

# What *isn't* social tolerance? The past, present, and possible future of an overused term in the field of primatology

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## Abstract

In the past four decades, the term *social tolerance* has been utilized to describe, explain, and predict many different aspects of primates' sociality and has been measured with a large range of traits and behaviors. To date, however, there has been little discussion on whether these different phenomena all reflect one and the same construct. This paper opens the discussion by presenting the historical development of the term social tolerance and a structured overview of its current, overextended use. We argue that social tolerance has developed to describe two distinct concepts: social tolerance as the social structure of a group and social tolerance as the dyadic or group-level manifestation of tolerant behaviors. We highlight how these two concepts are based on conflicting theoretical understandings and practical assessments. In conclusion, we present suggestions for future research on primate social tolerance, which will allow for a more systematic and comparable investigation of primate sociality.

## KEYWORDS

despotism, egalitarianism, phylogenetic model, primate behavior, social style, social tolerance, socio-ecological model, systematic variation

## 1 | INTRODUCTION

*Social tolerance* has become a pivotal construct in primatology, used by a plethora of studies to describe, explain, and predict primate social structures and behaviors. As such, it is frequently presented as one of the necessary preconditions for both the evolution and the performance of particular phenomena of human and non-human primate sociality, such as prosociality, cooperation, and social learning.<sup>1–12</sup> For instance, macaque species (*Macaca* spp.) have been organized into four grades of social style according to their levels of social tolerance, as typically measured by rates of aggression, counter-aggression, and post-conflict reconciliation.<sup>13</sup> Membership in these grades has been used to predict differences in, among others, resource partitioning,<sup>14</sup> reproductive skew,<sup>15</sup> and prosocial behavior.<sup>16</sup> With a similar aim, van Schaik and colleagues<sup>17</sup> assessed

social tolerance in orangutans (*Pongo* spp.) and chimpanzees (*Pan troglodytes* spp.) with measures relating to time spent in (foraging) parties and food-sharing and used this operationalization to predict sub-species and group differences in tool use. Socially tolerant behavior—measured yet differently with experimental dyadic cofeeding paradigms—has also been central in comparisons between bonobos (*Pan paniscus*) and chimpanzees. Here, differences in the socially tolerant behaviors among the two species have been used to explain differences in, for example, cooperation<sup>2</sup> and social inhibition.<sup>18</sup> These studies are exemplary of the broader field of research on social tolerance, whose definitions and measures have grown to encompass a large range of behaviors as well as attributes of dominance hierarchies. While all of these different phenomena are termed *social tolerance*, there has been, to date, little discussion on whether they actually reflect the same construct.

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This paper aims to bring structure and clarity to the study of social tolerance, which will enable a more systematic understanding of primate sociality. In pursuing this aim, we first present a short historical overview of the emergence and propagation of the term social tolerance in primatology. Based on this historical overview, we demonstrate how previous understandings of social tolerance do not reflect the same underlying construct. We argue that they have instead developed to describe what we see as two distinct concepts: social tolerance as a behavioral concept, referring to the dyadic or group-level manifestation of a specific behavior, and social tolerance as a structural concept, describing the social structure of a group, which is based on multiple traits and behaviors. We then present a structured overview of the most commonly used measures for social tolerance. Throughout, we highlight conflicting definitions and assessments. We conclude with suggestions for future research on primate social tolerance, which will allow for a more comparable investigation of primate sociality.

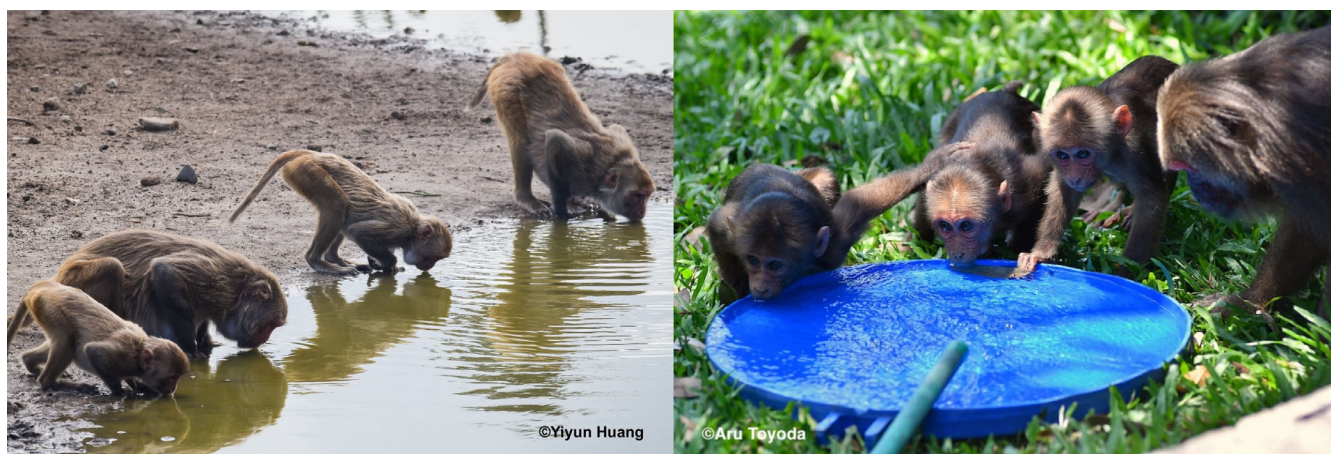
## 2 | THE PAST: WHERE DID THE TERM SOCIAL TOLERANCE COME FROM?

In the field of primatology, *social tolerance* was first coined by de Waal in 1986 in his paper “Class structure in a rhesus monkey group: the interplay between dominance and tolerance”<sup>19</sup> and was further elaborated on in his subsequent 1986 publication “The integration of dominance and social bonding in primates.”<sup>20</sup> *Social tolerance* was assessed by de Waal with different measures of dyadic codrinking and dyadic resource-proximity<sup>19</sup> and was later defined as the phenomenon that dominant individuals refrain from using their superior position to monopolize resources.<sup>20</sup> This was not in itself an entirely new concept, and de Waal referred to previous descriptions such as “concessionary behavior,” “respect for possession,” “control over the desire for exclusive possession,” and “special tolerance” (de Waal,<sup>20(p463)</sup>) as

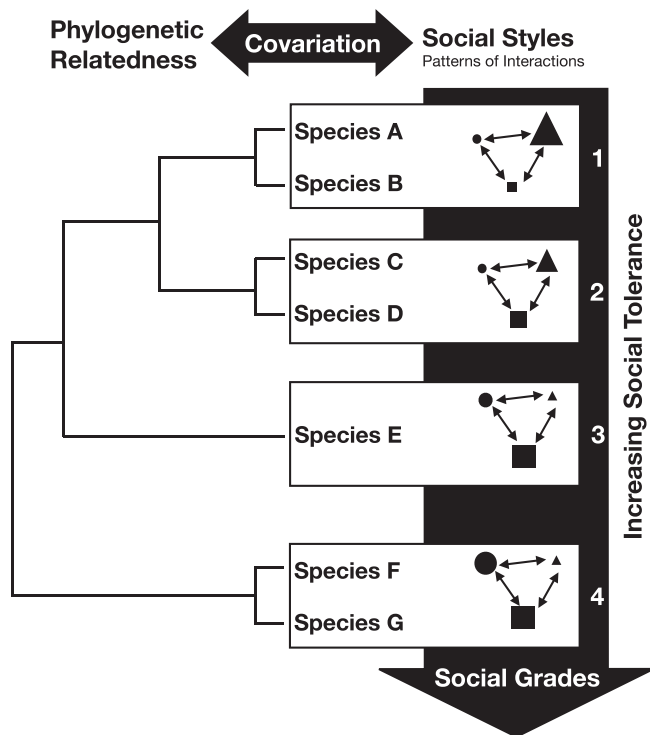
representing the same construct—but it was the first time that such a phenomenon was referred to as *social tolerance*.

