Tolerance of Muzzle Contact Underpins the Acquisition of Foraging Information in Vervet Monkeys (*Chlorocebus pygerythrus*)

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Muzzle contact, where one animal brings its muzzle into close proximity to that of another, has often been hypothesized as a straightforward means of socially mediated food investigation. Using 2,707 observations of muzzle contact occurring across 3 troops of wild vervet monkeys (*Chlorocebus pygerythrus*), we tested this social learning hypothesis. We first explored the social structuring of muzzle contact by analyzing the characteristics of initiators and receivers. Similar to previous research, juveniles initiated contact at higher rates than adults, particularly toward adult females and animals with lower dominance rankings. The highest number of contacts occurred between kin compared to contacts between nonkin. However, on the whole, contacts occurred at low rates, even among kin dyads. We next determined whether muzzle contact was used as a means to learn socially, specifically by animals seeking foraging information. We found that initiators did not overwhelmingly target foragers, meaning animals do not appear to directly seek information about food during muzzle contact. However, animals that contacted foragers were more likely forage themselves in comparison to those that contacted nonforagers, suggesting that foragers do provide food information. These findings indicate that both kin and low-ranking animals serve as discriminative stimuli for social tolerance and that foraging animals serve as discriminative stimuli for food availability. We conclude that broad social tolerance, rather than the recipient's knowledge, is the most likely antecedent to muzzle contact and that animals engage in this behavior as a low-cost means of maintaining a baseline level of information about their environment.

Keywords: social learning, social tolerance, information acquisition, foraging, *Chlorocebus pygerythrus*

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All foraging animals need to locate food, obtain a balance of necessary nutrients, and avoid toxins (King, 1994b). Many taxa use olfaction to investigate potential food stuffs, and, for gregarious animals, such investigation can be socially mediated (Hoppitt & Laland, 2013). Social contact during foraging allows animals to acquire information about novel foods and to avoid consuming those that are harmful (Hoppitt & Laland, 2013). For example, Galef and Wigmore (1983) notably demonstrated that rat food preferences can depend on odor cues found on the breath of conspecifics, an advantageous mechanism given that rats lack emesis abilities and are subsequently more at risk of poisoning if they ingest toxic substances. Similar socially-mediated food preferences via olfaction has been found in mice (Valsecchi & Galef, 1989), bats (O'Mara et al. 2014), even in invertebrates, most famously among the social insects (Farina et al. 2012; Hasenjager et al. 2020; Provecho & Josens, 2009).

Primates can also use olfaction to identify foods, and some primates have particularly developed olfactory systems that are useful for foraging (strepsirrhines) or social communication (platyrrhines) (Barton et al. 1995; Heymann, 2006; Zschoke & Thomsen, 2014). For example, Laidre (2009) found that three species of cercopithecenes (*Mandrillus sphinx*, *Mandrillus leucophaeus*, and *Papio anubis*) often seek olfactory cues when foraging, including from the mouths of others, and Tonkean macaques (*Macaca tonkeana*) can locate food sites and discriminate food availability and quality after sniffing the mouths of conspecifics (Chauvin & Thierry, 2005; Drapier et al. 2002). Furthermore, muzzle–muzzle contact (hereafter muzzle contact; Figure 1) has been proposed as a mechanism by which infant vervet monkeys (*Chlorocebus pygerythrus*; Lycett & Henzi, 1992) and yellow baboons (*Papio cynocephalus*; King, 1994b) can gather information about food. Gaining information about food is an essential stepping stone to foraging independence throughout primate ontogeny (King, 1994a), and muzzle contact could possibly afford such information acquisition (Lycett & Henzi, 1992). The prevalence of muzzle contact is likely to reflect species-relevant sensory modalities. For example, Lycett and Henzi (1992) suggested that olfactory information was more salient than visual information for vervet monkeys, given Cambefort's (1981) finding that vervets did not discriminate

Figure 1
A Juvenile Male Muzzle Contacts Its Mother

Note. Photo, S. Morris. See the online article for the color version of this figure.

aversive visual foraging cues provided by other troop members. Lycett and Henzi (1992) therefore suggested that muzzle contact might act to allow vervets to gain information efficiently from other troop members, particularly infants from their mothers.

Primates have been suggested to possess particularly skillful social learning abilities, but such abilities could also be a byproduct of their social organization (Coussi-Korbel & Fragaszy, 1995; Heyes, 2012; King, 1994b; Shettleworth, 2010; Tomasello, 1996; Visalberghi & Fragaszy, 1990; Visalberghi & Fragaszy, 1996). Certain behavioral features and ecological characteristics of vervets might help tease apart whether the social learning features of primates are particular to the primate order, or can instead be explained by more straightforward social tendencies. For example, vervets are omnivorous generalists, and generalist species have been hypothesized to benefit more from public information concerning foods because the large variation in generalist diets potentially increases the probability of encountering something toxic (Galef & Giraldeau, 2001). In addition, vervet mothers are tolerant of infants while foraging (and sometimes allow infants to take food from their mouths Hauser, 1993, 1994), and vervets are capable of socially transmitting arbitrary food preferences (van de Waal, et al., 2013).

