PNAS RESEARCH ARTICLE | PSYCHOLOGICAL AND COGNITIVE SCIENCES OPEN ACCESS

Social tolerance and success-biased social learning underlie the cultural transmission of an induced extractive foraging tradition in a wild tool-using primate

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Edited by Laurel Fogarty, Max-Planck-Institut fur evolutionare Anthropologie, Leipzig, Germany; received February 21, 2024; accepted September 18, 2024 by Editorial Board Member Marcus W. Feldman

The last two decades have seen great advances in the study of social learning (learning from others), in part due to efforts to identify it in the wild as the basis of behavioral traditions. Theoretical frameworks suggest that both the dynamics of social tolerance and transmission biases (or social learning strategies) influence the pathways of information diffusion in social groups. Bearded capuchins (*Sapajus libidinosus*) inhabiting the semiarid seasonal caatinga biome of the Serra da Capivara National Park (SCNP) form highly tolerant societies that possess the largest "tool-kit" described for monkeys, a feat likely facilitated by social learning. Here, we used social network analysis and an open diffusion experiment using an extractive foraging task to identify the occurrence of social learning and describe the pathways of social transmission of information in two wild primate populations. The dynamics of social tolerance outside of task introductions predicted opportunities for social learning, but it was tolerance during task introductions that predicted the actual pathways of social information diffusion. Our results also indicated that the capuchins mainly learned from others via direct observation and naïve individuals exhibited an observation bias toward successful males. This study supports the claims of cultural transmission in robust capuchins and empirically supports the role of social tolerance and social learning strategies in human and nonhuman primate cultural evolution.

social learning | social tolerance | social dynamics | transmission biases | social learning strategies

The study of cultural evolution spans a broad range of areas, such as biology, psychology, and anthropology. Through combining empirical studies with theoretical and mathematical modeling of cultural change, changes in socially transmitted beliefs, knowledge, customs, skills, attitudes, languages, or other behaviors are studied (1–3). Such modeling of the spread of cultural practices in human populations shows that cultural variation is not a random process, but governed by generalizable rules and acquired by social learning. The same is true for nonhuman animals, for which a diversity of behavioral traditions have been reported, especially in cetaceans, primates, and birds (4). As in humans, animal culture is fueled by social learning, defined as "learning influenced by the observation of, or interaction with, a conspecific, or its products" (5), and its study is relevant to understanding the evolution of human culture (6). Social learning allows naïve individuals to acquire information about different patterns of behavior and adopt those that are beneficial. Thus, patterns of behavior have different transmissibilities. Therefore, in cultural inheritance, transmission biases or social learning strategies, influencing when, what, and from whom individuals learn, seem to be the rule rather than the exception (reviewed in ref. 7). However, it is hypothesized that the social tolerance of humans (toward others in proximity) may be one of the underlying factors that facilitates our social learning and innovation, enabling the unique extent of cumulative culture in our species (8).

Building on Cavalli-Sforza and Feldman's (9, 10) pioneering importation of theoretical population genetics methods into the study of cultural evolution, Richerson and Boyd (2) used mathematical modeling to describe forces that specify when an individual is more likely to learn from a conspecific, and which conspecifics they may learn from, subdividing the types of transmission biases into *content-based (or direct) biases*, such as "copy greater pay-off behavior" and *context-based (or indirect) biases,* such as "copy the traits exhibited by dominant individuals." Transmission biases are also termed *social learning strategies* that influence "when to copy," "what to copy," and "whom to copy" (11, 12). Multiple such strategies may be deployed simultaneously, individuals can switch between strategies flexibly, and there is no one-to-one correspondence between psychological heuristics deployed

Significance

The influence of social tolerance in animal social learning has been scarcely investigated empirically. Social tolerance determines who is allowed in proximity to whom and granted access to resources such as food or social information. Therefore, tolerance toward others in proximity is necessary for the spread of social information, linking theories of cultural transmission and animal traditions (or culture). Here, we find evidence that naïve individuals attend to, and potentially learn from, successful conspecifics. Further, we find that social tolerance influences pathways of information transmission. Understanding the role of observation biases and social tolerance dynamics in the spread of novel foraging behavior in a tool-using primate may shed light on the evolutionary forces involved in primate cultural abilities.

Author contributions: C.G.C., E.B.O., and R.L.K. designed research; C.G.C. performed research; C.G.C. and I.G.-N. analyzed data; and C.G.C., I.G.-N., E.B.O., and R.L.K. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission. L.F. is a guest editor invited by the Editorial Board.

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This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2322884121/-/DCSupplemental.

Published November 18, 2024.

and resulting population-level patterns observed (7). Note, we use the term "copy" synonymously with social learning and not form-copying/imitation.

The pathways of information diffusion are also influenced by demographic factors (e.g., sex, age, social rank, kinship) that shape the occurrence and strength of social relations or social dynamics (13). Coussi-Korbel and Fragaszy (14) outlined how social tolerance (tolerance toward others in proximity) influences opportunities to observe and hence learn from conspecifics. According to this framework, different levels of social tolerance may lead to different patterns of social diffusion of information. *Nonspecific social learning*, where information spreads evenly across groups, is predicted to occur in egalitarian species. In contrast, *directed social learning*, which is influenced by the demonstrator's identity, resulting in an uneven spread of information across groups (e.g., only within cliques/subgroups), will occur in more despotic societies due to the asymmetry of social relationships (14). Importantly, care must be taken not to infer social learning strategies (e.g., copy same-sex conspecifics) before considering whether the pattern of information diffusion is due to directed social learning (e.g., individuals may only have the opportunity to observe those of the same sex as tolerance of proximity between sexes is lacking). Accordingly, to fully evidence a model-based social learning strategy, an assessment of whether preferential observation of specific individuals is influential in determining the behavior of observers, is required (15).

