

Lemurs groom-at-a-distance through vocal networks

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Vocal exchanges are predicted to serve a social bonding function by allowing conspecifics to 'groom-at-a-distance'. If vocalizations play a role in bonding, then they should be mainly exchanged between the socially bonded group members, and thus display high social selectivity that characterizes other affiliative behaviours such as grooming. However, whether or not vocal exchanges are driven by social bonds remains unclear. We investigated vocal selectivity by studying the relationships between contact-calling networks and grooming networks in multiple free-ranging groups of ringtailed lemurs, *Lemur catta*. Lemur grooming interactions were socially selective and were directed towards only some of their group members. However, their vocal exchanges displayed even higher levels of social selectivity. Instead of exchanging vocalizations with each group member they groomed, lemurs reserved their vocal responses mainly for the group members whom they had frequently groomed. We tested this vocal selectivity through a playback experiment in which we presented lemurs' calls to their group. Lemurs responded only to the playbacks of the conspecifics whose calls they had responded to while free-ranging, confirming that selective vocal responses do not depend on proximal (i.e. visual or olfactory) cues from the vocalizing lemur. These robust relationships between grooming and contact-calling networks in lemurs, a species that lives in small groups where grooming frequency reflects bond strength, demonstrates that vocal exchanges indicate the strong social bonds between conspecifics. Contact calls may serve a bonding function in social species by allowing the strongly bonded group members to groom-at-a-distance when they are separated from each other.

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Grooming (or preening) is the main social bonding method in most social species and has multiple benefits beyond health maintenance and hygiene (Barton, 1985; Cords, 1997; Silk, 2007; Silk, Altmann, & Alberts, 2006). However, grooming is very time consuming, requiring animals to be selective in whom they groom (Dunbar, 2003, 2004; Lehmann, Korstjens, & Dunbar, 2007). Pairs with strong social bonds devote more time to grooming each other than do pairs with weak or no bonds, and the frequency of grooming between two individuals reflects the strength of their bond (Silk et al., 2006). Grooming also requires close physical proximity, restricting conspecifics' ability to maintain bonds when they are separated from each other during daily activities such as foraging and movement. Together, these limitations introduce a challenge to group-living animals: when grooming the group

members with whom they share social bonds becomes impractical, what additional methods exist for maintaining these bonds?

Vocalizations may provide a solution to this problem by taking on a social bonding function. Vocal communication has several functions that range from territorial defence to individual recognition and group synchronization (reviewed in Fichtel & Manser, 2010). Most of these functions are achieved through specific types of vocalizations. For example, contact calls serve as a long-distance signal for group members to locate each other, and are thus critical for group cohesion (Kondo & Watanabe, 2009). Production of a contact call by a group member usually elicits vocal responses from conspecifics, resulting in the vocal exchanges that have been detected in multiple bird and mammal species (Fedurek, Machanda, Schel, & Slocombe, 2013; Nakahara & Miyazaki, 2011; Soltis, Bernhards, Donkin, & Newman, 2002; Soltis, Leong, & Savage, 2005; Takahashi, Narayanan, & Ghazanfar, 2013; Yosida & Okanoya, 2009). Because vocal exchanges are not as time consuming as grooming, do not require close proximity between the participating group members and can be effective at long distances, they may overcome some of the main challenges presented

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by grooming (Dunbar, 2003). Consistent with these advantages, it has been suggested that vocal exchanges may allow animals to maintain social bonds by ‘grooming-at-a-distance’ (Dunbar, 1993, 2003, 2004). If vocal exchanges have a social bonding function, then they should be socially selective and reflect the bonds among the affiliated group members. However, whether or not vocal exchanges rely on high social selectivity that is characteristic of other social bonding behaviours, such as grooming, is not well established.

In this study, we investigate whether vocal exchanges reflect the social bonds among conspecifics. Positive relationships between vocalizations and social context are present in multiple taxa. For example, male budgerigars, *Melopsittacus undulatus*, imitate the calls of their partners (Hile, Plummer, & Striedter, 2000), the song-sharing patterns of European starlings, *Sturnus vulgaris*, reflect their group structure (Hausberger, Richard-Yris, Henry, Lepage, & Schmidt, 1995) and Campbell’s monkey, *Cercopithecus campbelli campbelli*, grooming partners develop similar acoustic properties in their contact calls (Lemasson, Ouattara, Petit, & Zuberbühler, 2011). In addition, chacma baboons, *Papio hamadryas ursinus*, form vocal alliances that persist through playbacks of threat-grunts (Wittig, Crockford, Seyfarth, & Cheney, 2007) and male chimpanzees, *Pan troglodytes schweinfurthii*, tend to join the pant-hoots in which their short-term affiliates participate (Fedurek et al., 2013). Furthermore, bottlenose dolphins, *Tursiops truncatus*, respond to the playbacks of the calls of their offspring (Sayigh et al., 1999), while African elephants, *Loxodonta africana*, and common squirrel monkeys, *Saimiri sciureus*, respond to the playbacks of their affiliates, when physical proximity is used for quantifying affiliation (Soltis et al., 2002, 2005). More evidence is needed, however, to establish whether or not robust positive relationships between vocalizations and social bonds are present at the group level, in particular, beyond the bonds that exist due to of kinship or mating interactions.

