Modeling the Origins of Primate Sociality:

Kin Recognition in Mouse Lemurs

by

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ABSTRACT

Arguments of human uniqueness emphasize our complex sociality, unusual cognitive capacities, and language skills, but the timing of the origin of these abilities and their evolutionary causes remain unsolved. Though not unique to primates, kin-biased sociality was key to the success of the primate order. In contrast to ancestral solitary mammals, the earliest primates are thought to have maintained dispersed (non-group living) social networks, communicating over distances via vocalizations and scent marks. If such ancestral primates recognized kin, those networks may have facilitated the evolution of kin-biased sociality in the primate order and created selection for increased cognitive and communicative abilities. I used the gray mouse lemur (*Microcebus murinus*) to model whether vocalizations could have facilitated matrilineal and patrilineal kin recognition in ancestral primates. Much like mouse lemurs today, ancestral primates are thought to have been small-bodied, nocturnal creatures that captured insects and foraged for fruit in the thin, terminal ends of tree branches. Thus, the mouse lemur is an excellent model species because its ecological niche is likely to be similar to that of ancestral primates 55-90 million years ago. I conducted playback experiments in Ankarafantsika National Park, Madagascar testing whether mouse lemur agonistic calls contain matrilineal kin signatures and whether the lemurs recognize matrilineal kin. In contrast to large-brained, socially complex monkeys with frequent coalitionary behavior, mouse lemurs did not react differently to the agonistic calls of matrilineal kin and nonkin, though moderate signatures were present in the calls. I tested for patrilineal signatures and patrilineal kin recognition via mating and alarm calls in a colony with known pedigree relationships. The results are the first to demonstrate that a nocturnal, solitary foraging mammal gives mating calls with patrilineal signatures and recognizes patrilineal kin. Interestingly, alarm calls did not have signatures and did not facilitate kin recognition, suggesting that selection for kin recognition is stronger in some call types than others. As this dissertation is the first investigation of vocal kin recognition in a dispersed-living, nocturnal strepsirrhine primate, it greatly advances our knowledge of the role of vocal communication in the evolution of primate social complexity.

DEDICATION

I dedicate this dissertation to my father, Garry Kessler, with whom I learned as a child to enjoy, cherish, and be intrigued by nature.

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CHAPTER 1

INTRODUCTION

Since Hamilton's ground-breaking theory of inclusive fitness in 1964, kin-biased behavior has been theorized to have played a crucial role in the evolution of mammalian sociality (Chapais & Berman, 2004; de Waal & Tyack, 2003; Hamilton, 1964). Given the amount of research attention given to the topic over the subsequent decades, it is surprising that although group-living and social complexity has evolved multiple times in mammals (de Waal & Tyack, 2003; Müller & Thalmann, 2000; Waser & Jones, 1983), we still know very little about how this process occurs.

Ancestral mammals are believed to have been asocial, as are many extant mammal species (Müller & Thalmann, 2000; Waser & Jones, 1983). These species forage alone and maintain no relationships outside of the mating and infant-rearing seasons (Müller & Thalmann, 2000; Waser & Jones, 1983). Interactions between adults, including adult kin are marked by avoidance and aggression (Müller & Thalmann, 2000; Waser & Jones, 1983). This is note-worthy because in many species, females typically disperse shorter distances than males, leading to a spatial clustering of female kin (Maher, 2009b; Stoen, Bellemain, Saebo, & Swenson, 2005; Waser & Jones, 1983). For many theorists, it is this spatial clustering of kin which is the first step towards increasing sociality (Lutermann, Schmelting, Radespiel, Ehresmann, & Zimmermann, 2006; Meshriy, Randall, & Parra, 2011; Messier, Garant, Bergeron, & Reale, 2012; Perrin & Lehmann, 2001; Waser & Jones, 1983). The transition to group-living is believed to have occurred through solitary foraging (Müller & Thalmann, 2000). Extant solitary foragers forage alone, but in contrast to the asocial mammalian ancestors, maintain year-round social networks, communicating with conspecifics via scent-marks and vocalizations (Müller & Thalmann, 2000; Nash, 2004). Individuals may interact affiliatively during their active periods and sometimes sleep in social groups, often consisting of matrilineal kin, during the inactive periods (i.e., (Eberle & Kappeler, 2006; Radespiel, Sarikaya, Zimmermann, & Bruford, 2001), review: (Müller & Thalmann, 2000)). These social networks are believed to have been the foundations from which group-living evolved (Müller & Thalmann, 2000); if these social networks enabled solitary foragers to recognize their kin, they could have facilitated kin selection (the preferential treatment of genetic relatives) (Hamilton, 1964; Kessler, Scheumann, Nash, & Zimmermann, 2012; Müller & Thalmann, 2000; Nash, 2004). This, in turn, may have lead to the formation of kin-based foraging groups and the diversity of complex social systems seen today in mammals (Müller & Thalmann, 2000; Perrin & Lehmann, 2001; Waser & Jones, 1983).

However, this transition from solitary foraging with kin-based networks to kin-based foraging groups hinges upon the ability of individuals to use these social networks to recognize kin. In order to better understand how this transition occurred, I focus on Primates, an order where kin-based group-living has evolved multiple times (Müller & Thalmann, 2000). Though kin-biased sociality is not unique to primates (review: (de Waal & Tyack, 2003), i.e., hyenas (Holekamp, Smith, Strelioff, Van Horn, & Watts, 2012), killer whales (Yurk, Barrett-Lennard, Ford, & Matkin, 2002), elephants (McComb, Moss, Sayialel, & Baker, 2000)), it is argued to have been a vital adaptation in the primate order (Chapais & Berman, 2004; Dunbar, 1998; Silk, 2002, 2007b, 2009). Today, the primate order contains diverse social systems including both group-living and dispersed systems (Kappeler, 1997a; Kappeler & van Schaik, 2002; Müller & Thalmann, 2000; Strier, 2007). Group-living (gregarious) primates form their groups so that the benefits of group-living (e.g., increased protection from predators, foraging benefits, affiliative social interactions) are given to themselves and their kin (kin selection) (Chapais & Berman, 2004; Hamilton, 1964; Silk, 2002, 2007b, 2009; Strier, 2007). Group-living primates forage in many different types of groups (e.g., multiple males and multiple females; one male and multiple females; one female and multiple males; monogamous pairs; fission-fusion communities that break apart and join together into different subgroups; or multi-level societies with smaller permanent units embedded within them) (Kappeler & van Schaik, 2002; Strier, 2007).

The dispersed social systems are also complex (Müller & Thalmann, 2000; Nash, 2004). Although primates with dispersed social systems usually forage solitarily, they have overlapping ranges and maintain social networks (Müller & Thalmann, 2000; Nash, 2004). Though less is known about solitary foragers, they may gain a similar advantage by directing the benefits of their dispersed social networks to their kin (Nash, 2004). The structure of these networks varies across species to include, at a minimum, dispersed multi-male / multi-female, dispersed monogamy, and dispersed harem systems (Müller & Thalmann, 2000; Nash, 2004). They use vocalizations to interact with individuals who are distant in space and leave scent-marks to communicate with individuals who are distant in time (Müller & Thalmann, 2000; Nash, 2004).

The last common ancestor of primates is believed to have been a nocturnal solitary forager which diverged from other primitive mammals between 90 and 55 million years ago (Bloch, Silcox, Boyer, & Sargis, 2007; Gingerich & Uhen, 1994; Martin, 1993; Martin, Soligo, & Tavare, 2007; Müller & Thalmann, 2000; Springer, Murphy, Eizirik, & O'Brien, 2003; Steiper & Seiffert, 2012; Strier, 2007; Tavaré, Marshall, Will, Soligo, & Martin, 2002). Therefore, studies of extant nocturnal, solitary foragers are of great theoretical value because these primates have social systems and ecology (small-bodied, foraging alone at night) that is thought to be similar to those of the hypothesized last common ancestor of the primate order (Cartmill, 1972, 1974, 1992; Dammhahn & Kappeler, 2008; Gebo, 2004; Kappeler, 1997a, 1998; Kappeler & van Schaik, 2002; Kappeler, Wimmer, Zinner, & Tautz, 2002; Martin et al., 2007; Müller & Thalmann, 2000; Radespiel, 2006; Rasmussen, 1990, 2002; Ravosa & Dagosto, 2007; Sussman, 1991; Thoren et al., 2011). Mouse lemurs, in particular, make excellent ancestral primate models because they fit two major theories of primate origins. The first is the visually directed predation theory (Cartmill, 1972, 1974, 1992, 2012) which hypothesizes that the last common ancestor of primates was small-bodied with convergent eyes and grasping hands with which they preyed upon insects in the forest canopy and undergrowth. This is supported by fossils indicating that some of the earliest primates were small-bodied insectivores (i.e., *Teilhardina asiatica* dated to 55 mya (Ni, Hu, Wang, & Li, 2005; Ni, Wang, Hu, & Li, 2004)). The second major theory of primate origins is the angiosperm co-evolution theory (Sussman, 1991; Sussman, Rasmussen, & Raven, 2013; Sussman & Raven, 1978) which predicts that the last common ancestor of primates exploited the fruits, nectar, flowers (and insects attracted to them) in the thin terminal ends of angiosperm tree branches. This theory is supported by the relatively complete skeleton of the plesiadapiform *Carpolestes simpsoni* dated between 55 and 56 mya (Bloch & Boyer, 2002). This fossil has an opposable hallux (big toe) adapted for grasping, with a nail rather than a claw, a low-crowned molar teeth indicating fruigovory, thus supporting the angiosperm co-evolution theory (Bloch & Boyer, 2002; Sussman et al., 2013). In addition, *C. simpsoni* has divergent orbits which are inconsistent with the visual predation hypothesis (Bloch & Boyer, 2002; Sussman et al., 2013). However, it has been suggested that these two theories are not necessarily mutually exclusive (Rasmussen, 1990) and given that there is a mismatch between the divergence times estimated from the fossil record (first primates ~55 mya, i.e., (Ni et al., 2005; Ni et al., 2004)) and divergence times estimated from molecular clock studies (~82 mya (Tavaré et al., 2002), 76-63 mya (Steiper & Seiffert, 2012)), many open questions remain.

Thus, living models for ancestral primates remain an important contribution to this debate both because they provide comparative data from species in similar ecological niches and because they serve as models for those aspects of primate evolution that do not fossilize or get recorded in the genome, i.e. social behaviour (i.e., (Gebo, 2004; Müller & Thalmann, 2000)). Among the extant taxa used as ancestral primate models (i.e., shrews, tree-shrews, mouse lemurs, galagos, marsupials, colugos (Gebo, 2004; Müller & Thalmann, 2000; Rasmussen, 1990)), mouse lemurs are among the most frequently used (i.e., (Charles-Dominique & Martin, 1970; Gebo, 2004; Müller & Thalmann, 2000; Sussman & Raven, 1978), and are compatible with both the visual predation theory and the angiosperm co-evolution theory. Like the visually directed predation hypothesis (Cartmill, 1972, 1974, 1992, 2012) predicts for ancestral primates, mouse lemurs have convergent eyes and grasping hands with which they prey upon insects in the forest canopy and undergrowth (Dammhahn & Kappeler, 2008; Dammhahn & Kappeler, 2009, 2010; Goerlitz & Siemers, 2007; Piep, Radespiel, Zimmermann, Schmidt, & Siemers, 2008; Radespiel, 2006; Radespiel, Reimann, Rahelinirina, &

Zimmermann, 2006; Siemers et al., 2007; Thoren et al., 2011; Toussaint et al., 2013). As predicted by the angiosperm coevolution theory (Sussman, 1991; Sussman et al., 2013; Sussman & Raven, 1978), mouse lemurs forage for fruits and nectar in the thin terminal ends of branches (Dammhahn & Kappeler, 2008; Dammhahn & Kappeler, 2009, 2010; Radespiel, 2006; Siemers et al., 2007; Thoren et al., 2011; Toussaint et al., 2013). Furthermore, as *Microcebus* are the smallest primates, this makes them particularly useful models for estimates of ancestral primate body size that put ancestral primates at or smaller than the size of all living primates (e.g., (Gebo, 2004; Silcox, Boyer, Bloch, & Sargis, 2007), but see (Soligo & Martin, 2006; Soligo & Müller, 1999)). For example, based on fossil evidence suggesting that the last common ancestor of primates was likely smaller than extant primates, Gebo (2004) estimated that ancestral primates would have been approximately shrew-sized (10-15g) and exhibited a mixture of behavioural traits similar to shrews and mouse lemurs (but see (Soligo & Martin, 2006; Soligo & Müller, 1999)).

Of the mouse lemurs, the gray mouse lemur (*Microcebus murinus*) in particular, has been extremely valuable due to the unusual depth and breadth of knowledge that we have on this species. Unlike many of the other proposed ancestral primate models, mouse lemurs have been subjects of study at multiple long-term study sites in the wild (i.e., Ankarafantsika, Kirindy) providing us with an understanding of the variation in their social systems and ecology over time and across populations (i.e., (Eberle & Kappeler, 2004a, 2004b, 2006; Radespiel, 2000; Radespiel, Ehresmann, & Zimmermann, 2001; Radespiel, Sarikaya et al., 2001)). Therefore, I propose to continue in this tradition and use the dispersed social networks of living gray mouse lemurs (*M. murinus*) to model ancestral primate social organization and to reconstruct the social behavior patterns from which present-day primate diversity evolved (Müller & Thalmann, 2000).

Sociality and the Importance of Vocalizations

As social species, all primates require mechanisms for maintaining their social relationships (Müller & Thalmann, 2000). This means keeping some degree of contact with individuals who are out of sight, either for long or short periods of time, due to dense vegetation for forest dwelling species, darkness for nocturnal species, and/or distance for dispersed species (Müller & Thalmann, 2000; Nash, 2004). Therefore vocalizations are expected to be vitally important for both group-living and solitary foraging species (Altenmüller, Schmidt, & Zimmermann, 2013; Snowdon & Hausberger, 1997; Zimmermann, Newman, & Jürgens, 1995). Vocalizations have the advantage of transmitting under circumstances where visual and/or olfactory cues may not be possible (Bearder, Honess, & Ambrose, 1995; Mitani, GrosLouis, & Macedonia, 1996; Müller & Thalmann, 2000; Nash, 2004; Zimmermann, 1995a), thus they are important for facilitating group cohesion, inter- and intra-group spacing, mate advertisement, etc. (Braune, Schmidt, & Zimmermann, 2005; Braune, Schmidt, & Zimmermann, 2008; Delgado, 2006; Mitani et al., 1996; Rasoloharijaona, Randrianambinina, Braune, & Zimmermann, 2006). These social functions of vocalizations have likely selected for the calls to transmit a great deal of information about the caller (Braune et al., 2005; Braune et al., 2008; Delgado, 2006; Mitani et al., 1996; Rasoloharijaona et al., 2006). For example, cotton-top tamarin calls are distinctive by individual, sex, and group (Weiss, Garibaldi, & Hauser, 2001); baboons produce calls distinctive by sex and individual

(Owren, Seyfarth, & Cheney, 1997; Rendall, Owren, Weerts, & Hienz, 2004); and the calls of common marmosets (Jones, Harris, & Catchpole, 1993), pygmy marmosets (Snowdon & Cleveland, 1980), squirrel monkeys (Boinski & Mitchell, 1997), Thomas langurs (Wich, Koski, de Vries, & van Schaik, 2003), rhesus macaques (Rendall, Owren, & Rodman, 1998; Rendall, Rodman, & Emond, 1996), silvery gibbons (Dallmann & Geissmann, 2001), agile gibbons (Oyakawa, Koda, & Sugiura, 2007), and chimpanzees (Kojima, Izumi, & Ceugniet, 2003; Mitani et al., 1996) contain individual signatures.

Among the strepsirrhine primates, signatures have been detected for individuals in the gray mouse lemur (Zimmermann & Lerch, 1993), for groups in the golden brown mouse lemur (Braune et al., 2005), and for sex and pair identity in Milne Edwards' sportive lemurs (Rasoloharijaona et al., 2006) and sex and individual in sifakas (Patel & Owren, 2012). It is worth noting that much of the vocal analyses that have been done on nocturnal, solitary foragers have emphasized phylogeny and taxonomy, including the use of vocalizations as a fingerprint for distinguishing taxa (galago species (Ambrose, 2003; Anderson, Ambrose, Bearder, Dixson, & Pullen, 2000; Bearder et al., 1995; Butynski, de Jong, Perkin, Bearder, & Honess, 2006; Zimmermann, 1990), greater galagos (Masters, 1991; Zimmermann, 1990), tarsiers (Nietsch, 1999), and lemurs (Braune et al., 2008; Mendez-Cardenas, Randrianambinina, Rabesandratana, Rasoloharijaona, & Zimmermann, 2008; Stanger, 1995; Zimmermann & Radespiel, 2014; Zimmermann, Vorobieva, Wrogemann, & Hafen, 2000)). Collectively, these studies indicate that, similar to large-brained, group-living primates, the calls of nocturnal, solitary foragers also often contain vocal signatures from which a listener could potentially perceive a great deal of information about the caller.

Overall, more than three decades of research suggest that vocalizations are crucial for maintaining social relationships in both group-living and solitary foraging species (citations above). This suggests that if kin selection was creating pressure for kin recognition in ancestral primates, vocalizations would be a highly likely cue through which kin recognition could be facilitated. However, in order for kin recognition via vocalizations to occur, two pre-requisites must be fulfilled. First, the vocalizations of kin must be distinguishable from those of nonkin; kin signatures must be present in the calls. Then, listeners must be able to perceive these differences (kin recognition). Multiple cognitive mechanisms for this perception have been proposed. I will use the following three definitions based on Komdeur and Hatchwell (1999) (page 238, Box 2):

1. **Phenotype matching**: the individual's own phenotype or that of closely related conspecifics is learned and used as a template against which unknown individuals are compared. Kin are recognized based on how well they match the template.
2. **Familiarity**: individuals learn who their kin are during a period of familiarization (i.e., maturation, nursing, etc).
3. **Spatially based recognition**: individuals located in a specific place (i.e., the nest) are treated as kin.

Though there is a commonly discussed fourth mechanism in the literature, recognition alleles (a specific gene produces a recognizable phenotype and the ability to recognize that gene in others), this mechanism is believed to be largely theoretical with very little empirical support, particularly among complex organisms (Komdeur & Hatchwell, 1999). Therefore, I have excluded it here. Phenotype matching and familiarity are the main mechanisms proposed for mammals (Widdig, 2007), and these are two that I focus on most throughout this dissertation, though spatially based recognition is also discussed in the General Discussion (Chapter 5).

Because our current understandings of matrilineal and patrilineal kin recognition suggest that they occur at different rates and have different mechanisms (Rendall, 2004; Widdig, 2007), I will review what is known about each, separately, in the following two sections.

Matrilineal Kin Recognition

Within mammals, primates are no exception in that their social behavior is highly structured by matrilineal kin relationships (i.e., hyenas (Holekamp et al., 2012), killer whales (Yurk et al., 2002), elephants (McComb et al., 2000), mongooses (Schneider & Kappeler, 2014), primates (Chapais & Berman, 2004; Silk, 2002, 2007b, 2009), see also (Hrdy, 2009)). These kin-biased behaviours include alloparenting (Eberle & Kappeler, 2006), cooperation and coalitionary support of kin (Chapais, 1995; Perry, Manson, Muniz, Gros-Louis, & Vigilant, 2008; Silk, Alberts, & Altmann, 2004), etc. In 1980, a seminal study demonstrated that vervet monkey mothers recognized the screams of their infants (Cheney & Seyfarth, 1980). Since then, matrilineal kin recognition has been documented to be widespread among highly social mammals (i.e., hyenas (Holekamp et al., 1999), elephants (McComb et al., 2000; McComb, Reby, Baker, Moss, & Sayialel, 2003), pinnipeds (Insley, Phillips, & Charrier, 2003), goats (Briefer & McElligott, 2011; Briefer, de la Torre, & McElligott, 2012), bats (Balcombe, 1990; Knoernschild & Von Helversen, 2008)), including many socially complex primate species (i.e., squirrel monkeys (Symmes & Biben, 1985), baboons (Cheney & Seyfarth, 1999; Rendall, Cheney, & Seyfarth, 2000), macaques (Fischer, 2004; Fugate, Gouzoules, & Nygaard, 2008; Rendall et al., 1996). The only primate from the suborder Strepsirrhini in which vocal recognition of matrilineal kin has been demonstrated is the ring-tail lemur, which is both diurnal and group-living (Nunn, 2000). No nocturnal, solitary forager has yet been tested for vocal recognition of matrilineal kin.

Vocalizations are a likely medium for matrilineal kin recognition in solitary foraging primates due to both heritable and environmental factors. Applying source filter theory can explain how heritable morphological differences can produce audible differences in vocalizations (i.e., Ey, Pfefferle, & Fischer, 2007; Fant, 1960; Fant, Kruckenberg, & Liljencrants, 2000; Fitch, 2010; Fitch & Hauser, 1995; Hauser, Evans, & Marler, 1993; Owren & Linker, 1995; Owren & Rendall, 2001). Source filter theory explains that the vibration rate of the vocal folds produces the first harmonic (F_0 or fundamental frequency) and frequencies at integer multiples of that base rate (Ey et al., 2007; Fant, 1960; Fant et al., 2000; Fitch, 2010; Fitch & Hauser, 1995; Hauser et al., 1993; Owren & Linker, 1995; Owren & Rendall, 2001). This vibration rate is a result of both the air pressure and vocal fold morphology (length, thickness and tension) (Ey et al., 2007; Fant, 1960; Fant et al., 2000; Fitch, 2010; Fitch & Hauser, 1995; Hauser et al., 1993; Owren & Linker, 1995; Owren & Rendall, 2001). In low frequency calls with closely spaced harmonics, formants are often highly pronounced (Ey et al., 2007; Fant, 1960; Fant et al., 2000; Fitch, 2010; Fitch & Hauser, 1995; Hauser et al., 1993; Owren & Linker, 1995; Owren & Rendall, 2001). Formants are emphasized frequency bands produced as the tissues of the vocal tract act as a filter, emphasizing and dampening different frequencies of the waveform (Ey et al., 2007; Fant, 1960; Fant et al., 2000; Fitch, 2010; Fitch & Hauser, 1995; Hauser et al., 1993; Owren & Linker, 1995; Owren & Rendall, 2001). For high frequency calls with widely spaced harmonics, signatures can be coded in the contour of the fundamental frequency (Ehret, 2006; Leliveld, Scheumann, & Zimmermann, 2011). Thus, inherited morphological traits could produce vocalizations that are kin group specific. Although it is difficult to collect morphological measurements on the vocal tracts of live animals, a growing body of literature is teasing apart the relationships between body size measures, vocal tract morphology, and acoustic characteristics of vocalizations (e.g., (Ey et al., 2007; Fitch, 1997; Pfefferle & Fischer, 2006; Rendall, Kollias, Ney, & Lloyd, 2005; Riede & Fitch, 1999)).

Environmental factors, particularly learning, could also produce matrilineal kin group specific vocalizations in solitary foragers. Because all primates are nursed by their mothers during infancy, the offspring have the opportunity to hear their mothers' calls and the calls of other dependent young (Rendall, 2004). This exposure may help the newborns to learn to produce similar sounding calls and indeed, primates, with their prolonged periods of infant dependency, long life spans, overlapping generations, high intelligence and large brains, have been argued to recognize their kin through patterns of familiarity acquired during development (Rendall, 2004). Because immature primates associate closely with maternal kin, they are most familiar with their maternal kin and progressively less familiar with more distant relatives, producing a reliable correlation between maternal kinship and familiarity (Rendall, 2004). Not surprisingly, familiarity appears to be a highly pervasive proximate mechanism for matrilineal kin recognition (Rendall, 2004).