Here, we test the idea that muzzle contact has functional consequences for vervet monkeys (Lycett & Henzi, 1992). We begin by determining whether it is mediated by demographic and/or social characteristics (referred to as "phenotypes" by Carter et al. 2016). There some is prior work that allowed us to make a few specific predictions regarding the structure of muzzle contact. In addition, we conducted exploratory analyses regarding the phenotypic characteristics of initiators and receivers (whether contacts differentiated by age, sex, rank, or kinship) alongside the tests of our direct predictions (Gelman, 2003). Based on previous work, we predicted (a) that juveniles would initiate muzzle contact more often than adults (Grampp, et al., 2019; King, 1994b; Lycett & Henzi, 1992), (b) that the initiators of muzzle contact would be less likely to direct muzzle contact to higher ranking animals, given that muzzle contact requires close proximity and increases the risk of being bitten; and (c) that animals of all ages would target adult females, given that philopatric females are the focus of social attention and might also be expected to have experienced the range of local foods (King, 1994b; Renevey, et al., 2013). We also predicted that (d) the majority of muzzle contact would be directed toward kin and that (e) related dyads would have a higher number of muzzle contacts between them, as previous work on vervets has shown both that muzzle contacts are most frequent between infants and mothers (Lycett & Henzi, 1992) and that infants acquire foraging behavioral variants from their mothers (van de Waal, et al., 2014).

We then answer our key question of whether muzzle contact affords information acquisition. If animals do indeed initiate muzzle contact to acquire foraging information, and initiators are faced with the choice to target either foragers or nonforagers, then (f) initiators should disproportionately target foragers more than what is expected by chance (i.e., greater than 50% of the time; King, 1994b). To the extent that initiators do target foragers, we predicted that (g) initiators would forage immediately after contact. We make this prediction in accordance with three lines of evidence. The first is that by foraging immediately after contacting a forager, initiators and receivers can engage in simultaneous foraging behaviors, which is a form of behavioral matching. Behavioral matching has been

proposed as an important mechanism in novel foraging information acquisition in vervets (van de Waal et al., 2012). The second is that foraging immediately after contact affords selective practice, or the engagement in novel behaviors within an affording context (particularly useful to unskilled animals; Schuppli et al. 2016). Finally, foraging after contact allows animals to immediately capitalize on the benefits of social learning and reduce its potential costs (learning socially can be costly to an animal if the acquired information is outdated, but this cost can be reduced if the learner applies acquired information quickly, for example, in the presence of the relevant food item: Dunlap & Stephens, 2016).

To the extent that animals forage themselves immediately after contacting foragers, we predicted that (h) initiators would be more likely to do so after contacting foragers that are eating rarely encountered foods because new information should be sought more often from foods that are rarely encountered (Barrett et al., 2017). As overall food availability is likely to be implicated in all predictions, we controlled for this in our analyses, although we could not specify the direction of any effects. That is, animals may well turn to olfactory cues when food is generally scarce, and there is the strong possibility of missing a valuable or rare food, but, equally, they may also do so when food availability is high and new dietary items are appearing in the home range.

Method

Study Site and Subjects

We collected data between 2016 and 2018 at the Samara Private Game Reserve, Eastern Cape, South Africa from three troops ("PT," "RST," and "RBM") of vervet monkeys that occupy adjacent and overlapping territories in semiarid riparian woodland (Pasternak et al., 2013). These troops have been continuously studied since 2008 (RST, RBM) and 2012 (PT), and all animals are uniquely identifiable from natural markings. Group composition varied throughout the study period (Table 1).

Behavioral Data Collection

Christina M. Nord and three assistants used electronic data loggers to conduct behavior sampling (explained later) of agonistic interactions and muzzle contacts across a 9-month period from September 2016 to May 2017 and again during a 3-month period

Table 1
Composition of Study Troops Throughout the Study Period

Age-Sex	Count range	M
RST adult females	8–13	9
RST adult males	6–10	8
RST juvenile females	14–16	15
RST juvenile males	4–11	10
PT adult females	8–9	9
PT adult males	5–9	6
PT juvenile females	8–10	9
PT juvenile males	13–16	15
RBM adult females	5–10	7
RBM adult males	4–7	6
RBM juvenile females	14–16	15
RBM juvenile males	10–13	12

between March and May 2018. In all, 16,594 observations of decided agonistic interactions ($N_{RBM} = 5,061$; $N_{RST} = 5,914$; $N_{PT} = 5,619$) and 2,707 muzzle contact observations were collected across 1,107 observer days ($N_{RBM} = 339$; $N_{RST} = 441$; $N_{PT} = 327$).

Observers were trained to identify individual animals, relevant behaviors, vegetation, and how to record occurrences and outcomes of agonistic interactions by experienced field assistants as part of training to collect baseline data (Young et al., 2017). Muzzle contacts were not part of the baseline data collection, and as such, Christina M. Nord trained field assistants to identify muzzle contact and its duration. Consistency and accuracy were ensured by spot checks in the field on a regular basis to ensure interobserver agreement on particular cases. Given that we collect data for 10 hr a day, 5 days a week, there is some time during which animals are not observed. As such, we describe our behavioral data collection as behavior sampling (Martin & Bateson, 2007) rather than "all-occurrence sampling," as behavior sampling describes the recording of each instance of a behavior during a set observation period.