To determine whether vocal exchanges are informative about the social bonds between group members, we studied the relationships between grooming interactions and vocalizations in free-ranging ringtailed lemurs, *Lemur catta*. Lemurs live in stable female-dominated groups that include fewer than 25 group members (average group size 11.16; Gould, Sussman, & Sauther, 2003; Jolly, 1966a, 1966b; Jolly et al., 2002; Sussman, 1991). These group sizes are small enough to allow frequent grooming between the strongly bonded group members. Lemurs have a large vocal repertoire which includes contact calls (Fig. 1) that contain identity

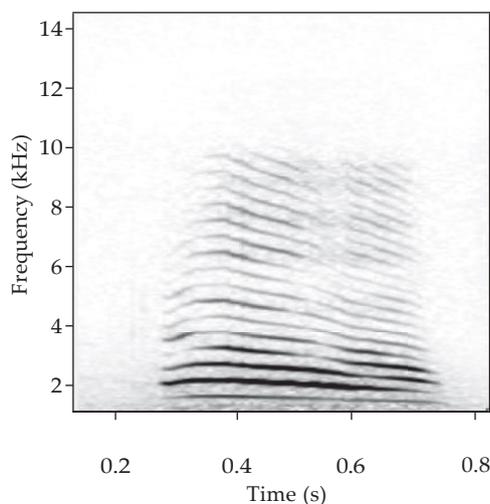


Figure 1. Spectrogram of a ringtailed lemur contact call. Lemur contact calls are long-distance calls that elicit vocal responses from group members.

information used for individual recognition (Kulahci, Drea, Rubenstein, & Ghazanfar, 2014; Macedonia, 1986, 1993). In this study, we focus only on contact calls, because they frequently result in vocal exchanges among the group members. Contact calls are also known as ‘cohesion calls’ because they serve as a long-distance signal during group movement or when a conspecific has been out of visual range (Macedonia, 1993). Notably, individuals do not typically exchange contact calls with each other while grooming or while they are in close proximity to each other. Therefore, any relationships between contact calls and grooming are unlikely to be due to temporal or spatial associations between the two behaviours.

We used social network analysis to examine the relationships between grooming interactions and vocalizations. Social network analysis provides a robust method for characterizing social interactions and for investigating the relationships between different social behaviours, while also accounting for individual variation in social behaviour (Croft, James, & Krause, 2008; Wey, Blumstein, Shen, & Jordan, 2008). If one of the functions of lemur contact calls is to maintain social bonds, then the socially bonded individuals (as determined by their grooming interactions) should be more likely to respond to each other’s calls. This would be detected as positive correlations between the grooming networks (based on who grooms whom) and the vocalization networks (based on who produces contact call responses upon hearing whose contact calls). In addition, if contact calls function as grooming-at-a-distance, then they should be sufficient to elicit selective vocal responses even when the vocalizing conspecific is not in close proximity. If so, then the playback of a conspecific’s contact call should elicit vocal responses only from the group members who had responded to that conspecific while free-ranging. This would lead to a positive correlation between the vocalization networks (obtained from data during observations while lemurs free-range) and the playback networks. Together, these results would suggest that contact calls indicate the social bonds between the group members and may allow them to groom-at-a-distance.

METHODS

Study Groups

We worked with four lemur groups. Two groups (N 7, 8) semifree-ranged in large forest enclosures at the Duke Lemur Center in North Carolina, U.S.A. We observed these groups during June–August in 2010 and 2011. Group enclosures were separated from each other by chain-link fences that allowed visual, acoustic and olfactory contact, but prevented movement between groups. The other groups free-ranged on St Catherines Island in Georgia, U.S.A. One of these groups (N 21) was observed during September–November 2011 and June–August 2012, the other (N 17) was observed during July–November 2013. On St Catherines Island, lemurs were free to interact with the members of the other groups and move between the groups. All procedures were approved by the Institutional Animal Care and Use Committees at Duke University (A121-10-05 for Duke Lemur Center research) and at Princeton University (protocol number 1868 for St Catherines Island research).

Data Collection

Using all-occurrence sampling, we collected data on vocalizations, grooming and aggression. Vocalizations were based on who produced a contact call and who responded with a contact call.

Grooming data included both mutual grooming (two lemurs simultaneously groom each other) and nonreciprocal grooming

(one lemur grooms another). Aggression data included chases and physical fights. Each group was observed a minimum of four times per week for at least 3 h per day. All lemurs were individually identifiable through visual features, collars and tail shaves.