By inducing novel foraging opportunities in wild animal groups, we can establish whether social learning is occurring and then move on to identifying influences on the transmission pathways (here social tolerance dynamics and the types of transmission biases at play), while maintaining the ecological validity lacking in laboratory experiments (16, 17). Such experimental designs with multiple freely moving demonstrators/models and observers (i.e., open diffusion experiments: 18) were scarce in wild primates until recently, but are important in allowing us to investigate biases in who is attended to and copied (e.g., older/dominant/successful individuals) and the influence of social dynamics (social tolerance), in naturalistic contexts. With the advent of statistical methods such as Network-based Diffusion Analysis (NBDA: 19, 20), researchers have demonstrated that social interactions, such as those based on affiliative behaviors (or social tolerance), do indeed represent opportunities for social learning in several wild primates (ring-tailed lemurs: 21; red-fronted lemurs: 22; vervet monkeys: 23). In addition, observation networks, which indicate tolerance of proximity in a competitive context, have evidenced social learning using NBDA in wild (chimpanzees: 24; vervet monkeys: 23) and free-ranging (Barbary macaques: 25) primates. Moreover, open-diffusion studies are conducive to registering multiple transmission events, which in turn allows us to investigate transmission biases. Indeed, such studies have found evidence consistent with transmission biases in wild gracile capuchin monkeys (*Cebus sp.*) including *copy most frequent behavioral variant* (26) and *copy highest payoff* (27).

Studies of wild primates help elucidate factors (cognitive and social) that underlie cultural evolution in human and nonhuman animals (28). The bearded capuchin (*Sapajus libidinosus*) is considered an intermediate species in the despotic-egalitarian spectrum within capuchins given their nonlinear dominance hierarchies and asymmetric distribution of aggression between dyads. This fosters diversity in social tolerance among individuals (29–31) making them ideal to investigate the role of social tolerance in social learning. In addition, there is no empirical evidence for social learning, nor transmission biases, in wild robust capuchin monkeys (*Sapajus sp.*). Yet, our study population of bearded capuchins (*Sapajus libidinosus*) in the Serra da Capivara National Park presents a uniquely large "tool-kit" for capuchins and the largest outside of the great apes. They use stones (for nut/seed-cracking, pulverizing stone, digging for tubers, roots and spiders, and throwing in proceptive displays) and sticks (as probes for honey, insects, and water) sometimes in combination and serially (32–35). Tool use seems to be acquired by social learning, for which different observation biases have been described in a semi-free ranging group (36, 37), making them a good candidate species to investigate social learning in the wild.

Here, we report an open-diffusion field experiment, where a novel extractive foraging task—with two possible actions to access rewards—was introduced to two groups of wild bearded capuchins and diffusion of solutions tracked. Using NBDA, we investigated whether behaviors spread at a higher rate between individuals who are more strongly connected through more frequent associations and/or interactions, indicating social learning (19). We considered specific social affiliative networks (social proximity, social play, grooming, and cofeeding) indicative of social transmissions pathways pertaining to tolerance and discuss the transmission of behaviors aided by close observation. We also investigate whether naïve individuals display biases in whom they observe interacting with the novel task addressing social learning strategies of "whom to copy."

Results

Open Diffusion Experiment. An open diffusion experiment was conducted with two groups of wild bearded capuchins [Jurubeba (JB) and Pedra Furada (PF)] and involved a foraging task (a food-dispensing puzzle-box) which could be solved one of two ways, *lift* or *pull* (Fig. 1 and *SI Appendix*, Fig. S3.1). This two-action paradigm (38, see ref. 39 for first use in the wild) allows testing for option preferences at the individual or group level. One monkey in each group had been trained as a demonstrator and was included as such in further analyses. The remaining monkeys observed (i.e., head oriented toward the task within a ten-meter radius) a conspecific solving the task at least once, before solving the task themselves. By the end of the open-diffusion experiment, a total of 34 individuals across both groups (N_{JB} = 23 of 40; N_{PF} = 11 of 30) had solved the task (whether by lifting or pulling) successfully at least once. Due to a bias for "lift" we do not analyze the diffusion of variants but focus on task solution (*SI Appendix*, section S3). The diffusion pattern of task solution presented a gradual increase in the proportion of informed individuals, stabilizing at 57.5% (JB) and 36.7% (PF) of group members (*SI Appendix*, Fig. S3.2). The task was solved a total of 8,671 times (N_{JB} = 4,591, N_{PF} = 4,080), with 92% of these observed by at least one conspecific. As there was often more than one observer, 33,177 observation events (N_{JB} = 15566, N_{PF} = 17611) were recorded.

The Influence of Observation Networks during Task Introductions. To investigate the role of observational learning, we conducted two separate NBDAs for each group using the time of acquisition diffusion analysis (cTADA, see *Materials and Methods*). For each group, we ran models informed by three observation networks each reflecting different observation distances (indicative of different learning processes) and compared models with social transmission (and asocial transmission, "social model") and without social transmission ("asocial model") using likelihood ratio tests (LRT) to quantify the evidence of social transmission and its level of significance (*P*). Maximum likelihood methods determined which model better explained the observed data (having the lowest AICc and highest Akaike weight).