These papers were written as an answer to the limited operationalization of dominance hierarchies in the existing literature. At the time, the common approach for experimentally studying dominance hierarchies was to create an artificial resource competition in which dyads or groups of conspecifics were deprived of either food or water and were subsequently given access to the resource.<sup>20</sup> This was done in a manner that only one individual could gain access—effectively ruling out any sort of tolerance.<sup>21</sup> This approach resulted in competitive situations that had only two possible outcomes: an individual was either dominant and won the competition, or subordinate and lost accordingly.<sup>20</sup> De Waal made the case that this approach poorly reflected group-living animals' natural dynamics in which individuals are rarely confronted with such binary outcomes. Instead, they are more likely to face resources that are spread out over large areas, which afford them with the additional options of either avoiding the situation or tolerating one another.<sup>20</sup> Therefore, he created a group-feeding context in which multiple individuals (but not the whole group) could simultaneously access a drinking resource.<sup>19</sup>

At this point, social tolerance referred to a characteristic of a dominant individual or a dyadic relationship. The first study that defined social tolerance as a characteristic of an entire group was from de Waal and Luttrell,<sup>22</sup> in which they compared dominance styles of rhesus (*Macaca mulatta*) and stump-tail macaques (*Macaca arctoides*) (see Figure 1). Social tolerance was again measured with a codrinking paradigm and operationalized in two manners: the first measure focused on the percentage of tolerant interactions (i.e., two individuals codrinking, or the presence of subordinates in the vicinity of the water while dominants were drinking). The second measure, which the authors claimed to be especially indicative of social tolerance, was the number of instances in which dominant individuals attempted to exclude subordinates from the water resource but were unsuccessful.<sup>22</sup> In this paper, social tolerance is proposed to be one of



**FIGURE 1** Rhesus macaques (left) and stump-tail macaques (right) codrinking (photos not from the original experiment). Left: Free-ranging rhesus macaques codrinking at Cayo Santiago, Puerto Rico. Photo credit: Yiyun Huang (University of Michigan). Right: Semi-wild stump-tail macaques codrinking at the Khao Krapuk Khao Taomor (KKP) Non-hunting Area, Thailand. Photo credit: Aru Toyoda (Chubu University)



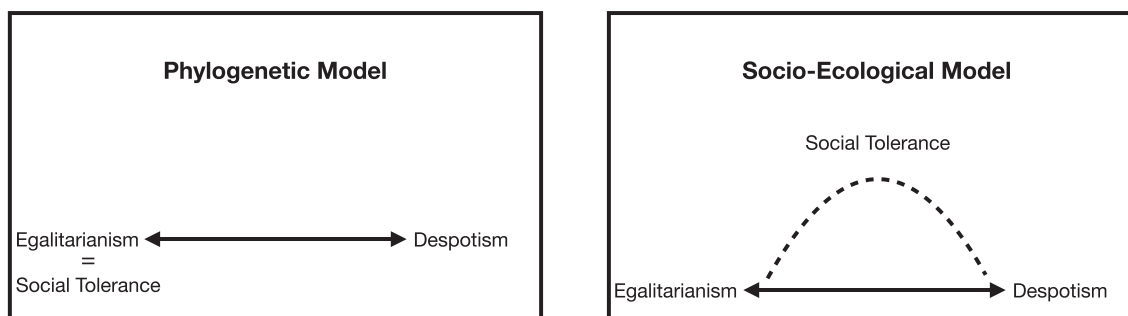
**FIGURE 2** Covariation between the phylogenetic relatedness and social styles of macaques. According to the phylogenetic model, the phylogenetic relatedness of macaque species (here illustrated by the phylogenetic tree) covaries with their social styles (here illustrated by arbitrary symbols representing different patterns of interactions). These social styles are organized into four grades of increasing social tolerance

many characteristics (e.g., reconciliation, aggression, grooming) that represent a specific dominance style that might covary with primate species' socioecology.<sup>22</sup>

While de Waal and colleagues' initial papers used social tolerance to describe specific, tolerant behaviors, social tolerance became most widely known through its use in what has been termed *systematic variation hypotheses*.<sup>23–25</sup> Systematic variation hypotheses encompass multiple theories that all assume that different aspects of primate social structures covary,<sup>23–25</sup> in particular “traits related to conflict and conflict management” (Cooper & Bernstein,<sup>26(p226)</sup>). Within some of these hypotheses, social tolerance progressed from being one of many covarying traits (e.g., de Waal & Luttrell<sup>22</sup>) to being used to describe an entire social structure or social style encompassing multiple covarying traits. A prominent model in this tradition is the phylogenetic model, which is based on a series of studies on macaques,<sup>13</sup> most of which have focused on female social behavior (see, e.g., Thierry et al.,<sup>27</sup> Balasubramaniam et al.<sup>28,29</sup>). According to this model, macaque species' social structures can be characterized by specific patterns of systematic variation in their behaviors, especially those relating to conflict management. These similarities in social styles are assumed to covary with the species' phylogenetic relatedness<sup>13</sup> (see Figure 2). Thierry<sup>13,30</sup> defined four social styles ranging from socially intolerant/despotic to socially tolerant/egalitarian and

postulated that each macaque species could be assigned to exactly one grade. According to Thierry's<sup>13</sup> approach, macaque species in the more socially tolerant grades have lower-severity conflicts involving more protests and counterattacks, which are then followed by more reconciliation. These socially tolerant macaque species are further characterized by fewer or less formalized submissive displays and are less affected by dominance and female kinship relationships compared with the less socially tolerant species.<sup>13</sup>