During the majority of the vocal exchanges, we were able to determine the identity of the vocalizing lemurs. In three instances, multiple lemurs simultaneously vocalized from different locations. These calls were excluded from the data because we could not identify all lemurs who responded. Calls that were used in the playback experiment were recorded using an HD camcorder equipped with an external directional microphone (Sennheiser ME66; 40 Hz–20 kHz, ± 2.5 dB) at Duke Lemur Center during June–August 2010 and in June 2011. Calls were normalized to 100% of peak amplitude in Adobe Audition CS4 (Adobe Systems Incorporated, San Jose, CA, U.S.A., version 4.0).

Vocalization Playbacks

We ran playback experiments with the two groups at the Duke Lemur Center during July–August 2011. All lemurs were habituated to the observer (I.G.K.) and over 1 year old at the time of testing. Vocalization of each group member was presented once to the group. We used small outdoor pens as testing arenas (3.05 \times 2.4 \times 2.4 m high). During the day of the trials, we moved the whole group to a single outdoor test arena. We then separated the focal lemur (whose vocalization we presented) into an indoor enclosure away from the test arena to prevent olfactory, acoustic and visual contact between the group and the focal lemur. Playing the call of the focal lemur allowed us to replicate the natural conditions where a group member produces a contact call when separated from the group. We played the vocalizations from an iPod connected to a mobile speaker (Anchor Audio AN-30 Portable 30W Speaker, 100 Hz–15 kHz, ± 3 dB). Before playing the call, we waited until all lemurs ceased vocalizing and were in close proximity to each other. All trials were recorded with a hand-held HD camcorder. Because we ran our trials in small arenas, we were able to record all group members simultaneously (except the one whose call was presented), allowing us to determine who vocalized in response to the playbacks. During two playbacks, one male stayed away from the rest of the group and was not visible in the videos. We could reliably determine when he produced a vocal response because the rest of the group was visible in the videos.

Data Analysis

We converted vocalization, grooming, aggression and playback data into directed network matrices that we analysed in UCINET (Borgatti, Everett, & Freeman, 2002). In grooming and aggression networks, the actor was the lemur who initiated the interaction. In vocalization and playback networks, the actor was the lemur who produced a vocal response. All networks except the playback network were analysed as weighted networks that included information about the interaction frequency between individuals. Weighted networks are particularly useful in understanding the social structure of small groups in which the frequency of connections is more informative than just their presence (Cantor & Whitehead, 2013; Lusseau, Whitehead, & Gero, 2008). We calculated grooming and vocalization network outdegrees to quantify the number of group members towards whom each lemur initiated grooming interactions and vocal responses. A lemur's grooming outdegree was defined as the number of group members that she groomed, while vocalization outdegree was defined as the number of group members that she produced a vocal response towards upon hearing their call.

To address the possibility that lemurs respond to the calls of same-sex conspecifics or to the calls of relatives, we calculated matrices based on sex similarity and kinship (Borgatti, Everett, & Johnson, 2013). In sex similarity matrices, if lemurs A and B were both males, we entered '1' in the cell corresponding to this pair. If A was a male and B was a female, we entered '0'. Kinship matrices were based on the coefficient of maternal relatedness because paternity data was unavailable for the St Catherines's groups. Sex similarity and kinship matrices were entered into a matrix regression analysis together with vocalization, grooming and aggression matrices in UCINET (multiple regression quadratic assignment procedure, MRQAP, double Dekker semipartialling variant) (Borgatti et al., 2013; Dekker, Krackhardt, & Snijders, 2007; Krackhardt, 1988). We used MRQAP to determine whether lemurs vocalized in response to the calls of the conspecifics they groomed, while accounting for the possibility that they assess other factors when deciding whose call to respond to. Vocalization matrix was the dependent matrix in the regression, while grooming, aggression, kinship and sex similarity were the independent matrices. MRQAP accounts for the nonindependent nature of network data through the use of randomization procedures. The first step is a regression test for the corresponding cells of each matrix. The second step permutes the rows and the columns of the dependent matrix, runs the regression again and repeats this procedure multiple times (we ran 10 000 permutations). A significant relationship between two matrices is concluded if the regression coefficient from the first step is larger than 95% of the random coefficients from the second step, demonstrating that the relationship between matrices is unlikely to be due to chance (Borgatti et al., 2002; Borgatti et al., 2013).

Our observations of one St Catherines group spanned 2 years ($N = 21$ in 2011 and 2012). The group size stayed the same between years. However, because group composition changed due to births, deaths and male movement, we had to treat networks from each year as separate networks. This gave us a total of five groups for matrix analyses (see Results, Table 1). For all other analyses that required us to pool data from all groups, we took two measures to reduce pseudoreplication. First, we excluded three males who moved into this group ($N = 3$) from the other group ($N = 17$). Second, we averaged the data from the lemurs who were in this group for both years. We were able to combine data from 2010 and 2011 from Duke, because the group compositions remained relatively consistent between these years (lemurs received contraception and movement between groups was restricted).