We found evidence (ΔAIC > 2 between social and asocial models, as per ref. 19), for social learning of task solution for all

Fig. 1. The two-action extractive foraging task. Food rewards slide down a shaft into a tray at the *Bottom* of the task. Here, an adult male solves the task using *lift* (the blue flap) instead of *pull* (the green nob), with three monkeys observing within 5 m.

observation networks (at different distances) in both groups (Table 1). These results were confirmed by the percentage of events that occurred by social transmission (%ST) and a likelihood ratio test comparing the asocial to the social model (LRT), with $P < 0.05$ indicating evidence of an effect consistent with social transmission. The 95% CI were consistent with evidence of social learning (s' = 0 not included in the interval), but the effect of social transmission was small for JB and large CI95% ranges indicate uncertainty in the strength of the effect for PF (Table 1). In JB, NBDA found stronger support (ΔAIC) for the social model over the asocial model when individuals observed task manipulations within 1 m than when they were beyond 1 m. However, we found contrasting results in PF, with stronger evidence of social learning when individuals observed task manipulations from beyond 5 m than within 5 m or 1 m. Differences in social structure and dynamics between both groups may explain these contrasting results (*SI Appendix*, section S4 and *Discussion*).

Individual-level variables (ILVs), of sex, age, rank, neophobia, and task monopolization, were included in the models to assess their potential influence on the social or asocial learning rates to avoid erroneous identification of social learning (Table 2). ILVs may influence only the asocial learning rates (additive model), or both learning rates equally (multiplicative model) or independently (unconstrained model). In both groups, inclusion of a variable describing the latency to touch novel objects (of those that entered 5 m of the object) improved the model fit for observation networks within 1 m and 5 m of the task in both groups, indicating that increasing "neophobia(latency to touch)" slowed asocial and social learning rates. In JB, sex influenced social diffusion in observation networks beyond 5 m, indicating that males had higher learning rates than females. Finally, in PF, the best model for the observation network beyond 5 m was influenced by a variable describing the avoidance of novel objects (including those that never entered 5 m of the object) with decreasing "neophobia(avoidance)" accelerating asocial and social learning rates (*SI Appendix*, section S8). The ILV monopolization of resources did not improve model fit in any case (*SI Appendix*, section S5).

Additive models were a better fit than multiplicative models when testing social transmission in all observation networks except for that beyond 5 m in JB, for which the multiplicative model was a better fit. Thus, excepting one case, the social transmission of task solving was a direct consequence of observing those manipulating the task (or observational learning) rather than indirect social learning processes (42).

The Social Context Fostering Cultural Transmission. Social networks were created, and SNA metrics were calculated for each group. PF was a more cohesive group (network density: PF range 0.11 to 0.74, mean 0.34 ± 0.28; JB range 0.11 to 0.56, mean 0.28 ± 0.18) than JB, the larger group, that had a more cliqued social structure (clustering coefficient: PF range 0.29 to 0.79, mean 0.60 ± 0.18, JB range 0.16 to 0.67, mean 0.47 ± 0.17; see *SI Appendix*, section S4).

In a second set of NBDA models, we investigated whether social structure and dynamics outside the experimental context of task introduction predicted the information transmission observed (43). In both groups, the ΔAIC < 2 indicated insufficient support of social transmission when the NBDA was informed with the socio-positive networks (social proximity, cofeeding, and grooming). However, results of the LRT indicated significant evidence ($P < 0.05$) consistent with social transmission when models were informed by cofeeding in JB (social model exp(0.5*ΔAIC) = 1.89× more support than asocial model) and grooming in PF (social model 1.91× more support than asocial model). Accordingly, in both cases, less than 60% of learning events (57% when using the cofeeding network in JB; 26% when using the grooming network

Table 1. Results for continuous time of acquisition diffusion analysis (cTADA)

	Jurubeba					Pedra Furada				
Network informing the social model	ΔAIC	Akaike weights (ω)	LRT *P*value	%ST	CI95%	ΔAIC	Akaike weights (ω)	LRT (*P*)	%ST	CI95%
Observation<1 m	25.87*	1	28.57 <0.001*	71.96	s′ = 6.20 L = 1.42 U = 40.29	2.11*	0.74	6.39 0.011*	83.79	s′ = 314.94 L = 45.44 U = 2,539.47
Observation<5 m	13.45*	1	16.16 <0.001*	75.46	s′ = 1.45 L = 0.31 U = 18.95	3.82*	0.87	8.11 0.004*	85.68	s′ = 317.50 L = 47.47 U = 2,113.76
Observation>5 m	13.34*	1	16.04 <0.001*	68.86	s′ = 22.67 L = 5.39 U = 105.67	8.89*	0.99	13.18 <0.001*	78.24	s′ = 199.79 L = 46.61 U = 1,348.82
Grooming	-0.16	0.48	2.54 0.111	33.11	s′ = 1,987.93 L = 0.00 U = 8,988.62	1.29	0.66	5.58 0.018*	26.32	s′ = 12312.89 L = 672.77 U = 56683.98
Social proximity	−0.65	0.42	2.05 0.152	44.59	s′ = 5.01 L = 2.19 U = 85.51	−3.00	0.18	0.21 0.645	0.00	s′ = 0.00 L = 0.00 U = 6.92
Cofeeding	1.28	0.65	3.98 0.046*	56.78	s′ = 8.53 L = 0.06 U = ∞	−4.29	0.11	0.00 1.00	0.00	s′ = 0.00 L = 0.00 U = 7.89
Social play	−2.70	0.21	0.00 1.00	0.00	s′ = 0.00 L = 0.00 U = 59.85	−4.29	0.11	0.00 1.00	0.00	s′ = 0.00 L = 0.00 U = 17.04