Observers also recorded agonistic interactions and muzzle contacts while performing other data collection duties (e.g., scan sampling, fecal sample collection) that required them to search for every individual every half hour. Given this, and that our study site is characterized by generally high visibility and animals are well-habituated, we are confident that data were collected without systematic bias.

Agonistic interactions included lunges, charges, chases, displacements, and supplants (Young et al., 2017). We defined muzzle contact as a directed dyadic behavior that began when one animal (the initiator) brought its muzzle to within 1 cm of another animal (the receiver), and ended when the dyad members' muzzles were more than 2 cm apart (Figure 1). We recorded dyad member identities and date and time of muzzle contact, along with approximate duration, bracketed as 1–3 s, 3–5 s, 5–10 s, or 10+ s. We also recorded whether or not dyad members foraged in the 5 s before muzzle contact began, and/or in the 5 s after muzzle contact ended. Foraging was defined as actively gathering (e.g., pulling grass, pulling leaves), searching for (digging through dirt or grass, chasing insects), and ingesting food (putting food in the mouth, biting food, or chewing food). If animals did forage, we also recorded the food type. As our study troops' territories overlapped, we also observed and recorded muzzle contacts between members of different groups.

Age

Subjects were categorized as either juvenile or adult in relation to sexual maturity (Jarrett et al. 2018; birth to less than ~3.5 years for females; or less than 5 years for males).

Relatedness

The identities of mothers, their offspring, and maternal siblings have been collected since 2013 as part of the Samara Vervet Monkey Project's ongoing baseline data collection. We included only muzzle contacts initiated by juvenile animals in our relatedness analyses because, whereas the relatedness between all juvenile–juvenile and juvenile–adult dyads for the current study is known, relatedness between adults born before 2013 is largely unknown.

Table 2
Summary of the Predictions Made, Variables Included, and the Subsequent Findings

Prediction	Response variable	Predictor variables (grouping variables)	Covariates	Finding
(a) Juveniles initiate muzzle contact more often than adults	Count of contacts initiated	Initiator age/sex, initiator average rank (initiator ID, initiator troop)	N/A	Juvenile females had the highest rate of initiating muzzle contacts per the study period (Table 3, Figure 2a)
(b) Initiators direct less muzzle contact to higher ranking animals	Count of contacts received	Receiver age/sex, average receiver rank (receiver ID, receiver troop)	N/A	Lower ranking animals received more muzzle contacts than did higher-ranking animals (Table 4, Figure 2b)
c) Animals target adult females	Count of contacts received	Receiver age/sex, average receiver rank (receiver ID, receiver troop)	N/A	Adult females received muzzle contact at the highest rates, and females overall received muzzle contacts at higher rates than did males (Table 4, Figure 2b)
(d) The majority of contact is directed towards kin	Kin and nonkin dyads	Initiator sex, receiver sex, initiator age (initiator ID, receiver ID, initiator troop, receiver troop)	NDVI	9.3% of contacts occurring between kin (Table 5)
(e) Related dyads have more contacts between them	Counts of kin and nonkin dyads	Initiator sex/receiver sex, dyad relatedness, average dyad rank difference, initiator age (initiator ID, receiver ID, initiator troop, receiver troop)	N/A	Kin-based muzzle contacts occurred at the highest rates per the study period compared to nonkin-based muzzle contacts (Table 6, Figure 3)
(f) Initiators target foragers greater than 50% of the time	Contacts to foragers vs. nonforagers	N/A (initiator ID, receiver ID, initiator troop, receiver troop)	NDVI	Initiators targeted foragers 46.7% of the time (Table 7)
(g) Initiators forage immediately after contact	Initiators foraged post contact (yes/no)	Foraging receiver (yes/no), initiator age/sex, dyad rank difference (initiator ID, receiver ID, initiator troop, receiver troop)	Approximate duration, NDVI	There was a higher probability that an initiator would forage immediately following contact with a forager than with a non-forager (Table 8, Figure 4)
(h) Initiators forage immediately after contact more so after contacting foragers who are eating rarely encountered foods	Initiators foraged post contact (yes/no)	Initiator age/sex, dyad rank difference, receiver food type frequency (initiator ID, receiver ID, initiator troop, receiver troop)	Approximate duration, NDVI	No clear effect of rarely encountered foods (Table 9)

Note. NDVI = Normalized Difference Vegetation Index.

Dominance Rankings and Dominance Rank Differences

These analyses focus on the structure and function of muzzle contact between all group members, so we calculated dominance ranks across all members of each troop rather than within specific age and sex classes, allowing us to compare muzzle contact and agonistic interactions directly.

We generated dominance hierarchies from decided agonistic dyadic interactions for all troop members. We first determined if rank changed by dividing the 12-month study period into four 3-month blocks and calculated rank as standardized (allowing comparison across troops), normalized David's scores using the R package "compete" (Curley et al., 2015) in R 3.5.2 (R Core Team, 2018). The divisions ensured adequate sample sizes with which to estimate ranks. After confirming that rank varied within animals (we measured variation by calculating the SD of each animal's ranks throughout the study period; mean SD = .116, range SD = 0-.385), we used these

Table 3
Posterior Estimates of Muzzle Contact Initiation Rate

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population-level effects	Intercept (adult females)	−2.797	0.142	−3.077	−2.485
	Juvenile females	0.536	0.130	0.289	0.796
	Adult males	−0.674	0.153	−0.979	−0.372
	Juvenile males	0.159	0.129	−0.096	0.412
	Average rank	0.326	0.182	−0.025	0.688
Group-level effects	SD (ID)	0.454	0.042	0.379	0.543
	SD (Troop)	0.141	0.192	0.003	0.657

Note. Age-sex is relative to adult females. Estimates are on the log scale; CI = credible interval. N = 145. R^2 marginal = .427; R^2 conditional = .903.