Patrilineal Kin Recognition

Far less is known about recognition of paternal kin in mammals, though it is expected to shape the evolution of social behavior through paternal kin selection and inbreeding avoidance (Chapais & Berman, 2004; Hamilton, 1964; Widdig, 2007). Initial studies of paternal kin recognition looking to isolate the cues and mechanisms produced results that were difficult to replicate (for review, see (Rendall, 2004)): Macaques reared apart from kin preferred unfamiliar patrilineal kin over unfamiliar nonkin (Wu, Holmes, Medina, & Sackett, 1980). However, follow up work with larger sample sizes were unable to replicate the results (Fredrickson & Sackett, 1984; Sackett & Fredrickson, 1987). Similarly, adult male macaques and their infants spent more time together than males and unrelated infants, but this effect was also shown to be related to mothers' relationships with the offsprings' fathers (Berenstein, Rodman, & Smith, 1981). Furthermore, later work in sooty mangabeys did not replicate the preferential associations between fathers and offspring (Gust et al., 1998). These inconsistent results for paternal kin biases in behaviour lead some researchers to conclude that beyond possible familiarity effects, no paternal kin recognition occurs (Rendall, 2004).

More recently, though, there has been a resurgence in interest in paternal kin recognition. Long-term behavioral studies suggest that mammals often behave as if they recognize paternal kin (baboons: (Buchan, Alberts, Silk, & Altmann, 2003), hyenas: (Van Horn, Wahaj, & Holekamp, 2004; Wahaj et al., 2004). In addition, studies have begun to find evidence of preferential behaviour being given to paternal kin, though the bonds are often weaker than with maternal kin (rhesus macaques: (Widdig, Nurnberg, Krawczak, Streich, & Bercovitch, 2002), baboons: (Alberts, 1999; Smith, Alberts, & Altmann, 2003), mandrills: (Charpentier, Peignot, Hossaert-Mckey, & Wickings, 2007), reviews: (Widdig, 2007, 2013).

Overall, work on vocal recognition of paternal kin has been rare. Macaques have been shown to recognize paternal kin via vocalizations (Pfefferle, Ruiz Lambides, & Widdig, 2014). In rodents, odor has been shown to be highly important (Widdig, 2007), but in species that rely less heavily on olfactory cues, or have long lifespans, large brains and complex relationships (i.e., primates), other cues or combinations of cues such as vocalizations, visual cues, and/or personality may be emphasized (Rendall, 2004; Widdig, 2007).

Within group-living species with a high male reproductive skew and short male breeding tenure, familiarity may facilitate patrilineal kin recognition because age-based cohorts will have an increased likelihood of being paternal siblings (Widdig, 2013). For these species, shared environmental factors including social learning of vocalizations modelled after the father (i.e., possibly the alpha male, if still present in the group (Widdig, 2013)), would be possible. In addition, signatures might be produced by shared, inherited morphology (see source filter theory: i.e., Ey et al., 2007; Fant, 1960; Fant et al., 2000; Fitch, 2010; Fitch & Hauser, 1995; Hauser et al., 1993; Owren & Linker, 1995; Owren & Rendall, 2001). In contrast, in species in which males obtain matings through scramble competition and paternal half-siblings are not likely to grow up together (i.e., (Eberle & Kappeler, 2004a, 2004b; Radespiel, Ehresmann et al., 2001)), phenotype matching based on signatures produced by inherited morphology would be necessary.

Phenotype matching has been suggested to be selected for in species which (a) do not provide paternal care, (b) have multiple paternity litters, and/or (c) nest communally

(Mateo, 2004). This makes mouse lemurs a particularly interesting species in which to investigate phenotype matching because they fulfil these criteria. First, males do not provide paternal care, co-nest, or co-forage with their mates or with their young (Eberle & Kappeler, 2006; Radespiel, Sarikaya et al., 2001). This strongly limits the effectiveness of the familiarity-based mechanisms often seen in more gregarious species with cohesive foraging groups (i.e., primates (Rendall, 2004; Widdig, 2007)). Second, mouse lemur litters can have multiple paternities within the same litter (Eberle & Kappeler, 2004a; Radespiel et al., 2002), thus infant mouse lemurs could be expected to evolve self-referential phenotype matching to distinguish between full-siblings and maternal half-siblings in the nest. Finally, given that multiple females may breed in the same nest (Eberle & Kappeler, 2006), infant mouse lemurs could potentially encounter paternal half siblings within the other mother’s litter and use self-referential phenotype matching to recognize them. Self-referential phenotype matching has been observed in ground squirrels using olfactory cues (Mateo, 2010).

Current Knowledge on the Gray Mouse Lemur

Our current knowledge of the gray mouse lemur makes it a useful species in which to investigate vocal recognition of kin and to model ancestral primate social behavior. Like the hypothesized ancestral primates (Cartmill, 1974, 2012; Müller & Thalmann, 2000; Rasmussen, 1990; Sussman, 1991; Sussman et al., 2013; Sussman & Raven, 1978), gray mouse lemurs are small-bodied, nocturnal, solitary foragers that have dispersed social networks (Braune et al., 2008; Eberle & Kappeler, 2002; Leliveld et al., 2011; Radespiel, 2000). Male dispersal and female philopatry (residence) are common

(Radespiel, Lutermann, Schmelting, Bruford, & Zimmermann, 2003; Radespiel, Sarikaya et al., 2001; Schliehe-Diecks, Eberle, & Kappeler, 2012). Both sexes forage solitarily in ranges that overlap with those of the opposite sex (Eberle & Kappeler, 2002; Radespiel, 2000). During the day, adult males sleep alone (Eberle & Kappeler, 2006; Radespiel, Cepok, Zietemann, & Zimmermann, 1998). The philopatric females usually form sleeping groups with female kin and cooperatively raise their young in nests (Eberle & Kappeler, 2006; Radespiel, Sarikaya et al., 2001). Immature males and females are socialized within these groups (Eberle & Kappeler, 2006; Radespiel, Sarikaya et al., 2001).

Mouse lemurs have an elaborate vocal repertoire and use vocalizations in a diversity of social contexts (e.g., mating contexts (Braune et al., 2008; Buesching, Heistermann, Hodges, & Zimmermann, 1998), mother-infant communications (Scheumann, Zimmermann, & Deichsel, 2007), emotional state (Altenmüller et al., 2013)). Several call types are in the high frequency/ultrasonic range, which is believed to be important for maintaining crypsis and avoiding predators which either do not hear the ultrasonic frequencies or cannot easily localize the high frequencies (Zimmermann, 1995a). As owls may predate over 25% of the mouse lemur population per year, crypsis is crucial for mouse lemurs (Goodman, O'Connor, & Langrand, 1993).

Among the most frequently given call types are the agonistic call, the alarm call, and the mate advertisement call (Leliveld et al., 2011). I expected these call types to facilitate kin recognition due to their functions and their acoustic structures. The agonistic call is given in aggressive/defensive situations and is a short, frequency modulated call, which starts lower, peaks in the middle, and then decreases in frequency at the end

(Leliveld et al., 2011). Because kin recognition of agonistic calls has been observed in monkeys and hyenas with frequent kin-biased coalitionary behavior (Cheney & Seyfarth, 1980, 1999; Fischer, 2004; Fugate et al., 2008; Holekamp et al., 1999), I expected to find it in mouse lemurs as well, as this could facilitate the recruitment of kin support. The alarm call is given in disturbance situations and is a short, relatively non-modulated call (Leliveld et al., 2011). I hypothesized that kin recognition via alarm calls could facilitate the defense of kin from predators (defense of nonkin has been observed in mouse lemurs (Eberle & Kappeler, 2008)). Both of the agonistic and the alarm calls are short, but often given in rapid succession (Leliveld et al., 2011). The mate advertisement call is frequent during the breeding season and is a longer call with multiple modulations (Leliveld et al., 2011; Zimmermann & Lerch, 1993). Kin recognition via the mating call is expected to be important for preventing inbreeding (Rendall, 2004; Widdig, 2007). Each of these three call types contain individual signatures which are encoded largely within the contour of the fundamental frequency (Leliveld et al., 2011; Zimmermann & Lerch, 1993), as is expected for high frequency calls (Ehret, 2006).

Three threads of previous work on gray mouse lemurs are consistent with the idea that their calls could be shaped, at least in part, by social learning: **(1)** genetically and morphologically indistinguishable groups of wild *M. murinus* have distinguishable dialects (Hafen, Neveu, Rumpler, Wilden, & Zimmermann, 1998); **(2)** in a study of three pairs of males, males housed together produced calls that were more similar to each other than to the other males' calls (Zimmermann, 1995b; Zimmermann & Lerch, 1993); and **(3)** young mouse lemurs produce a highly variable "proto-trill" that becomes more stereotyped as they mature (Zimmermann, 1995b), unless they are socially deprived, in which case the proto-trill does not stabilize (Zimmermann, 1991).

It is also highly possible that vocalizations may also be shaped by inherited morphological characteristics (see source filter theory, i.e., Ey et al., 2007; Fant, 1960; Fant et al., 2000; Fitch, 2010; Fitch & Hauser, 1995; Hauser et al., 1993; Owren & Linker, 1995; Owren & Rendall, 2001). Morphological traits of the vocal tract, vocal cords and lung capacity may be inherited, and if so, could result in related individuals producing similar calls (see source filter theory: i.e., Ey et al., 2007; Fant, 1960; Fant et al., 2000; Fitch, 2010; Fitch & Hauser, 1995; Hauser et al., 1993; Owren & Linker, 1995; Owren & Rendall, 2001). These two proximate mechanisms are not likely to be mutually exclusive, but rather occur simultaneously.

Thus, our current understanding of the socio-ecology, life history, and vocal communication of the gray mouse lemur makes it an excellent species in which to investigate vocal recognition of kin. This deep understanding of the gray mouse lemur's social system and feeding ecology is particularly necessary when we wish to apply the results to model the social behavior of the ancestral primates from which present-day primate diversity evolved (Müller & Thalmann, 2000).

Organization of the Dissertation

This dissertation presents the results from both a field study investigating matrilineal kin recognition and a laboratory study which investigated patrilineal kin recognition. The field study was conducted in Ankarafantsika National Park in north-western Madagascar with female *M. murinus.* Chapters 2 and 3 present the results from the field study and Chapter 4 presents the laboratory study conducted at the Institute of Zoology at the University of Veterinary Medicine Hannover. In Chapter 2 (Kessler et al., 2014) I address whether matrilines have distinctive signatures in their agonistic calls and whether increasing acoustic distance correlates with decreasing genetic relatedness. I recorded agonistic calls from female mouse lemurs during social interactions while they were kept in temporary captivity. I conducted a multi-parametric analysis of the acoustic structure of the calls and tested whether the calls could be accurately classified by matriline. I also genotyped the population and calculated pairwise relatedness using seven microsatellite loci and sequenced the D-loop of the females in order to determine matrilineal relatedness. For each dyad of females, I calculated pairwise acoustic distance and genetic relatedness and tested whether they are negatively correlated.

In Chapter 3, I present the results from the playback study testing whether females respond differently to calls from matrilineal kin and nonkin, and differently to familiar and unfamiliar individuals. When each lemur was trapped, it was injected with a microchip transponder and released at its capture site. The playback experiments were then conducted on feeding platforms that contained a microchip reader (Joly, Scheumann, & Zimmermann, 2008). When the female ate at the feeding platform, the platform read her microchip (Joly et al., 2008), thus identifying the female and enabling me to select and play a stimulus call. This protocol allowed me to individually identify these elusive, nocturnal, visually very similar lemurs as they foraged and to conduct playback experiments on wild, free-ranging subjects under semi-controlled conditions.

The results from the laboratory study are presented in Chapter 4 (Kessler et al., 2012). This study was conducted in a well established colony where genetic relationships and social histories (i.e., which animals have shared a cage together) are known. This enabled me to test for patrilineal kin recognition, while controlling for familiarity. I tested whether females respond differently to mating calls and alarm calls from their fathers and an equally familiar unrelated male. Chapter 5 discusses the significance of the findings for the evolution of primate social complexity and makes recommendations for future research.

Taken together, this dissertation tests for both matrilineal and patrilineal kin recognition, tests three call types, discusses the findings in terms of two major kin recognition mechanisms (familiarity and phenotype matching), and models how kin recognition may have occurred in solitary foraging ancestral primates.

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CHAPTER 2

MODELING THE ORIGINS OF MAMMALIAN SOCIALITY: MODERATE EVIDENCE FOR MATRILINEAL SIGNATURES IN MOUSE LEMUR VOCALIZATIONS

Abstract

Maternal kin selection is a driving force in the evolution of mammalian social complexity and it requires that kin are distinctive from nonkin. The transition from the ancestral state of asociality to the derived state of complex social groups is thought to have occurred via solitary foraging, in which individuals forage alone, but, unlike the asocial ancestors, maintain dispersed social networks via scent-marks and vocalizations. We hypothesize that matrilineal signatures in vocalizations were an important part of these networks. We used the solitary foraging gray mouse lemur (*Microcebus murinus*) as a model for ancestral solitary foragers and tested for matrilineal signatures in their calls, thus investigating whether such signatures are already present in solitary foragers and could have facilitated the kin selection thought to have driven the evolution of increased social complexity in mammals. Because agonism can be very costly, selection for matrilineal signatures in agonistic calls should help reduce agonism between unfamiliar matrilineal kin. We conducted this study on a well-studied population of wild mouse lemurs at Ankarafantsika National Park, Madagascar. We determined pairwise relatedness using seven microsatellite loci, matrilineal relatedness by sequencing the mitochondrial D-loop, and sleeping group associations using radio-telemetry. We recorded agonistic calls during controlled social encounters and conducted a multi-

parametric acoustic analysis to determine the spectral and temporal structure of the agonistic calls. We measured 10 calls for each of 16 females from six different matrilineal kin groups. Calls were assigned to their matriline at a rate significantly higher than chance (pDFA: correct=47.1%, chance=26.7%, p=0.03). There was a statistical trend for a negative correlation between acoustic distance and relatedness (Mantel Test: g=-1.61, Z=4.61, r=-0.13, p=0.058). Mouse lemur agonistic calls are moderately distinctive by matriline. Because sleeping groups consisted of close maternal kin, both genetics and social learning may have generated these acoustic signatures. As mouse lemurs are models for solitary foragers, we recommend further studies testing whether the lemurs use these calls to recognize kin. This would enable further modeling of how kin recognition in ancestral species could have shaped the evolution of complex sociality.

Introduction

Maternal kin selection (the preferential treatment of matrilineal relatives (Hamilton, 1964; Rendall, 2004)) has been argued to be one of the driving forces in the evolution of mammalian sociality, underpinning some of the most complex and intriguing social behaviors including communal infant rearing and socialization, the evolution of group-living, alliance formation and cooperation (Altenmüller et al., 2013; Chapais & Berman, 2004; de Waal & Tyack, 2003; Hamilton, 1964). While such manifestations of kin selection are well documented in gregarious species that live in complex social groups (Chapais & Berman, 2004; de Waal & Tyack, 2003), its evolutionary foundations are likely to have emerged in less complex, ancestral species ((Müller & Thalmann, 2000), but see (Shultz, Opie, & Atkinson, 2011)). Given that ancestral mammals are believed to have been asocial with no social relationships maintained outside of mating and rearing infants (Müller & Thalmann, 2000), tracing how maternal kin selection may have formed the backbone for this transition is likely to be crucial to understanding how social complexity evolves.

A prerequisite of maternal kin selection in any mammalian social system is that maternal kin must be sufficiently distinctive from nonkin that they can be recognized and thus receive preferential treatment (Hamilton, 1964; Rendall, 2004). For the asocial and nocturnal ancestral mammals (Müller & Thalmann, 2000), this would have also meant being distinctive over distances, through darkness, and dense foliage where visual and olfactory cues would have been inefficient. Mammals under these conditions would be expected to benefit from having matrilineal signatures in their vocalizations.

To date, much of the attention that has been given to investigating matrilineal signatures in mammalian vocalizations has focused on social species (ie. goats (Briefer et al., 2012; Briefer & McElligott, 2012), meerkats (Townsend, Hollen, & Manser, 2010), marmots (Blumstein, Nguyen, & Martin, 2013), sperm whales and killer whales (Tyack, 2008; Whitehead, Dillon, Dufault, Weilgart, & Wright, 1998; Yurk et al., 2002), bats (Chaverri & Kunz, 2011; Gillam & Chaverri, 2012; Scherrer & Wilkinson, 1993) and the socially variable house mouse (Hoffmann, Musolf, & Penn, 2012; Latham & Mason, 2004)). Much less has been done on solitary species (i.e., pandas (Charlton, Zhang, & Snyder, 2009)). In the solitary pandas, individual signatures were found, but there was no correlation between overall acoustic distance between individuals and their relatedness, and only a few individual parameters correlated with relatedness (Charlton et al., 2009). Though the authors did not clarify whether relatedness was matrilineal, patrilineal, or both, the lack of stronger results may still indicate that pressure to encode kinship within vocalizations may not be as strong as in the more social species (Charlton et al., 2009). Each of these studies that investigated kin signatures, either exclusively focused on matrilineal relatedness or had a high likelihood of relatedness from both patrilineal and matrilineal relationships, thus suggesting that matrilineal relatedness had a strong role in the signatures found. We differentiate between *individual* signatures that may be recognized by kin (i.e., primates: (Nunn, 2000; Rendall et al., 2000; Rendall, Notman, & Owren, 2009; Rendall et al., 1996), pinnipeds (Insley et al., 2003), elephants (McComb et al., 2000), dolphins (Sayigh et al., 1998)) and *matrilineal* signatures. Matrilineal signatures have the important distinction that they may enable the recognition of unfamiliar maternal kin via the similarity to known maternal kin, thus facilitating the preferential treatment of unfamiliar maternal kin.

In order to better understand the evolutionary transition from asociality to social complexity, we focus on primates, an order in which some lineages have evolved highly complex, cohesive social groups while other lineages are believed to have retained the social system that is believed to be ancestral to primates: solitary foraging (Müller & Thalmann, 2000). In the lineages that evolved social systems with cohesive social groups, the ancestral solitary foragers are believed to have been a transition phase between asociality and group-living (Müller & Thalmann, 2000). Solitary foragers forage alone, but maintain a dispersed social network of relationships with conspecifics communicating through vocalizations and scent-marks, and often have consistent co-sleeping associations (Müller & Thalmann, 2000). It is these dispersed social networks in ancestral primates that are thought to have been the foundation for the evolution of more complex primate social systems (Müller & Thalmann, 2000), thus they are likely to have been crucial for kin networks and a likely pathway for kin selection (Kessler et al., 2012; Nash, 2004).

In order to determine whether matrilineal signatures in vocalizations may have facilitated matrilineal kin selection in solitarily foraging ancestral primates, we use the gray mouse lemur (*Microcebus murinus*) to model ancestral primates. Mouse lemurs are frequently used as ancestral primate models because their socioecology is thought to be similar to that of the last common ancestor of the primate order (Cartmill, 1972, 1974, 1992; Charles-Dominique & Martin, 1970; Gebo, 2004; Kappeler, 1997a, 1998; Martin et al., 2007; Müller & Thalmann, 2000; Piep et al., 2008; Radespiel, 2000, 2006; Radespiel et al., 1998; Radespiel, Sarikaya et al., 2001; Rasmussen, 1990, 2002; Ravosa & Dagosto, 2007; Sussman, 1991). Like mouse lemurs today, ancestral primates are thought to have been small-bodied, small-brained nocturnal solitary foragers that forage for fruits and insects in the thin, terminal ends of branches (Cartmill, 1972, 1974, 1992; Charles-Dominique & Martin, 1970; Gebo, 2004; Kappeler, 1997a, 1998; Martin et al., 2007; Müller & Thalmann, 2000; Piep et al., 2008; Radespiel, 2000, 2006; Radespiel et al., 1998; Radespiel, Sarikaya et al., 2001; Rasmussen, 1990, 2002; Ravosa & Dagosto, 2007; Sussman, 1991). Therefore, we use the dispersed social networks of living mouse lemurs to model ancestral primate social organization and to reconstruct the social behavior patterns from which present-day primate diversity evolved (Müller & Thalmann, 2000).

Our current knowledge of the gray mouse lemur's dispersed social networks makes it an excellent model species in which to test for matrilineal signatures. Male dispersal and female philopatry are common (Radespiel et al., 2003; Schliehe-Diecks et al., 2012). Both sexes forage solitarily in home ranges that overlap with those of other individuals of both sexes (Eberle & Kappeler, 2002; Radespiel, 2000). During the day, adult males sleep alone (Eberle & Kappeler, 2006; Radespiel et al., 1998). Females form sleeping groups with female kin and cooperatively raise their young in tree holes (Eberle & Kappeler, 2006; Radespiel, Sarikaya et al., 2001). Immature males and females are socialized within these groups (Eberle & Kappeler, 2006; Radespiel, Sarikaya et al., 2001) and thus have ample opportunity to hear and learn the calls of their matrilineal kin. However, given that larger nest groups may split, subsequent generations may encounter matrilineal kin with whom they personally did not share a nest (Radespiel, Sarikaya et al., 2001). It is also possible that inherited vocal tract morphology (see source-filter theory:

i.e., (Ey et al., 2007; Fitch & Hauser, 1995; Owren & Rendall, 1997)) could cause related individuals to produce similar calls. Thus, both genetic factors and social learning could contribute to the development of matrilineal signatures in this species.

Mouse lemurs have an elaborate vocal repertoire and use vocalizations in a diversity of social interactions (e.g., mating contexts (Braune et al., 2008; Buesching et al., 1998), mother-infant communications (Scheumann et al., 2007), emotional state (Altenmüller et al., 2013; Zimmermann, 2009), paternal kin recognition (Kessler et al., 2012)). We chose to investigate the individually distinctive agonistic call (Leliveld et al., 2011). It is a short, frequency modulated vocalization with an upward and downward sweep (Fig. 1) containing harmonics in both the audible and ultrasonic range (Leliveld et al., 2011).

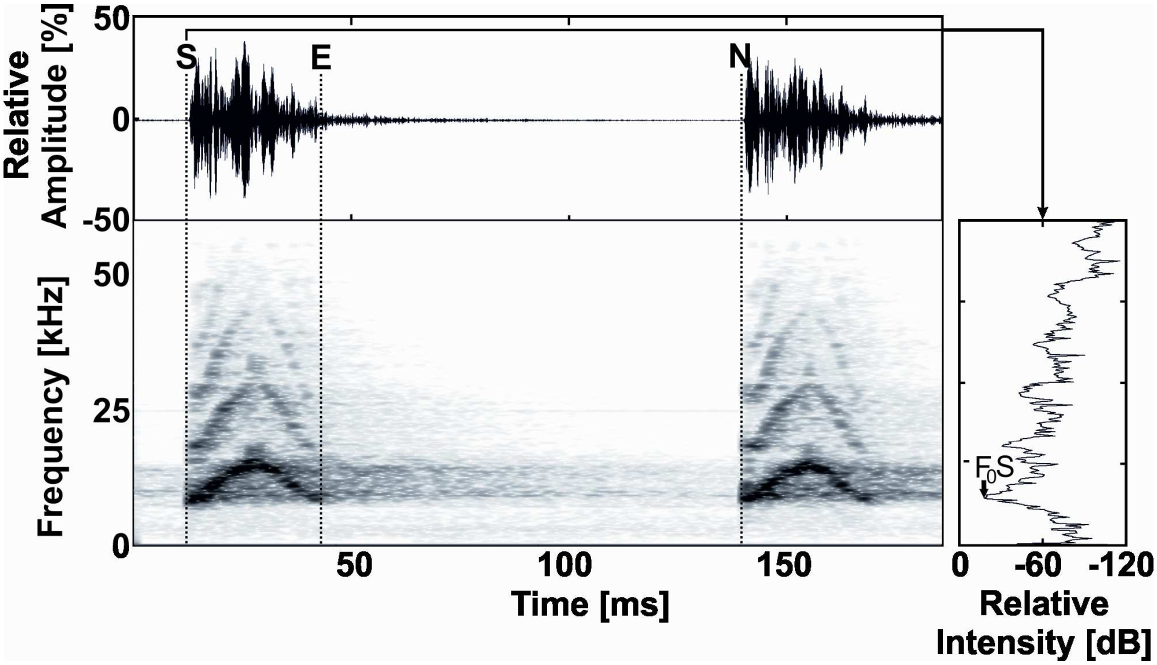

Figure 1. An oscillogram, spectrogram and power spectrum depicting some of the acoustic parameters of the agonistic call. S, E, and N show the start time, end time, and start of the next call, respectively. F_0S shows the measurement of the fundamental frequency on the power spectrum. Figure produced in BatSound Pro 3.31 (Pettersson Elektronik AB, Upsala Sweden) according to (Leliveld et al., 2011). For more information see Table 1 and (Leliveld et al., 2011).