An ΔAIC of at least 2 points indicates a better fit of one model over the other: ΔAIC > 2 = social model selected (*) and ΔAIC < 2 = asocial model selected. Akaike weights (ω) represent the weight or likelihood of a model relative to other candidate models (40). Observation networks were collected during task introductions, whereas the remaining networks were collected outside of task introductions. $\Delta AIC = AIC_{asocial\ model} - AIC_{social\ model.}$ %ST: the percentage of events that occurred by social transmission. LRT: a likelihood ratio test comparing both agent-based models. CI95%: 95% confidenceintervals for the social parameter *s′* which determines the strength of social transmission relative to asocial learning. L: Lower value of the CI95%. U: Upper value of the CI95%. When models provided the same results using different approaches and rates, LRT and CI95% were calculated for those with better estimates of the s′ parameter. * indicates models that provide evidence of social transmission. For interpretation of CI95% for the *s′* parameter, refer to Table 1 and SI Appendix in ref. 41.

in PF) occurred by social transmission and a large CI95% range of the s' parameter indicated uncertain strength of the social transmission effect (Table 1). Sex influenced learning rates in both cases, with males learning faster than females (PF, grooming: 154× faster; JB, cofeeding: 17× faster), although results must be taken with caution due to the wide CI95% (Table 2). Consistent with the weak social transmission effects, the best models were obtained using multiplicative approaches, indicating that cofeeding and grooming relations provided opportunities for indirect social learning processes such as local/stimulus enhancement, or social/response facilitation.

To further explore how the patterns of affiliative social relations established outside task introductions may predict observation opportunities in a social learning context, we conducted permutation-based linear mixed model regressions (Table 3). In JB, observation networks within 1 m and 5 m of the task were predicted by cofeeding, grooming, and proximity within 1 m outside of task introductions. In most of those cases, the socio-positive-observation relationship was significantly influenced by social rank similarity (Table 3) such that frequent affiliative partners that are more similar in rank, more frequently observed each other during task introductions than those more dissimilar in rank. Observations beyond 5 m

Table 2. Contribution of the ILVs in social learning for models providing evidence of social transmission

Group	Network	Approach	ILV	Effect (95%CI)
Jurubeba	Observation within 1 m relative frequency	cTADA Additive	Neophobia (latency touch)	0.38 (0.19, 0.73)
	Observation within 5 m relative frequency	cTADA Additive	Neophobia (latency touch)	0.32 (0.12, 0.64)
	Observation beyond 5 m relative frequency	cTADA Multiplicative	Sex	6.19 (1.95, 27.72)
	Cofeeding	cTADA Multiplicative	Sex	16.75 (5.54, 72.34)
Pedra Furada	Observation within 1 m relative frequency	cTADA Additive	Neophobia (latency touch)	0.68 (0.15, 39.81)
	Observation within 5 m relative frequency	cTADA Additive	Neophobia (latency touch)	0.76 (0.15, 70.32)
	Observation beyond 5 m relative frequency	cTADA Additive	Neophobia (avoidance)	1.57 (0.17, 14.41)
	Grooming	cTADA Multiplicative	Sex	154.42 (14.38, 3,352.05)

Approach: cTADA= Continuous time of acquisition NBDA; Additive, indicative of direct social learning/observational; Multiplicative, indicative of indirect social learning such as stimulus enhancement. ILV: Individual-level variable. Effect: The degree to which social and asocial learning increase as measures of the parameters (ILVs) increase, calculated as exp (MLE). For example, in the first line, social and asocial learning rates decrease by a factor of 0.38× per 1 value increase of neophobia (latency to touch the novel object).

Table 3. Results of the permutation-based linear mixed model regressions

Group	Socio-positive network	Observation <1 m	Observation <5 m	Observation >5 m
Jurubeba	Cofeeding	$r_{COF} = 2.492$ ($P < 0.001$)* SR = −0.072 ($P < 0.001$)*	$r_{COF} = 3.889$ ($P < 0.001$)* SR = −0.082 ($P < 0.001$)*	$r_{COF} = 1.035$ ($P = 0.429$) SS = −6.04E-04 ($P = 0.023$)*
	Grooming	$r_{GRO} = 1{,}575$ ($P < 0.001$)* SR = −0.084 ($P < 0.001$)*	$r_{GRO} = 2.939$ ($P < 0.001$)* SR = −0.099 ($P < 0.001$)*	$r_{GRO} = 1.463$ ($P < 0.001$)* SS = −4.45E-04 ($P < 0.001$)*
	Social play	$r_{PLA} = 0.559$ ($P = 0.086$) SR = −0.084 ($P < 0.001$)*	$r_{PLA} = 0.689$ ($P = 0.134$) SR = −9.89E-05 ($P = 0.079$)	$r_{PLA} = -0.139$ ($P = 0.594$) SS = −6.22E-04 ($P < 0.001$)*
	Proximity 1 m	$r_{PR1} = 0.772$ ($P < 0.001$)* SR = −7.89E-05 ($P = 0.018$)*	$r_{PR1} = 1.298$ ($P < 0.001$)* SR = −0.091 ($P < 0.001$)*	$r_{PR1} = 0.556$ ($P = 0.012$)* SS = −5.16E-04 ($P < 0.001$)*
Pedra Furada	Cofeeding	$r_{COF} = 3.066$ ($P = 0.002$)* SS = 0.001 ($P = 0.717$)	$r_{COF} = 3.335$ ($P < 0.001$)* SS = 5.76E-04 ($P = 0.737$)	$r_{COF} = 0.064$ ($P = 0.358$) AS = 5.71E-04 ($P = 0.345$)
	Grooming	$r_{GRO} = 1.364$ ($P = 0.045$)* SS = 0.001 ($P = 0.565$)	$r_{GRO} = 1.621$ ($P = 0.064$) SS = 0.001 ($P = 0.634$)	$r_{GRO} = 0.693$ ($P = 0.363$) AS = 5.35E-04 ($P = 0.349$)
	Social play	$r_{PLA} = 2.260$ ($P = 0.042$)* SS = 0.001 ($P = 0.776$)	$r_{PLA} = 2.927$ ($P = 0.043$)* SS = 0.001 ($P = 0.779$)	$r_{PLA} = 1.460$ ($P = 0.858$) AS = −5.64E-04 ($P = 1.000$)
	Proximity 1 m	$r_{PR1} = 1.395$ ($P < 0.001$)* SS = 0.001 ($P = 0.627$)	$r_{PR1} = 1.568$ ($P < 0.001$)* SS = 0.001 ($P = 0.646$)	$r_{PR1} = 0.313$ ($P = 0.513$) AS = −5.02E-04 ($P < 0.001$)*