Figure 2

Rates of Muzzle Contact (a) Initiation and (b) Receiving by Age-Sex Category
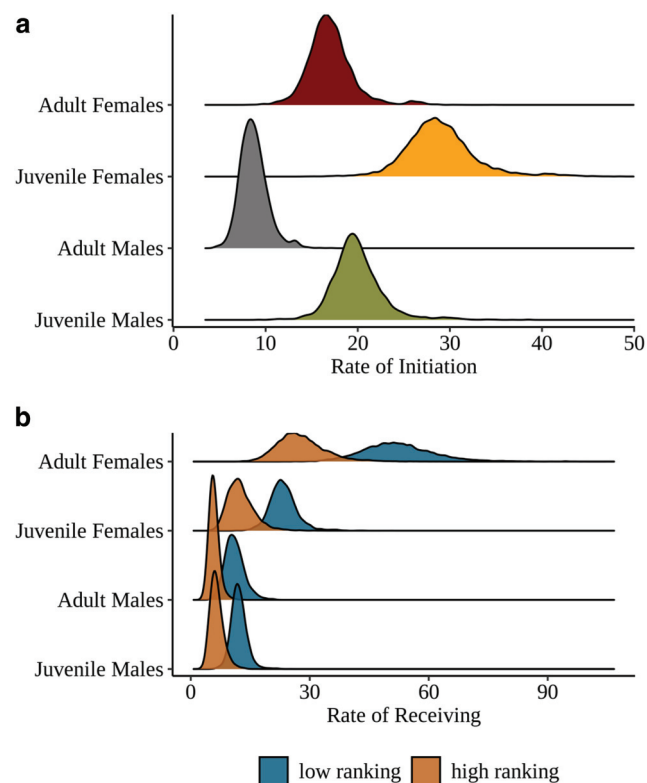
Note. Density plots present the range of rates predicted by the model, with the height of the density curve indicating the probability of the predicted rate, and the spread of the curve indicating its uncertainty (Tables 3 and 4). Rates are back-transformed from the log scale into the original scale. In this context, rate refers to the number of contacts initiated (a) and received (b) per the study duration. See the online article for the color version of this figure.

dynamic rank estimates (i.e., our 3-month block estimates) in our analyses.

For all models exploring dyadic relationships, we used differences in dominance rank (initiator–receiver), where positive values indicate that the initiator was higher ranking than the receiver. Dominance ranks were averaged across the study period for all Poisson models. For muzzle contacts that occurred across troops, differences in dominance rank were relative to each dyad

members' within-troop rankings, as dominance ranking were only calculated from within-troop agonistic interactions.

Relative Frequencies of Food Types

The relative frequency with which animals encountered different foods was derived from the foods that recipients were eating prior to muzzle contact.

Troop-Level Estimates of Resource Availability

We used the Normalized Difference Vegetation Index (NDVI) to model differential resource availability experienced by the three troops, as this has been shown to be a strong correlate of food availability to wild vervets (Willems, et al., 2009). NDVI estimates were obtained using Moderate Resolution Imaging Spectroradiometer (MODIS) NDVI data downloaded from NASA's "Reverb | ECHO" site (Didan, 2015). The Earth Observing System (EOS) satellites Terra (EOS AM-1) and Aqua (EOS PM-1) collect MODIS data with a return-to-site periodicity of 16 days (Didan, 2015). We then used "ArcGIS" Version 1.6.1 to overlay the MODIS data onto the three territories, with each territory represented as a regular series of points 10-m apart. NDVI values were then extracted from the MODIS rasters at each point. Area-weighted averages for each territory were generated every 16 days by averaging all NDVI values for points falling within the territory's 95% isopleth and weighted by the troop's differential usage of its territory during that period.

Statistical Analyses

We constructed multilevel regression models within a Bayesian framework (Gelman & Shalizi, 2013) using the package "brms" (Bürkner, 2017) in R 3.5.2 (R Core Team, 2018). Sample sizes of observed muzzle contacts varied with respect to the variables included in each tested model. We specified four chains and 3,500 iterations for all models. All models included weakly informative priors ($M = 0$, $SD = 1$). All r^s = 1.0, confirming model convergence (Gelman & Shirley, 2011). Using the "DHARMa" package in R (Hartig, 2017), we tested residual assumptions for each dataset all data sets met model assumptions except for our model investigating muzzle contact interaction indices between related dyads (see the following sections). In addition, we used directed dyads because we were interested in whether or not specific animals were being targeted for contact, and, given cross-troop contact, we included initiator and/or receiver troop membership as random effects in all models.