In parallel to the growing use of social tolerance in macaque studies, social tolerance also took root in another systematic variation model: the socio-ecological model of female relationships.<sup>31,32</sup> This model proposes that primate females' social relationships can be explained by a combination of ecological and social variables such as predator vulnerability, food distribution, population density, and the corresponding levels of inter- and intragroup competition.<sup>31,33,34</sup> The resulting relationships between females were initially proposed to vary along two dimensions: individualistic to nepotistic and egalitarian to despotic.<sup>33</sup> Social tolerance was later added as a third dimension<sup>31</sup> and describes the situation in which dominant individuals concede their priority to food resources or mating opportunities to subordinate individuals. In this context, therefore, social tolerance requires a certain level of despotism—that is, the presence of clearly established dominance hierarchies<sup>31</sup>—and nepotism. Dominant individuals are most likely to concede their priority of access in societies that have dominance hierarchies but in which dominant individuals rely on the support of subordinates<sup>35</sup> (also known as “subordinate leverage” [van Schaik,<sup>36(p269)</sup>]). This dynamic results in less active and more formal dominance relationships, which are based on specific indicators of submission and dominance.<sup>22,31,35,36</sup> Similar to the phylogenetic model, the socio-ecological model presents socially tolerant societies as characterized by less severe (but still common) aggression, more threats toward dominant group members, and more behaviors that enhance group cohesion.<sup>31</sup> The two models differ, however, in how they propose that despotism will affect social tolerance levels. Most studies working with the phylogenetic model use the term social tolerance synonymously with egalitarianism and despotism synonymously with intolerance (e.g., Adams et al.<sup>37</sup>; Kawazoe<sup>38</sup>; Balasubramaniam et al.<sup>39</sup>; Ciani et al.<sup>40</sup>; Matsumura<sup>41</sup>; Sueur et al.<sup>42</sup>; cf. Thierry<sup>43</sup>; Berman et al.<sup>44</sup>). Despotism is therefore considered to decrease social tolerance (see Figure 3). Following de Waal and Luttrell's statement that formal dominance need not vary with the outcomes of actual competitive interactions,<sup>22</sup> the socio-ecological model places tolerance on a dimension separate from despotism. Further, it proposes that a certain level of despotism (based on a formal dominance hierarchy) is necessary for social tolerance to be displayed, since only in a clearly defined dominance hierarchy would there be an incentive for dominant individuals to be socially tolerant of their subordinates.<sup>22,31,35</sup> The relationship between despotism and social tolerance, as described by the socio-ecological model, might be best understood as an inverted U-shape: both a lack of a dominance hierarchy (i.e., egalitarianism) and high levels of despotism prohibit social tolerance, while an intermediate level of despotism, combined with the reliance of dominant individuals on coalitionary support fosters social tolerance<sup>31,35,36</sup> (see Figure 3).



**FIGURE 3** Relationship between despotism and social tolerance in the phylogenetic and socioecological model. Left: In the phylogenetic model social tolerance is seen as synonymous with egalitarianism. Right: In the socioecological model the relationship is an inverted U-shape. Both very high and very low levels of despotism (i.e., egalitarianism) prohibit social tolerance

Finally, social tolerance also became a central component of what we consider to be yet another systematic variation hypothesis: the self-domestication model.<sup>1,9</sup> This model posits that the selection for socially tolerant and *against* aggressive behavior has led to the development of a whole array of behavioral, cognitive, and physical characteristics, including prosocial and cooperative behavior.<sup>1,9,45</sup> Without specific emphasis, the self-domestication model wields social tolerance as an all-encompassing concept referring roughly to various nonaggressive behaviors (e.g., peaceful cofeeding and food sharing).

While much of the previous literature has utilized social tolerance to describe a social structure encompassing multiple covarying traits, social tolerance has also continued to be used to describe specific, tolerant behaviors. As a behavioral concept, building on the early work by de Waal,<sup>19,20</sup> it has come to be defined in the primate literature as, for instance, “the willingness of individuals to interact non-agonistically with each other and to spend time in proximity to their social partner” (Rina Evasoa et al.,<sup>46(p12)</sup>), which was assessed with measures of cofeeding, proximity, (lack of) general aggression and dyadic dominance, “low competitive tendency, especially by dominants towards subordinates” (de Waal,<sup>21(p246)</sup>) which was based on previous studies measuring social tolerance with cofeeding and proximity,<sup>19,22</sup> “the probability that individuals will be in proximity to conspecifics around valuable resources with little or no aggression” (Cronin & Sánchez,<sup>47(pp1250066-4)</sup>) based on previous literature reporting measures of proximity, food-sharing and cofeeding,<sup>17</sup> and “low probability of attack when two animals are in close proximity in a particular context” (Burkart & van Schaik,<sup>8(p2)</sup>), which was operationalized as the evenness of access to a food source within a group.

### 3 | THE PRESENT: WHAT IS SOCIAL TOLERANCE?

In this section, we try to bring structure to the varied and, at times, inconsistent usage of social tolerance by identifying what we see as two diverging concepts of social tolerance. We then present an overview of previously used measures of social tolerance, following our proposed framework. Finally, we illustrate the limitations of the current, indiscriminate use of social tolerance measures.

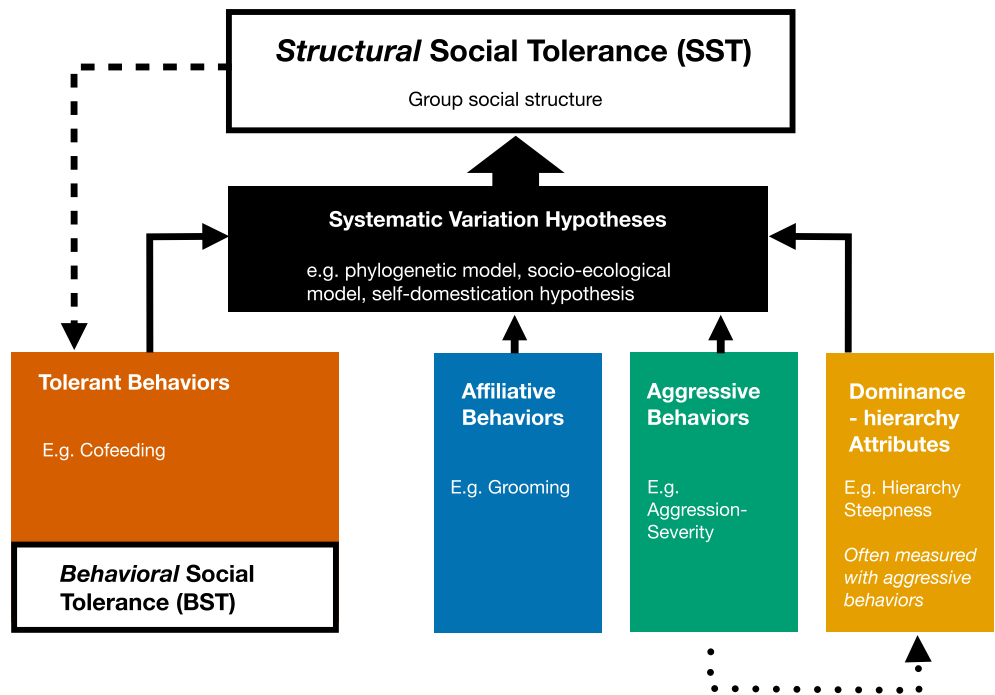
#### 3.1 | Two concepts of social tolerance

The historical developments presented above have resulted in what we posit are two separate, yet not wholly independent concepts of tolerance (see Figure 4): social tolerance as a *behavioral construct* that is used to describe specific tolerant behaviors, and social tolerance as a *structural construct*, that is used to describe specific social styles and social structures of a group.