r: regression coefficient of the independent network. GRO: Grooming. COF: Cofeeding. PLA: Social play. PR1: Proximity 1 m. SS: regression coefficient for sex similarity. AS: regression coefficient for age similarity. SR: regression coefficient for social rank similarity. *P*: *P*-values. Only regression coefficients and *P*-values of significant variables in the fitted model are reported. *$P < 0.05$.

of the task were only predicted by grooming and proximity within 1 m and, in both cases, relationships were influenced by sex similarity. In PF, observation networks within 1 m and 5 m of the task were predicted by cofeeding, social play, and proximity within 1 m. Only grooming significantly predicted observations within 1 m of the task and no socio-positive network significantly predicted observations beyond 5 m (Table 3).

Transmission Biases. To investigate model-based biases, a GLM analysis with a gamma log link function was run to determine whether any model characteristics (sex, age, dominance, and task success) predicted whom was most frequently observed by naïve conspecifics when interacting with the task. When the overall fitted model was compared against the intercept-only model, a significant fit was found (likelihood ratio chi-square = 80.127, d.f. = 15, $P < 0.001$), indicating that at least one of the factors/covariates characterizing models was predictive of observation frequency. Both the ratio of successful to unsuccessful task manipulations (success ratio) as a main factor and the interaction between sex and success ratio were predictive of the frequency with which a model was observed by naïve conspecifics (Table 4). Sociograms (Fig. 2) indicate that, for both groups, successful males were attended to by naïve individuals most often. Unfortunately, there was insufficient variation in the task option used (lift/pull) in each group to enable analysis of whether the observation bias translated into learning of the behavior exhibited by “successful males” (*SI Appendix*, Fig. S6.1).

Discussion

Detecting Social Learning. The results herein provide empirical evidence for social learning in wild robust capuchin monkeys (*Sapajus sp*), supporting the claims of culture in this clade (44), and as suggested by a similar study of wild gracile capuchins (*Cebus capucinus*: 27). Hoppitt (45) empirically demonstrated that observation networks are a direct and powerful way to detect social transmission, even when there is no social structure information or when other networks (e.g., affiliative) cannot provide evidence of social learning. Observation networks predicted the diffusion of social information regarding task solutions in all cases, with the additive model being the best model in all but one case. This indicates that social learning of the foraging tasks was a direct consequence of observation (e.g., observational learning: 3). These findings for this exceptional tool-using species echo the belief that observational learning supports the maintenance of complex cultural behaviors such as tool use (46, but see ref. 47). In contrast, the multiplicative model selection when NBDA was applied using socio-positive networks outside of task introductions (grooming, social play, social proximity, and cofeeding) to inform the social model reiterates that these relationships reflect opportunities to learn by indirect learning processes such as social facilitation, or local enhancement (*Materials and Methods*).

The Role of Social Dynamics and Social Tolerance. The NBDA findings, the regressions of observation networks with socio-positive networks, and the fact that the individual level variable (ILV) of monopolization did not improve the model fit in any case point to the importance of social tolerance in the dissemination of information through these groups, as seen in several species (chimpanzees: 48, 49; ravens: 50; squirrel monkeys: 51; Barbary macaques: 25).

The observational learning, identified above, requires behavioral coordination in space and time, for which individuals must tolerate

Table 4. Results for the generalized linear model analysis, testing for model-based biases in the choice of observational targets during the lift–pull task experiment

Model fit	Likelihood ratio Chi-square	d.f.	Sig.
Group	2.740	1	0.098
Sex	0.049	1	0.825
Age	0.526	1	0.468
Dominance	0.638	2	0.727
Success ratio	3.959	1	**0.047****
Sex*Age	0.924	1	0.336
Sex*Dominance	1.978	2	0.372
Age*Dominance	2.056	2	0.358
Sex*Success ratio	7.349	1	**0.007****
Age*Success ratio	3.168	1	0.075
Dominance*Success ratio	1.093	2	0.579

$^{**}P < 0.05$.

