, 20241452. (<https://doi.org/10.1098/rspb.2024.1452>)
- Rochat, Philippe, 2015, "Self-Conscious Roots of Human Normativity", *Phenomenology and the Cognitive Sciences*, vol. 14, no. 4, pp. 741–753.
- Roma, Peter G., Alan Silberberg, Angela M. Ruggiero, Stephen J. Suomi, 2006, "Capuchin Monkeys, Inequity Aversion, and the Frustration Ef-

- fect”, *Journal of Comparative Psychology*, vol. 120, no. 1, pp. 67–73. (<https://doi.org/10.1037/0735-7036.120.1.67>)
- Samuni, Liran, Franziska Wedgell, and Martin Surbeck, 2020, “Behavioural Diversity of Bonobo Prey Preference as a Potential Cultural Trait”, *eLife*, vol. 9, e59191. (<https://doi.org/10.7554/eLife.59191>).
- Silberberg, Alan, Lara Crescimbene, Elsa Addressi, James R. Anderson, and Elisabetta Visalberghi, 2009, “Does Inequity Aversion Depend on a Frustration Effect? A Test with Capuchin Monkeys (*Cebus apella*)”, *Animal Cognition*, vol. 12, pp. 505–509. (<https://doi.org/10.1007/s10071-009-0211-6>)
- Sterelny, Kim, 2021, *The Pleistocene Social Contract*, Oxford University Press, Oxford.
- Surbeck, Martin, Leveda Cheng, Melodie Kreyer, Gerrit Gort, Roger Mundry, Gottfried Hohmann, and Barbara Fruth, 2025, “Drivers of Female Power in Bonobos”, *Communications Biology*, vol. 8, 550. (<https://doi.org/10.1038/s42003-025-07900-8>)
- Tokuyama, Nahoko, and Takeshi Furuichi, 2016, “Do Friends Help Each Other? Patterns of Female Coalition Formation in Wild Bonobos at Wamba”, *Animal Behaviour*, vol. 119, pp. 27–35. (<https://doi.org/10.1016/j.anbehav.2016.06.021>).
- Tokuyama, Nahoko, Tetsuya Sakamaki, and Takeshi Furuichi, 2019, “Inter-Group Aggressive Interaction Patterns Indicate Male Mate Defense and Female Cooperation across Bonobo Groups at Wamba, Democratic Republic of the Congo”, *American Journal of Physical Anthropology*, vol. 170, no. 4, pp. 535–550. (<https://doi.org/10.1002/ajpa.23929>)
- Tomasello, Michael, 2019, “The Moral Psychology of Obligation”, *Behavioral and Brain Sciences*, vol. 43, no. 2020, pp. 1–58. (<https://doi.org/10.1017/S0140525X19001742>)
- Tomasello, Michael, 2016, *A Natural History of Human Morality*, Harvard University Press, Cambridge, Mass.
- van Leeuwen, Edwin J. C., Nicky Staes, Jonas Verspeek, William J.E. Hoppitt, and Jeroen M.G. Stevens, 2020, “Social Culture in Bonobos”, *Current Biology*, vol. 30, no. 6, pp. R261–R262. (<https://doi.org/10.1016/j.cub.2020.02.038>)
- van Leeuwen, Edwin J.C., Nicky Staes, Marcel Eens, and Jeroen M.G. Stevens, 2024, “Group-Level Signatures in Bonobo Sociality”, *Evolutionary Human Sciences*, vol. 6, e48. (<https://doi.org/10.1017/ehs.2024.44>)
- Verspeek, Jonas, and Jeroen M.G. Stevens, 2022, “Behavioral and Physiological Response to Inequity in Bonobos (*Pan paniscus*)”, *American Journal of Primatology*, vol. 85, no. 1, e23455. (<https://doi.org/10.1002/ajp.23455>)
- Vervaecke, Hilde, Han de Vries, and Linda van Elsacker, 2000, “Distribution and Function of Coalitions in Captive Bonobos (*Pan paniscus*)”, *Primates*, vol. 41, no. 3, pp. 249–265. (<https://doi.org/10.1007/BF02557595>)

- Westra, Evan, and Kristin Andrews, 2022, “A Pluralistic Framework for the Psychology of Norms”, *Biology & Philosophy*, vol. 37, no. 40. (<https://doi.org/10.1007/s10539-022-09871-0>)
- Westra, Evan, Simon Fitzpatrick, Sarah F. Brosnan, Thibaud Gruber, Catherine Hobaiter, Lydia M. Hopper, Daniel Kelly, Christopher Krupenye, Lydia V. Luncz, Jordan Theriault, Kristin Andrews, 2024, “In Search of Animal Normativity: A Framework for Studying Social Norms in Non-Human Animals”, *Biological Reviews*, vol. 99, no. 3, pp. 1058–1074. (<https://doi.org/10.1111/brv.13056>)
- Whiten, Andrew, 2020, “Social Learning: Does Culture Shape Hunting Behavior in Bonobos?”, *eLife*, vol. 9, e62104. (<https://doi.org/10.7554/eLife.62104>)

Received: July 7, 2025; accepted: January 31, 2026.