Because aggressive/defensive encounters have the potential to be very costly due to injuries sustained, we predicted that it would be advantageous for agonistic calls to contain matrilineal signatures so that aggression amongst matrilineal relatives could be minimized. We hypothesized that these agonistic calls will be distinctive by matrilineal kin group and that the genetic relatedness of female dyads will negatively correlate with their acoustic distance. We found moderate evidence for matrilineal signatures and a trend suggesting that increasing relatedness is associated with decreasing acoustic distance. Further studies are needed to determine whether mouse lemurs use these signatures to recognize kin.

Results

Acoustic differences in agonistic calls between matrilines. Qualitative differences are visible between matrilines (Appendix A) in both frequency and temporal parameters. For example, several individuals in matriline 6 gave calls with an unusually high peak frequency, matriline 5 gave calls of longer duration, and matrilines 1 and 3 typically gave lower frequency calls, with the calls of matriline 1 being generally qualitatively shorter than those of 3.

The principal component analysis produced two components which together explained 66.2 % of the variation in the original dataset. The first component was highly correlated (>0.4 or <-0.4) with all original acoustic parameters, but correlated most strongly (>0.7) with the frequency parameters, and thus, it is referred to as the frequency component (48.6% of the total variation). The second component correlated highly (>0.4 or <-0.4) with call duration and inter-call interval and is thus called the time component (17.5% of the total variation). Table 1 shows the 25% quartile, median, and 75% quartile for each of the original acoustic parameters and their loadings on the frequency component and the time component.

Table 1

The 25%, 50%, and 75% Quartiles of the Original Acoustic Parameters and the Loadings for Each Parameter on the Frequency (Component 1) and Time (Component 2) Components.

Parameters	Quartiles			Component loadings	
	25%	Median	75%	Component 1	Component 2
F_0S (Hz)	10156	11133	12061	**0.828**	0.330
F_0Peak (Hz)	12500	13770	16602	**0.785**	0.064
F_0E (Hz)	10156	11523	12891	**0.805**	-0.253
Start Bandwidth (Hz)	3062	3749	4646	**0.590**	0.263
Call Duration (ms)	32	40	48	**-0.624**	**0.658**
Time to Peak (ms)	17	20	26	**-0.696**	0.280
Inter-call Interval (ms)	101	148	197	**-0.481**	**-0.685**

Note. Parameters classified as highly loaded (>0.4 or <-0.4) are shown in bold

Table 2 shows the matrix of pairwise acoustic distances calculated for each dyad of females (bottom matrix).

Table 2.

Pairwise Relatedness Values Between Females (top matrix) (Goodnight & Queller, 1999; Queller & Goodnight, 1989) and Acoustic Distances for the Female Dyads (bottom matrix).

	06-09	**10-10**	**11-11**	**101-10**	**112-10**	**113-10**	**17-10**	**19-10**	**28-09**	**36-11**	**41-11**	**45-10**	**46-11**	**51-10**	**52-11**	**58-10**
06-09		0.11	0.25	-0.18	0.03	-0.15	-0.17	**0.61**[a]	-0.22	-0.20	**0.29**[b]	0.12	0.05	0.12	-0.14	0.09
10-10	0.38		0.04	-0.08	**0.41**[a]	-0.02	-0.15	0.10	-0.03	-0.09	0.00	-0.02	0.00	-0.02	-0.02	0.01
11-11	1.27	1.65		0.06	0.28	0.05	-0.17	0.24	-0.22	-0.03	-0.03	0.14	0.16	**0.34**[c]	-0.04	**0.62**[a]
101-10	0.14	0.24	1.41		0.08	0.01	-0.10	-0.20	0.00	-0.05	0.03	**0.51**[a]	-0.22	0.01	0.16	-0.12
112-10	1.00	**0.62**	2.27	0.85		-0.01	-0.12	-0.06	0.06	-0.07	-0.14	0.08	0.09	-0.09	0.07	0.09
113-10	0.15	0.23	1.42	0.01	0.85		-0.05	-0.08	-0.02	0.01	0.19	0.09	0.11	0.09	**0.36**[a]	0.02
17-10	1.96	2.34	0.69	2.10	2.95	2.11		-0.28	**0.52**[a]	**0.49**[a]	-0.02	-0.14	**0.44**[a]	-0.05	-0.04	-0.19
19-10	**0.08**	0.46	1.19	0.22	1.08	0.23	1.88		-0.31	-0.05	**0.44**[a]	0.10	-0.06	0.20	-0.24	0.16
28-09	1.02	1.40	0.25	1.16	2.01	1.17	**0.94**	0.94		**0.23**[b]	-0.08	-0.19	**0.17**[b]	-0.02	0.06	-0.15
36-11	2.82	3.20	1.55	2.96	3.82	2.97	**0.87**	2.74	**1.81**		-0.06	-0.08	**0.38**[a]	0.10	0.01	-0.05
41-11	**0.50**	0.89	0.77	0.65	1.50	0.65	1.45	**0.42**	0.51	2.32		0.28[c]	0.03	0.10	-0.08	-0.01
45-10	0.17	0.55	1.10	**0.31**	1.17	0.32	1.79	0.09	0.85	2.65	0.33		0.01	0.09	-0.10	-0.03
46-11	0.07	0.45	1.20	0.21	1.07	0.22	**1.89**	0.01	**0.95**	**2.75**	0.43	0.10		-0.09	0.01	0.08
51-10	0.95	1.33	**0.32**	1.09	1.94	1.10	1.01	0.87	0.07	1.88	0.44	0.78	0.88		-0.19	**0.29**[b]
52-11	0.38	0.77	0.88	0.53	1.38	**0.53**	1.57	0.31	0.63	2.44	0.12	0.22	0.32	0.56		-0.07
58-10	0.42	0.81	**0.85**	0.57	1.42	0.57	1.53	0.34	0.59	2.40	0.08	0.25	0.35	**0.52**	0.04	

[a] P<0.001, Likelihood ratio > 37.02, Type II error <0.77

[b] P<0.01, Likelihood ratio > 11.95, Type II error <0.59

[c] P<0.05, Likelihood ratio > 3.31, Type II error <0.36.

Note. In both matrices, bold values show dyads from the six kin groups (compare Table 3).

Genetic relatedness. Median pairwise relatedness for all dyads in the population is r=-0.02 (n=107 individuals, min=-0.38, max=0.91). Median pairwise relatedness for the females within the kin groups was r=0.41 (n=16 females, min=0.30, max=0.52, Table 3), whereas the between kin group median relatedness was r=-0.02 (n= 16 females, min=-0.12, max=0.06).

Table 3.

The Six Kin Groups, their Co-sleeping Behavior, Relatedness Values Calculated from Seven Microsatellites, Allelic Exclusions from the Microsatellites (Number of Loci with No Shared Alleles), and the Mitochondrial D-loop Haplotype.

Kin group	Dyad	Co-sleep	Relatedness	Allelic Exclusions	Haplotype
1 (n=3)	06-09 & 19-10	No	0.61[a]	0	06-09: H6
	06-09 & 41-11	??	0.29[b]	1	41-11: H6
	19-10 & 41-11	Yes	0.44[a]	0	19-10: ??
2 (n=3)	51-10 & 58-10	Yes	0.29[b]	0	All: H6
	51-10 & 11-11	Yes	0.34[c]	2	
	58-10 & 11-11	Yes	0.62[a]	0	
3 (n=2)	10-10 & 112-10	Yes	0.41[a]	0	All: H6
4 (n=2)	45-10 & 101-10	Yes	0.51[a]	0	All: H3
5 (n=2)	113-10 & 52-11	No	0.36[a]	0	All: H3
6 (n=4)	28-09 & 17-10	Yes	0.52[a]	0	All: H4
	28-09 & 36-11	??	0.23[b]	3	
	28-09 & 46-11	??	0.17[b]	2	
	17-10 & 36-11	Yes	0.49[a]	0	
	17-10 & 46-11	Yes	0.44[a]	0	
	36-11 & 46-11	Yes	0.38[a]	1	

[a] P<0.001, Likelihood ratio > 37.02, Type II error <0.77

[b] P<0.01, Likelihood ratio > 11.95, Type II error <0.59

[c] P<0.05, Likelihood ratio > 3.31, Type II error <0.36.

Note. ?? means data not available. Allelic exclusions were included to faciliatate comparisons with previous genetic analyses on sleeping groups in this population of mouse lemurs (e.g., (Radespiel, Sarikaya et al., 2001)).

Table 2 (top matrix) shows the pairwise relatedness values of all the females in the kin groups. Within the females in the population, we found seven mitochondrial haplotypes (Figure 2). The kin groups in this study belonged to the three most frequent haplotypes (H3, H4, H6).

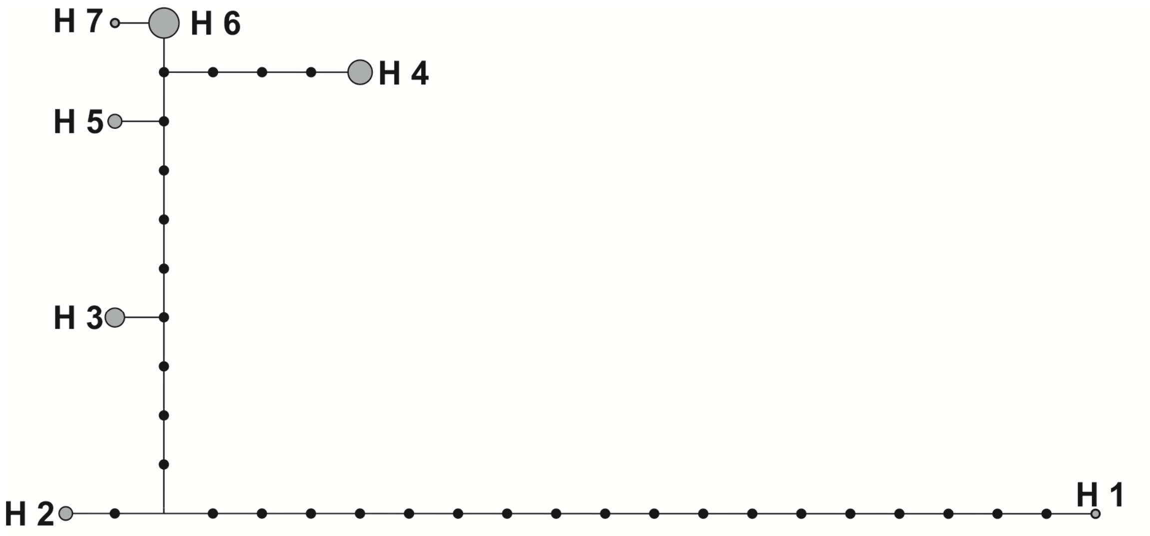

Figure 2. A mitochondrial D-loop haplotype network of the population. Kin groups 1-3 are from haplotype 6. Groups 4 and 5 are from haplotype 3 and group 6 is from haplotype 4.

Kin group signatures and correlation between acoustic distance and genetic relatedness. The pDFA correctly classified 47.1% of the 160 calls by kin group (pDFA, chance level=26.7%, p=0.03). Figure 3 shows the separation of the kin groups produced by the frequency and time components (classification table produced by a non-permutated DFA is presented in Appendix B).

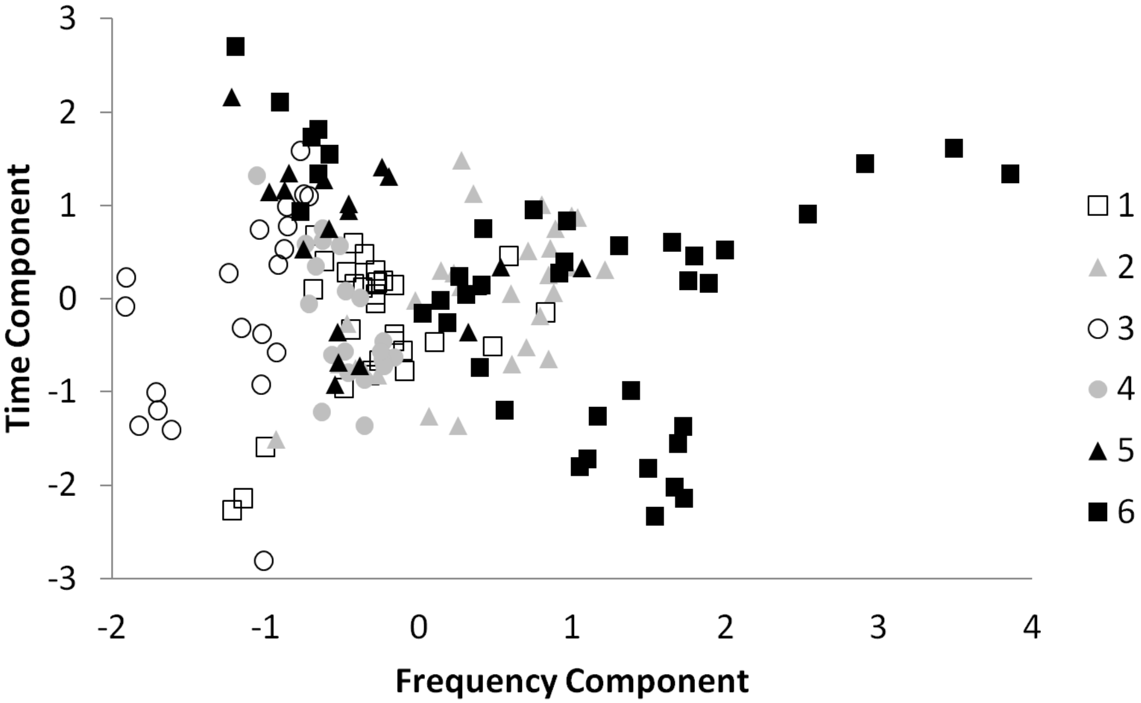

Figure 3. A scatterplot showing the separation of the kin groups produced by the frequency and time components of the principal component analysis. Individual symbols each represent one of the 160 analyzed calls.

In addition, we found a statistical trend for a weak, negative correlation between genetic relatedness and acoustic distance among the 16 females (Mantel Test, g=-1.61, Z=4.61, r=-0.13, p=0.058, Fig. 4). Thus, an increase in relatedness was associated with a tendency towards a decrease in acoustic distance.

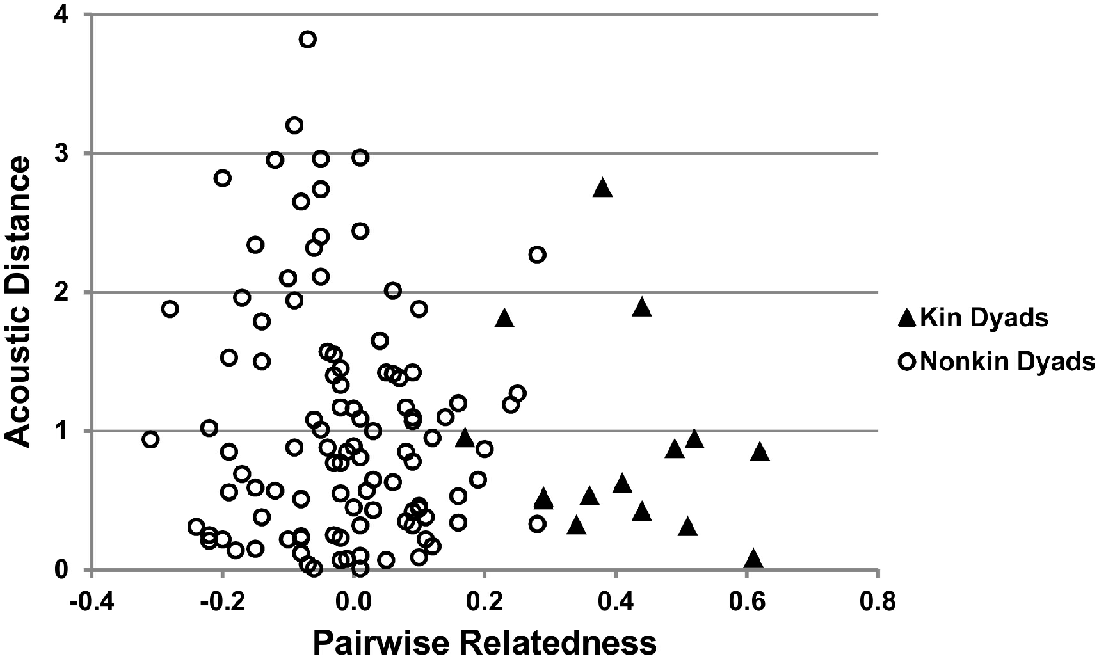

Figure 4. A scatterplot showing a weak negative relationship between pairwise genetic relatedness (X axis) and acoustic distance between dyads (Y axis).

Discussion

We found moderate evidence for matrilineal signatures in mouse lemur agonistic calls. While the calls were classified to the correct matriline at a rate significantly higher than chance (47% correct vs. 26.7% chance), the false classification was still made more than half the time. In addition, while we found a statistical trend for a negative relationship between genetic relatedness and acoustic distance, the correlation coefficient was relatively low.

Given that the dispersed matrilineal social system of mouse lemurs provides the opportunity for matrilineal signatures to occur through both inherited traits in vocal morphology (see source filter theory, i.e., (Ey et al., 2007; Fant, 1960; Fant et al., 2000;

Fitch, 2010; Fitch & Hauser, 1995; Hauser et al., 1993; Owren & Rendall, 1997)) and through social learning (Eberle & Kappeler, 2006; Radespiel, Sarikaya et al., 2001), both may have been important proximate mechanisms for the moderate signatures found in this study. Offspring may inherit vocal tract morphology affecting vocal cord length and thickness which would in turn affect the fundamental frequency of the calls (Ey et al., 2007; Fant, 1960; Fant et al., 2000; Fitch, 2010; Fitch & Hauser, 1995; Hauser et al., 1993; Owren & Rendall, 1997). And indeed, fundamental frequency parameters were important in this analysis, loading highly on principle component 1. Offspring could also inherit traits having to do with lung capacity which could influence breathing rate and thus affect acoustic parameters such as call duration and inter-call interval (see source filter theory, i.e. (Ey et al., 2007; Fant, 1960; Fant et al., 2000; Fitch, 2010; Fitch & Hauser, 1995; Hauser et al., 1993; Owren & Rendall, 1997)), both of which loaded highly on component 2. Unfortunately, it was not possible to collect measurements of vocal tract morphology (ie, length and thickness of vocal folds, length of vocal tract) as this would be highly invasive and, in the field, very complicated. Thus, it is not possible for us to test for a relationship between vocal tract morphology and acoustics. Furthermore, we do not expect less targeted morphological measures (ie. body mass, body length, head size, etc) to be useful proxies for heritability of vocal tract morphology, because they will often vary with pregnancy status, age, season, and the availability of sufficient nutrition for the developing females, none of which we could control for in this population of wild mouse lemurs. Additionally, previous reviews have shown that body size tends to correlate with acoustic differences across age and sex classes in monkeys and humans, but within those classes the relationship is less clear (Ey et al., 2007; Rendall et al., 2005).

In addition to genetic mechanisms, it is possible that offspring may also learn to produce calls similar to the calls of the matrilineal relatives from the same nest, which they hear during socialization (Eberle & Kappeler, 2006; Radespiel, Sarikaya et al., 2001). Prior research has shown that infant mouse lemurs produce highly variable infant calls that then stabilize into the adult form around the time of weaning (Zimmermann, 1991). This could mean that social learning during development may be crucial for the development of kin signatures. Similar findings have been found in birds (Sharp, McGowan, Wood, & Hatchwell, 2005) and other mammals (i.e., (Briefer & McElligott, 2012)). Unfortunately our data do not allow us to separate the effects of social learning and heritability. While co-sleeping promotes familiarity and thus generates opportunities for social learning, we cannot reliably compare co-sleepers with non-co-sleepers. We cannot exclude the possibility that the non-co-sleeping dyads may have co-slept when they were younger, but no longer did during our study. This is particularly likely for 28-09 and 36-11 and for 28-09 and 46-11 who were not observed to co-sleep. However, since 28-09 was not recaptured in the second year of the study, we do not know if she was still alive. If she was still alive when 36-11 and 46-11 were born, she may have co-slept with them until her death. Similarly, 06-09 was not captured the second year of the study when 41-11 was first caught, thus we do not know if both members of this dyad were alive at the same time. In addition, 19-10 and 06-09 were both at least one year old at the start of the study. Thus, they could be a sibling dyad or mother-daughter dyad which was part of a sleeping group which split as the lemurs aged. However, while it is not possible to distinguish between the two mechanisms here (genetics and social learning), we suspect that the two proximate mechanisms are not mutually exclusive and may even have additive effects (though additional interaction effects could also be possible). Thus, we expect that both mechanisms are likely to have contributed to the evolution of the moderate matrilineal signatures present in the calls.

While these matrilineal signatures are statistically present, their weakness brings up several intriguing questions. The first is whether the lemurs would be expected to use them to recognize kin. Prior work on mouse lemurs showed that females responded differently to calls from paternal kin and nonkin when the classification rate was 79% (mating calls), but not when it was 45% (alarm calls) (Kessler et al., 2012). Though our current study focuses on only the agonistic calls, future work testing other call types for matrilineal signatures would be very valuable. It would contribute to an increasing body of literature which suggests that the strength of acoustic signatures and the corresponding responses from conspecifics varies greatly by call type (i.e., (Leliveld et al., 2011; Mitani et al., 1996; Rendall et al., 2009; Rendall et al., 1998; Rendall et al., 1996)). However, while playback studies like those above focus exclusively on acoustic cues, in the wild kin recognition is a multi-modal process and the relative strength of each of the cue types may vary depending upon the context in which selection is expected to occur. It is possible that weaker signatures might be present in calls typically used at short distances when visual and olfactory cues would also be available (Leliveld et al., 2011; Mitani et al., 1996). Given that agonistic calls are frequently given during close-range conflicts, and mouse lemurs have not been documented to recruit kin for alliances, it is possible that kin signatures in agonistic calls may not be under strong selection (though see (Eberle & Kappeler, 2008) for a case of nonkin recruitment).

