



## 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, & Slocumbe, 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

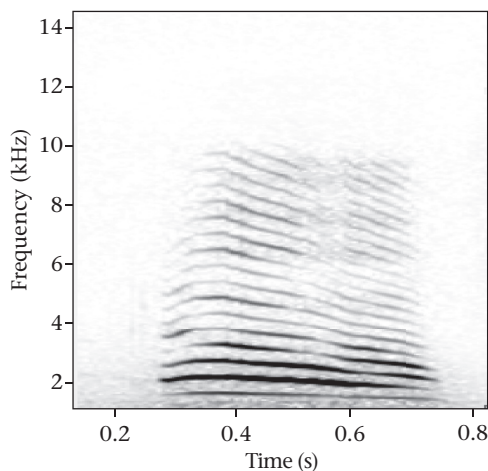
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by grooming (Dunbar, 2003). Consistent with these advantages, it has been suggested that vocal exchanges may allow animals to maintain social bonds by ‘grooming-at-a-distance’ (Dunbar, 1993, 2003, 2004). If vocal exchanges have a social bonding function, 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, & Jordán, 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

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