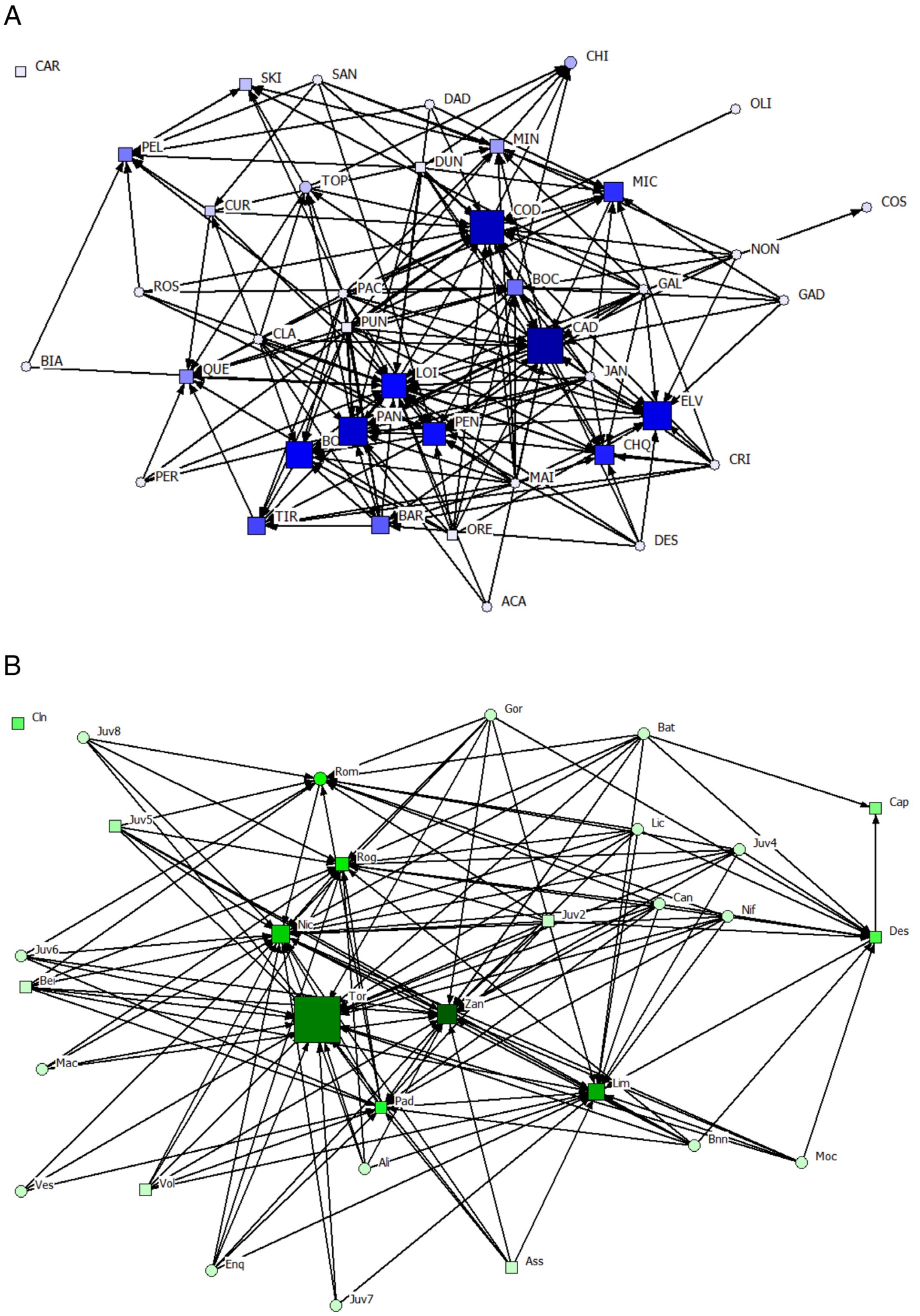

Fig. 2. Observation within 5-m radius networks for (*A*) Jurubeba and (*B*) Pedra Furada. Larger nodes indicate higher in-degree centrality (frequency that a monkey was observed by a naïve conspecific while task solving); darker colors indicate higher success ratios in task solving. Circle = female and square = male.

others in proximity (14). Moreover, socio-positive networks outside of task introductions that were consistent with social transmission in the NBDA were cofeeding (for JB) and grooming (for PF). These represent interactions that are more indicative of tolerance than proximity associations in cohesive groups (e.g., captive starlings: 52) and may be more important than in more fluid fission-fusion groups where proximity associations can predict social learning (e.g., great tits: 53; whales: 54). In a highly competitive context as in our experiment, where the task is a monopolizable resource, social affiliation is a determining factor to be tolerated near, or granted access to, the task (55–57). As visual attention is required for behavioral coordination and any bias in individuals' attention toward closely bonded conspecifics increases the likelihood of acquiring information from those particular individuals via social learning (58) we conducted network regressions. Here, social tolerance represented by grooming, social play, social proximity, and cofeeding (outside of task introductions) were variously predictive of who observed whom (at either 1 m or 5 m) during task presentations, confirming the importance, as predicted by Coussi-Korbel and Fragaszy (14), of social tolerance and diverse relationships in the pathways of information transmission.

Together, results of NBDA and network regressions provide further support that tolerance in the bearded capuchin groups was key in enabling social learning. This corresponds with the assertion of Pasqueretta et al. (59) that, across 78 primate groups, more tolerant groups (with little clustering or variance in individuals' centrality) have more efficient networks in terms of information flow. The sociograms and SNA metrics (*SI Appendix*, section S4), indicate this may be true for PF as a more cohesive group and within each clique/subgroup in the larger JB group, each of which was generally composed of a large male and encircling females. Indeed, the influence of ILVs in the NBDA analysis and network regressions attests to the influence of social structure on the diffusion of information with greater evidence of potential directed social learning (14) in the cliquey JB than PF group. In observation networks beyond 5 m, sex influenced the diffusion of information in JB, with males having a higher learning rate than females, whereas in the cohesive PF it was neophobia(avoidance). Thus, during task introductions in JB, each male had preferential access to the task in front of an audience mostly composed of females from his clique. In fact, in these wild groups, female capuchins are less frequent tool users (34, 60), meaning that natural social diffusion of behavioral traits such as tool-use skills and access to these resources is favored among adult males. Finally, in network regressions, rank similarity (for close-range observation networks) and sex similarity (for observations>5 m network) were determining factors in JB, but no ILVs were relevant in the more cohesive PF. We note, however, that contrary to expectations of directed social learning, the spread of novel task solutions was faster and more encompassing in the "cliquey" JB than the more cohesive PF. This may be explained by the lower connectivity in observation networks (*SI Appendix*, Table S4.1) of PF than JB, due to the greater number of central individuals (large males) in JB that naïve individuals (encircling females) may observe. However, the identity of the "innovator" or trained individual may also have been influential, being a mid-ranking female in JB, yet a subordinate, hence less observed (15), male in PF.