As solitary foragers are thought to be the intermediary link between the solitary ancestral mammalian condition and the more complex, derived forms of gregarious primate sociality (Müller & Thalmann, 2000), our results suggest that ancestral solitary foragers may also have had moderate matrilineal signatures in their vocalizations. Such signatures, if used for kin recognition, may have been a crucial element of the dispersed social networks from which more complex, gregarious sociality is thought to have evolved in primates. However, if these signatures are not recognized, then it would lend support to an alternative theory of cryptic kin selection (Hatchwell, 2010) in which kin-based sociality is thought to have evolved from the spatial proximity of kin alone. As mouse lemur females (as well as females of many other species (Widdig, 2013)) are philopatric, they could interact preferentially with kin simply because kin are there, rather than because they discriminate kin and nonkin, and this could then be the foundation from which more complex forms of kin-based sociality evolved (Hatchwell, 2010). Future work is underway to test for the vocal recognition of matrilineal kin in this population and is expected to facilitate testing hypotheses about the possible influences of kin-biased behavior on the evolution of complex sociality (ie., (Shultz et al., 2011)).

The presence of both matrilineal and individual signatures in several species (i.e., the gray mouse lemur (Leliveld et al., 2011), bats (Gillam & Chaverri, 2012)) brings up the question of whether different pressures select for kin vs. individual signatures (Grafen, 1990; Rendall, 2004; Tang-Martinez, 2001). It could be that there is an optimal amount of divergence between individuals within a kin group which optimizes both types of signatures, thus enabling an individual to be categorized by kin group and be simultaneously individually distinctive within its kin group (Fripp et al., 2005; Tyack, 2008). Or, it is possible that one of the two levels of distinctiveness is more strongly targeted by selection and that the other is merely a side effect of inherited vocal tract morphology and social learning of call production (Rendall, 2004). For example, if individual distinctiveness is highly selected for, how distinctive an individual could be might be constrained by inherited vocal tract morphology and socially learned call production (Rendall, 2004). Alternatively, if kin group distinctiveness is highly selected for, within kin group similarity might be constrained by their individual genetics and individual learning experiences. To tease the two apart, future work should compare the acoustic distances between individuals within kin groups across species with different social systems. Future work should also examine whether females use these moderate signatures to discriminate familiar kin, unfamiliar kin, and familiar nonkin. If only familiar kin are recognized, then it would suggest that the recognition of kin occurs primarily through familiarity with individuals who happen to be kin (see (Sharp et al., 2005) for work on cooperatively breeding birds). Such future work, testing whether the lemurs actually recognize matrilineal kin will be highly important to determining the biological and evolutionary significance of these signatures.

Conclusions

We found moderate evidence for matrilineal signatures in mouse lemur agonistic calls. In addition, there was a tendency for acoustic distance between individuals to decrease as relatedness increased. We expect that both inherited morphological traits and social learning are proximate mechanisms for these signatures. Given that mouse lemurs are solitary foragers, they serve as models for the ancestral solitary foragers that are believed to have been the link between ancestral solitary mammals and derived, more complex forms of sociality in primates (Müller & Thalmann, 2000). Thus, our results suggest that the ancestral solitary foragers might have had similar, moderate, matrilineal signatures in their calls and we recommend further studies testing whether the lemurs use these calls recognize kin. Such studies would enable further modeling of how kin recognition in ancestral primates might have impacted the evolution of more complex forms of sociality in primates.

Methods

Field site and animal housing. This study was conducted at the Ankarafantsika National Park near the Ampijoroa forestry station (16°19’S, 46°48’E) in northwestern Madagascar during the dry seasons (May through November) of 2010 and 2011 in the designated research area of the park called Jardin Botanique A (JBA). Mouse lemurs were trapped in Sherman Live Traps baited with banana, marked with subcutaneously injected, individually distinctive transponders (ID-100, Trovan Small Animal Marking System, Telinject®, Römberg, Germany), and had small (1-2 mm^2) ear biopsies taken as genetic samples. Previous generations were already marked (for methodological details regarding trapping and sampling techniques see: (Radespiel et al., 2002; Radespiel, Sarikaya et al., 2001)). Tissue samples were stored in approximately 1 ml of Queen’s lysis buffer (Seutin, White, & Boag, 1991) for up to 7 months at ambient temperature in the field and then at 4ºC until extraction (up to 6 years for archived samples collected in prior years) (Radespiel, Sarikaya et al., 2001).

A subset of the trapped lemurs were temporarily kept in cages in the forest near the campsite to facilitate recording of vocalizations (total number trapped lemurs =107, total caged lemurs=45). No lactating females were kept in the cages. Animals were kept either singly in cages of 0.5 m by 0.5 m by 1 m (width x depth x height) or in small groups (two to four animals) in sets of two adjoining cages, each approximately 1 m wide by 1.2 m high by 0.5 m deep. Each set of cages had two passages (0.3 m x 0.2 m x 0.2 m) connecting them. Cardboard cans were provided as nest boxes (one for each lemur) and the cages were furnished with branches for climbing. The lemurs were fed fresh fruit and could be observed catching insects that flew into the cages. They were provided with additional insects as often as possible. Water was available *ad libitum*. These housing conditions are comparable to those in captive colonies (Wrogemann, Radespiel, & Zimmermann, 2001) and no lemurs were injured by the cages or by a cage-mate. Lemurs were released at their capture site after recording was completed (1 night – approximately 2 weeks, mean=5 nights). Methods were approved by Madagascar National Parks (2010 permits: N102/ 10/MEF/SG/DGF/DCB.SAP/SCBSE, N103/10/MEF/SG/DGF/DCB.SAP/SCBSE, 2011 permits: N101/11/MEF/SG/DGF/DCB.SAP/SCB, N102/11/MEF/SG/DGF/DCB.SAP/SCB) and the Arizona State University Institutional Animal Care and Use Committee (Protocol: 10-1077R).

Before release, 25 adult female gray mouse lemurs (2010: n=13, 2011: n=15, three collared in both years, adult = 50 g) were fitted with a radio-collar (either a PicoPip or a Pip3 collar from BioTrack Ltd., United Kingdom, weight 2.3-3.1 g). We then used radio-telemetry to locate the females' daytime sleeping sites using a TR-4 receiver (Telonics, Mesa, AZ, USA). We read the transponders of lemurs sleeping inside the nests with a handheld microchip reader (Trovan Small Animal Marking System, Telinject®, Römberg, Germany). We checked the sleeping sites on a total of 118 days (65 days in 2010, 53 days in 2011), which resulted in a range of 11-74 days of data per collared female (mean=29 days), depending on the lifespan of the radio-collar and survival of the female.

Recording methods and acoustic measurements. We recorded all calls given during controlled social encounters when two lemurs were introduced within the cages (or, occasionally during coincidental encounters when a free-ranging lemur outside the cage approached). The introductions inside the cages were observed and the elicited calls were considered to be agonistic when they were associated with aggressive/defensive behaviors such as fighting, chasing, fleeing, etc. When the lemurs were first introduced, the experimenter remained present during the entire night so that she could separate the lemurs if necessary. However, this was rarely necessary, and no lemurs were injured during the introductions.

We recorded the calls with a D1000X Bat Detector (flat frequency response: 5-235 kHz, sampling frequency 200 kHz, 16-bit resolution, Pettersson Elektronik, Upsala, Sweden) from a distance of approximately 2-4 meters from the inside of an observation tent. Under these conditions, agonistic calls were recorded from 15 female gray mouse lemurs. None of the lemurs were caged with female kin group members when the calls were recorded. For one additional female, calls were recorded at a distance of approximately 3 meters while she ate at a feeding platform in the forest after a conflict with another lemur.

Calls were measured in Signal 4.0 (Engineering Design) using the macro written by M. Scheumann for agonistic gray mouse lemur calls and used in earlier studies (Leliveld et al., 2011). Ten high quality calls were selected from each female. High quality calls were those that had a clearly visible fundamental frequency, low background noise, and no overlaps with other sound-producing organisms. As the calls are typically given in series, we selected 2-3 series per lemur. Each series consisted of 2-7 calls for a total of 10 calls for each of the 16 lemurs. Fig 1 (above) and Table 4 provide a description of the acoustic parameters that were measured or calculated.

Table 4.

Measured and Calculated Acoustic Parameters.

Measured Parameters	Definition	Source
*F_0S (KHz)	Freq. of F_0 with highest amplitude at start	Osc. & PS
*F_0Peak (KHz)	Freq of F_0 with highest amplitude at max of F_0	Spect. & PS
*F_0E (KHz)	Freq. of F_0 with highest amplitude at end	Spect. & PS
SB_Max	Frequency at 20dB above F_0S	PS
SB_Min	Frequency at 20 dB below F_0S	PS
S (ms)	Start time of call	Osc.
P (ms)	Time of highest point of F_0	Spect.
E (ms)	End time of call	Spect.
N (ms)	Start time of next call	Osc.
Calculated Parameters	**Definition**	**Calculation**
*Start Bandwidth (KHz)	Bandwidth of F_0 at start	SB_Max – SB_Min
*Call Duration (ms)	Time between start and end of call	E – S
*Time to Peak (ms)	Time between start and peak of call	P – S
*Inter-call Interval (ms)	Time between end of the call and start of the next call	N – E

Note: Osc. = Oscillogram, PS = Power spectrum, and Spect. = Spectrogram. *parameters included in the principal component analysis. For more information see Fig. 1 and (Leliveld et al., 2011).

Genetic analyses. Genetic analyses were conducted at the University of Veterinary Medicine Hannover in the Institute of Zoology. Extractions were performed with a proteinase K digestion and a phenol / chloroform extraction. Eight microsatellite loci were successfully amplified using one of three methods: 1) We used a Qiagen Multiplex PCR Kit (Qiagen, Hilden, Germany) following the manufacturer's instructions, but reduced to the final reaction volume to 10 µl. Ratios followed the instructions with the exception that only 1 µl of Q Solution was used. Cycling conditions followed the provided protocol with annealing temperatures of 48-58ºC and up to 48 cycles. 2) We used a MyTaq DNA Polymerase kit (Bioline GmbH, Luckenwalde, Germany) following the manufacturer's instructions and concentrations, but reducing the reaction volume to 10 µl and using 0.15 µM of each primer and 0.05 µl MyTaq. 3) We performed PCR reactions with final concentrations of 1.5-2.0 mM $MgCl_2$ Solution (Invitek , Berlin, German), 1 x NH_4-reaction buffer (50 mM Tris-HCL (pH8.8), 16mM $(NH_4)_2SO_4$, 0.1% Tween ©20, Invitek, Berlin, Germany) or 1 x PARR buffer (Cambio, Cambridge, UK), 225 µM of each dNTP (Fermentas Life Sciences), 0.15-0.5 µM of each primer, and 0.025 U of *Taq* DNA Polymerase. Cycling conditions for this procedure and the MyTaq kit consisted of an initial denaturation phase of 2-4 min at 92-94ºC, denaturing for 20-60s at 92-94ºC, annealing for 20-60s at 48-58ºC, extension for 30-90s at 72ºC, and a final extension phase of 5-7min at 72ºC. We used up to 48 cycles. For one marker, M3, the cycling conditions were as follows: initial denaturing at 94ºC for 4min, denaturing at 94ºC for 30s, annealing at 55ºC for 20s, extension at 72ºC for 30s (6-7 cycles), denaturing at 94ºC for 30s, annealing at 53ºC for 20s, extension at 72ºC for 30s (6-7 cycles), denaturing at 94ºC for 30s, annealing at 50ºC for 20s, extension at 72ºC for 30s (25-30 cycles), and a final extension phase at 72ºC for 7min.

The length of the resulting PCR products were determined on an Applied Biosystems 3500 capillary sequencing machine (Applied Biosystems, Life Technologies, GmbH, Darmstadt, Germany). Alleles were scored in Genemapper 4.1 (Applied Biosystems, Life Technologies, GmbH, Darmstadt, Germany) and checked by eye. All homozygous samples were amplified at least twice, following the procedures in prior studies (i.e., (Radespiel, Juric, & Zimmermann, 2009; Radespiel, Sarikaya et al., 2001)).

The mitochondrial D-loop was sequenced using the universal mammalian control region primers H16498 and L15997 (Guschanski, Olivieri, Funk, & Radespiel, 2007) for all captured females. PCR was conducted in a 25 µl reaction volume with the following concentrations: 3 mM $MgCl_2$, 1 x NH_4-reaction buffer (50 mM Tris-HCL (pH8.8), 16mM $(NH_4)_2SO_4$, 0.1% Tween ©20, Invitek, Berlin, Germany), 400 µM of each dNTP (Fermentas Life Sciences), 0.8 µM of each primer, 0.125 U of *Taq* DNA Polymerase. We used an initial denaturation phase of 3 min at 94ºC, a denaturing phase of 1 min at 94ºC, an annealing phase of 1 min at 50ºC, an extension phase of 1 min at 72ºC (35-50 cycles), and a final extension phase of 5 min at 72ºC. For samples that did not amplify well and were weak when visualized on a 1.5% agarose gel (containing 1.3×10^{-4} mg/ml ethidium bromide), we used the MyTaq DNA Polymerase kit (Bioline GmbH, Luckenwalde, Germany). We followed the manufacturer's instructions and concentrations, but reduced the reaction volume to 25 µl and used 1 µl of each primer (10 pM/µl) and 0.1 µl MyTaq. Cycling conditions were the same as above. PCR products were then cleaned using the MSB Spin PCRapace kit (Stratec Molecular GmbH, Berlin, Germany). Sequencing followed one of two procedures. We either mailed the samples to Macrogen Ltd. (http://dna.macrogen.com) where they were sequenced using an ABI 3730XL automatic DNA sequencer or we performed the sequencing reactions ourselves using the ABI Prism BigDye Terminator v. 3.1 Cycle Sequencing Kit (Applied Biosystems, Life Technologies, GmbH, Darmstadt, Germany). We used 10 µl reactions consisting of 6.5 µl cleaned PCR product, 1 µl ABI Prism BigDye Terminator Ready Reaction Mix, 2 µl 5x Sequencing Buffer, and 0.5 µl primer (10 mM) and performed 25 cycles of 96ºC for 10s, 57ºC for 5s, and 60ºC for 3 min. After a final cleaning step with an ethanol precipitation, subsequent sequencing was performed on an Applied Biosystems 3500 capillary sequencer.

Sequences of 446-563 bp (mean=531.6) were edited, analyzed and aligned in SeqMan 7.0 (DNASTAR Inc., Madison, WI, USA). The final alignment and a matrix of the number of pairwise differences was calculated in Mega 5 (Tamura et al., 2011), and a haplotype network was produced in Network 4.6.1.1 (Fluxus Technology Ltd., Suffolk, UK).

Sequences have been deposited in GenBank (Accession numbers: KJ183142-KJ183177).

Relatedness calculations. Of the eight microsatellite markers, one (M21) was not in Hardy-Weinberg equilibrium and displayed a significant deficit in heterozygotes (F_{is}=0.155, P=0.0003, calculated in Fstat 2.9.3.2 (Goudet, 1995)). Because this could influence the relatedness calculations, this marker was dropped from the analysis. The remaining markers and the calculations over all loci were in Hardy-Weinberg equilibrium (Table 5) and were therefore included in the relatedness calculations.

Table 5.

Characteristics of the Microsatellite Markers.

Marker	N	Alleles	H_e	H_o	F_{is}	P	Citation
M2	107	9	0.74	0.69	0.062	0.1401	(Radespiel, Funk, Zimmermann, & Bruford, 2001)
M3	107	15	0.81	0.84	-0.041	0.8827	(Radespiel, Funk et al., 2001)
M9	106.5	16	0.90	0.89	0.010	0.4226	(Radespiel, Funk et al., 2001)
M10	105	24	0.93	0.90	0.041	0.0839	(Radespiel, Funk et al., 2001)
M21	105	11	0.83	0.70	0.155	0.0003*	(Hapke, Eberle, & Zischler, 2003)
M22	107	11	0.84	0.80	0.047	0.1429	(Hapke et al., 2003)
M39	107	25	0.94	0.94	-0.004	0.6133	(Hapke et al., 2003)
PVCA1	107	13	0.86	0.88	-0.018	0.7316	(Wimmer, Tautz, & Kappeler, 2002)
Overall	**106.6**	**16.1**	**0.86**	**0.85**	**0.013**	**0.1490**	**-----**

Note: N shows the number of individuals typed at each locus. “Alles” is the number of alleles observed at each locus. H_e is expected heterozygosity. H_o is observed heterozygosity. F_{is} is the heterozygote deficit within the population. The P value of the heterozygote deficit. Significant p-values are Bonferroni corrected to be <0.00714. “Overall” shows the calculations performed across the seven loci retained in the analysis (excluding M21). The citations indicate where the primer sequences are published. The decimal N indicates individuals where only one of two alleles could be determined at that locus.

While we acknowledge that increasing the number of markers improves the resolution of the kinship relationships (Harrison, Saenz-Agudelo, Planes, Jones, & Berumen, 2013), using 7 microsatellites is within the range used in similar studies on mouse lemurs (7 microsatellites: (Radespiel, Sarikaya et al., 2001), 6 microsatellites: (Radespiel et al., 2009; Wimmer et al., 2002)). In addition, we maximized the genetic information obtained from these microsatellites we used by selecting markers that are highly polymorphic (9-25 alleles, see Table 5) (Harrison et al., 2013).

We calculated pairwise relatedness in Kinship 1.3.1 (Goodnight & Queller, 1999) according to Queller and Goodnight’s estimate of relatedness (Queller & Goodnight,

1989) based on the genotypes of 107 individuals (72 males, 35 females) that were captured during the study period. We chose this relatedness estimator for two reasons. First, it has been shown to perform well on samples with a high percentage of highly related pairs (Csilléry et al., 2006), which we expected to have, given that we were focusing on co-sleeping females. (Prior research has shown that co-sleeping females are typically closely related (Radespiel, Sarikaya et al., 2001), and indeed, in this study, all co-sleeping dyads were closely related). Second, it will allow for comparisons with previous studies on mouse lemur relatedness using this estimator (i.e., (Radespiel, Sarikaya et al., 2001; Rode et al., 2013)). Using Kinship we used a simulation procedure which uses the allele frequencies within the population to test the likelihood that the r-value between each dyad was produced by a relationship of $r_{maternal}$=0.5 and $r_{paternal}$=0 against a null hypothesis of $r_{maternal}$=0 and $r_{paternal}$=0. This was performed for all possible dyads among the 107 individuals. By doing so, we distinguished between dyads with a close matrilineal relatedness and dyads that were matrilineally unrelated. This procedure is based upon prior work showing that though pairwise relatedness may not be precise enough to distinguish small differences in relatedness (e.g., full- and half-siblings), unrelated dyads can be accurately distinguished from closely related dyads and vice versa (Van Horn, Altmann, & Alberts, 2008). Closely related dyads are rarely misclassified as unrelated and unrelated dyads are rarely misclassified as closely related (Van Horn et al., 2008, page 1177, Table 1). Kinship's pairwise relatedness values have been shown to correlate with known pedigree relationships (Van Horn et al., 2008), and negatively with allelic exclusions in this population (Radespiel, Sarikaya et al., 2001).

Distinguishing $r_{maternal}$=0.5 and $r_{paternal}$=0 from $r_{maternal}$=0.0 and $r_{paternal}$=0.5 was possible because we integrated the pairwise relatedness data with the mitochondrial haplotype data and co-sleeping data (discussed in greater detail below). The mitochondrial data enabled us to exclude closely related pairs with no matrilineal relationship. While we acknowledge that it could be possible for closely related paternal relatives to have the same mitochondrial haplotype, it is very unlikely that such dyads would also co-sleep as prior research on this population (Radespiel, Sarikaya et al., 2001) and others (Eberle & Kappeler, 2006) showed that sleeping groups consist of close matrilineal, not patrilineal, relatives.

The probability of identity between two individuals in the population was $<1^{-6}$ (Botstein, White, Skolnick, & Davis, 1980), calculated in PopAssign 3.9e (written by S.M. Funk). The probabilities of exclusion (Jamieson & Taylor, 1997), calculated in PopAssign 3.9e, were 0.999941 for one parent, 1.000000 for the second parent, and 0.998505 in the case of a missing parent. Alpha was set at 0.05 for all statistical tests in this study unless otherwise specified.

Marker characteristics are shown in Table 5 (above). Expected and observed heterozygosity (H_e and H_o) for each locus and over all loci were calculated in PopAssign 3.9e. The observed F_{is} for each locus and over all loci and the associated P values testing for a deficit in heterozygotes were calculated in Fstat 2.9.3.2 (Goudet, 1995). The statistical error p was calculated by randomizing alleles among individuals over 7000 randomizations. P values are the proportion of randomizations that gave a larger F_{is} than the observed. The Bonferroni corrected alpha was set at <0.00714.

Kin group selection. In order to minimize the confounding effects of paternal relatedness when testing for matrilineal signatures, we selected dyads of females within kin groups that had high pairwise relatedness and strong genetic and behavioral evidence of matrilineal relationships. While we realize that the inclusion of full sister dyads (and therefore some cases of paternal relatedness) cannot be excluded with certainty, we assume that due to the promiscuous mating system, possible multiple paternities within litters, and the high turn-over rate of mouse lemurs across field seasons (Eberle & Kappeler, 2004a, 2004b; Radespiel et al., 2002), most of our dyads are likely to consist of mother-daughter pairs or half sisters. This would mean that on average, barring severe inbreeding, matrilineal relatedness should be much higher than patrilineal relatedness within the dyads. We grouped the dyads into matrilineal kin groups based upon three criteria. Within a kin group: 1) females had the same mitochondrial haplotype, 2) behavioral evidence showed that they co-sleep, and 3) females had a Queller and Goodnight relatedness value (Queller & Goodnight, 1989) that is significantly likely to result from a maternal relatedness of 0.5 with *all* other individuals in the group. In three out of six groups all dyads met all three criteria for kin groups. Within the remaining three groups (groups 1, 5, and 6) not all of the criteria were fulfilled for all dyads (Table 3). Within group 1, female 06-09 was not observed to share a sleeping site with the other females in her group. However, because she shared her mitochondrial haplotype with one of the other females in the group (the third could not be determined), and was closely related to both of the other two females ($r=0.61$, $P<0.001$ and $r=0.29$, $P<0.01$), 06-09 is included in the kin group. The mitochondrial haplotype of a second female (19-10) from kin group 1 was unknown, but she shared a nest and had an r-value likely to result from a maternal relatedness of 0.5 (r=0.44, P<0.001) with one of the other females in her group. As sleeping groups in this population have been shown to typically consist of close matrilineal relatives (Radespiel, Sarikaya et al., 2001), 19-10 is also included in this matrilineal kin group. Within group 5, the two females were not observed to co-sleep, but they fulfilled the other two criteria, including having a significant r value (r = 0.36, P<0.001) and thus are still considered a kin group. Within sleeping group 6, co-sleeping data is unavailable for two dyads. However, 17-10 co-slept with 28-09 in 2010 and with 36-11 and 46-11 in 2011. It is unknown whether 28-09 lived long enough to have the opportunity to share a sleeping site with 36-11 and 46-11 because she was not recaptured in 2011. In total, we divided the 16 females into 6 kin groups: one group of four females, two groups of three females, and three groups of two females (Table 3).

Test of kin group signatures. In order to test whether agonistic calls are distinctive by kin group, we conducted a discriminant function analysis. We performed a principal component analysis with no rotation on the correlation matrix conducted in SPSS 21 to reduce the dimensionality of the dataset. Then, because we have a nested design (individuals are nested within kin groups), we conducted a permutated linear discriminant function analysis (pDFA) in R 2.14.0 (The R Foundation for Statistical Computing, 2011) with kin group as the test factor and individual as the control factor (Mundry & Sommer, 2007) and 10,000 permutations. As the maximum number of input parameters is one less than the number of objects in the smallest class (two individuals in some of the kin groups), we could only include one principal component in the analysis (Mundry & Sommer, 2007). We included the first principal component because it accounted for the greatest amount of variation in the original dataset relative to the other components. Cross-validation was performed using the leave-one-out method (Mundry, R., personal communication). Because the pDFA does not produce a classification table, we present the table produced by a nonpermutated discriminant function analysis conducted in SPSS 21.