For social tolerance as a behavioral construct, we suggest using the term behavioral social tolerance (henceforth “BST”). There is currently no shared understanding of what exactly a socially tolerant behavior is. Most existing definitions describe peaceful, non-agonistic interactions but diverge on whether these interactions are posited to be between dyads (see Burkart & van Schaik<sup>8</sup>) or among groups (see Cronin & Sánchez<sup>47</sup>), whether they focus on the internal motivation (see Rina Evasoa et al.<sup>46</sup>), or on the behavioral outcome (e.g., Burkart & van Schaik<sup>8</sup>; Cronin & Sánchez<sup>47</sup>), or emphasize competitive contexts (e.g., Cronin & Sánchez<sup>47</sup>; de Waal<sup>21</sup>). Definitions such as “the willingness of individuals to interact non-agonistically with each other and to spend time in proximity to their social partner” (Rina Evasoa et al.,<sup>46(p12)</sup>) also do not differentiate *tolerant* behavior from overtly beneficial behavior and could be used to describe beneficial or prosocial behaviors such as social grooming. In the course of this paper, we will therefore develop and propose a working definition that focuses on behavior and encompasses many of the previously studied aspects of BST while also distinguishing BST from more generally affiliative behavior.

BST can be measured at the individual level, such as the time an individual spends cofeeding with a conspecific (e.g., de Waal & Luttrell<sup>22</sup>), at the dyadic level, such as the time a dyad spends cofeeding (e.g., Hare et al.<sup>2</sup>), or at the group level with group-level paradigms such as the proportion of a group gathered to cofeed (e.g., DeTroy et al.<sup>48</sup>). As an outcome of interest, BST is usually analyzed and discussed on the dyadic, group, or even species level (e.g., Rina Evasoa et al.<sup>46</sup>). It is important to note that BST as a *group* trait in contrast to social tolerance as a structural construct is not tied to any further assumptions concerning the social style of the group or any covariation of other traits. It does not describe the social structure of a group but instead is employed to measure the group-level

**FIGURE 4** Schematic of structural social tolerance (SST) and behavioral social tolerance (BST). SST represents the covariation of various tolerant, affiliative, and aggressive behaviors as well as dominance-hierarchy attributes, which are depicted by the solid arrows. Attributes of the dominance hierarchy are based on aggressive behaviors as depicted by the dotted arrow. The extent and direction of the covariation are determined by the respective systematic variation hypothesis. BST represents the dyadic or group-level manifestation of socially tolerant behaviors. SST enables BST as depicted by the dashed arrow



manifestation of specific socially tolerant behaviors (such as average dyadic cofeeding duration or average duration of social proximity).

Social tolerance as a structural construct (henceforth “structural social tolerance” [SST]) is used to describe specific social structures. These social structures encompass multiple behaviors as well as dominance-hierarchy attributes, such as the hierarchy linearity and steepness (e.g., Balasubramaniam et al.<sup>28</sup>; Duboscq et al.<sup>49</sup> Thierry<sup>13</sup>). The behaviors used to describe and measure SST can be (i) behaviorally tolerant (i.e., BST), such as food sharing (e.g., van Schaik et al.<sup>50</sup>) or tolerated infant handling (e.g., Berman et al.<sup>44</sup>), (ii) generally affiliative, such as grooming behavior (e.g., Ciani et al.<sup>40</sup>) or post-conflict reconciliation (e.g., Duboscq et al.<sup>49</sup>), or (iii) aggressive, such as counter-aggression (e.g., van Schaik et al.<sup>50</sup>) or aggression rates (e.g., Duboscq et al.<sup>49</sup>). While SST measures can therefore include BST measures (as graphically depicted in Figure 4), the outcome of interest is not the behavior itself but the social structure at a group- or species-level. Despite this focus, SST is rarely assessed with group-level measures and instead is predominantly assessed with aggregations of individual or dyadic measures. For instance, the SST levels of two groups of female wild crested macaques (*Macaca nigra*) were measured with, among others, aggregations of individual rates of proximity, grooming, reconciliation, aggression rates, and counter-aggression.<sup>49</sup> Which exact selection of behaviors and attributes of the dominance hierarchy are considered to represent SST depends on the respective systematic variation hypothesis (see the historical overview and the following section for more details).

Our scheme (as presented in Figure 4) is strongly inspired and influenced by the framework presented by Hinde.<sup>51</sup> Hinde developed a framework for describing and studying human and nonhuman social interactions and social structures. In this framework, he discusses

different levels of abstraction in describing societies, moving from individual interactions to relationships, from relationships to the surface structure of the group, and through further abstractions to the possible structures of entire species and on to the so-called *deep structure*—the general explanatory models of social interactions and relationships. Our understanding of BST corresponds to Hinde’s levels of relationships (when describing dyadic BST), surface structure (when describing group-level BST), and structure (when generalized to describe the BST of entire species), while SST would best correspond to Hinde’s concept of the deep structure, which can be seen as based on interactions (e.g., rates of grooming or aggression), relationships (e.g., dyadic dominance relationships, measures of counter-aggression) and surface structural elements (e.g., the linearity or steepness of the dominance hierarchy).

While these two diverging concepts have been indirectly addressed in such descriptions as the following: “macaques with a tolerant dominance style [-SST] often show (...) tolerance around limited resources [-BST] (...) [and] maternal tolerance for infant handling [-BST]” (Cooper & Bernstein,<sup>26(p226)</sup>; text within brackets by the authors of the current paper), to our knowledge, this distinction has yet to be explicitly discussed.

### 3.2 | An overview of social tolerance measures

In the following, we present a non-exhaustive overview of selected primate research on social tolerance from the past four decades. Literature was selected to include the variable *social tolerance*, either as an outcome or a covariate, and with the intent to represent as wide an array of measures as possible (see Table 1). This overview should enable a summary of previously used measures and highlight the most

TABLE 1 Overview of social tolerance measures. Overview of literature using measures of social tolerance either as an outcome or a covariate

Title	Authors, Year	Tolerant Behaviors			Affiliative Behaviors			Aggressive Behaviors			Dominance-hierarchy Attributes			
		Co-feeding	Food-sharing	Proximity	Other	Grooming	Reconciliation	Other	Rates	Severity	Counter-Aggression	Other	Hierarchy steepness	Hierarchy linearity
Aversion to violation of expectations of food distribution: (...)	Anici et al., 2012	X												
Hierarchical steepness, counter-aggression, and macaque social style scale	Balasubramaniam et al., 2012 <sup>b</sup>							X				X		Social grades <sup>a</sup>
The influence of phylogeny, social style, and sociodemographic factors on macaque social network structure	Balasubramaniam et al., 2017				X									Dominance network indices
Group service in macaques ( <i>Macaca fuscata</i> ), capuchins ( <i>Cebus apella</i> ) and marmosets (...)	Burkart & van Schaik, 2013	X												
The evolutionary origin of human hyper-cooperation.	Burkart et al., 2014									X				
Social tolerance and adult play in macaque societies: (...)	Ciani et al., 2012				X		X		X		X			Agonistic support rates
Population-level variability in the social climates of four chimpanzee societies	Cronin et al., 2014		X											
Bonobos show limited social tolerance in a group setting: (...)	Cronin et al., 2015		X											
Social tolerance in wild female crested macaques (...)	Dubosq et al., 2013			X			X		X		X		X	Rate of approaches, response to non-agonistic approach
														Measures of power asymmetry
														Displacement rates, responses to aggression
														Affiliative expressions, contacts and interactions