The playback networks were based on binary instead of valued (weighted) data, because each lemur's call was presented only once. To compare playback networks to observation-based vocalization networks, we transformed the vocalization networks into binary networks by including data only about the presence, but not about the frequency, of the responses. Quadratic assignment procedure (QAP) correlations between playback and vocalization matrices allowed us to determine whether lemurs vocalized in response to the same group members in observations and in playbacks. All playback videos were scored by two people who were blind to the identity of the focal lemur whose vocalization was presented in the video (interobserver reliability: 96%).

RESULTS

Lemur Vocal Responses Display High Social Selectivity

We found high individual variation in the frequency with which contact calling and grooming were exhibited. Some lemurs were very social and frequently engaged in grooming interactions while also frequently producing vocal responses to the calls of others.

Table 1
Relationships between vocal networks and four other networks of ringtailed lemurs

Group size (N)	Groom		Aggression		Kinship		Similarity in sex	
	r	P	r	P	r	P	r	P
7	0.269	0.051	-0.022	0.491	0.634	0.006	0.115	0.199
8	0.465	0.011	0.182	0.075	0.161	0.139	0.348	0.009
17	0.306	0.001	0.128	0.062	0.037	0.287	-0.017	0.389
21	0.202	0.002	0.061	0.119	-0.041	0.299	0.054	0.148
21	0.274	0.001	-0.020	0.385	0.119	0.053	0.118	0.024

The regression value (r) for each network is provided with the corresponding P value from MRQAP run with 10 000 permutations (bold indicates significant P values). Across groups of all sizes, lemurs produced frequent vocal responses to the calls of the group members that they frequently groomed.

Other lemurs were less socially active and rarely groomed or vocalized in response to their conspecifics. Overall, lemurs who frequently engaged in grooming interactions also frequently responded to conspecifics' calls (Pearson correlation: $r_{49} = 0.567$, $P < 0.001$; Fig. 2a). Lemurs' grooming outdegrees were positively correlated with their vocalization outdegrees ($r_{49} = 0.436$, $P = 0.001$; Fig. 2b), suggesting that lemurs who groomed more conspecifics also vocalized in response to more conspecifics.

As group sizes increased, lemurs groomed more group members (grooming outdegree: $r_{49} = 0.313$, $P = 0.025$; Fig. 2c) and were groomed by more group members (grooming indegree: $r_{49} = 0.39$, $P = 0.005$). However, they did not direct vocalizations towards more group members (vocal outdegree: $r_{49} = 0.181$, $P = 0.206$; Fig. 2c) or receive vocalizations from more group members (vocal indegree: $r_{49} = 0.214$, $P = 0.131$). Normalized outdegrees, which convert raw outdegrees to percentages by accounting for group size, revealed that lemurs actually became more selective in their grooming interactions and vocal responses as groups got larger (Fig. 2d). Although lemurs groomed almost all group members in smaller groups ($N = 7, 8$), they groomed a lower percentage of their group members in larger groups ($N = 17, 21$). In addition, across

groups of all sizes, normalized grooming outdegrees were higher than normalized vocalization outdegrees (Fig. 2d; mean normalized outdegree \pm SE: grooming: $58.188 \pm 3.85\%$; vocalization: $23.129 \pm 3.37\%$, $N = 51$). Together, these results reveal that lemurs vocalized in response to a smaller subset of their group members than they groomed, regardless of group size.

Lemurs Respond to the Calls of the Group Members They Frequently Groom

We used the multiple regression quadratic assignment procedure (MRQAP) to determine which factors influenced vocal responses (dependent matrix: vocalization; independent matrices: grooming, aggression, kinship, sex similarity). In each group, we found strong relationships between the grooming and the vocalization network matrices (MRQAP: $r = 0.269$, $N = 7$, $P = 0.051$; $r = 0.465$, $N = 8$, $P = 0.011$; $r = 0.306$, $N = 17$, $P = 0.001$; $r = 0.202$, $N = 21$, $P = 0.002$; $r = 0.274$, $N = 21$, $P = 0.001$; Table 1, Fig. 3a, b). Lemurs were more likely to respond to the group members with whom they engaged in grooming interactions (ANOVA: $F_{1,41} = 10.135$, $N = 7$, $P = 0.003$; $F_{1,55} = 23.85$, $N = 8$, $P < 0.001$;