Table 4

Posterior Estimates of Muzzle Contact Receiving Rates

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population-level effects	Intercept (adult females)	−1.890	0.136	−2.164	−1.600
	Juvenile females	−0.804	0.130	−1.053	−0.552
	Adult males	−1.565	0.155	−1.873	−1.264
	Juvenile males	−1.462	0.132	−1.721	−1.202
	Average rank	−0.425	0.183	−0.778	−0.059
Group-level effects	*SD* (ID)	0.479	0.042	0.403	0.567
	SD (Troop)	0.150	0.202	0.003	0.742

Note. Age-sex is relative to adult females. Estimates are on the log scale; CI = credible interval. $N = 145$. R^2 marginal = .515; R^2 conditional = .945.

Table 5
Posterior Estimates of Whether Juveniles Contacted Kin (y/n)

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population-level effects	Intercept (juvenile females)	−2.359	1.195	−5.011	0.062
	Rank difference	−0.785	0.326	−1.413	−0.151
	Male initiators	0.451	0.229	0.012	0.917
	Male receivers	−1.422	0.325	−2.076	−0.788
	Initiator age	−0.875	0.130	−1.129	−0.617
Group-level effects	SD (initiator)	0.702	0.144	0.436	1.000
	SD (initiator troop)	0.984	1.452	0.021	5.112
	SD (receiver)	1.252	0.173	0.946	1.626
	SD (receiver troop)	1.041	1.533	0.018	5.281

Note. Sex is relative to (a) females and (b) female–female dyads. All initiators are juveniles. Estimates are on the logit scale; CI = credible interval. N = 1,964. R^2 marginal = .092; R^2 conditional = .314.

We explored whether specific social and demographic phenotypes influenced muzzle contact (predictions a-c) by constructing two Poisson models, one modeling the characteristics of initiators, and the other the characteristics of receivers. For both models, age-sex categories and rank served as predictor variables, whereas the number of times an animal acted as an initiator served as the response variable in the initiator model, and the number of times an animal acted as a receiver served as the response variable in the receiver model. We entered the ID and troop membership as random effects, as well as an offset variable accounting for the number of days each animal was present during the sample period.

We then assessed the relationship between relatedness and muzzle contact (Prediction d). Because relatedness between adults was largely unknown, we explored this question for only juvenile-initiated dyads by constructing a Bernoulli model to determine how often juveniles contacted kin as compared to nonkin. For this model, whether or not the receiver was related to the juvenile initiator (yes/no) served as the response variable, and differences in dominance rank, receiver sex, and initiator age at the time of contact (calculated by adding days since birth to the time of muzzle contact; these values were centered and scaled, resulting in ages represented as SDs above and below the mean value) were entered as predictor variables, with receiver ID, initiator troop membership, and receiver troop membership as crossed random effects.

We were also interested in the effect of relatedness on muzzle contact interaction rates, that is, the total number of contacts

per the study duration, between specific dyads initiated by juveniles (prediction e), so we constructed a Poisson model to determine the rates of juvenile-initiated muzzle contacts. Using rates allowed us to calculate interaction indices for muzzle contact and determine if certain dyads made contact at higher rates than others. Given that our response variable for this model was dyadic, so too were all of our fixed effects (e.g., the fixed effect "sex" included the sexes of both dyad members, either male-male, male-female, female-male, or female-female). Thus, we specified the identities of each dyad as our response variable and included sexes of the dyad, dominance differences between the dyad, average age of the initiator during the study period, and whether or not the dyad was related (yes/no) as fixed effects. Initiator ID, receiver ID, and troop memberships of the initiator and the receiver were entered as crossed random effects. Our analysis of residuals for this model (which used a Poisson distribution) revealed underdispersion in the data—the model did not account for many of the dyads that interacted only one time. Running this model using a hurdle Poisson distribution (Hilbe, 2017) removed the underdispersion and revealed the same relative estimates as our original, underdispersed Poisson version of the model. Given this, we present the results from the simpler Poisson model in the following text and provide results from the hurdle Poisson version of the model in the Supplementary Materials.

We then explored whether muzzle contact affords information acquisition by constructing three Bernoulli models (Predictions

Table 6
Posterior Estimates of Dyad Association Indices

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population-level effects	Intercept (Female–female dyads)	−4.896	0.225	−5.372	−4.401
	Average rank difference	0.014	0.090	−0.164	0.191
	Relatedness	0.718	0.062	0.592	0.837
	Female–male dyads	−0.520	0.090	−0.696	−0.348
	Male–female dyads	−0.236	0.062	−0.357	−0.114
	Male–male dyads	−0.499	0.096	−0.688	−0.313
	Average initiator age	0.026	0.040	−0.051	0.103
Group-level effects	SD (initiator)	0.119	0.040	0.034	0.194
	SD (initiator troop)	0.199	0.331	0.003	1.063
	SD (receiver)	0.222	0.031	0.164	0.286
	SD (receiver troop)	0.189	0.303	0.003	1.005

Note. Sex is relative to (a) females and (b) female–female dyads. All initiators are juveniles. Estimates are on the log scale; CI = credible interval. N = 1,105. R^2 marginal = .199; R^2 conditional = .305.