Correlation between acoustic distance and genetic distance. We used the first principal component to calculate an acoustic distance for all dyads. First we calculated a mean value for each individual for PCA1. We then calculated the Euclidean distances between each pair of individuals producing a matrix of acoustic distances between the individuals. We conducted a Mantel test in Mantel 2.0 (Liedloff, 1999) using 1000 permutations to test for a correlation between acoustic distance and genetic relatedness.

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CHAPTER 3

KIN RECOGNITION AND THE EVOLUTION OF COALITIONARY BEHAVIOR

Abstract

Frequent kin-biased coalitionary behavior is a hallmark of mammalian social complexity. Furthermore, selection to understand complex social dynamics is believed to underlie the co-evolution of social complexity and large brains. Vocalizations have been shown to be an important communication channel with which large-brained monkeys living in complex social groups recognize the agonistic calls of their kin and are recruited to give coalitionary support. We test whether such vocal kin recognition also occurs in a less socially complex species, the small-brained, solitary foraging mouse lemur (*Microcebus murinus*). As mouse lemurs are frequent models for ancestral solitary foraging primates, this study models whether kin recognition using agonistic calls in a solitary foraging species might have been an important element from which more complex, kin-based coalitionary behavior may have evolved in primates. We test whether wild mouse lemurs in Ankarafantsika National Park, Madagascar react differently to agonistic calls from kin and nonkin and to calls from familiar and unfamiliar individuals. Subjects did not distinguish between any of these call categories. Results suggest that this solitary foraging species does not use agonistic calls to recognize kin and monitor agonistic interactions involving kin unlike several species of Old World monkeys. While kin discrimination did not occur via the agonistic calls, future work testing other call types and additional sensory modalities (i.e., olfaction) is urgently needed.

Introduction

Frequent kin-biased coalitionary behavior kin is a hallmark of mammalian social complexity (Chapais, 1995; de Waal & Tyack, 2003; Dunbar, 1998, 2003; Silk, 2007b). The selective pressure to monitor the multiple, complex dyadic relationships occurring in social groups is argued to underlie the co-evolution of social complexity and large brains (Chapais, 1995; de Waal & Tyack, 2003; Dunbar, 1998, 2003; Silk, 2007b). Among the most difficult to monitor are likely to be coalitionary behaviors in which the interactions between one dyad have implications for a third individual (i.e., third party interventions, coalitionary aggression (sensu (Gompper, Gittleman, & Wayne, 1997)) (Dunbar, 1998). These agonistic interactions may be costly in terms of injuries sustained or by a decrease in inclusive fitness (sensu: (Hamilton, 1964)) when harm to kin is not prevented ((i.e., lethal aggression: (Gilby et al., 2013; Gros-Louis, Perry, & Manson, 2003; Talebi, Belatrão-Mendes, & Lee, 2009)). Furthermore, agonistic interactions are fast-paced and may occur out of sight due to dense foliage, distance, or darkness, making monitoring them all the more difficult. Thus, kin selection (Hamilton, 1964) should select for agonistic signals which will effectively recruit aid from kin under these circumstances.

Among mammals, matrilineal kin are expected to be more widely recognized due to the obligate relationship between infants and their mother during nursing (Rendall, 2004) and are thus more probable coalition partners than paternal kin. This extended period of infant care provided by mammalian mothers ensures the opportunity for mothers, current offspring, and often siblings to become highly familiar with each other, and thus facilitates kin recognition via the proximate mechanism of familiarity (Rendall, 2004). Vocalizations are a likely medium for the recruitment of kin for two reasons. First, they have the advantage that they may convey information to conspecifics that are out of sight and second, they are a widely used cue for matrilinear kin recognition among both large and small brained mammals (i.e., primates (Cheney & Seyfarth, 1980; Nunn, 2000; Rendall, 2004; Rendall et al., 2009; Rendall et al., 1996; Seyfarth & Cheney, 2003), hyenas (Holekamp et al., 1999), elephants (McComb et al., 2000; McComb et al., 2003), pinnipeds (Insley et al., 2003), goats (Briefer & McElligott, 2011; Briefer et al., 2012), bats (Balcombe, 1990; Knoernschild & Von Helversen, 2008)).

This widespread recognition of maternal kin via vocalizations suggests that, if agonistic calls can also be used for kin recognition, they might also be sufficient to recruit kin. And, indeed, multiple studies of large-brained, socially complex mammals known to engage in high rates of coalitionary behavior with maternal kin (Chapais, 1995; Silk, 2002, 2007b; Silk et al., 2004) show that such species recognize the agonistic calls of their kin and, for some, the kin relationships among conspecific dyads as well (i.e., (Cheney & Seyfarth, 1980, 1999; Fugate et al., 2008; Wittig, Crockford, Seyfarth, & Cheney, 2007)). Baboon females react more strongly to threat grunts from kin of a previous conflict partner than to kin of a female with whom they just interacted peacefully (Wittig et al., 2007). And after hearing calls mimicking an agonistic encounter between female kin and nonkin group-mates, a female listener is more likely to behave aggressively to the kin of the female that was in conflict with her kin (Cheney & Seyfarth, 1999). Vervet and spotted hyena mothers respond more strongly to distress screams of their own infants than did control mothers (Cheney & Seyfarth, 1980; Holekamp et al., 1999). Control vervet mothers looked at the mother of the infant that screamed after the playback, though control hyena mothers did not (Cheney & Seyfarth, 1980; Holekamp et al., 1999). In addition, similar studies have shown that macaques also recognize kin via agonistic vocalizations ((Fischer, 2004; Fugate et al., 2008), but see (Rendall et al., 1998; Rendall et al., 1996)). While identical studies have not been done in chimpanzees, agonistic screams are individually distinctive (Kojima et al., 2003) and chimpanzees monitor social interactions, reacting more strongly to vocalizations sequences that violated established dominance hierarchies than to those that were consistent with established hierarchies (Slocombe, Kaller, Call, & Zuberbuhler, 2010). While kin recognition via agonistic calls in chimpanzees has not been tested, it seems likely that they may be capable of discerning kinship and using that information when deciding whether to intervene on the behalf of kin.

However, all of these species known to use agonistic vocalizations for kin recognition have large-brains and live in complex social systems (see citations above). Far less is known about small-brained or solitary species. Coalitionary behavior benefitting kin has been observed in smaller brained, social species (lemurs: (Nakamichi, Rakototiana, & Koyama, 1997; Pereira & Kappeler, 1997; Roeder, Duval, & Gosset, 2002), coatis: (Gompper et al., 1997), but see (Russell, 1983)), but the role of vocalizations was not investigated. For solitary species, there are far fewer opportunities for coalitionary behavior, however, it has still been observed (Hauver, Hirsch, Prange, Dubach, & Gehrt, 2013). The socially flexible, though generally solitary, raccoon has been observed to engage in the occasional coalitionary defense of food resources, though this behavior did not appear to be driven by kin relations (Hauver et al., 2013). These authors do not provide information as to whether coalitionary support was recruited in any way (Hauver et al., 2013). (For the purposes of this paper, we are following the definition of coalitions used by (Gompper et al., 1997) which restricts coalitions to short-term interactions, thus excluding the relatively long-term male-male associations in some otherwise solitary species (mongooses: (Schneider & Kappeler, 2014; Waser, Keane, Creel, Elliott, & Minchella, 1994), hyenas: (Wagner, Creel, Frank, & Kalinowski, 2007; Wagner, Frank, & Creel, 2008), cheetahs: (Caro & Collins, 1987; Dalton, Charruau, Boast, & Kotze, 2013; Marker et al., 2008)). More detailed behavioral data are needed to determine whether these male-male associations may also engage in kin-biased coalitionary agonistic interactions and use vocalizations for kin recruitment.) To our knowledge, no study has tested whether a non-group living mammal can recognize maternal kin via agonistic calls.

Because kin recognition via agonistic calls would be a highly important catalyst for kin-biased coalitionary behavior, we aim to investigate the evolution of this trait in an order which is well known for kin-based coalitions: primates (i.e., (Chapais, 1995; Perry et al., 2008; Silk, 2007b; Silk et al., 2004)). We focus on the small-brained, solitary foraging gray mouse lemur (*Microcebus murinus*) (Müller & Thalmann, 2000). Mouse lemurs forage alone at night, but maintain a dispersed social network, communicating with conspecifics via scent-marks and vocalizations (Müller & Thalmann, 2000; Nash, 2004). This solitary foraging pattern is believed to be ancestral to primates and the social networks are thought to have been the foundation from which more complex forms of sociality evolved in primates (Müller & Thalmann, 2000). Therefore, if kin recognition via agonistic calls is found in this species, it could model how this trait may have facilitated the evolution of the kin-biased coalitionary behavior frequently seen in many primates today.

Mouse lemurs make useful models for ancestral primates because, like the hypothesized last common ancestor of primates, they are small-bodied, nocturnal, solitary foragers that forage for fruit, insects, and gums in a fine branch niche (Cartmill, 1974; Müller & Thalmann, 2000; Radespiel, 2000; Rasmussen, 1990; Rendigs, Radespiel, Wrogemann, & Zimmermann, 2003; Sussman, 1991; Sussman & Raven, 1978; Thoren et al., 2011). Their social system is strongly structured by kin relationships (Eberle & Kappeler, 2006; Radespiel, Sarikaya et al., 2001). Males sleep alone and disperse whereas females are philopatric and remain near their natal range (Eberle & Kappeler, 2006; Radespiel et al., 1998; Radespiel et al., 2003; Radespiel, Sarikaya et al., 2001; Schliehe-Diecks et al., 2012; Wimmer et al., 2002). This produces a spatially structured population with predominantly male-mediated gene flow and clusters of highly related females (Fredsted, Pertoldi, Olesen, Eberle, & Kappeler, 2004; Fredsted, Pertoldi, Schierup, & Kappeler, 2005; Radespiel et al., 2003; Wimmer et al., 2002). This has been suggested to facilitate increased cooperation and sociality among the females including matrilineal sleeping groups of female kin where the females breed cooperatively and co-nurse each other's young (Eberle & Kappeler, 2006; Lutermann et al., 2006; Radespiel, Sarikaya et al., 2001; Wimmer et al., 2002).

Mouse lemurs are highly vocal using vocalizations in a variety of contexts (i.e., mating (Braune et al., 2008; Buesching et al., 1998), agonism (aggression/defense) (Leliveld et al., 2011), disturbance situations (Leliveld et al., 2011), mother-infant contexts (Scheumann et al., 2007), and in connection with varying emotional states (Altenmüller et al., 2013; Zimmermann, 2009)). Thus, their sleeping groups provide ample opportunity to become familiar with the calls of matrilineal kin. And indeed, immature gray mouse lemurs have been shown to give highly variable infant calls which then stabilize into their adult forms around the time of weaning (Zimmermann, 1991), suggesting that both social learning and physical maturation (of potentially heritable morphology) are likely to play a role in this process. In this study we focus on agonistic *tsäk* calls, which have been shown to be individually distinctive (62% correct classification by individual (Leliveld et al., 2011)) and contain some signatures of matrilineal kin group (47% correct classification by matriline, (Kessler et al., 2014), Chapter 2). The agonistic call is one of the most frequently heard calls (Leliveld et al., 2011). It is a harmonic, frequency modulated call with harmonics in the audible and ultrasonic ranges (Leliveld et al., 2011). It is given at a relatively high amplitude during agonistic encounters and thus should be audible to surrounding conspecifics (Leliveld et al., 2011). Therefore, if this call were to facilitate kin recognition, it could function to recruit aid from kin during agonistic interactions.

In order to test for kin recognition via agonistic vocalizations in gray mouse lemurs, we performed playback experiments on wild mouse lemurs at feeding platforms in Ankarafantsika National Park, Madagascar. Subjects heard calls from matrilineal kin, a neighbor, a cage-mate (from temporary captivity during recording), and a stranger. We hypothesized that subjects would recognize their kin based on the proximate mechanism of familiarity. Thus we expected subjects to react differently to the calls according to the continuum of familiarity: kin (very familiar), neighbors and cages-mates (less familiar), and strangers (unfamiliar). Subjects showed no differences in reactions to the different stimuli, thus they did not react differently based upon kinship or familiarity. We discuss our results in terms of their significance for the evolution of coalitionary behavior and social complexity and for future avenues of research.

Results

Genetic relatedness. Median pairwise relatedness for all dyads in the population is r=-0.02 (n=107 individuals, min= -0.38, max=0.91). Median pairwise relatedness within kin dyads was r=0.44 (n=19 dyads, min=0.17, max=0.62), whereas median relatedness was r=0.01 between neighbor dyads (n=7 dyads, min=-0.05, max=0.11), r=-0.02 between cage-mate dyads (n=11 dyads, min=-0.12, max=0.16), and r=-0.04 between stranger dyads (n=20 dyads, min=-0.28, max=0.19) (Appendix C). We found seven mitochondrial haplotypes in the females of this population ((Kessler et al., 2014)). Females included in this study belonged to H1, H3, H4, H5, H6, and H7 (Appendix C). See Chapter 2 (Kessler et al., 2014) for a haplotype network.

Differences in reactions to kin, cage-mates, neighbors, and strangers. Though some of the pairwise tests (Mann Whitney U and Wilcoxon Matched Pairs Tests) found significant differences across call types, none were significant after a Bonferroni correction (Appendix D). No significant dyad effects were found by the linear mixed models for any of the behavioral variables or the reaction index at any of the time intervals even before a Bonferroni correction (3, 5.5 or 11.96s, Appendix E and Appendix F). Figure 5 shows that *feed, latency stop feed, vigilant* and *latency vigilant* were very similar after hearing the different types of calls.

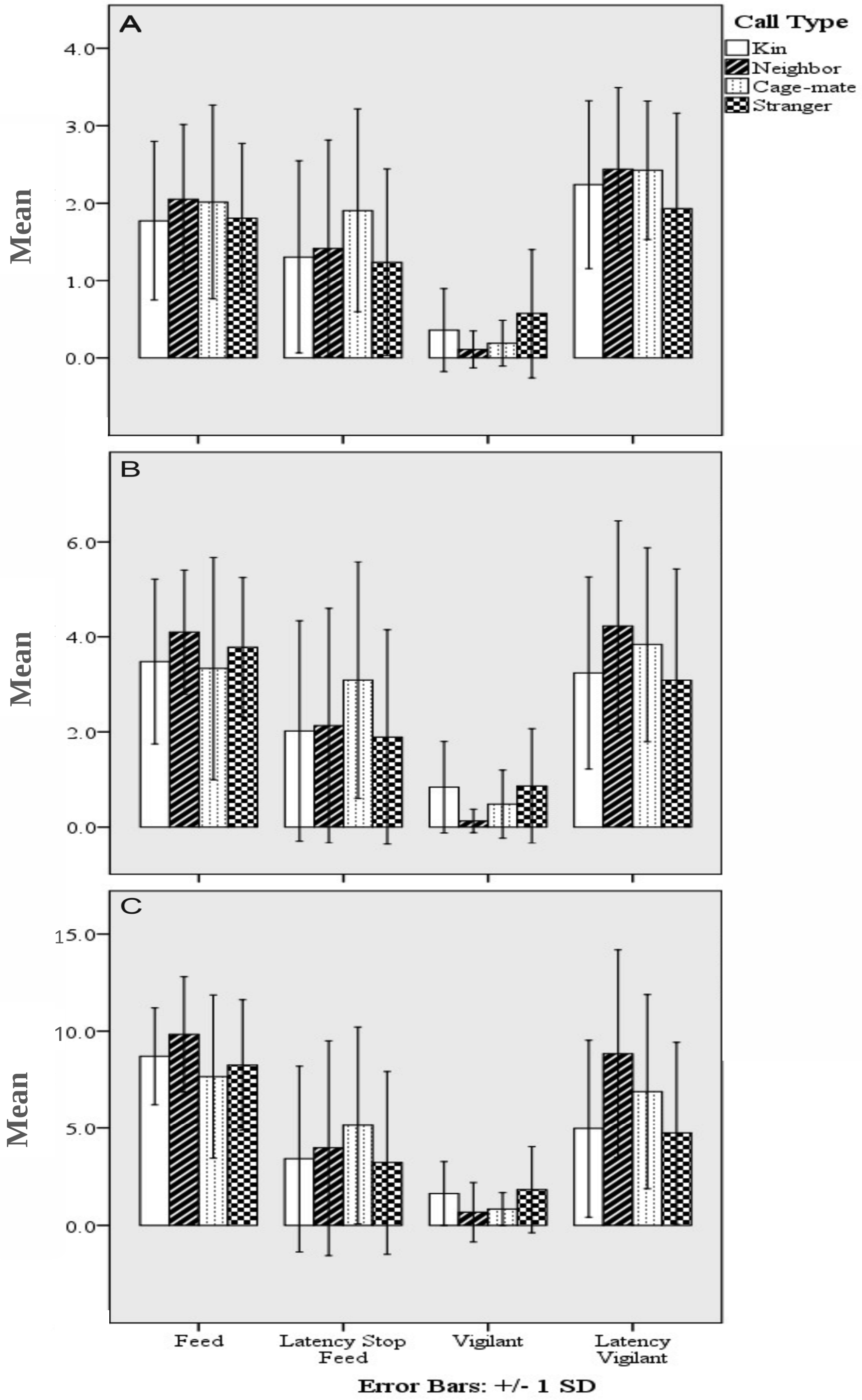

Figure 5. Graphs of *feed*, *latency stop feed*, *vigilant*, and *latency vigilant* at 3 (a), 5.5 (b), and 11.96 (c) seconds after the onset of the playback. The Y-axis is time (s). No significant differences were found between the call types at any of the three time points (Appendix C and Appendix E).

Figure 6 shows that the differences in *look*, *latency to look*, and *PCA Look*, the variables expected to be the most sensitive, were very small across call types and that the standard deviations were very large.

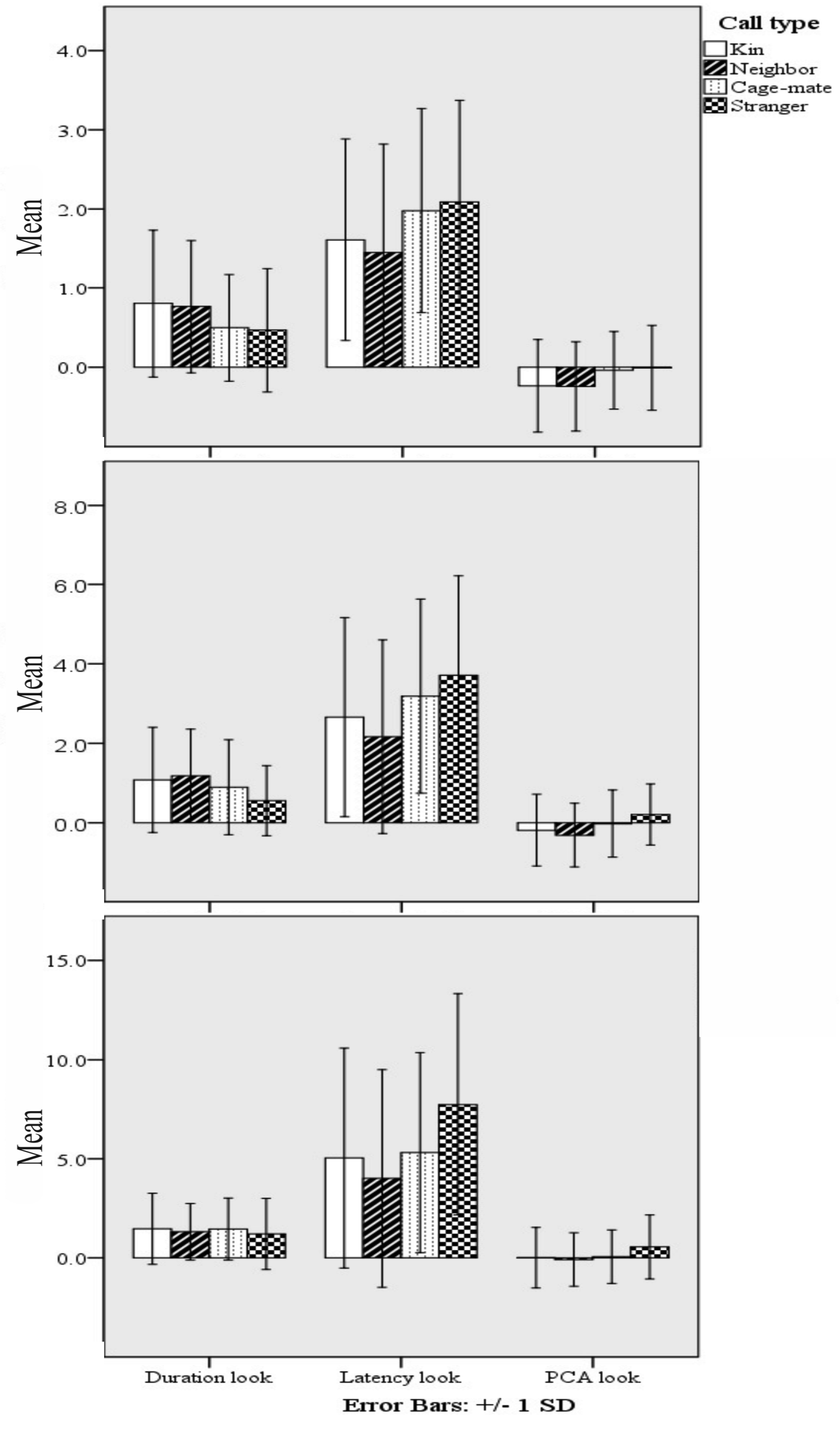

Figure 6. Graphs of *look, latency look*, and *PCA look* at 3 (a), 5.5 (b), and 11.96 (c) seconds after the onset of the playback. For *look* and *latency look* the Y-axis is time (s), for *PCA look*, the Y-axis is the component score. No significant differences were found between the call types at any of the three time points (Appendix C and Appendix E).

Results from the linear mixed models are shown in Appendix E, and Appendix G provides descriptive statistics including the means and standard deviations for each variable at the three time intervals.

Overall, *PCA Look* explained 75.8% of the variation in the original behavioral variables of *look* and *latency look* and was highly correlated with both (loading = -0.871 and 0.871, respectively). However, *PCA Look* did not show significant differences between call types even before a Bonferroni correction (Appendix E and Appendix F). Appendix G shows the means, standard deviations and other descriptive statistics for *PCA look* across the different call types.

When an interaction term is included there were no significant effects for call type or call type*order for any of the linear mixed models (Appendix H).

Order effects. Order effects appeared to be stronger than the effects of call type, with *latency stop feed* and *reaction index* at 3, 5.5, and 11.96 s and *latency look* and *PCA look* at 11.96 s having significant order effects after a Bonferroni correction (Appendix E and Appendix F). When order effects were present before or after a Bonferroni correction, they suggested that subjects habituated overtime. *Feed* increased, *look* decreased, *latency look* increased, *latency stop feed* increased, *reaction index* decreased (smaller values indicate a weaker reaction), and *PCA Look* increased (indicated longer *latency look* and shorter *look*).

Discussion

Power and habituation effects. Our results showed that female gray mouse lemurs did not react significantly differently to the stimuli based on kinship or familiarity.