TABLE 1 (Continued)

Title	Authors, Year	Tolerant Behaviors		Affiliative Behaviors			Aggressive Behaviors			Dominance-hierarchy Attributes			
		Cofeeding	Food-sharing	Proximity	Other	Grooming	Reconciliation	Other	Rates	Severity	Other	Hierarchy steepness	Hierarchy linearity
Measuring social tolerance: (..)	Fichtel et al., 2018	X											
Food sharing across borders	Fruth & Hohmann, 2018 <sup>6</sup>		X										
Tolerance allows bonobos to outperform chimpanzees on a cooperative task	Hare et al., 2007	X											
Shades of gray mouse lemurs: (..)	Hohenbrink et al., 2015						X						
Tolerant food sharing and reciprocity is precluded by despotism among bonobos but not chimpanzees	Jaeggi et al., 2010 <sup>b</sup>		X										
High but not low tolerance populations of Japanese macaques solve a novel cooperative task	Kaigaishi et al., 2019												Predetermined by previous literature
The effects of social context and food abundance on chimpanzee feeding competition	Koomen & Herrmann, 2018 <sup>67</sup>	X											
An experimental, comparative investigation of tool use in chimpanzees and gorillas	Lonsdorf et al., 2009	X					X						
Generous leaders and selfish underdogs: (..)	Massen et al., 2010												Social grades <sup>a</sup>
Engineering cooperation in chimpanzees: (..)	Melis et al., 2006		X										

(Continues)

TABLE 1 (Continued)

Title	Authors, Year	Tolerant Behaviors			Affiliative Behaviors			Aggressive Behaviors			Dominance-hierarchy Attributes		
		Cofeeding	Food-sharing	Other	Grooming	Reconciliation	Other	Rates	Severity	Other	Hierarchy steepness	Hierarchy linearity	Other
Sources of variation in social tolerance in mouse lemurs ( <i>Microcebus spp.</i> )	Rina Evasoa et al., 2019	X	X					X				Dyadic dominance relationship	
Local traditions in orangutans and chimpanzees: (...)	van Schaik, 2003	X	X										
The conditions for tool use in primates: (...)	van Schaik et al., 1999	X	X	X	X	X		X	X			Habitat productivity, collaborative hunts, medicinal plant use	
Male reproductive skew, paternal relatedness, and female social relationships	Schülke & Ostner, 2008											Social grades <sup>a</sup>	
A comparative network analysis of social style in macaques	Sueur et al., 2011		X		X					X		Dominance network indices	
Success and understanding in cognitive tasks: (...)	Visalberghi, 1997 <sup>8a</sup>											Predetermined by previous literature	
Class structure in a rhesus monkey group: (...)	de Waal, 1986	X								X			
Towards a comparative socioecology of the genus <i>Macaca</i> : (...)	de Waal & Luttrell, 1989	X								Attempt to exclude others from codrinking			
Bonobos exhibit delayed development of social behavior and cognition relative to chimpanzees	Wobber et al., 2010 <sup>b</sup>	X	X										

Note: Cells with "X" denote the measure(s) of social tolerance employed in the respective study.

<sup>a</sup>Social tolerance levels are not directly measured but are assigned based on membership in a specific social grade.

<sup>b</sup>These papers write of (interindividual) tolerance instead of social tolerance. As they are all cited by subsequent literature in reference to social tolerance<sup>4,49,53,81</sup> and two of them<sup>18,28</sup> also use the same measures that have been used by other studies assessing social tolerance,<sup>2,39</sup> we have chosen to include these studies into the overview.



commonly used ones. It should also illustrate the extent to which operationalizations have diverged, with the result that social tolerance currently encompasses measures as varied as medicinal plant use<sup>50</sup> and dyadic proximity (e.g., Hohenbrink et al.<sup>52</sup>). Following the structure described above (see Figure 4), we present four categories of tolerance measures: measures of *tolerant behaviors* (i.e., BST) and measures of behaviors and traits that are not explicitly tolerant but are used to measure socially tolerant structures (i.e., SST), namely *affiliative behaviors*, *aggressive behaviors*, and attributes of the *dominance hierarchy*.

### 3.2.1 | Tolerant behaviors

This category represents behaviors that are in themselves socially tolerant. Since a common definition is currently lacking, we provisionally include peaceful, non-agonistic interactions between individuals. We exclude behaviors that are potentially advantageous to the tolerating individual(s) to distinguish tolerant from affiliative behaviors.

One of the most common measures of tolerant behavior is *cofeeding*: one or more individuals allowing the close proximity of other individuals while eating or drinking.<sup>4,22,47,53,54</sup> We also include food-sharing, as most of the operationalizations termed as food-sharing in studies on social tolerance include either versions of *cofeeding*<sup>5,18</sup> or cases of *passive food-sharing* (i.e., *tolerated food-theft*)<sup>7,17</sup> and rarely *proactive food donations* (which would be more accurately attributed to *affiliative behaviors*). The final category comprises measures of *general* (i.e., non-food-related) proximity. While proximity can be disadvantageous (i.e., the proximity of a male rival during mating) and as such must be *tolerated*, it can also be beneficial (i.e., the proximity of closely affiliated conspecifics). The context, in which proximity is measured, however, is seldom reported.<sup>17,49,54</sup> This makes a distinction between different forms of proximity infeasible in many cases. Generally, though, proximity (in the absence of aggression) is seen as a behavior in which the presence of a conspecific is tolerated in close distance.<sup>47</sup> Therefore, it can best be viewed as a form of BST (but see the later section on “The possible future” for further discussion). As previously stated, socially tolerant behaviors are used to assess the dyadic- or group-level manifestation of BST, but also to measure SST (in combination with other covarying traits; see Figure 4).