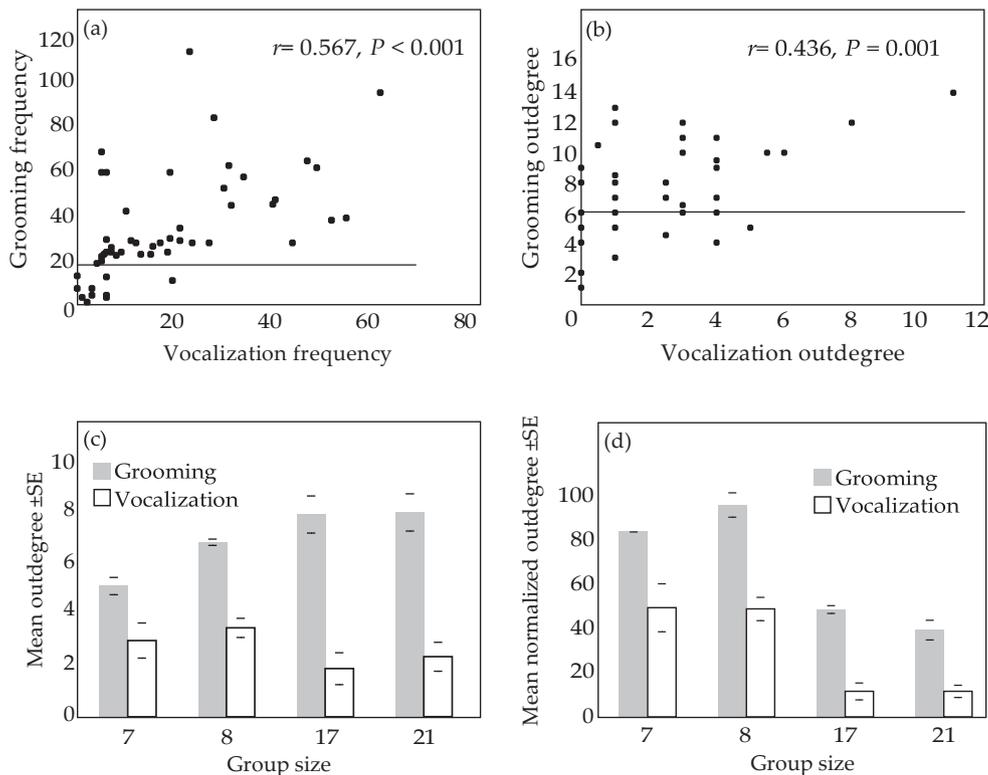


Figure 2. (a) Relation between grooming frequency and vocalization frequency in ringtailed lemurs. (b) Relation between grooming outdegree and vocal outdegree. (c) Mean \pm SE grooming and vocalization outdegree relative to group size. (d) Mean \pm SE normalized grooming and vocalization outdegree relative to group size. $N = 51$.

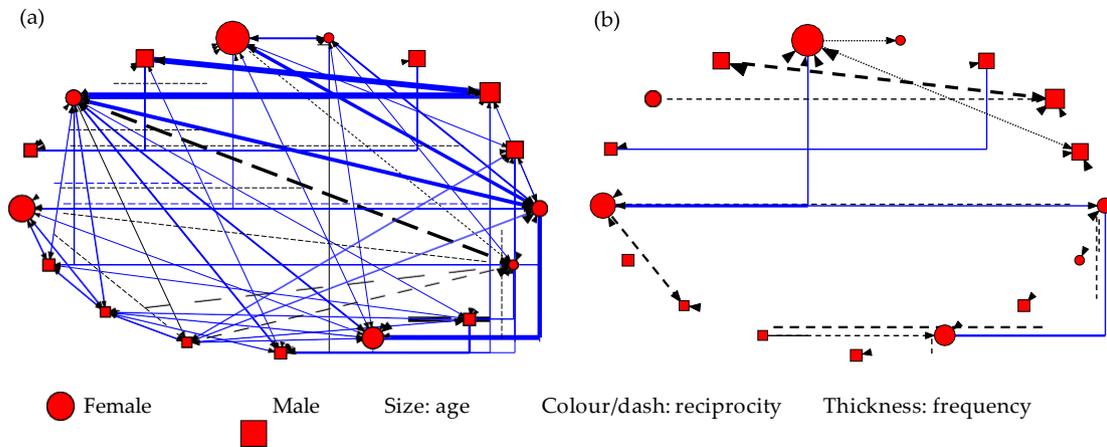


Figure 3. Representative (a) grooming and (b) vocalization networks from one group of ringtailed lemurs ($N = 17$). Thicker lines indicate frequent grooming interactions (a) or vocal responses (b). Arrows point towards the recipient. In the vocalization network, arrows point towards the lemur receiving a vocal response after having vocalized first. Blue solid lines indicate reciprocal interactions or responses (i.e. individual A responded to individual B, and individual B responded to individual A at another time); black dashed lines indicate nonreciprocal interactions or responses.

$F_{1,127} = 36.525, N = 17, P < 0.001$; $F_{1,840} = 96.97\%, N = 21, P < 0.001$; Fig. 4). Because grooming and vocalization matrices included information about how frequently each interaction occurred, as well as who initiated it, MRQAP results revealed that lemurs frequently produced vocal responses to the contact calls of group members that they frequently groomed. Matrices based on aggressive interactions, maternal kinship and similarity in sex all failed to consistently predict who responded to whose call. Thus, regardless of group size, a lemur's decision of whose contact call to respond to was mainly determined by the frequent grooming interactions.