Though some variables did find weak trends for effects of call type, we do not expect the lack of statistical significance to be driven by a lack of power for three reasons. 1) When we ran the linear mixed model comparing only the kin and stranger dyads (N=19 and 20, respectively) we did not find a significant effect of call type even though these were the groups we expected to evoke the strongest differences in reactions and they were the groups with the largest sample sizes (results not shown). 2) In addition, we expect our sample size to be a biologically relevant sample size. We tested a total of 57 dyads, for which 16 individual females were listeners to at least one of four types of stimuli. This is a sizeable percentage of the total number of females in the JBA population. During our two field seasons we caught a total of 37 female gray mouse lemurs (23 in 2010, 20 in 2011) in the JBA research grid. Thus our sample size of 16 individual female listeners is 43% of the total number of females trapped during the study period and 70% and 80% of the total number of females found in JBA during 2010 and 2011, respectively. While it is possible that a few females in the grid were not trapped, we followed a well established routine of intensive trapping that has been used successfully for the long-term study of this population (i.e., (Radespiel et al., 2003; Radespiel, Sarikaya et al., 2001)). Thus, we expect to have detected and tested many of the available females in the population. In order to obtain a larger sample size within JBA, it would be necessary to do this study over more than two years, to establish multiple teams of researchers that could run several platforms simultaneously during one field season thus testing closer to 100% of the females per season, or to increase the study area (not permitted by the park service). 3) Furthermore, we expect that our within-subjects design of four different call types is a realistic test of the cognitive challenges facing female mouse lemurs. Female mouse lemurs, relative to other mammals (i.e., colony-living bats (Balcombe, 1990; McCracken & Gustin, 1991)), do not have an extremely large number of same-sex interaction partners. Because females have home-ranges of 1-3 hectares, they are unlikely to interact with all, or even most, of the other females on the 30 hectare research grid. In a previous study on this population, 12 females over two years were radio-collared and it was found that females had range-overlaps with an average of 1.5 other females (Radespiel, 2000). While this number is clearly limited by the number of collared animals, it does suggest that females generally interact with a small subset of the population. Therefore, we expect that the cognitive demands for distinguishing between four different call types (*kin, neighbors,* etc.) should not have been too difficult and it should have been representative of the number and type of female interaction partners available to the subjects in the wild. Thus, if recognition had occurred, we believe our experimental set-up should have been sensitive enough to detect it.

Though habituation effects (order effects) appeared to be stronger than kinship or familiarity effects (call type), we do not believe that this is driving our negative result for three reasons. 1) Variables that showed no order effects in the LMMs, also did not show effects of call type (Appendix E). 2) Running the LMM models with an interaction term for order*call type did not show significant interaction between the two variables (Appendix H). This indicates that subjects did not habituate faster to some call types than others (which would have indicated that they reacted differently to the different call types). 2) By entering order as a covariate, the LMM calculated what the effects of call type were after the order effects were separated out (Field, 2009). Therefore, this test would have been able to detect an effect of call type if it was significant after order effects were removed (Field, 2009). However, we do acknowledge that additional tests with an experimental set-up which tests each subject only once would be the ideal method of excluding habituation as a potential confound (i.e., two speaker choice (Fischer, Noser, & Hammerschmidt, 2013)). This is probably best performed in the lab where several generations could be tested under highly controlled conditions.

The negative result. Therefore, if we accept the negative result as valid, this raises two possibilities. The first is that the subjects recognized their kin, neighbors, cage-mates, and strangers, but did not react differently to the different call types using the variables we measured. The second is that the subjects did not recognize the different categories of callers and so did not react differently. It is difficult for us to determine which was occurring, however, in the second half of the dry season, when the experiments were performed, the banana used to bait the platform was clearly a highly valued food item for the lemurs. Up to nine individuals visited the same platform per night often returning multiple times (see also (Joly et al., 2008)), and at the very end of the dry season, nearly all of the females were possibly pregnant (Kessler, pers. obs.), increasing their nutritional needs even more. And, indeed, the mouse lemurs fed most of the time they were video-taped – after all four stimulus types (Fig. 5). Therefore, it is possible that the females were so hungry that they were not motivated to differentiate between the callers, even if they recognized who was calling.

The alternative explanation is that perhaps the lemurs did not respond differently to kin and nonkin because the calls do not contain sufficient kin-specific acoustic signatures. Previous studies showed that agonistic calls can only be classified by kin group at a rate of 47% (Kessler et al., 2014, Chapter 2) but by individual at a rate of 62%

(Leliveld et al., 2011). It may be that these signatures are simply not pronounced enough to facilitate kin recognition. Kessler et al. (2012) showed that female mouse lemurs discriminated paternal kin from nonkin based on mating call signatures with a 79% classification rate, but not based on alarm calls with a 45% classification rate (Chapter 4). Similar differences in reactions to acoustic signatures have been found across call types in other species ((Mitani et al., 1996; Rendall et al., 2009; Rendall et al., 1998; Rendall et al., 1996)). However, such classification percentages should still be viewed with caution, because what researchers measure and find to be statistically significant does not always match with what the subjects find to be biologically relevant (i.e., (Fugate et al., 2008)).

Given that other researchers have advocated for other experimental designs to test discrimination between stimuli (i.e., habituation-recovery, two speaker choice (Cheney & Seyfarth, 1988; Fischer et al., 2013)), we recommend further work testing for kin recognition in the lab with these methods. The laboratory would also have the added advantage of offering more control and minimizing distractions (i.e., other noises in the forest). However, regardless of which is the underlying cognitive process, the mouse lemurs showed a very different reaction to agonistic calls of kin than did large-brained, socially complex monkeys and hyenas (Cheney & Seyfarth, 1980, 1999; Holekamp et al., 1999). In contrast to the monkeys and hyenas (Cheney & Seyfarth, 1980, 1999; Holekamp et al., 1999), the mouse lemurs showed no sign of heightened attention to the agonistic calls of kin. Though coalitions and the recruitment of support from kin have not been documented in mouse lemurs, one prior study reported the recruitment of nonkin via vocalizations during a predator attack (Eberle & Kappeler, 2008). Recruited conspecifics then mobbed the snake (Eberle & Kappeler, 2008). Given that this was an isolated incident, it may not be indicative of widespread coalitionary behavior. Therefore, our findings are consistent with the lack of widespread coalitionary behavior in mouse lemurs and suggest that in contrast to large-brained, socially complex species (Cheney & Seyfarth, 1980, 1999; Holekamp et al., 1999), the small-brained, solitary foraging mouse lemur does not appear to use agonistic vocalizations to monitor agonistic interactions involving kin, or perhaps, any conspecifics engaged in conflicts with other conspecifics.

Given that we have only tested one call type, our results do not indicate that mouse lemurs are unable to recognize maternal kin via other vocalizations. Other researchers have argued that the noisy quality typical of agonistic calls makes them ill suited to displaying acoustic signatures (Owren & Rendall, 2001; Rendall et al., 1998; Rendall et al., 1996). While formants have been proposed to be highly important for individual signatures among larger species, i.e., anthropoid primates (Fitch, 1997; Owren & Rendall, 2001; Rendall, 2003; Rendall et al., 2005), formants are believed to be less significant among smaller species that give high frequency/ultrasonic calls, (Ehret, 2006; Leliveld et al., 2011). Prior research compared the strength of individual acoustic signatures across four call types in mouse lemurs and found that harmonic, long distance calls were more individually distinctive than the noisier (though still harmonic), short distance agonistic calls (Leliveld et al., 2011). Therefore, future work should investigate whether harmonic, long distance call types (i.e., gathering calls) are used for kin recognition in gray mouse lemurs. If matrilineal kin recognition were to be found to occur via long distance call types, it would suggest that the dispersed social networks of mouse lemurs were more important in facilitating kin selection than selective pressure for kin-biased coalitionary behavior. Further work should be done investigating other species, including solitary species, solitary foragers, and social species, to determine whether kin recognition via agonistic calls has evolved only in species with frequent kin-biased coalitionary behavior.

Given that agonistic calls are typically given at close range during a conflict (Leliveld et al., 2011), the caller's conflict partner would also have access to visual and olfactory cues at that moment. This combination of acoustic, visual, and olfactory cues may be sufficient to facilitate kin recognition and mitigate aggression among closely related individuals, though it would not be sufficient for the recruitment of coalitionary support from out of sight kin. Future work should also test for kin recognition via other cues (i.e., olfaction). Furthermore, given that solitary and solitary foraging mammals show a great diversity of social systems (Müller & Thalmann, 2000), additional work should be done to determine whether these differences correlate with differences in kin recognition, including within and among different mouse lemurs species. Because the social variation within and between mouse lemur species is only beginning to be discovered (i.e., (Dammhahn & Kappeler, 2005; Olivieri et al., 2007; Weidt, Hagenah, Randrianambinina, & Radespiel, 2004; Zimmermann, Cepok, Rakotoarison, Zietemann, & Radespiel, 1998)), the extent to which the findings in this paper can be generalized to other mouse lemur species is not yet clear and further investigations comparing kin recognition among the different mouse lemur social systems is a promising area for further research.

Conclusions

Gray mouse lemurs did not react differently to any of the call types. This suggests that the small-brained, solitary foraging, mouse lemurs do not use agonistic calls to monitor agonistic interactions involving their kin. This is in stark contrast to large-brained, socially complex monkeys and hyenas which engage in frequent kin-biased, coalitionary behavior (Cheney & Seyfarth, 1980, 1999; Holekamp et al., 1999). Future studies should be done to investigate whether mouse lemurs use other cues, like other vocalization types or olfaction, to recognize kin. Additional work should also be conducted on other solitary foraging and solitary species including both other mammals and nonmammals to isolate which mechanisms are used for kin recognition in which types of social systems.

Methods

Field site and trapping methodology. This study was conducted at the Ankarafantsika National Park near the Ampijoroa forestry station (16°19’S, 46°48’E) in the designated research area, Jardin Botanique A (JBA). JBA is a 30 hectare plot (approximately 600 m by 500 m) of dry deciduous forest with a grid of trails at approximately 50 m intervals (Fig. 7).

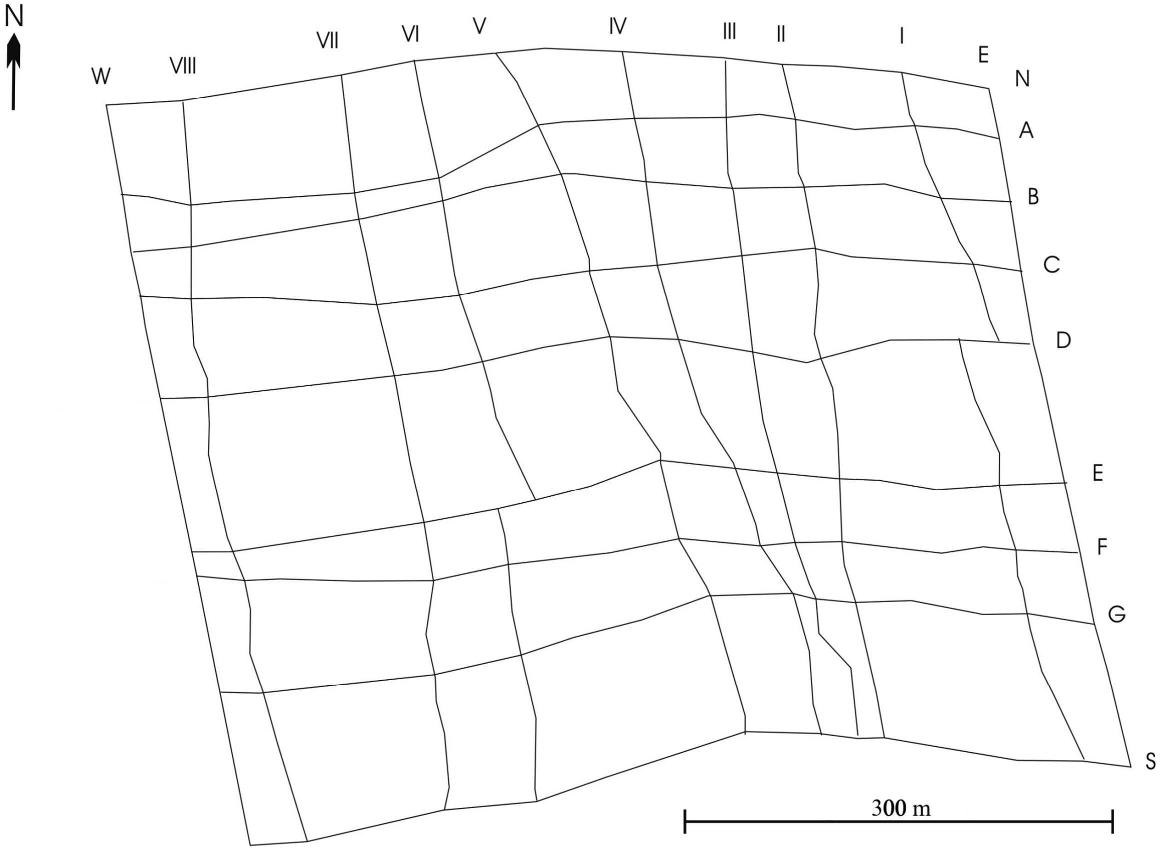

Figure 7. A map of the research grid, JBA, and the trails. The grid system of trails is labeled (top, L-R) W, VIII, VII, VI, V, IV, III, II, I, E and (right, top-bottom) N, A, B, C, D, E, F, G, S. W, E, N, and S refer to the cardinal directions. Intersections where subjects were captured are referred to in Table 1 with both the north-south and east-west trails, i.e., AI, BII, CIII, etc.

We conducted the fieldwork during the dry seasons in May through November of 2010 and 2011. A total of 107 *Microcebus murinus* were trapped in Sherman Live Traps baited with banana using established methods (i.e., (Radespiel, 2000; Radespiel et al., 1998; Radespiel, Sarikaya et al., 2001), data presented in full in (Kessler et al., 2014), Chapter 2). The trapped lemurs were marked with subcutaneously injected microchip transponders (ID-100, Trovan Small Animal Marking System, Telinject®, Römberg, Germany), and had small (1-2 mm^2) ear biopsies taken as genetic samples. Twenty-five adult females (2010: n=13, 2011: n=15, 3 collared in both years, adult≥50g) were fitted with radio-collars (either a PicoPip or a Pip3 collar from BioTrack Ltd., United Kingdom, weight 2.3-3.1 g) before release at their capture location. Radio-collared females were tracked to their daytime sleeping sites using a TR-4 receiver (Telonics, Mesa, AZ, USA). Then the collared lemurs' microchips and those of their co-sleepers were scanned with a hand-held transponder reader (Trovan Small Animal Marking System, Telinject®, Römberg, Germany), thus identifying co-sleeping lemurs (data presented in (Kessler et al., 2014), Chapter 2). We collected sleeping site data on a total of 118 days (65 days in 2010 and 53 days in 2011) and obtained 11-74 days of data per collared female (mean: 29 days).

Recording vocalizations. A subset of 45 lemurs was temporarily kept in captivity for recording following the protocol described in ((Kessler et al., 2014), Chapter 2). All recordings were made with a D1000X bat detector (flat frequency response: 5-235 kHz, sampling frequency 200 kHz, 16-bit resolution, Pettersson Elektronik, Upsala, Sweden) at a distance of approximately 2-4 m. Lemurs that were caged together to elicit calls usually engaged in agonistic encounters including fighting, chasing and fleeing during which agonistic calls were recorded. No injuries were observed in any of the lemurs. During the first night that the lemurs were caged together, the experimenter was present throughout the whole night and could separate the animals if necessary (very rare). Though multiple cardboard cans per cage were available as sleeping sites, the lemurs typically shared a sleeping site from the first night onwards when they were caged together. Methods were approved by Madagascar National Parks (2010 permits: N102/

10/MEF/SG/DGF/DCB.SAP/SCBSE, N103/10/MEF/SG/DGF/DCB.SAP/ SCBSE, 2011 permits: N101/11/MEF/SG/DGF/DCB.SAP/SCB, N102/11/MEF/SG/DGF/DCB. SAP/SCB) and the Arizona State University Institutional Animal Care and Use Committee (Protocol: 10-1077R). All animals were released at their capture locations after recording was completed (1 night – approximately 2 weeks, mean=5 nights).

Stimuli Preparation. Playback stimuli consisted of a series of 3-5 agonistic calls repeated three times separated by approximately 3.6 seconds of background noise from the original sound file (Fig. 8).

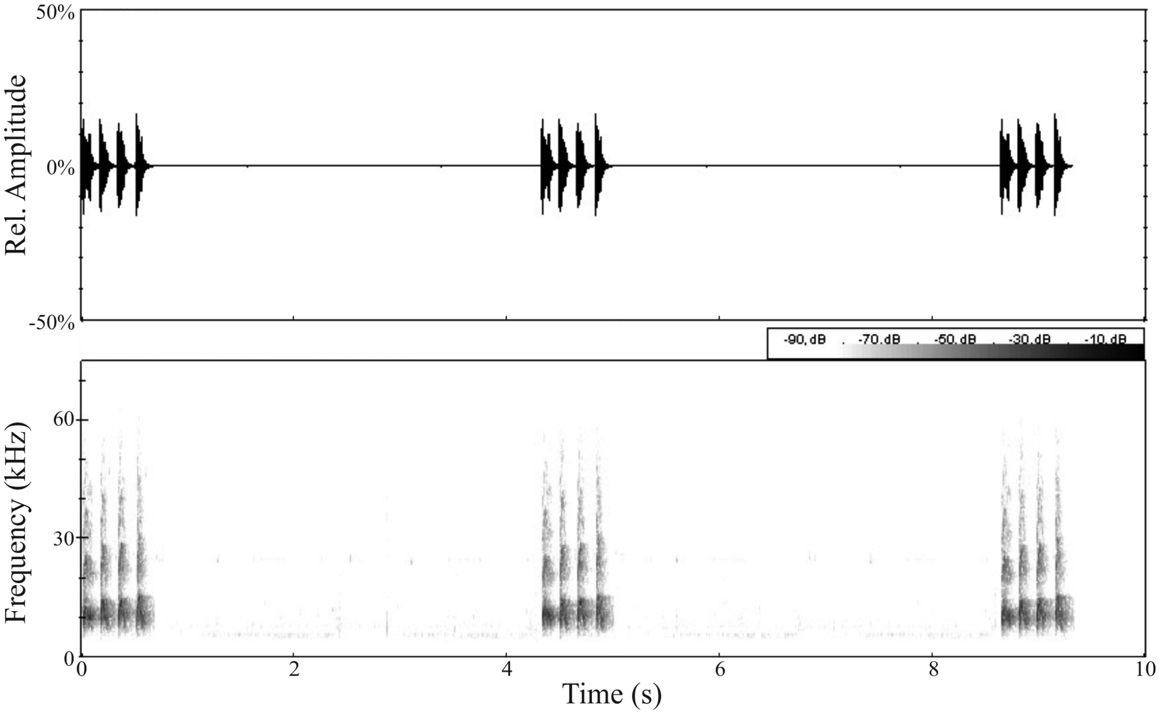

Figure 8. A spectrogram (bottom) and oscillogram (top) of a playback stimulus of the agonistic calls. Time (s) on the X-axis. Frequency (kHz) and relative amplitude (%) are on the Y-axis. Amplitude is shown on the gray scale in the spectrogram.

This stimulus format was chosen because it has been successfully used in other mouse lemur playback studies (i.e., (Kessler et al., 2012; Scheumann & Zimmermann, 2008)). In one female, the calling rate was slower than in the others, and so agonistic calls from this female were repeated only twice to produce a stimulus of approximately the same length. Playback stimuli were obtained from 22 females. The sound files were prepared in BatSound Pro 3.3.1 (Petterson Elektronik, Uppsala, Sweden), filtered with a band-pass filter (<5kHz, >90 kHz), and then uploaded from Madagascar via the internet to the bioacoustics lab at the Institute of Zoology, University of Veterinary Medicine Hannover in Germany where the calls were adjusted to be 75 +/- 1 dB at a distance of 1 m (see (Kessler et al., 2012), Chapter 4) for details of sound pressure adjustment). However, due to technical problems, not all calls could be adjusted and 18 (30%) of the stimuli were played at their original sound pressure level ranging from 75-80 dB, except for one stimulus which was 61 dB (mean pressure for all unadjusted stimuli: 76.94 dB, standard dev. 4.22 dB).

Genetic analyses. Genetic analyses were conducted at the Institute of Zoology at the University of Veterinary Medicine Hannover, Germany. Pairwise relatedness for all dyads of the 107 captured lemurs (72 males, 35 females) was calculated in Kinship 1.3.1. (Goodnight & Queller, 1999) based on multilocus genotypes produced by seven nuclear microsatellites. Matrilinear relationships were confirmed by sequencing the mDNA D-loop for all captured females using the universal mammalian control region primers H16498 and L15997 (Guschanski et al., 2007). Methodological details and the genetic data are presented in full in ((Kessler et al., 2014), Chapter 2).

Classification of kin, neighbor, cage-mate and stranger dyads. Dyads were classified as matrilinear kin, neighbors, cage-mates and strangers based on the following criteria (Appendix C). Kin i) had a pairwise relatedness value that was significantly likely to result from a relationship of $r_{maternal}$=0.5 and $r_{paternal}$=0, based on the permutations implemented in Kinship 1.3.1., ii) shared the same mitochondrial haplotype, and iii) co-slept (slept in the same sleeping site simultaneously). For three kin dyads, the co-sleeping requirement was not fulfilled. Dyads 28-09 and 36-11, and 28-09 and 46-11, respectively, were not observed to co-sleep, however, all three of these females co-slept with a fourth female, 17-10. Because 36-11 and 46-11 were only captured in the second field season and 28-09 only in the first, it is likely that 28-09 was dead in the second field season. However, if she was still alive when 36-11 and 46-11 were born, then she probably co-slept with them until her death. Females 52-11 and 113-10 were not observed to co-sleep, but the high relatedness between them (r=0.36), having the same mitochondrial haplotype, and eating at the same feeding platform suggest that they are likely to be kin from a sleeping group that underwent a group split at some earlier time point. This phenomenon has been documented in this population (Radespiel, Sarikaya et al., 2001). The mitochondrial haplotype could not be determined for one female, 19-10. However, she had was closely related (r=0.44) and co-slept with female 41-11, thus this dyad is also classified as kin.

Neighbors fed at the same feeding platform (though not necessarily simultaneously), but were not kin (pairwise relatedness was not significantly likely to result from a relationship of $r_{maternal}$=0.5 and $r_{paternal}$=0 and they did not co-sleep). Feeding at the same platform indicated that they had overlapping ranges and shared feeding sites, making it highly likely that they were familiar with each other.

Cage-mates both shared a cage during the recording and, during that time, heard agonistic calls from the other lemur, but did not co-sleep in the wild, did not share a feeding platform in their home ranges, and did not have an r value that was significantly likely to result from a relationship of $r_{maternal}=0.5$ and $r_{paternal}=0$.