Model-Based Observation Biases. Selective attention by naïve individuals toward proficient individuals (those with high success ratio) was found. Such may translate into a "copy successful" social learning strategy and resonates with what has been described for tool-aided nut cracking in semi-free (*Sapajus spp.*: 36, 37) and wild (*Sapajus libidinosus*: 61) capuchins. As in many natural foraging situations, the naïve individual could be attending to these models for scrounging opportunities. However, the motivation to do so, coupled with social tolerance, allows learning opportunities. Consequently, if more proficient individuals are attended to, there are better chances of a beneficial novel behavior spreading through the social group and fostering cultural evolution.

Here, in the early transmission phase of a tradition, more proficient males were the preferred target of naïve individuals while in Coelho et al.'s (37) study of an established nut-cracking tradition in a different population, age and dominance rank of models were influential as these characteristics reliably correlated with proficiency. Moreover, a study of wild vervet monkeys posed a foraging task (62), suggests that dominant females, rather than dominant males, are favored as a source of social information in species with female philopatry. This stands in opposition to our findings with bearded capuchins, despite them also displaying female philopatry, yet we note this may be explained by the male domination of tool use in this species (34, 60). Further investigations of observation biases for apparent learning purposes (in naïve individuals) are required to elucidate the factors involved in diverse species and contexts to build a better picture of the variety of ways social learning strategies may be combined (7). Such is not confined to model-based biases as indicated by wild vervet monkeys exhibiting a content/direct pay-off bias alongside a bias to copy higher rank individuals (63). Future studies will benefit from ensuring diverse trait variants (e.g., task options) are used by individuals within a group, even while perhaps manipulating their relative payoff, to enable investigation of the extent to which observation biases translate into social learning.

Final Remarks. As shown by our study, social tolerance facilitates the diffusion of social information within primate groups. Through a consequent increase of social learning opportunities such tolerant groups should generate more diverse local traditions (64; evidenced in orangutans: 65) and, according to the "cultural intelligence hypothesis"—that states that cultural effects had a role in the evolution of social tolerance and animal intelligence—ultimately enhanced cognitive abilities (66, 67) necessary for cultural evolution.

Populations of *Sapajus libidinosus* have produced the oldest known nonhuman tools (stone hammers and anvils) outside Africa (3000 y: 68) and, through their percussive activities, unintentionally produce stone flakes and cores that closely resemble those previously thought to be intentionally produced by extinct hominins (69). Moreover, capuchins in caatinga biomes live in unusually large group sizes (70), a demographic factor known to favor the emergence and spread of novel behavior in early humans (71, 72). Likewise, increased terrestriality has recently been linked to increased tool-kit size in these populations (73). Although no extant species is a perfect comparator for extinct hominins, our findings, regarding the importance of social tolerance and observation biases (alongside the influence of population size and terrestriality) for the transmission of novel foraging behavior, contribute to increasing understanding of human technological evolution and cumulative culture in the second half-century of cultural evolution research.

Materials and Methods

Data on group composition, behavioral data sampling and recording methods, and calculation of social ranks, that informed the analysis, are reported in *SI Appendix*, sections S1 and S2.

Open Diffusion Experiment. The lift–pull task consisted of a matte white acrylic box 20(w) × 30(h) × 20(d) cm. The two functional parts were a blue rectangular plate (10 × 8 cm), that could be lifted perpendicular to the front of the box, and a green knob (7 × 5 cm) at the end of a protruding rod, that could be pulled away from the box. Both actions, when successfully executed, triggered release of the same quantity and quality of food rewards (a mixture of corn, peanuts, and raisins) into a tray below (Fig. 1 and *SI Appendix*, Fig. S3.1). The blue plate or green knob would then automatically return to its initial position.

A pilot study with semi-free capuchin monkeys, at Tiete Park, Sao Paulo, indicated it would be unlikely that an individual capuchin would monopolize the task in order to learn it and act as demonstrator. We therefore seeded each wild group with a trained demonstrator by attracting an individual and demonstrating how to solve the task out of sight of other group members. In JB, a mid-ranking adult female (CHI), received a single training session encompassing 4 full demonstrations of the action lift and, when the open diffusion phase started, she was the first to solve the task in her group and did so using lift. In PF, a mid-ranking juvenile male (Lim) received a single demonstration of the pull action, after his group had departed. He then immediately approached the box and solved the task using pull. Note, that half of 14 asocial learning controls failed to solve the task in 4 × 5 min trials (*SI Appendix*, section S3). To further the goal of seeding one option in each group (lift for JB; pull for PF), the task was initially presented, to the entire group, with the appropriate option functioning and the alternative locked. This was maintained until approximately 10% of each group (5 monkeys in JB over 1 d; 3 monkeys in PF over 2 d) had solved the task at least once using the seeded action.

The open diffusion phase began with the task presented to each group with both options functioning for a total of 14 d for each group between September and October 2012 for JB and between March and April 2013 for PF. The task was offered for as long as the group remained in the experimental area or until they had consumed a maximum of 2 kg of food rewards per day. On average, JB spent 90 min around the task, before setting off on their daily routes, resulting in 19 h and 20 min of experimentation. PF would spend, on average, 120 min around the task, resulting in 29 h and 15 min of experimentation. For further details, see *SI Appendix*, section S3.