Figure 3

Muzzle Contact Rates as Predicted by the Model for Nonkin (Green, Light Grey) and Kin (Blue, Dark Grey) Dyads
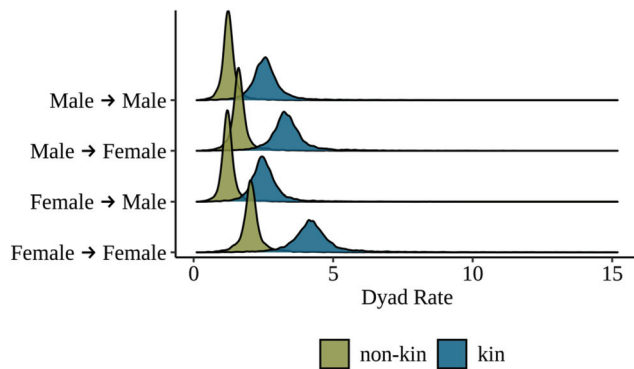
Note. Density plots present the range of rates predicted by the model, with the height of the density curve indicating the probability of the predicted rate, and the spread of the curve indicating its uncertainty (see Table 6). Rates are back-transformed from the log scale into the original scale. In this context, rate refers to the number of contacts per the study duration. See the online article for the color version of this figure.

f–h). We first determined if initiators targeted foragers significantly more than non-foragers (Prediction f) by creating a model with whether or not receivers forage after contact (yes/no) as the response variable, NDVI as the predictor variable, and initiator ID, receiver ID, and troop memberships of the initiator and receiver as crossed random effects. We next determined how often initiators foraged after contacting a forager (Prediction g) by constructing a model in which foraging post contact (y/n) was entered as our response variable, whether receivers foraged prior to contact (yes/no), age-sex, and differences in dominance rank as predictor variables, and receiver ID, initiator troop membership, and receiver troop membership as crossed random effects. Finally, to determine if rarely encountered foods increased initiator postcontact foraging (Prediction h), we specified whether initiators foraged post contact (y/n) as our response variable, relative food type frequency, age-sex, and differences in dominance rank as predictor variables, and receiver ID, initiator troop membership, and receiver troop membership as crossed random effects. We included NDVI in all information acquisition models to account for local ecological conditions, and duration of contact as a statistical control for the probability that information could be adequately transmitted during contact.

Model main effects are presented as summary statistics for posterior means, standard errors (*SE*s), and 95% credible intervals (CIs), along with group-level variation in our response variables.

Ethical Note

All protocols were noninvasive and adhered to the laws and guidelines of South Africa and Canada. Procedures were approved by the University of Lethbridge Animal Welfare Committee (Protocols 0702 and 1505). This study also adheres to the Association for the Study of Animal Behaviour/Animal Behaviour Society Guidelines for the Use of Animals in Research.

Data Availability

The data that support the findings of this Study and related R notebook are openly available in Figshare at https://doi.org/10.6084/m9.figshare.c.4794657.v2.

Results

All of the muzzle contacts we recorded were typical to our definition. We found that once initiators brought their muzzles within 1 cm of the receivers' muzzle, initiators were never refused or rejected, and we observed no agonistic interactions during muzzle contacts. Although it could be the case that potential receivers refused contact prior to initiation, such refusals would be impossible to record as they would have occurred before the 1 cm threshold in our definition of muzzle contact. (Video S1 in online supplemental material)

Predictions, variables, and findings are summarized in Table 2.

Initiator and Receiver Characteristics

Juvenile females had the highest rate of initiating muzzle contacts per the study period, whereas adult male–initiated muzzle contact at the lowest rates pre age/sex class (Table 3, Figure 2a). Dominance rank had little effect on the number of contacts initiated (Table 3). Adult females received muzzle contact at the highest rates per the study period, and females overall received muzzle contacts at higher rates per the study period than did males (Table 4). In addition, lower ranking animals received more muzzle contacts than did higher ranking animals (Figure 2b). The difference between the marginal and conditional R^2 values reveal that there remains unexplained variation (beyond our predictor variables) in our grouping variables, particularly between individual animals (as opposed to between observations within animals Nakagawa & Schielzeth, 2013), but not between troops (Table 3, Table 4).

Table 7

Posterior Estimates of Whether Initiators Contacted Foragers (y/n)

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population-level effects	Intercept	0.179	0.623	−1.060	1.563
	NDVI	−0.800	0.485	−1.797	0.131
Group-level effects	*SD* (initiator)	0.315	0.070	0.178	0.455
	SD (initiator troop)	0.495	0.779	0.008	2.781
	SD (receiver)	0.506	0.075	0.361	0.657
	SD (receiver troop)	0.471	0.766	0.009	2.611

Note. Estimates are on the logit scale; CI = credible interval. N = 2,707. R^2 marginal = .001; R^2 conditional = .069.

Table 8
Posterior Estimates of Initiators Foraging After Contacting Foragers

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population-level effects	Intercept (adult females)	−2.218	0.563	−3.300	−0.907
	Foraging receiver	2.148	0.105	1.947	2.355
	Juvenile females	0.232	0.138	−0.035	0.499
	Adult males	−0.177	0.210	−0.600	0.215
	Juvenile males	0.128	0.147	−0.151	0.428
	Approximate duration	0.018	0.042	−0.065	0.101
	NDVI	−0.010	0.532	−1.059	1.048
	Rank difference	−0.051	0.139	−0.324	0.228
Group-level effects	SD (initiator)	0.102	0.073	0.004	0.270
	SD (initiator troop)	0.406	0.627	0.008	2.232
	SD (receiver)	0.138	0.086	0.007	0.320
	SD (Receiver troop)	0.426	0.641	0.006	2.392

Note. Age-sex is relative to adult females. Estimates are on the logit scale; CI = credible interval. $N = 2,655$. R^2 marginal = .189; R^2 conditional = .201.