### 3.2.2 | Affiliative behaviors

Within the study of social tolerance, *affiliative behaviors* (i.e., behaviors that are potentially beneficial to the recipient) belong to the collection of covarying behaviors that are employed to measure SST. The most commonly employed affiliative measure is *social grooming*, which is often analyzed with social network analyses (i.e., statistical investigations of individual, dyadic, and supra-dyadic grooming interactions). Less modular and denser grooming networks are then considered to reflect more tolerant societies.<sup>39,49,55</sup> *Post-conflict reconciliation* (i.e., friendly contact after a conflict) is also frequently utilized to assess SST and is often combined with measures of

*aggressive behavior*.<sup>40,49,50</sup> According to the phylogenetic model, societies characterized by high levels of SST have high rates of post-conflict reconciliation.<sup>13</sup>

### 3.2.3 | Aggressive behaviors

Measures related to aggressive behaviors are also used to assess SST. The most commonly used measures are *aggression rates*,<sup>4,40,46,49</sup> *aggression severity*,<sup>46,49</sup> and *counter-aggression* (i.e., retaliation by the recipient of aggression).<sup>28,40,50</sup> This category forms the basis for the phylogenetic approach of measuring social tolerance,<sup>13</sup> and both phylogenetic and socio-ecological approaches treat this selection of measures as mutually codependent<sup>13,31,39</sup> with the occurrence of one variable indicating the presence of the others. As such, only a subset of this array is often actually measured. Groups with high SST are expected to have less severe aggression as well as higher rates of counter-aggression (because of the lesser risk for individuals when retaliating received aggression).<sup>13,28,49,56</sup>

There is some discrepancy concerning the relationship between rates of aggression and SST. Some studies do not differentiate between mild and severe aggression and consider high rates of general aggression indicative of socially intolerant relationships.<sup>46,57,58</sup> Other authors have made a distinction between mild and severe aggression and consider only high rates of severe aggression to characterize low SST; high rates of mild aggression, on the other hand, are considered to be characteristic of high SST<sup>22,40,41,59–61</sup> as mild aggression would have less severe consequences in societies with higher SST.<sup>22</sup> We will discuss this discrepancy in more detail in the later section on “The possible future.” Aggressive interactions are also frequently used to assess dominance hierarchies and relationships (as depicted by the dotted line in Figure 4), attributes of which form the final category of measures of SST.

### 3.2.4 | Dominance hierarchies

Attributes of the dominance hierarchy are either global measures of the dominance hierarchy, such as the hierarchy steepness or linearity,<sup>28,49</sup> or measures of dyadic dominance relationships between two individuals,<sup>46</sup> most often based on the outcomes of conflicts.<sup>28,46,49</sup> While the behaviors these measures are based on are often the same as those mentioned in the previous category, the outcome of interest and the level of analysis is different. Depending on whether social tolerance is viewed as distinct from or synonymous with egalitarianism, the presence of clearly established (formalized) hierarchies can either be expected to enable social tolerance<sup>22,31,35</sup> or to exclude it.<sup>13,39,42</sup> This discrepancy appears to have never been formally addressed in the literature. It has, however, led to less conflicting research than might be expected. While the concept of a formal dominance hierarchy played an important role in early hypotheses of social tolerance,<sup>22,31</sup> it has seldom been operationalized in studies on social tolerance (for an exception see Lu et al.<sup>56</sup>), and it remains debated to which extent such an additional layer of

dominance (distinct from the actual, active dominance hierarchy) exists.<sup>62–65</sup>

### 3.3 | Limitations of the current use of social tolerance

Much of the past literature has acknowledged the diversity in measures of social tolerance; however, the consensus is often that they all reflect one common underlying construct (see, e.g., Fichtel et al.<sup>4</sup>; Hare et al.<sup>9</sup>; Kaigaishi et al.<sup>3</sup>; Rina Evasoa et al.<sup>46</sup>). While this can be the case, for example, when similar measures are used to assess both BST and SST, some of the measures are so disparate as to result in contradicting assessments of social tolerance. This possibility can be illustrated by the case of the reportedly socially tolerant callitrichids (*Callitrichidae* spp.). Callitrichids are a family of New World monkeys and are characterized by their high levels of cooperative breeding, prosociality, and most frequently by their *social tolerance*.<sup>7,8,66–68</sup> This characterization of social tolerance is based on observations of high rates of affiliative behavior and low rates of aggression,<sup>69–71</sup> and experimental studies demonstrating a high evenness of food distribution, high levels of cofeeding, and large extent of food provisioning when compared to other primates.<sup>7,8,72</sup> In light of other measures of social tolerance, however, members of the callitrichid family would not be considered socially tolerant at all. For instance, callitrichids are characterized by reproductive suppression of subordinate females,<sup>73</sup> resulting in a strong reproductive skew,<sup>74</sup> which is often seen as a trait of a despotic dominance relationship (see Vehrencamp<sup>75</sup>; Burkart & van Schaik<sup>67</sup>; Sterck et al.<sup>31</sup>; cf. Thierry,<sup>13</sup> Schülke & Ostner<sup>15</sup>). Lion tamarins (*Leontopithecus* spp.) are reported to have strict dominance hierarchies,<sup>73,74,76</sup> and multiple callitrichid species are reported to have very low reconciliation rates.<sup>69,71,77</sup> Hence, studies basing their assessment of social tolerance on a few or single measures<sup>28,52,53,78</sup> could arrive on contradictory results concerning callitrichid social tolerance, depending on the operationalization.

This is not only the case for callitrichids: some species, such as bonobos, may have relatively flat dominance hierarchies (Stevens et al.<sup>64</sup>; Tokuyama & Furuichi,<sup>79</sup> but see Jaeggi et al.<sup>80</sup>), but may be relatively unwilling to gather in close proximity in the presence of valuable resources (Cronin et al.<sup>81</sup>; Jaeggi et al.,<sup>80</sup> but see Hare et al.<sup>2</sup>; Wobber et al.<sup>18</sup>), and exhibit high stress levels in such situations.<sup>82,83</sup> Other species, like chimpanzees, may have strict and linear dominance hierarchies,<sup>84</sup> but show higher levels of cofeeding tolerance as measured with group-level assays.<sup>81,85</sup> Depending on whether one assumes that despotism facilitates<sup>22,31,35</sup> or prohibits<sup>13,39,42</sup> social tolerance, these findings can also be seen as contradictory.

These reflections are not meant to conclude that callitrichids (or chimpanzees or bonobos) are socially tolerant of conspecific group members or not, but to exemplify that it is impractical and confounding to employ different measures of social tolerance and to compare units (e.g., groups or species) based on their respective results. Depending on the behavioral aspect measured and the theory invoked to draw inferences, it is currently possible to measure the

same group of individuals and come to very different conclusions concerning their levels of social tolerance (see, e.g., Amici et al.<sup>86</sup>).

Despite these disparities, it remains common for papers to present and discuss “social tolerance” by comparing the results from studies on SST and BST. For example, Fichtel et al.<sup>4</sup> state:

Social tolerance crucially affects several aspects of the social life of group-living animals, including (...) patterns of recruitment (Sueur & Petit, 2010), cooperation (Melis, Hare, & Tomasello, 2006; Range, Ritter, & Virányi, 2016), prosocial behavior (Burkart et al., 2014) (...), and the spread of knowledge within social groups ([...] van Schaik, Deaner, & Merrill, 1999).

These different correlates of social tolerance are based on such diverse assessment as the patterns of aggression and reconciliation,<sup>87</sup> dyadic cofeeding tolerance,<sup>5,88</sup> the equal distribution of resources,<sup>7</sup> and a whole range of behaviors and characteristics including habitat productivity, the occurrence of collaborative hunts, and medicinal plant use<sup>50</sup> (see Table 1 for more details).