Playbacks are Sufficient to Induce Selectivity in Vocal Responses

To test whether selectivity in vocal responses could be experimentally replicated, we ran a playback experiment in which we presented each lemur's vocalization once to their group. We then analysed the relationships between playback networks and vocalization networks. The vocalization networks were based on observational data that were collected as lemurs free-ranged, and thus included multiple vocalizations from each lemur. Even though the playback networks, which were based on a single presentation of each lemur's call, did not capture each vocal response that was present in the observation-based vocalization

networks, we found strong positive relationships between these two networks.

Presenting the call of a group member was sufficient to elicit vocal responses from the rest of the group. Lemurs that responded to the calls of more group members during our observations also responded to the playbacks of more group members' calls (correlations between observation-based vocalization network out-degree and playback network out-degree: $r_4 = 0.616, P = 0.014$). In particular, each focal lemur's playback call elicited responses from the group members that had responded to that lemur during our observations (QAP Pearson correlation between playback and vocalization networks: $r_6 = 0.489, P = 0.002$; $r_5 = 0.744, P < 0.001$; Fig. 5a, b). Although some playbacks elicited vocal responses from multiple lemurs, no playback received responses from more than four lemurs (Fig. 6a). Similarly, none of the vocalizations in our observations received responses from more than three lemurs (Fig. 6b). Notably, the lemurs that received multiple responses in the playbacks also received multiple overlapping responses in the vocalization networks (number of responses received in playbacks versus maximum number of simultaneous responses received in observations: $r_{13} = 0.66, P = 0.007$). Thus, selectivity in vocal responses was robust enough to be experimentally replicated and persisted even in the absence of olfactory and visual cues from the lemur who produced the initial call.

DISCUSSION

We provide evidence of the robust positive relationships between grooming and vocalizations in ringtailed lemurs, a species in which grooming is an efficient method of social bonding. Similar to other social species, lemurs are selective in whom they groom. However, we show that lemur vocal responses display even higher levels of social selectivity than their grooming interactions. Instead of responding to the contact calls of each group member they groomed, lemurs mainly responded to the calls of those they groomed most frequently. This suggests that vocalizations indicate the strong social bonds between group members, when bond strength is inferred from frequent grooming interactions. Furthermore, vocal selectivity persisted during playback experiments, revealing that vocal responses are independent of proximal cues (e.g. visual or olfactory cues) and may function as grooming-at-a-distance.

The positive links between contact calls and grooming suggests that one of the functions of vocalizations may be to complement

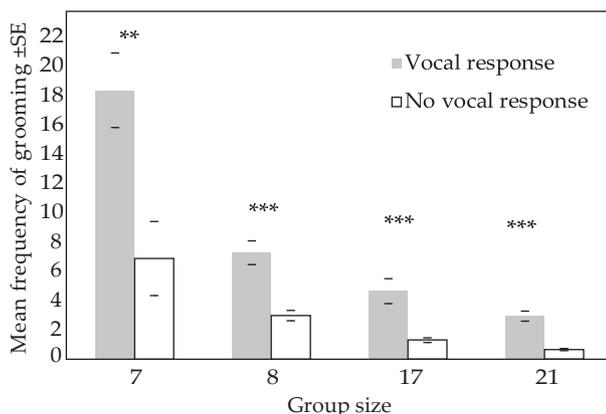


Figure 4. Mean \pm SE frequency of grooming by ringtailed lemurs based on their response to the contact calls of group members. $**P < 0.01$; $***P < 0.001$.

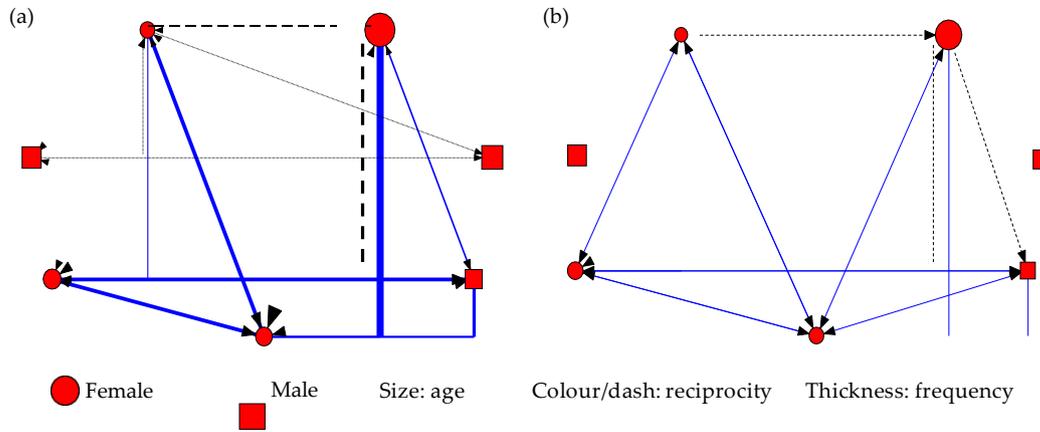


Figure 5. Representative (a) vocalization and (b) playback networks from one group ($N = 7$). Line thickness in the vocalization network (a), but not in the playback network (b), indicates frequency of vocal responses. The playback network includes information only about the presence (but not about the frequency) of vocal responses, because each lemur's vocalization was presented only once. Blue solid lines indicate reciprocal responses; black dashed lines indicate non-reciprocal responses. In both graphs, the arrows point towards the lemurs who received the vocal response.