Is There a Kin Basis to Muzzle Contact?

How Often Do Juveniles Contact Kin?

Our model testing whether related juveniles were more likely to contact kin compared to nonkin found little evidence that this was the case, with only 9.3% of contacts occurring between kin (Table 5; we calculated percentages using model marginal means and back-transformed this value into the original scale). There were, however, age and sex differences in kin-based contacts: Younger juveniles and juvenile males were more likely to direct contacts toward kin compared to nonkin, and juvenile males were less likely to be contacted by relatives. Comparison of marginal and conditional R^2 values reveals that overall model performance was, to a large degree, driven by unexplained variation in our grouping variables, including initiator and receiver identities, as well as initiator troop membership (Table 5).

Are Dyad Rates Influenced by Kinship?

Our model investigating the rates of contact per dyad found that most dyads occurred at low rates (Table 6). We also found that kin-based muzzle contacts occurred at the highest rates per the study period compared to nonkin-based muzzle contacts (Table 6, Figure 3). We found no effect of average initiator age between related dyads on this rate (Table 6). Comparison of marginal and conditional R^2 values reveals that unexplained variation remains among initiator and receiver identities (Table 6).

How Often Do Initiators Contact Foragers?

There was little evidence that initiators contacted foragers more frequently than nonforagers, doing so only 46.7% of the time (and therefore contacted nonforagers 53.7% of the time; Table 7; we calculated percentages using model marginal means and back-transformed this value into the original scale). We found little evidence that initiators were more likely to contact foragers during times of low resource availability (Table 7). This model accounted for minimal variance in the response variable, as indicated by the marginal R^2 and conditional R^2 values.

## Do Initiators Forage After Contacting a Forager?

There was a higher probability that an initiator would forage immediately following contact with a forager than with a nonforager (Table 8), with female juveniles being slightly more likely to do so compared to all other age-sex classes (Figure 4). Duration of muzzle contact, NDVI, and difference in dominance rank had little impact on the probability of subsequent foraging. The overall model explained approximately 20% of the variance, and comparison of marginal and conditional R^2 values indicates little contribution of grouping-level differences in either individual or troop identities, indicating that most observed variation was between observations rather than among particular grouping variables (Table 8).

Do Rarely Encountered Foods Affect Foraging After Contact?

We cannot be certain of any effect for rarely encountered foods, as the right tail of the CI for the estimate contains zero. However, the density of the CI could point toward a possible effect of rarely encountered foods, as most of the density lies within the negative range, indicating that the rarer the food foraged by the receiver, the more likely the initiator was to forage post contact. However, any

Figure 4
Probabilities of Initiators Themselves Foraging After Contacting Foragers (Yellow, Light Grey) and Nonforagers (Grey) by Age-Sex Categories
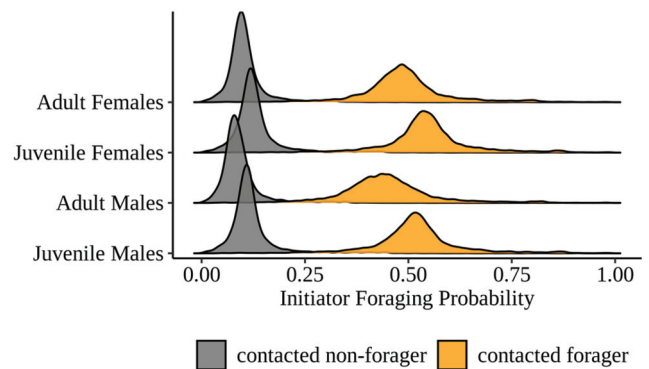
Note. Density plots present the range of probabilities predicted by the model, with the height of the density curve indicating the likelihood of the probability, and the spread of the curve indicating its uncertainty (Table 7). Probabilities are back-transformed from the logit scale into a probability scale. See the online article for the color version of this figure.

Table 9
Posterior Estimates of Initiators Foraging After Contacting Foragers Dependent Upon the Food Item Eaten by the Receiver

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population-level effects	Intercept (adult females)	−0.108	0.804	−1.886	1.646
	Juvenile females	0.258	0.160	−0.056	0.577
	Adult males	0.008	0.249	−0.484	0.479
	Juvenile males	0.115	0.168	−0.211	0.456
	Receiver foodtype frequency	−1.248	0.771	−2.759	0.277
	Approximate duration	0.010	0.048	−0.083	0.106
	NDVI	0.415	0.591	−0.727	1.562
	Rank difference	−0.343	0.168	−0.668	−0.004
Group-level effects	*SD* (initiator)	0.108	0.078	0.004	0.289
	SD (initiator troop)	0.547	0.851	0.010	2.928
	SD (receiver)	0.129	0.087	0.006	0.326
	SD (receiver troop)	0.722	1.348	0.009	5.300

Note. Age-sex is relative to adult females. Estimates are on the logit scale; CI = credible interval. $N = 1,305$. R^2 marginal = .012; R^2 conditional = .024.

effect of rare foods is uncertain. We found no effect of duration of contact, food availability, or age/sex class on the frequency of foraging post contact. We did find a small effect of rank difference on whether or not initiators foraged post contact given they had contacted a forager. However, comparing the conditional and marginal R^2 values indicate that our model accounts for minimal variance and reveals few differences among either individual or troop identities, again indicating that most observed variation was between observations rather than between particular grouping variables (Table 9).