We argue that this present-day approach of equating SST and BST glosses over profound differences, both in the theoretical framework (i.e., the covarying patterns of behavior (SST) or the dyadic manifestation of a specific behavior (BST)) and in the actual measurements used to assess them (i.e., rates of counter-aggression and reconciliation or dyadic cofeeding tolerance). Overlooking these differences can lead to the erroneous conclusion that there is a single construct—social tolerance—that concurrently affects (among others) patterns of aggression and affiliation, access to resources, recruitment, cooperation and prosocial behavior, fairness, and the spread of knowledge (see, e.g., Kaigaishi et al.<sup>3</sup>; Fichtel et al.<sup>4</sup>; Hare et al.<sup>9</sup>; Dubuc et al.<sup>10</sup>; Rina Evasoa et al.<sup>46</sup>).

## 4 | THE POSSIBLE FUTURE: HOW CAN THE STUDY OF SOCIAL TOLERANCE ARE IMPROVED?

To overcome the identified conflation of social tolerance conceptualizations and enable valid cross-studies comparisons, we suggest that primate social tolerance research enact two, overarching steps: First, a clear distinction should be made between social tolerance as a structural construct (SST) and behavioral structural construct (BST) and second, *within* these two constructs, it should be clarified which measures best represent the respective concepts. Both steps require theoretical and empirical work. In the following section, we present our proposal for how these steps should be best approached.

### 4.1 | Distinction between SST and BST

Structural social tolerance and behavioral social tolerance represent different concepts; SST refers to the social structure of a group as

expressed by the covariation of different behavioral traits and attributes of the dominance hierarchy, while BST refers to the expression of tolerant behaviors, at a dyadic or group level. These two concepts are not wholly independent of one another. We propose that SST can be understood as describing social structures that allow for socially tolerant behaviors between group members (as illustrated by the dashed arrow in Figure 4). Depending on the theoretical background and selected measures, the operationalizations used to measure SST can also include socially tolerant behaviors (BST) (though, in many cases, they do not; see Table 1). However, the outcome of interest of these two constructs is different. The focus of BST is to describe the manifestation of specific tolerant behavior, at a dyadic or group level. While SST is based on individual and dyadic measurements, the outcome of interest is the group structure that they represent.

## 4.2 | Clarification within BST

Most existing BST definitions describe peaceful, non-agonistic interactions but have been inconsistent in the level of interactions (dyadic or group level) they describe, such as, for example, “low probability of attack when two animals are in close proximity in a particular context” (Burkart & van Schaik,<sup>8(p2)</sup>) or “the probability that individuals will be in proximity to conspecifics around valuable resources with little or no aggression” (Cronin & Sánchez,<sup>47(pp1250066-4)</sup>) and whether they require a competitive context, such as “low competitive tendency, especially by dominants towards subordinates” (de Waal,<sup>21(p246)</sup>). Definitions such as “the willingness of individuals to interact non-agonistically with each other and to spend time in proximity to their social partner” (Rina Evasoa et al.,<sup>46(p12)</sup>), place emphasis on the motivation instead of the behavior and do not sufficiently differentiate BST from general affiliative behavior. We, therefore, propose a new definition of BST: *An individual shows behavioral social tolerance when they do not hinder one or more others from behaving in a way that is potentially disadvantageous to that individual, resulting in peaceful, non-agonistic interactions.* While this definition is based on the previous definitions mentioned earlier,<sup>8,21,46,47</sup> we find it to be an improvement in a number of aspects.

First, our definition focuses on the tolerant interaction instead of an internal tolerant motivation such as “willingness [...] to interact non-agonistically” (Rina Evasoa et al.,<sup>46(p12)</sup>), which can be difficult to validly measure across species. It does not limit the interaction to either a dyadic (e.g., Burkart & van Schaik<sup>8</sup>) or group setting (e.g., Cronin & Sánchez<sup>47</sup>).

Second, as some instances of BST, such as tolerated infant handling or proximity, are not always clearly competitive, we do not include the specification of competition as a necessary requirement in our BST definition. Instead, we specify that the behavior or presence should be potentially disadvantageous in order to distinguish BST from overtly beneficial behavior. We recognize that identifying what behaviors can be potentially disadvantageous will be challenging in some cases. However, we wish to distinguish BST from behaviors that directly benefit an individual in the immediate situation (i.e., prosocial

behaviors). We, therefore, recommend, as a minimal criterion, that the behaviors not be overtly beneficial, such as, for example, grooming or proactive food donations. What can be considered overtly beneficial will no doubt vary depending on the context and species and as such should be directly addressed in each study assessing this construct.

Finally, we state that BST should result in peaceful, non-agonistic interactions. This stipulation is meant to exclude aggressive interactions, even instances of “tolerated” counter-aggression by dominant individuals. Aggressive interactions, such as counter-aggression, are central to the assessment of SST. However, opening our definition of BST to non-hindered aggressions would move our definition too far away from what we have found to be a common denominator of previous definitions of BST: peaceful, non-agonistic interactions between individuals.

Our definition is limited to describing socially tolerant behavior, not the mechanisms behind it. The mechanisms by which BST arises and is maintained, both on a proximate and ultimate level, are manifold. For instance, dyadic cofeeding tolerance fulfills our criteria for BST: Two individuals do not hinder each other's presence, which is potentially disadvantageous (they might be able to eat more if alone), resulting in a peaceful interaction. However, there are multiple proximate processes that can lead to two individuals eating peacefully in close proximity: A dominant individual's willingness to concede their priority to food resources in exchange for coalitional support from a subordinate,<sup>35,36</sup> one or both individuals' inability to monopolize the resource,<sup>85</sup> or mutual respect of possession.<sup>36,89</sup>

On a more ultimate level, the systematic variation hypotheses describe group structures that evolved to enable or even require BST and discuss different mechanisms (both socio-ecological and phylogenetic) by which this could have happened. Numerous studies have further investigated the possible adaptive effects of BST and have posited that it enables cooperation, social learning, and prosociality.<sup>2,6-8,10,11,17</sup> A thorough discussion of the proximate and ultimate mechanisms underlying social tolerance is beyond the scope of this review but presents an important avenue for further research.

While there has been some initial work done comparing different measures of BST (e.g., Cronin and colleagues<sup>85</sup> operationalized “social tolerance” in terms of cofeeding tolerance, evenness of food distribution, and proximity networks—all forms of BST), we still know little about how different BST measures correspond to one another and to which extent results obtained with different operationalizations are commensurable. For instance, it is not inconceivable that group members act highly gregariously (as measured with, e.g., proximity network) in the absence of competition-eliciting factors like valuable food resources but show limited tolerance when scarce or depleting resources are present (as measured with, e.g., cofeeding).