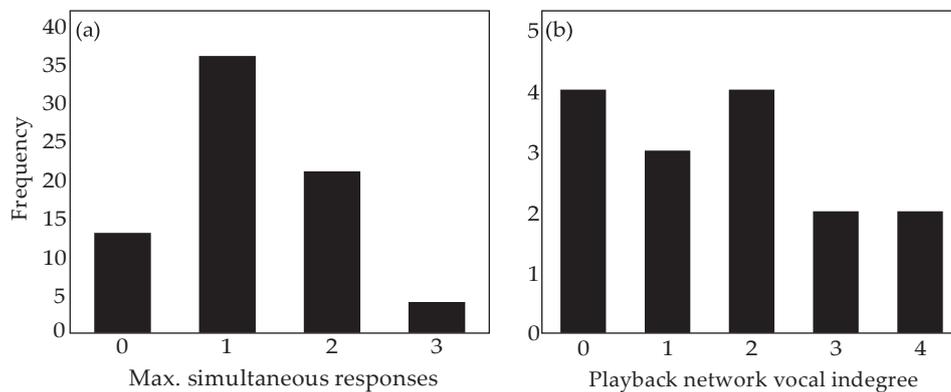


Figure 6. Vocal responses of ringtailed lemurs to contact calls of conspecifics during (a) observations (maximum number of simultaneous responses/call) and (b) playbacks (total number of lemurs responding, playback network vocal indegree).

grooming. Even though grooming is regarded as one of the best indicators of social bonds between individuals (Cords, 1997; Silk, 2007; Silk et al., 2006), it serves multiple functions: it is used for reconciliation, alliance formation, stress reduction and hygiene (Barton, 1985; Enquist & Leimar, 1993). Vocal exchanges could provide a more precise indication of who is strongly bonded with whom in social groups. By complementing their grooming interactions with vocal exchanges, strongly bonded conspecifics may reassure their bonds when they are separated from each other during foraging or group movement. As such, vocalizations may provide a bonding mechanism that allows strongly bonded conspecifics to groom-at-a-distance.

Previous studies have investigated vocalizations in relation to social context in multiple species ranging from birds to mammals (Fedurek et al., 2013; Hausberger et al., 1995; Hile et al., 2000; Lemasson et al., 2011; Smith, Newman, & Symmes, 1982; Soltis et al., 2002, 2005; Wittig et al., 2007). For example, bottlenose dolphins respond to the calls of their offspring, while elephants and squirrel monkeys respond to the calls of their affiliates, when affiliation is measured through physical proximity (Nakahara & Miyazaki, 2011; Sayigh et al., 1999; Soltis et al., 2002, 2005). Affiliated conspecifics in some species, including budgerigars and Campbell's monkeys, develop similar acoustic properties in their calls (Hile et al., 2000; Lemasson et al., 2011). Our results build on these studies to show that lemurs produce selective vocal responses to the contact calls of the group members with whom they are strongly bonded, when such strong bonds are quantified

through frequent grooming interactions, which provide a robust measure of affiliation.

By using regression analysis on multiple networks, we were able to rule out the possibility that aggressive interactions, kinship, and similarity in sex influence who responds to whose call. Grooming may function to reduce aggression between conspecifics (Cords, 1997; Silk, 2007; Silk et al., 2006). Although vocalizations may also help to reduce aggression through their social bonding function, we found no relationship between the vocalization and the aggression networks in any of the groups. Lemurs did not avoid responding to the calls of the conspecifics with whom they engaged in aggressive interactions, providing further evidence that selective vocal responses are driven by the affiliative interactions in lemurs.

Ringtailed lemur social behaviour and cognition are comparable to those of monkeys and apes (Jolly, 1966b; Sandel, MacLean, & Hare, 2011). Social selectivity in lemur grooming interactions supports the notion that grooming in lemurs, similar to grooming in monkeys and apes, has a social purpose in addition to its hygienic purpose. In our study, lemurs groomed more group members as group size increased. However, accounting for group size differences revealed that lemurs became more selective in the larger groups, by focusing their grooming interactions on a lower percentage of their conspecifics. Furthermore, vocalization network outdegrees were lower than grooming network outdegrees, indicating that lemurs' vocal responses display higher levels of social selectivity than their grooming interactions. This high vocal selectivity has major implications for one of the popular hypotheses

regarding the evolution of vocal communication in primates. We discuss these implications next.