To accurately record the activities at the task and the opportunities monkeys had of observing conspecifics solving it, the experiment was filmed with two video cameras: one zoomed in on the task to clearly register task manipulations (*SI Appendix*, Fig. S3.1) and one covering a 5 m radius around the task (Fig. 1). CGC also narrated the identity of all monkeys within a 10 m radius of the box and whether they had their heads oriented toward the task when a demonstration occurred, indicating observational opportunities of task solving. Videos were coded independently by two researchers registering i) which individuals solved the task, ii) latency from the beginning of the experiment until each successful task solution iii) which of the two options (lift or pull) was used, iv) the identity and v) distance of monkeys observing the task being solved by a conspecific, regardless of the option used (lift or pull) (for interobserver reliability, see *SI Appendix*, section S9).

Network-Based Diffusion Analysis. NBDA was applied to test for social learning (19). We informed the model with 1) the diffusion of the novel trait as the time or order in which each group member first solved the task and 2) a social network detailing the strength of connection between group members. We used both continuous time of acquisition diffusion analysis (cTADA) and order of acquisition diffusion analysis (OADA) following the guidelines and R codes provided by Hasenjager et al. (41). Results of both analyses were similar hence we report results for the more powerful cTADA (42).

We built networks of varying conspecific observation distances during task manipulations and socio-positive networks, outside of task introductions (grooming, social proximity, cofeeding, and social play). Observation networks during task introductions were used to identify social learning, whereas the socio-positive networks outside task introductions were used to identify potential pathways of social transmission of information. All networks were weighted with the strength of connections between individuals calculated using relative measures (see *SI Appendix*, section S4 and Figs. S4.1 and S4.2 for sociograms). Finally, since NBDA is susceptible to Type I error (20), six noncolinear individual-level variables (ILVs: sex, age, dominance rank, two measures of neophobia, and one measure of monopolization), were included in the NBDA (*SI Appendix*, section S5).

NBDA compared a purely asocial learning model with a social learning model to test whether the order or time of diffusion (task solving) followed the pattern of relations of the social networks. Multimodel inference was used to determine the best models (lowest AICc) in terms of ILV selection and influence on social and asocial learning rates (unconstrained, additive, and multiplicative models). In an unconstrained model, the effect that each ILV has on asocial and social learning rates is estimated independently. The additive model assumes that ILVs only influence asocial learning so that social transmission occurs as an independent process from asocial learning, meaning the total rate of trait acquisition is the sum of the rates of asocial learning and social transmission (i.e., social influence adds to the chances of individual learning). The additive model is, therefore, likely to be appropriate if individuals can acquire the trait as a direct consequence of observation (46) such as observational learning, including imitation. Conversely, the multiplicative model assumes that ILVs equally influence both learning rates and, therefore, the behavior of the demonstrator influences the naïve individual's behavior in a manner that leads indirectly to learning (i.e., whereby the social influence of the demonstrator multiplies the chances of individual learning, such as local/stimulus enhancement (*SI Appendix*, Fig. S6).

Correlations between Socio-Positive Networks and Observation Networks. To test whether affiliative relations outside of task introductions correlate with observation opportunities during task introductions, we used permutation-based mixed models where the socio-positive network was entered as the independent matrix and the observation network as the dependent matrix. Each model was informed with other independent variables or fixed effects (sex, age, and dominance ranks) and random effects (individual identity was used to control for the number of observations, a confounding factor that may bias effect sizes and hinder the interpretation of results: 74). Different models (combinations of fixed and random effects) were tested for the same pair-wise matrix comparison and the Akaike Information Criterion (AIC) used to determine which model better explained the data and Variance Inflation Factor to determine collinearity of variables (with none found) before each regression. The best model was used for regressions with the observed networks and each permutation of the dependent matrix. A total of 10,000 permutations were run for each pair-wise network comparison and *P*-values calculated based on the distribution of the regression coefficients of each permutation-based regression (*SI Appendix*, Fig. S7).

Model-Based Observation Biases. Four variables were considered as possible model-based factors/covariates in the GLM analysis: sex, age, dominance, and success at solving the task. Sex and age-category was known for all experimental subjects and their dominance ranks were determined for the months before, during, and after task introductions in each group. Individual's task-solving success was calculated as a success ratio by dividing the frequency of successful manipulations by the total frequency of (successful + unsuccessful) manipulations of the functional blue plate or green knob. The observation records used portrayed the frequency with which naïve observers (those yet to solve the task) saw the task being solved (and by whom), from close range (within 5 m). To control for individual differences in the frequency of solving the task (and consequent observation opportunities), observation matrices were normalized, along each column based on the maximum value of that column, using UCINET 6.0's "Normalization" procedure. To represent the relative frequency a given individual was observed by naïve conspecifics, while it solved the task, in-degree (which indicates how many edges arrive at the node) was calculated. A generalized linear regression analysis was then conducted to test whether the model-based factors (sex, age, dominance rank) or covariate (success ratio) were predictive of the response variable, the frequency an individual was observed by naïve individuals (in-degree for the model normalized for relative frequency of successful manipulations).

Data, Materials, and Software Availability. Data available at https://osf.io/s4fct/?view_only=43c4790a2025472b840c4c87c35ef1ec; UCINET, SOCProg, Gephi, R code adapted from Hasenjager et al. (41).

ACKNOWLEDGMENTS. FAPESP and CNPq funding to C.G.C. and E.B.O.; Royal Society Dorothy Hodgkin Fellowship funding to R.L.K.; Chico, B. Rawlings and C. Corat (fieldwork data collection), M. Miguel and I. Smith (video coding), Noel Santos (task building), Will Hoppitt (NBDA advice); Parque Nacional Serra da Capivara (ICMBio, Fumdham); Parque Ecologico do Tietê; Living Links, Edinburgh Zoo. Portions of the paper were developed from the PhD thesis of C.G.C.

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