Moreover, BST can be measured on the individual (e.g., time an individual spends cofeeding), dyadic (e.g., time spent dyadically cofeeding), and group level (e.g., the proportion of a group cofeeding). Aggregations of individual and dyadic measures are also often used to report group-level manifestations of BST (e.g., the average time an individual or a dyad spends cofeeding). The results of these different

levels are commonly integrated into discussions of social tolerance. For example, Fichtel et al.,<sup>4</sup> and Kaigaishi et al.<sup>3</sup> base their assessments of social tolerance on group-level cofeeding measurements and integrate their research into previous literature on cofeeding tolerance that is based on both dyadic as well as group-level measurements. We argue that discussing this distinction explicitly in the future will avoid the general assumption that measurements on any level assess the same socially tolerant tendency. We find it conceivable that groups might, for example, have high levels of BST as measured with a group-level paradigm (i.e., a large proportion of the group is willing to gather in proximity while cofeeding) but have low levels of BST as measured with a dyadic paradigm (i.e., on average individuals are not comfortable directly competing with a conspecific in a dyadic cofeeding task). To the best of our knowledge, there have been of yet no systematic comparisons of these different levels of measurement of BST. Future research should investigate the extent to which different levels of measurement correspond with one another.

### 4.3 | Clarification within SST

Social tolerance as a structural construct (SST) is used to describe social structures that enable BST. This concept is based on systematic variation hypotheses, the most prominent of these being the phylogenetic and the socio-ecological models. There is a rich and lively history of exchange and debate between proponents and critics of these two systematic variation models (e.g., Castles et al.<sup>23</sup>; Clutton-Brock & Janson<sup>90</sup>; Cooper & Bernstein<sup>26</sup>; Hemelrijk<sup>91</sup>; Koenig & Borries<sup>92</sup>; Thierry<sup>93</sup>), and it is beyond the scope of this paper to debate their respective merits and deficits. Concerning their concept of SST, the two models have a high level of correspondence: they both describe societies that have less severe aggression, more instances of counter-aggression, and more reconciliation.<sup>13,31</sup> The main point of contradiction in their respective concepts of SST is the role of the dominance hierarchy. Future research should clarify whether despotism—that is, the presence of a clearly defined dominance hierarchy—enables or precludes SST. To date, there is little support for the assumption that a certain level of formal despotism is necessary for other aspects of SST, such as high rates of counter-aggression and reconciliation (see Lu et al.<sup>56</sup>). Indeed there is overall little support for the existence of this proposed second layer of dominance relationships, separate from outcomes of actual agonistic and competitive interactions.<sup>62–65</sup> On the other hand, however, outside of research done with macaques (e.g., Balasubramaniam et al.<sup>39</sup>; Balasubramaniam et al.<sup>28</sup>; Thierry<sup>13</sup>), there is also little support that egalitarianism, that is, the lack of a clear dominance hierarchy, increases SST. The examples of callitrichids, bonobos, and chimpanzees suggest that species with supposedly despotic relationships (such as chimpanzees) can display some tolerant behaviors (such as group cofeeding) while species with supposedly egalitarian relationships (such as bonobos) may not. For these species, at least, attributes of the dominance hierarchy might be wholly independent of other aspects of SST. Further research among other primates besides

macaques is needed to disentangle the associations between aspects of the dominance hierarchy and other traits of SST.

Further, it remains unclear whether tolerant societies can be characterized by high rates of mild aggression. A part of the literature does not differentiate between severe and mild aggression and considers higher rates of aggression characteristic of lower social tolerance levels.<sup>46,57,58</sup> Other studies, however, do differentiate between severe and mild aggression, and only severe aggression is considered characteristic of low tolerance, while high rates of mild aggression are posited as characteristic of socially tolerant societies.<sup>17,22,41,59</sup>

Creating comparable categorizations of aggression severity will likely be challenging.<sup>94</sup> However, since these two different approaches can potentially contradict each other (i.e., rates of mild aggression indicating both high and low SST), we believe it is important to further investigate the extent to which societies with high levels of SST can be characterized by high rates of mild aggression. Future research should, therefore, continue to distinguish between mild and severe aggression.

Future studies should also bear in mind that there might not be one unifying system of covarying traits and attributes that can be applied to all or even most primate species (see Thierry<sup>93</sup>). For example, the traits listed in the phylogenetic model were compiled to describe the patterns observed specifically among (female) macaques. This pattern has not been consistently found in empirical studies (see Amici et al.,<sup>86</sup> Balasubramaniam,<sup>39</sup> Berman et al.,<sup>44</sup> and Cooper & Bernstein<sup>24,26</sup>), and macaques have also since been proposed to likely be unique among primates in the hypothesized consistency of the covariation of their social traits.<sup>39</sup> Future research should be open to the possibility that the selection of behaviors and structural traits that covary and characterize a socially tolerant society (SST) might differ from species to species, or that some models might better explain patterns of SST across clades while others more accurately explain the variation within.<sup>32</sup> Finally, much of previous research on SST has focused primarily on the behavior of female primates,<sup>59,93,95</sup> and as a result many of the identified patterns of behavior only apply to females. Further research is needed on SST among male primates.

## 5 | CONCLUSION

The term *social tolerance* has played an important role in sparking new research into the behavior and social structures of primates, leading to the study of many aspects of primate behavior and sociality that allow individuals to peacefully coexist and cooperate in social groups. To be able to understand the evolutionary pathways and causal mechanisms behind these phenomena, however, we require systematic comparisons of social tolerance across study groups and species. The current usage of the term social tolerance, as well as the variable underlying operationalizations, do not allow for valid, systematic comparisons. In this paper, we have illustrated past and current shortcomings and have presented our proposal for how to proceed—with a clearer understanding of what social tolerance is and what it isn't.

**BOX 1 GLOSSARY**

**Attributes of the dominance hierarchy:** Quantifiable characteristics of the dominance hierarchy of a group, such as steepness or linearity.

**Behavioral social tolerance (BST):** An individual shows behavioral social tolerance when they allow one or more other individual(s) to behave in a way that is potentially disadvantageous to them.

**Despotism:** Presence of a clearly defined dominance hierarchy.

**Dominance hierarchy:** Structure of dominance relationships within a group.

**Egalitarianism:** Absence of a clearly defined dominance hierarchy.

**Formal dominance hierarchy:** Dominance hierarchy primarily based on ritualized submission behaviors.

**Grades of social style/social grades:** Four different patterns of covarying traits and attributes of the dominance hierarchy that characterize specific macaque species, ranging from Grade 1 (socially intolerant/despotic) to Grade 4 (socially tolerant/egalitarian).

**Phylogenetic model:** Systematic variation hypothesis that states that (primarily female) macaque species' social styles/social structures covary with their phylogenetic relatedness.

**Socio-ecological models of female relationships:** Systematic variation model that states that primate females' social relationships can be explained by a combination of ecological and social variables.

**Social structure:** Group-level organization of interindividual relationships.

**Social style:** Group-level patterns of interactions often used interchangeably with “dominance style”.

**Structural social tolerance (SST):** Specific pattern of covarying traits and attributes of the dominance hierarchy that are considered to characterize a socially tolerant group, according to a systematic covariation hypothesis.

**Systematic variation hypotheses:** Hypotheses that state that different aspects of primate social structures and social styles covary.

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