Discussion

Our results confirm that muzzle contact is afforded and constrained by social structure and directed toward tolerant animals. In addition, we found that muzzle contact has the potential to afford foraging information. As predicted, muzzle contact was influenced by both demographic and social phenotypes. Juveniles initiated contact more so than adults, and contact was directed disproportionately toward adult females, replicating Lycett and Henzi's (1992) findings. In addition, dyads that had the largest number of muzzle contacts were more likely to be kin. Most dyads, however, did not interact very often, and these lower levels of interaction were not disproportionately kin-based.

In sum, we found evidence that muzzle contact had functional consequences for our monkeys: Animals were more likely to forage themselves after contacting foragers. This suggests that foragers provide salient information about local food availability. Given this, it seems reasonable to infer that muzzle contact may afford social learning for foraging (Hoppitt & Laland, 2013). Against this, initiators did not appear to target foraging animals specifically for muzzle contact, nor did they clearly adapt their behavior post contact in relation to the type of food eaten by receivers.[1] Thus, although muzzle contact is a potential means of information transfer, it appears that our animals did not always seek such information from others, nor did they vary their behavior with respect to the information they obtained.

Perhaps a more reasonable interpretation of our results is that foragers serve as discriminative stimuli for food availability, and kin and low-ranking animals serve as discriminative stimuli for social tolerance. That is, animals may have learned that by approaching foragers (i.e., coming within close proximity) they will often find food and that by approaching kin and low-ranking animals, they will often either gain access to social reinforcement (e.g., grooming partners;

positive reinforcement) or avoid social punishment (e.g., displacement; negative reinforcement). Any muzzle contacts that occur in these contexts could then be reinforced by either accessing food or gaining/avoiding social reinforcement. Thus, given our findings, it is likely that muzzle contact is multiply determined.

With respect to relatedness, our findings speak to an ongoing debate in the social learning literature: Do some animals fail to benefit from social learning because they lack certain adaptive strategies (Kendal et al. 2018); or because they are constrained by various phenotypic traits (Carter et al. 2016)? Our data suggest that, at least for our animals, this question cannot be answered in a binary fashion. Our findings do not follow from either the adaptation or constraint hypotheses. For example, while dyads with higher interaction counts were more likely to be related (which could be interpreted as a kin-biased adaptive learning strategy and thus consistent with the adaptation hypothesis), most dyads had low numbers of interaction, meaning that the large majority of contacts were between nonkin. In addition, because muzzle contact occurred mostly between nonkin, relatedness did not necessarily restrict any information potentially gained from muzzle contact, contradicting an interpretation that follows the phenotypic-constraint hypothesis.

Given this pattern of results, our hypothesis is that these animals use muzzle contact as a low-cost means of targeting socially-tolerant conspecifics in order to quickly and effectively update their knowledge of current resource availability, rather than to seek specific foraging information. The tolerance levels of recipients, rather than the quality of the "knowledge" they possess, thus serves as the impetus for muzzle contact. Our observation that juveniles engage in muzzle contact more than adults supports this interpretation: With less-established learning histories than adults, they will need to update their information more frequently.

Furthermore, muzzle contact might also have additional functions. As close facial contact is a significant pathway of pathogen transfer, muzzle contact could potentially transmit microbes in addition to transmitting foraging information. Tung et al. (2015) found that after

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[1] As pointed out by reviewers, an alternative null from which we could interpret these findings is that initiators do not always have equal access toforagers and nonforagers, and we could conclude that initiators aretargeting foragers if they do so more than 27.0% of the time, as this is the proportion of animals foraging at any given time (Table S3, Figure S8). The authors thank the editor and three anonymous reviewers for their comments and suggestions here and elsewhere, which greatly improved the manuscript.

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controlling for diet, kinship, and shared environments, variation in the gut microbiomes of yellow baboons (*Papio cynocephalus*) can be explained by social relationships. This finding underscores the significance of direct physical contact between social partners in gut microbial species transmission, which could in turn be consequential in the evolution of sociality. In addition, the patterns of juvenile engagement we found also suggest that muzzle contact might serve a social function, as a way to signal and assess interindividual tolerance, much as play signals do (cf., Bergman & Sheehan, 2013; Cordoni et al. 2018; Palagi et al. 2015). Older juveniles were less likely to contact kin than younger juveniles, suggesting that juveniles may use muzzle contact to learn who they can contact without adverse consequences as they grow older. This, in turn, might form part of a larger juvenile strategy to integrate themselves into networks beyond their kin-groups as they age, possibly affording the development of affiliative relationships beyond the broad social tolerance we find here (Jarrett et al., 2018). In this regard, it will be interesting to discover if factors beyond those associated with individual dyads (e.g., the structure of the network itself, which can be investigated via triadic relationships: Faust, 2010; Ilany et al. 2013; Wey et al. 2019) could help identify possible social affiliative functions of muzzle contact. A social affiliation component to muzzle contact would help explain why hypotheses related to information acquisition cannot fully account for the patterns we observe, and add to our findings of broad social tolerance.

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