Dyads were classified as strangers when they were captured more than approximately 300 m apart from each other. This is based upon the sum of the known ranging radius and dispersal threshold for females in this population (Radespiel et al., 2003; Radespiel, Sarikaya et al., 2001). Prior work on this population demonstrated that females have home-ranges of 1-3 hectares which remain stable across years (Radespiel, Sarikaya et al., 2001). Assuming a circular home-range, this can be converted to a ranging radius of 50-87 m. Furthermore, adult females are largely philopatric and are rarely found to have dispersed further than one home-range from the natal range (median dispersal distance: 63 m, lower quartile 23 m, upper quartile: 119 m) (Radespiel et al., 2003). Therefore, to calculate a conservative estimate we multiplied the larger home-range radius (87 m) by two and added the upper quartile of the dispersal distance (119 m) to obtain 293 m as a distance beyond which females are highly unlikely to be familiar with each other. We then rounded up to approximately 300 m. Appendix C summarizes the characteristics of the dyads and lists the trail intersections at which each female was captured. Figure 7 shows the grid system of trails. Three of 20 stranger dyads had capture locations that were closer than 300 m. For 06-09 and 14-09, 17-10 and 10-10 this distance was very close to 300 m (Appendix C, Fig. 7). For one additional dyad, 46-11 and 10-10, their nearest capture locations were only ~200 m apart from each other (Appendix C, Fig. 7). However, they were not captured in the same year. Given that only 38 of 69 lemurs, 55%, captured in 2011 were recaptures from prior years, the turnover rate in the population is likely to be quite high. This is in agreement with long-term studies in this population showing similar turnover rates (Radespiel et al., 2003). Therefore, we conclude that it is likely that 10-10 died before 46-11 was born and this dyad is included as a stranger dyad.

Playback experiments. Playback experiments were conducted at feeding platforms in the forest based upon the set-up used in prior work (Joly et al., 2008) (See diagram in Fig. 9).

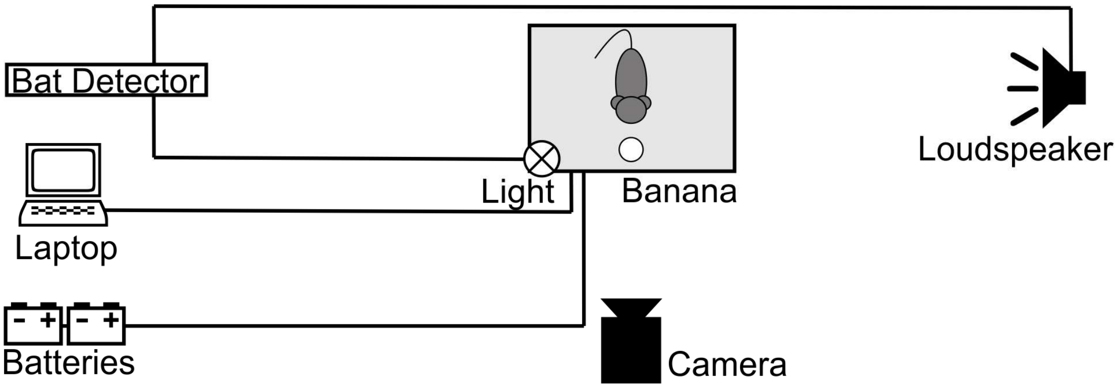

Figure 9. A top-view diagram of the set-up for the playback experiments.

The platform itself consisted of a wooden shelf (29 by 40 cm) on a plastic pipe approximately 1 m high. We placed a transponder reader (EURO ID GmbH, Weilerswist, Germany) on the platform. The reader consisted of an AAN FK2 antenna (EURO ID, 370 x 267 x 49 mm) connected to a EUR 4100-24 reader device (EURO ID) and then to a laptop (Lenovo Thinkpad T410). It was powered by two 12V car batteries. Approximately 1 m from the feeding platform was a second platform with an ultrasonic loudspeaker with a built in amplifier (Petterson Elektronic, Uppsala, Sweden), which was connected to the ultrasonic/audible output of the D1000X bat detector. The audible output (where headphones could be attached) was connected to a set of infra-red lights which would light up when the playback started. The lights were completely in the infra-red spectrum. Infra-red light is not visible to the human eye and the lemurs were not observed to look at them even when their pupils were open wide. The experiments were video-taped using the nightshot mode (which records infra red frequencies, thus displaying the infra-red lights at the onset of the playback) of a digital Sony video camera (DCR-SR210).

Calls were played while the subject ate the banana that was offered on the platform. This guaranteed that the female's head was in a standardized position at a standardized distance (1 m) from the loudspeaker. Call types (*kin*, *neighbor*, *cage-mate*, and *stranger*) were played in a pseudo-randomized order with a minimum of 5 minutes between two stimuli. No subject heard all of its stimuli on the same night.

A frame-by-frame analysis was conducted in Observer XT 10 (Noldus Information Technology) by an observer who was blind to which stimulus the subject heard (because the calls are high frequency with harmonics in the ultrasonic range, it is not possible to distinguish the caller while listening to the videos (recorded with a camcorder that is not specialized for high frequency recording). We analyzed 11.96 s (one frame less than 12 s) after the onset of the playback (marked by the infra-red lights), measuring seven behavioral variables: duration of time the lemur was on the platform, duration of time the lemur looked at the loudspeaker, duration of time the lemur was vigilant without looking at the loudspeaker, duration of time the lemur ate banana, latency to look at the loudspeaker, latency to be vigilant, latency to stop feeding (detailed ethogram in Table 6, diagram of experimental set-up in Fig. 9).

Table 6.

Behavioral Variables Measured or Calculated from the Playback Videos

Measured Variables	D/E	Definition
Onset of playback	E	First frame in which the lights are lit up, while subject is on platform and feeding (see below and text)
On platform	D	**Start:** Onset of playback **End:** Lemur's front feet have left the platform
Feed	D	**Start:** Onset of playback, thereafter when lemur bites/licks the banana **End:** animal has stopped biting/licking the banana
Look	D	**Start:** Lemur is within one frame of looking at the loudspeaker (90º to the right/left of platform) **End:** Lemur is not looking at the loudspeaker (+/- one frame)
Vigilant	D	**Start:** lemur is looking around, but not at the loudspeaker **End:** one frame before lemur looks at loudspeaker or feeds
Reaction index	E	0 = no reaction, 1 = vigilance, 2 = look at speaker, 3 = left platform
Calculated Variables	D/E	Calculation
Latency Look	D	Start of Look – Onset of playback
Latency Vigilant	D	Start of Vigilance – Onset of playback
Latency Stop Feed	D	The smaller of latency to look at loudspeaker or latency to be vigilant

Note. D/E shows whether the variable was considered a duration or an event. *Feed, Look,* and *Vigilant* are mutually exclusive.

We also scored a reaction index (0 = no reaction to the playback, 1 = vigilant (looked around but not at loudspeaker), 2 = looked at loudspeaker, 3 = left platform).

Using the values of the behavioral variables obtained from 11.96 s, we tested for intra-observer reliability by re-coding 22% of the videos and testing for differences between the two sets of data with a Wilcoxon Matched Pairs test. Though two behavioral variables were significantly different after a Bonferroni correction (Wilcoxon Matched Pairs Test, $Z_{\text{latency vigilant}}$=-3.072 and $Z_{\text{latency stop feed}}$=-2.869, N=24, test-wide alpha>0.05), they were retained in the analyses because the mean differences between the two codings were small (*latency vigilant* = 1.4 s and *latency stop feed* = 0.1 s).

All statistical tests were run in SPSS 20-22 (IBM Corp.) and test-wide alpha for each comparison type (i.e., reactions to kin vs. neighbors) was set at 0.05. Bonferroni corrections were performed including the eight variables *feed*, *look*, *vigilant, latency look, latency vigilant, latency stop feed, reaction index*, and *PCA Look.*

Sound pressure level. Using the values of the behavioral variables obtained for 11.96 s after the onset of the playback, we tested whether sound pressure level represented a significant confound by comparing the behavioral variables (*feed, look, vigilant, latency look, latency vigilant, latency stop feed*) measured from trials where the sound pressure level was adjusted to 75 +/- 1 dB to those trials where the sound pressure level was not adjusted using a Mann Whitney U test. Aside from one trial with a sound pressure level of 61 dB, all unadjusted stimuli were 75 dB or louder, thus we expected reactions to be stronger to the unadjusted stimuli than to the adjusted stimuli. Therefore we excluded the trial with 61 dB from this test. Because none of the tests were significant after a Bonferroni correction (Mann Whitney U test, $U \geq 225$, $N_{adjusted}=39$, $N_{unadjusted}=17$, test-wide alpha>0.05), we retained all trials in the analyses.

Screening within the 12 seconds. Given that mouse lemurs are small-bodied mammals with a high predation rate (Goodman et al., 1993), we reasoned that a fast reaction time to auditory stimuli could be under high selection (bats have been shown to react to playback stimuli within 200 ms (Kastein, Winter, Kumar, Kandula, & Schmidt, 2013)). We wished to exclude the possibility that our analyzed time interval was too long, thus causing a significant difference in reactions to be diluted by extraneous behavior due to distractions in the forest (i.e., background noises from other species, weather, branches falling, etc.). Therefore, we screened half second intervals from 1-11.96 s. We did not test for effects at time intervals longer than 12 s because it was evident from watching the videos that the amount of behavior unrelated to the stimuli increased with the time since the playback's onset (i.e., subject looked towards other noises in the forest).

We conducted pairwise nonparametric tests testing for differences in reactions to kin vs. neighbors with a Mann Whitney U test on the results of independent dyads, and for reactions to kin vs. cage-mates, kin vs. strangers, and neighbors vs. strangers with Wilcoxon Matched Pairs tests with the pairs matched by the listening female (Appendix C and Appendix D).Because the lemur left the platform in only 4 of 57 trials, we discarded the variable *duration on the platform* due to a lack of variation.

During this screening, we identified 3 possible time intervals in which differences or trends toward differences between reactions to the four dyads appeared evident before a Bonferroni correction: 3s, 5.5s, and 11.96s after the onset of the playbacks. Then, because we expected the subjects to habituate to the experimental set-up, and this could influence the reactions, we conducted a multi-level linear mixed model in SPSS 22 using the maximum likelihood method. Following published methods (Field, 2009), we used the call type (*kin*, *neighbor, cage-mate,* and *stranger,* range: most to least familiar) and order (the trial number for that individual, range: 1-13) as fixed covariates. Both were nested within the random factor subject, which had a random intercept. The eight dependent variables were *feed, look, vigilant, latency look, latency vigilant, latency stop feed, reaction index,* and *PCA look* (described below). We also ran these models including an interaction term of call type*order (Appendix H).

Because we expected the most sensitive behavioral variables to be latency to look to the loudspeaker and duration of the look to the loudspeaker, we performed a principal components analysis (no rotation) on the correlation matrix of these two variables and extracted one principal component. We called it *PCA look* due to the input variables. The scores were saved, and for each of the time periods (3s, 5.5s, and 11.96s) we tested *PCA look* as the dependent variable in the multi-level general linear mixed model described above.

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CHAPTER 4

PATERNAL KIN RECOGNITION IN THE HIGH FREQUENCY / ULTRASONIC RANGE IN A SOLITARY FORAGING MAMMAL

Abstract

Kin selection is a driving force in the evolution of mammalian social complexity. Recognition of paternal kin using vocalizations occurs in taxa with cohesive, complex social groups. This is the first investigation of paternal kin recognition via vocalizations in a small-brained, solitary foraging mammal, the gray mouse lemur *(Microcebus murinus*), a frequent model for ancestral primates. We analyzed the high frequency/ultrasonic male advertisement (courtship) call and alarm call. Multi-parametric analyses of the calls' acoustic parameters and discriminant function analyses showed that advertisement calls, but not alarm calls, contain patrilineal signatures. Playback experiments controlling for familiarity showed that females paid more attention to advertisement calls from unrelated males than from their fathers. Reactions to alarm calls from unrelated males and fathers did not differ. Findings provide the first evidence of paternal kin recognition via vocalizations in a small-brained, solitarily foraging mammal. High predation, small body size, and dispersed social systems may select for acoustic paternal kin recognition in the high frequency/ultrasonic ranges, thus limiting risks of inbreeding and eavesdropping by predators or conspecific competitors. Paternal kin recognition via vocalizations in mammals is not dependent upon a large brain and high social complexity, but may already have been an integral part of the dispersed social networks from which more complex, kin-based sociality emerged.

Introduction

Though kin selection (the preferential treatment of genetic relatives) has been theorized to be one of the most important forces driving the evolution of social complexity in mammals, we still know surprisingly little about how this process occurs (Chapais & Berman, 2004; Hamilton, 1964). Vocalizations are an important cue for the recognition of maternal kin (related through the mother) in species with large brains, complex social systems and cohesive foraging groups (primates (Rendall et al., 2000; Rendall et al., 2009; Seyfarth & Cheney, 2003), hyenas (Holekamp et al., 1999), elephants (McComb et al., 2000; McComb et al., 2003), dolphins (Sayigh et al., 1998), pinnipeds (Insley et al., 2003), (Barton, 1996, 2006; Barton & Dunbar, 1997)) and in small-brained species with varying degrees of social complexity (colony-living bats: (Balcombe, 1990; Knoernschild & Von Helversen, 2008), small-brained, group-living lemurs (Nunn, 2000), and the socially variable house mouse (full-sibling recognition: (Hoffmann et al., 2012; Latham & Mason, 2004; Musolf, Hoffmann, & Penn, 2010)). Far less is known about recognition of paternal kin (related through the father), though it is expected to shape the evolution of social behavior through paternal kin selection and inbreeding avoidance (Chapais & Berman, 2004; Hamilton, 1964; Widdig, 2007). Long-term field studies of species with complex social systems suggest they often behave as if they recognize paternal kin (baboons: (Buchan et al., 2003), hyenas: (Van Horn et al., 2004; Wahaj et al., 2004), reviews: (Silk, 2009; Widdig, 2007)). Studies investigating the cues have shown that large-brained macaques use vocalizations for paternal kin recognition (Pfefferle et al., 2014) and that small-brained laboratory rodents use olfaction (i.e., (Kruczek & Golas, 2003; Todrank, Busquet, Baudoin, & Heth, 2005), review: (Widdig, 2007)). To our knowledge, our study is the first to demonstrate acoustic patrilineal signatures and paternal kin recognition via vocalizations in a solitary-foraging mammal, suggesting that this ability can evolve independently of social complexity.

We investigated the gray mouse lemur (*Microcebus murinus*) as a model for small-brained mammals with relatively simple social systems (Barton, 2006; Müller & Thalmann, 2000). Within primates, it retains basal morphological traits including a small brain-size relative to body size (Barton, 2006) and has been suggested to represent an ancestral primate model (Martin, 1972; Müller & Thalmann, 2000). It is a tiny, nocturnal strepsirrhine primate endemic to Madagascar that maintains social networks involving shared home ranges and sleeping sites, but forages alone for insects and fruit in thin, terminal ends of tree branches in tropical forests (Eberle & Kappeler, 2006; Radespiel, 2000; Radespiel et al., 1998; Radespiel, Sarikaya et al., 2001). This is a particularly interesting species in which to investigate paternal kin recognition via vocalizations, because in the wild females are philopatric and cooperatively raise their young in nests with maternal kin (Eberle & Kappeler, 2006; Radespiel, Sarikaya et al., 2001). Males provide no paternal care and do not co-nest with their mates or with their young, thus limiting the opportunities for the familiarity-based mechanisms seen in species with more complex social systems ((Eberle & Kappeler, 2006; Mateo, 2004; Radespiel et al., 1998; Radespiel, Sarikaya et al., 2001; Rendall, 2004; Widdig, 2007)). However, inbreeding avoidance is still likely to be highly important, because males may remain in the same area for multiple years and during the breeding season they can expand their ranges to be more than twice as large as the females' ranges, making it likely that adult males' ranges will overlap the ranges of their daughters from previous mating seasons (Radespiel, 2000; Radespiel et al., 2002).

Because mouse lemurs are nocturnal, solitary-foragers living in dense forests, vocal communication is highly important for regulating social interactions across distances where visibility is poor and olfactory communication is limited (Zimmermann, 1995a). Mouse lemurs suffer from high predation (Goodman et al., 1993), and their high frequency and ultrasonic calls have been suggested to be an anti-predator strategy by calling above the hearing range of owls (Zimmermann, 1995a). Two of the most frequent calls are the mate advertisement call and the alarm call. The mate advertisement call is used in social and sexual contexts (Leliveld et al., 2011; Zimmermann & Lerch, 1993). It is a complex, high frequency / ultrasonic vocalization that starts with a whistle unit, followed by an upward sweep, and a highly modulated tail unit (Leliveld et al., 2011; Zimmermann & Lerch, 1993). The alarm call is given in social and disturbance contexts and it is a short, almost non-modulated, high frequency call (Leliveld et al., 2011). Both call types contain individual signatures (Leliveld et al., 2011; Zimmermann & Lerch, 1993). If used for paternal kin recognition, both call types could facilitate kin selection, and the advertisement call could also enable inbreeding avoidance in sexual contexts.

We tested two hypotheses in each call type: (i) *Patriline Signature Hypothesis:* calls will be distinctive by patriline, and (ii) *Patriline Recognition Hypothesis:* females will respond differently to calls from their fathers and unrelated males when familiarity is controlled. We found patrilineal signatures and paternal kin recognition in the high frequency/ultrasonic male advertisement call but not in the high frequency alarm call. These findings suggest that paternal kin recognition via vocalizations can emerge in mammals independently of a large brain and high level of social complexity.

Results

Patriline signatures. Advertisement calls, but not alarm calls, contained patrilineal signatures. Seventy nine percent of the advertisement calls and 45% of the alarm calls were correctly assigned to their respective patrilines (permutated discriminant function analysis, chance=33%, $P_{advertisement\_call}$=0.0398, P_{alarm_call}=0.609). Figure 10 shows the separation of advertisement calls and alarm calls by patriline produced by the principal components analyses (see also Appendix I and Appendix J, which summarize the data).

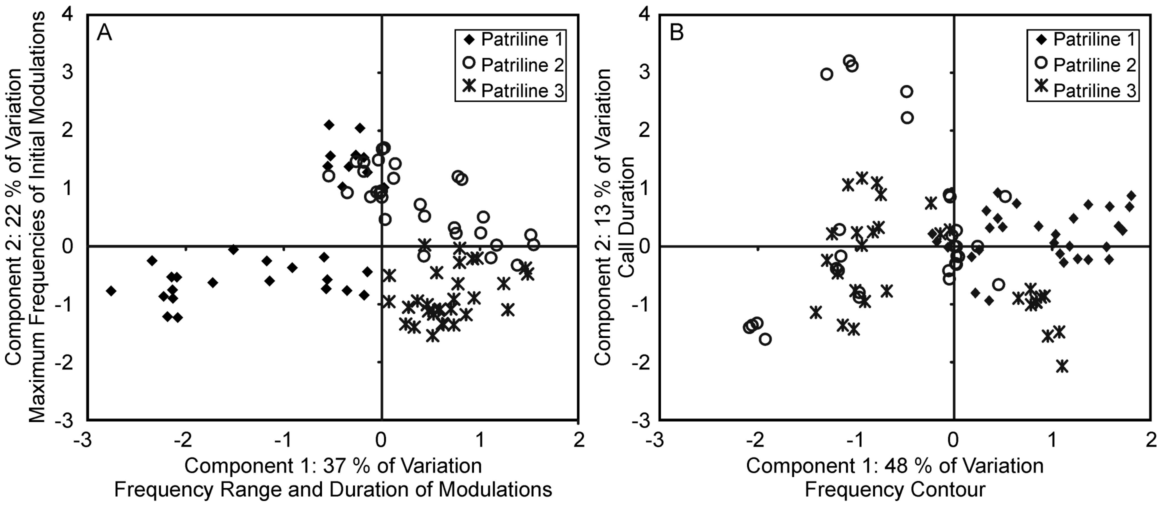

Figure 10. Separation of calls by patriline produced by components 1 and 2. **A:** advertisement calls, **B:** alarm calls. Only the advertisement calls showed statistically significant classification by patriline. See Appendix I and Appendix J for the quartiles of each acoustic parameter and their loadings on the components.

Because the acoustic structures of the calls are complex, principal components analysis was used to reduce the number of parameters (Field, 2009). For the advertisement calls, high positive values on component 1 (37% of the variation) were associated with modulations of a longer duration and a greater frequency range and higher maximum frequencies in the tail modulations. High positive values on component 2 (22% of the variation) are associated with high maximum frequencies in the first seven modulations.

Acoustic dissimilarity between dyads correlated significantly with patrilineal genetic dissimilarity between dyads (Mantel test: r=0.191, g=1.9327, Z=6.5104, p=0.028) and did not correlate with matrilineal genetic dissimilarity between dyads (Mantel test: r=-0.0721, g=-0.3679, Z=7.1612, p=0.4120).

Patriline recognition. The females paid more attention to advertisement calls from unrelated males than from their fathers, but showed no differences in response to alarm calls from unrelated males and from their fathers (Fig. 11, see also Table 7 and Appendix K, which summarize the data).

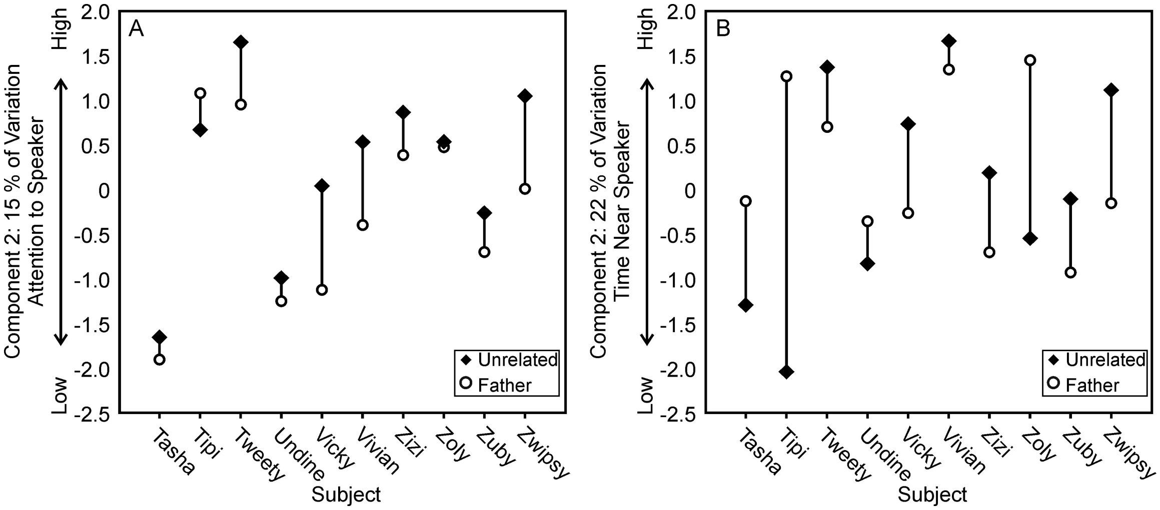

Figure 11. Females' responses to advertisement calls (A) and alarm calls (B) from their fathers and unrelated males. **A:** Component 2 showed that nine of 10 females paid more attention to the advertisement calls of the unrelated (control) males than to calls from their fathers. High values on component 2 correlated with looking towards the speaker faster, approaching the speaker sooner, and spending more time near the speaker. **B:** Component 2 did not show a significant difference between responses to alarm calls from fathers and unrelated males. High values on component 2 correlated with approaching the speaker sooner and spending more time near the speaker. See Table 7 and Appendix K for the quartiles of each behavioral variable and their loadings on the components.

Table 7.