Primate Vocal Communication and Dunbar's 'Gossip' Hypothesis

One of the hypotheses regarding the evolution of primate vocal communication predicts that when increasing group size precludes grooming as a viable bonding mechanism, primates living in large groups switch to using vocal exchanges to groom-at-a-distance (Dunbar, 1998, 2003, 2004; Freeberg, 2006; McComb & Semple, 2005). According to Dunbar's hypothesis, as primate groups get larger, group members start to form social bonds with more conspecifics (Dunbar, 2003, 2004). Eventually, group size reaches a threshold, where grooming each conspecific with whom a bond is shared becomes too time consuming, requiring animals to focus their grooming interactions on a specific set of group members (Dunbar, 1993, 2003, 2004). Dunbar's hypothesis suggests that vocalizations provide a bonding mechanism that allows individuals to maintain bonds with more group members than grooming does, eventually taking the place of grooming interactions in large groups (Dunbar, 1993, 2003, 2004).

There are two core assumptions behind Dunbar's hypothesis. The first assumption is that there is a positive relationship between vocalizations and social bonds. Our results provide support for this assumption. In our study, strong social bonds between individuals (indicated by frequent grooming) best predicted who responded to whose call. The second assumption is that vocalizations allow animals to maintain bonds with more group members than grooming interactions do. Social species living in groups that have not reached a group-size threshold, which precludes grooming as an efficient bonding mechanism, provide a special opportunity to address this assumption. As group size increases, animals should bond with (and groom) more conspecifics. If the second assumption behind Dunbar's hypothesis is true, then animals should produce vocal responses to all conspecifics with whom they share bonds, eventually responding to more conspecifics as group size increases. At the group level, these changes would be detected as positive correlations between group size, the number of group members groomed and the number of group members with whom vocalizations are exchanged. Such correlations would provide evidence that vocalizations keep up with the increasing numbers of social bonds as groups get larger, and potentially allow more group members to maintain bonds with each other than would grooming interactions.

However, our results show that the number of group members with whom vocalizations are exchanged can be limited. Consistent with the prediction that animals form social bonds with more group members as group size increases (Dunbar, 1993, 2003, 2004), several monkey and ape species groom more conspecifics in larger groups (Lehmann et al., 2007). Similar to monkeys and apes, lemurs also groomed more conspecifics as group size increased, suggesting that they were bonded with more group members in larger groups. Yet, they did not vocalize in response to more conspecifics as group size increased, nor did they respond to the calls of each group member they groomed. This selectivity in vocal responses was present across all of the group sizes that we studied. Thus, even before groups got too large and bonding via grooming became too time consuming, we observed a limit to the number of group members with whom lemurs exchanged contact calls. Importantly, lemurs' responses were not random but were instead reserved specifically for the group members they frequently groomed, suggesting that vocalizations complement the grooming interactions of the strongly bonded conspecifics.

If similar types of high vocal selectivity are detected in other species, it will be critical to address whether it is caused by a

cognitive constraint in discriminating, learning and remembering individual vocalizations, or whether it is the consequence of a social decision to selectively respond to certain group members. We suspect that, in lemurs, the second possibility is most likely, as lemurs can recognize the vocalizations of individual group members and integrate this information across sensory modalities (Kulahci et al., 2014), but they respond mainly to the calls of those with whom they share strong bonds.

Conclusion

Vocalizations have been suggested to serve a social bonding function, but empirical evidence showing robust relationships between vocal exchanges and grooming interactions (a frequent method of assessing social bonds) has been lacking. We demonstrate that vocal exchanges indicate the strong social bonds between conspecifics, when strong bonds are inferred from frequent grooming interactions. Our results also have implications for Dunbar's hypothesis about the evolution of vocal communication in primates. Vocalizations have been hypothesized to be advantageous over grooming by allowing more group members to maintain bonds with each other than grooming would. However, we demonstrate that vocalizations, similar to grooming interactions, are also subject to social selectivity. In fact, our results suggest that lemur contact calls rely on a higher social selectivity than do lemur grooming interactions, as contact calls are exchanged mainly between the group members who frequently groom each other. Thus, contact calls provide reliable indicators of the strong social bonds between group members, and may allow bonded conspecifics to maintain bonds when they are physically separated from each other. Consequently, grooming-at-a-distance through vocalizations is likely to be a widespread phenomenon among social species in which vocal communication is frequent.

Acknowledgments

We are grateful to the Duke Lemur Center and St Catherines Island. We thank Robin Dunbar for comments on a previous version of the manuscript. This study was funded by grants to I.G.K. from the Animal Behavior Society, the American Society of Mammalogists, the American Society of Primatologists and Princeton University Department of Ecology & Evolutionary Biology. This is Duke Lemur Center publication number 1296.

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