Quartiles of the Behavioral Responses to Advertisement Calls and their Loadings on the Principal Components

Behavior	Quartiles			Component Loadings		
	25	50	75	Component 1	Component 2	Component 3
Latency to Leave Bottle Area	114.00	214.00	673.00	0.870	0.148	0.051
Latency to Box Area	136.25	376.50	673.00	0.869	0.231	0.127
Duration in Bottle Area	483.00	652.00	813.63	0.841	0.137	0.183
Latency to Speaker Area	697.13	1420.50	1500.00	0.735	**-0.585**	-0.101
Latency to Box	340.00	890.50	1465.88	0.722	0.342	0.487
Duration Look to Speaker	18.25	33.50	61.50	0.628	-0.055	-0.614
Duration in Box	14.50	221.00	407.75	-0.580	-0.441	-0.367
Duration in Speaker Area	0.00	63.50	218.00	-0.716	**0.591**	0.183
Duration in Box Area	115.13	185.75	299.13	-0.513	**0.539**	-0.291
Latency to Look to Speaker	22.50	144.00	295.38	-0.266	**-0.528**	0.687
Duration Look to Box	0.00	13.75	21.25	-0.518	-0.148	0.480

Note. Components 1, 2, and 3 are 47%, 15%, and 15% percent of the variation, respectively. Behavioral variables that correlated highly (<-0.5 or >0.5) with component 2 are in bold. Frequency is measured in Herz and time is in frames (resolution of 25 frames/s).

The components of the females' responses to advertisement calls accounted for 47%, 15%, and 15% of the variation in the original response behaviors. Component 2, the attention to speaker component, showed that nonestrous females paid more attention to the advertisement calls of the unrelated males than to calls from their fathers (Bonferroni corrected Wilcoxon matched pairs test, Z=-2.395, n=10, P=0.017). High values on component 2 correlated with looking towards the speaker faster, approaching the speaker sooner, spending more time near the speaker, and spending more time in the box area. (After looking towards/approaching the loudspeaker and finding no lemur, sometimes the subject would then approach the nest box and appear to look inside. Because the lemurs are transported from cage to cage using the nest boxes, the nest box may be a second place for the subjects to look for another lemur).

Using component 2 scores, nine of the 10 females paid more attention to the unrelated males' advertisement calls than to those of their fathers (Fig. 11). Components 1 and 3 did not differentiate between responses to fathers' and control males' advertisement calls (Bonferroni corrected Wilcoxon Matched Pairs Test, Component 1: Z=-0.561, n=10, p=0.575, Component 3: Z=-1.58, n=10, p=0.114).

The components of the responses to alarm calls accounted for 39%, 22% and 16% of the variation in the original response behaviors. None of the components differentiated between responses to fathers' and control males' alarm calls (Fig. 11, Bonferroni corrected Wilcoxon Matched Pairs Test, Component 1: Z=-1.172, n=10, P=0.241; Component 2: Z=-0.051, n=10, P=0.959; Component 3: Z=-0.968, n=10, P=0.333).

To exclude the possibility that arousal confounded our results, we measured parameters *most likely* to vary with arousal (Schehka, Esser, & Zimmermann, 2007), and tested for differences between the stimulus calls of related and control males. We measured the peak frequency of the fundamental, the call duration, number of modulations and the modulation rate (number of modulations/duration) of the advertisement calls (BatSound Pro 3.31, Pettersson Elektronik AB, Uppsala, Sweden). Peak frequency of the fundamental, call duration, and modulation rate did not differ between the five father-control male dyads (Wilcoxon matched pairs tests, peak frequency of the fundamental: Z=-0.67, n=5, P=0.50; call duration: Z=-1.21, n=5, P=0.23; modulation rate: Z=-1.48, n=5, P=0.14). The number of modulations showed a trend (Wilcoxon matched pairs tests, Z=-1.63, n=5, P=0.10), but was not significantly correlated with the Attention to Speaker component (Spearman Correlation, rho≥-0.099, n=20, P=0.339). Therefore, we concluded that the arousal state of the caller did not confound our results.

Discussion

We found that male gray mouse lemur advertisement calls, but not alarm calls, contain acoustic patrilineal signatures. Furthermore, females paid more attention to the unrelated males' advertisement calls than those of their fathers. Though the females were not in estrous at the time, this increased attention to unrelated males suggests that such discrimination may be an important mechanism for inbreeding avoidance.

The two main kin recognition mechanisms proposed for mammals are familiarity and phenotype matching (sensu (Widdig, 2007): matching an unknown individual either to oneself or to known kin). In our study subject females were equally familiar with the calls of both their fathers and their control males, but this does not exclude the possibility that the females used their own calls and/or calls of their full-siblings as a template against which the stimulus calls were compared (Mateo, 2004; Penn & Frommen, 2010). (Both males and females give these highly modulated advertisement calls). Thus, inbreeding avoidance could be accomplished if females prefer males with calls that are different from their own and their paternal/full siblings' calls, and alternatively, kin selection could occur if mouse lemurs give preferential treatment to lemurs with calls similar to their own and their paternal/full siblings' calls.

Phenotype matching has been said to be selected for in species with (i) a lack of paternal care, (ii) multiple paternity litters, and/or (iii) communal nesting (Mateo, 2004). Thus, the social system of mouse lemurs should favor phenotype matching: (i) Since males do not provide paternal care and do not co-nest or co-forage with their mates or with their young (Eberle & Kappeler, 2006; Radespiel, Sarikaya et al., 2001), this strongly limits the effectiveness of the familiarity-based mechanisms often seen in more gregarious species with cohesive foraging groups (i.e., primates (Rendall, 2004; Widdig, 2007), elephants (McComb et al., 2000)). (ii) Mouse lemur litters can have multiple paternities within the same litter (Radespiel et al., 2002), thus infant mouse lemurs could be predicted to evolve self-referential phenotype matching to distinguish between full-siblings and maternal half-siblings in the nest. (iii) Given that multiple females may breed in the same nest (Eberle & Kappeler, 2006), infant mouse lemurs could potentially encounter paternal half siblings within the other mother's litter and use self-referential phenotype matching to recognize them. Self-referential phenotype matching has been observed in ground squirrels using olfactory cues (Mateo, 2010) and future work on mouse lemurs will aim to distinguish between self-referential phenotype matching and phenotype matching using kin as templates.

The difference in kin recognition between the two call types may be due both to the structure of the call types and to their role in the social system of this nocturnal, solitary foraging mammal. The advertisement call has a highly complex modulated structure that is well-suited to display patrilineal signatures. The alarm call is a shorter, non-frequency modulated call that may provide less opportunity to display the subtle differences between callers that appear necessary for patrilineal signatures. The lack of kinship signatures in the alarm calls also fits well with a prior report of cooperative mobbing of snakes by wild mouse lemurs which resulted in the rescue of an unrelated conspecific (Eberle & Kappeler, 2008). It suggests that mouse lemurs do *not* behave in the wild as if they are using kin signatures from the alarm calls (commonly given during predator mobbing) to selectively give aid to kin (Eberle & Kappeler, 2008). The costs of responding to a related conspecific’s mate advertisement call (inbreeding) may be high enough and the costs of responding to an alarm call low enough, that patrilineal signatures may be more strongly selected for in the advertisement call than the alarm call. Our results on paternal kin recognition, combined with prior work showing differences in maternal kin recognition across call types (Rendall et al., 2009; Rendall et al., 1998; Rendall et al., 1996), indicate that the selective pressures that drive the evolution of acoustic kin recognition are not uniform throughout all aspects of the communication system and that kin recognition in different calls may evolve independently.

The costs of sociality for a small-bodied, nocturnal mammal with a dispersed social system may have selected for higher frequencies in the social advertisement calls than in the alarm calls. Alarm calls are typically given in the context of a present threat when crypsis appears to no longer be the primary tactic of predator/threat avoidance (Gursky, 2005, 2006). In contrast, advertisement calls are social/mating calls and may facilitate interactions in close proximity, leading to an increased risk of detection due to the movements of multiple, rather than one, animal. The increased crypsis offered by the ultrasonic frequencies may help limit eavesdropping opportunities for predatory birds to only movement-related and not vocalization-related acoustic cues (Arch & Narins, 2008; Goodman et al., 1993; Zimmermann, 1995a). Additionally, the evolution of patrilineal signatures and kin recognition in these calls may enable listeners to choose *not* to approach the caller, thus avoiding the extra predation risk inherent in approaching the caller should the caller not be an advantageous mate. Such discrimination could be advantageous to both the listener and the caller.

An additional, non-mutually exclusive possibility is that the advertisement call may have been under more selective pressure due to interference from environmental background noise (Arch & Narins, 2008). Male mouse lemurs leave their sleeping sites earlier in the night than the females during the breeding season and use that time to go to the females’ sleeping sites and potentially monitor their estrous status (Radespiel, 2000; Radespiel, Ehresmann et al., 2001). If this early evening/dusk time is critical for finding mates, it may coincide with a time of heightened background noises, including rising winds due to changing temperatures and increased insect activity (S. Kessler, pers. obs., 2010). This increased noise at this time of night could select for the calls to be given at higher frequencies, thus enabling individuals to maintain a better signal-to-noise ratio if there is a lot of background noise in the lower frequencies (Arch & Narins, 2008) . In addition, in this context, where the caller and receiver are in close proximity (female inside the sleeping site, and male outside) it may be advantageous that the ultrasonic frequencies will rapidly scatter and not be heard by other conspecific competitors (Arch & Narins, 2008).

This suggests that high predation pressure and basal mammalian traits such as small body size and dispersed social systems select for paternal kin recognition in the high frequency and ultrasonic range, thus limiting the risks of inbreeding and being eavesdropped by predators or competitor conspecifics. Future analyses will determine which acoustic parameters make this kin recognition possible and will involve experimentally manipulating the acoustic parameters.

To our knowledge, our study is the first to demonstrate that that acoustic paternal kin recognition in mammals can evolve independently of a large brain, cohesive foraging groups, and a complex social system, and that it can also evolve in small-bodied, nocturnal solitary foragers whose main predator defense is crypsis. Given that more complex forms of sociality with cohesive foraging groups are thought to have evolved from an ancestral solitary forager much like the gray mouse lemur (Müller & Thalmann, 2000; Shultz et al., 2011), this suggests that mechanisms for kin recognition like those seen in this solitary forager may have been the foundation from which more complex forms of kin-based sociality evolved.

Conclusions

We provide the first evidence for paternal kin recognition using vocalizations in a small-brained, nocturnal, solitary foraging mammal, indicating that high predation, and basal mammalian traits, such as small body size and a dispersed social system, may select specifically for paternal kin recognition in the high frequency/ultrasonic ranges, thus limiting the risks of inbreeding and eavesdropping by predators or competitor conspecifics. Paternal kin recognition via vocalizations in mammals is not dependent upon a large brain and high social complexity, but may already have been an integral part of the dispersed social networks from which more complex, kin-based sociality is thought to have evolved.

Methods

Patriline Signatures. All calls for this study were used from the sound archive of the Institute of Zoology, University of Veterinary Medicine Hannover or newly recorded in 2008. All recordings were made with one of two previously published methods. For the first we connected the high frequency output of a bat detector (U30, Ultra Sound Advice, frequency range: >100 kHz) via a control filter unit (Pettersson box F2000) to a high-speed A/D card (DAS 16/330) in a laptop (Compaq Armada) equipped with the recording software BatSound Pro 3.31 (Pettersson Elektronik AB, Uppsala, Sweden).

(For additional details: (Scheumann et al., 2007)). For the second set-up consisted of connecting the high frequency output of a bat detector (frequency range: 8–100 kHz) to a high-speed analog-to-digital (A/D) card in a laptop (sampling frequency: 200–500 kHz) using the program NiDisk (for more details see: (Leliveld et al., 2011)). All calls were recorded at 16-bit per sample with a sampling frequency of 200 kHz or higher, and when higher, were resampled to 200 kHz. Mating calls were recorded during the breeding season from the male in the presence of a female. Alarm calls were recorded in disturbance/social contexts (novel object in the cage, after hearing a novel sound, predator call, conspecific alarm call, or in the context of a social interaction).

We analyzed advertisement and alarm calls from three patrilines housed at the University of Veterinary Medicine Hannover. Matrilineal and patrilineal relatedness values were calculated for all dyads within and between patrilines (see Tables 8 and 9) using breeding colony records maintained since the founding of the colony in 1985 and containing a pedigree depth of up to nine generations.

Table 8.

Patrilineal Relatedness Within and Between the Patrilines in the Patriline Signature Analysis.

	Eddie	Beetle	Amigo	Adrian	Xaver	Uli	Yves	Vito	Vincent
Eddie									
Beetle	**0.500**								
Amigo	**0.281**	**0.516**							
Adrian	0.000	0.000	0.000						
Xaver	0.043	0.027	0.021	**0.500**					
Uli	0.111	0.098	0.056	**0.250**	**0.500**				
Yves	0.195	0.141	0.100	0.063	0.094	0.117			
Vito	0.113	0.086	0.058	0.063	0.063	0.070	**0.514**		
Vincent	0.113	0.086	0.058	0.063	0.063	0.070	**0.514**	**0.257**	

Note. Relatedness within the three patrilines is shown in bold.

Table 9.

Matrilineal Relatedness Within and Between the Patrilines in the Patriline Signature Analysis.

	Eddie	Beetle	Amigo	Adrian	Xaver	Uli	Yves	Vito	Vincent
Eddie									
Beetle	**0.000**								
Amigo	**0.031**	**0.016**							
Adrian	0.000	0.000	0.000						
Xaver	0.066	0.059	0.035	**0.000**					
Uli	0.193	0.070	0.066	**0.000**	**0.039**				
Yves	0.023	0.031	0.014	0.063	0.094	0.055			
Vito	0.059	0.031	0.140	0.000	0.041	0.054	**0.014**		
Vincent	0.059	0.031	0.140	0.000	0.041	0.054	**0.014**	**0.257**	

Note. Relatedness within the three patrilines is shown in bold.

When a dyad had a common ancestor who was a maternal relative for one individual and a paternal relative for the other, that ancestor's portion of the relatedness value was divided by two and half was attributed to the dyad's maternal relatedness and half to the dyad’s paternal relatedness. The paternity of one male (not a stimulus male) within the pedigree was both unknown and could have influenced calculations. This case was resolved with the goal of maximizing inbreeding, thus minimizing genetic separation between patrilines and being conservative regarding our hypotheses. Mean patrilineal relatedness within and between patrilines was 0.426 and 0.073, respectively (Table 8). Mean matrilineal relatedness within and between patrilines was 0.041 and 0.053, respectively (Table 9). When animals have r values higher than 0.5, they are slightly inbred. (For colony management details: (Wrogemann et al., 2001)).

We measured ten advertisement calls and ten alarm call series from each of nine adult males, three males/patriline. Male ages in years when advertisement calls were recorded are: patriline 1: 4-9 (mean=6), patriline 2: 2-5 (mean=3), patriline 3: 4-6 (mean=5). Male ages in years when alarm calls were recorded are: patriline 1: 4-6 (mean=5), patriline 2: 3-6 (mean 5), patriline 3: 2-4 (mean=3). All males were sexually mature at the time of recording. (Mouse lemurs are sexually mature at one year old (Zimmermann & Radespiel, 2007)). We used the same macros as in prior work (Leliveld et al., 2011) in Signal 4.0 (Engineering Design, Belmont, USA). See Figure 12 for sample oscillograms, spectrograms, and power spectrums showing how measurements were made and Appendix L and Appendix M for definitions of advertisement call and alarm call parameters, respectively.

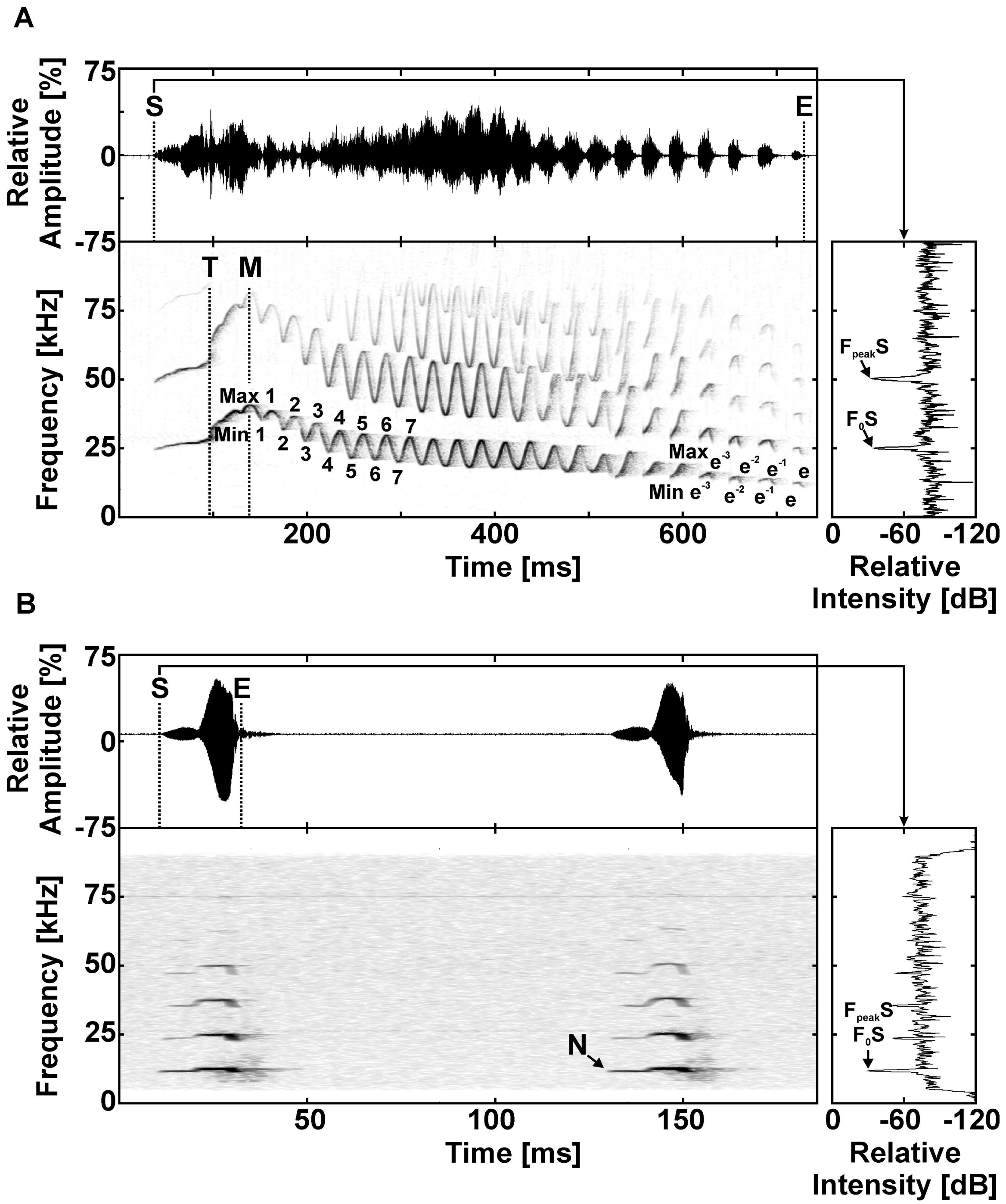

Figure 12. Oscillogram, spectrogram, and power spectrum showing the highly modulated advertisement call (**A**) and the almost non-frequency modulated alarm call (**B**). Some acoustic parameters are depicted. $F_{peak}S$ is the peak frequency of the start and F_0S is the fundamental frequency of the start. Figure produced in BatSound Pro 3.31 (Pettersson Elektronik AB, Uppsala, Sweden) according to published work (Leliveld et al., 2011). See Appendix L and Appendix M for more information.

Figure 12, Appendix L, and Appendix M were produced according to published work (Leliveld et al., 2011). We measured 45 acoustic parameters in the advertisement calls and 10 parameters in the alarm calls. These parameters were chosen to provide a detailed characterization of the contour of the fundamental frequency for each call type. As is evident in Figure 12, the advertisement call is far more structurally complex than the alarm call, thus more parameters are required to characterize it.

We used principal components analysis (Factor analysis, principal components method on the correlation matrix, no rotation, SPSS 20, Chicago, USA) to reduce the data to two components for each call type. Then, for each call type, the component scores were put into a permutated linear discriminant function analysis with individual nested within patriline (Mundry & Sommer, 2007). Cross-validation was performed with the leave-one-out method (Mundry, R. pers. com. 2008). Alpha was set at 0.05. This statistical technique of first conducting principal components analysis for parameter reduction (Field, 2009) and then putting the component scores into a discriminant function analysis is widely accepted in the acoustic literature across taxa (i.e., gibbons (Oyakawa et al., 2007), langurs (Wich, Schel, & De Vries, 2008), wolves (Passilongo et al., 2010), baboons (Rendall et al., 2009), macaques (Rendall et al., 1998), mouse lemurs (Leliveld et al., 2011), flycatchers (Lein, 2008), bats (Balcombe & McCracken, 1992; Knoernschild, Nagy, Metz, Mayer, & Von Helversen, 2012)). Such parameter reduction is important because the permutated discriminant function analysis is sensitive to the number of predictor variables (Mundry & Sommer, 2007) and the principal components analysis enables one to retain more information from the original parameters than could be included when just a small subset of the original parameters was chosen (Field, 2009).

We verified that the patrilineal signatures we found are related to patrilineal relatedness, not matrilineal relatedness between subjects by performing Mantel tests investigating the relationship between 1) acoustic dissimilarity and paternal relatedness and 2) acoustic dissimilarity and maternal relatedness. Paternal and maternal relatedness values are shown in Tables 8 and 9. For both tests acoustic dissimilarity was calculated as follows using an acoustic dissimilarity index (Kastein et al., 2013).

First each call parameter for each call was normalized to have a value between 0 and 1 using:

$$p_{ni}=(p_i - p_{min})/(p_{max} - p_{min}) \tag{1}$$

where p_{ni} is the normalized parameter value, p_i is the raw parameter value, and p_{max} and p_{min} are the maximum and minimum values of that parameter across the entire dataset. Second, we calculated a dissimilarity index for each parameter for each individual:

$$\text{Dissimiliarity}_{\text{parameter per individual}} = \sqrt{\frac{\sum_{i=1}^{n_c}(p_{ni} - p_{median})^2}{n_c}} \tag{2}$$

p_{ni} is the normalized parameter calculated in the previous formula, p_{median} is the median for that parameter across the whole dataset, and n_c is the number of calls per individual. Third, we combined these dissimilarity indexes across parameters within individuals using root mean squares. We followed the parameter groupings of the principal components analysis. Thus we calculated, for each individual, a root mean square of the acoustic parameters in component 1, and a second root mean square of the acoustic parameters in component 2. Fourth, we used these two dissimilarity indexes to calculate Euclidian distances between all possible dyads, producing a matrix of acoustic dissimilarity. We transformed the relatedness matrices (Tables 8 and 9) into relatedness *dis*similarity matrices by subtracting each value from 1 (a father-son dyad is related patrilineally by 0.5, thus they would also have a patrilineal genetic *dis*similarity index of 0.5). We then conducted Mantel tests in Mantel 2.0 (Liedloff, 1999) using 1000 permutations to test for a correlation between acoustic dissimilarity and patrilineal genetic dissimilarity and between acoustic dissimilarity and matrilineal genetic dissimilarity.

Patriline Recognition. We conducted playback experiments at the University of Veterinary Medicine Hannover in 2008. Ten adult *nonestrous* females (ages 2-8 years) heard advertisement calls and alarm calls from their genetic father and an unrelated control male ($r \leq 0.141$) played in a randomized order. As can be seen in Tables 10 and 11, patrilineal relatedness between fathers and daughters was high (mean=0.506) while matrilineal relatedness was low (mean=0.019). In contrast, both patrilineal relatedness and matrilineal relatedness was low between the females and their control males (mean patrilineal relatedness: 0.054, mean matrilineal relatedness: 0.049).

Table 10.

Patrilineal Relatedness Between the Female-Father Dyads and Between Female-Control Male Dyads.

Female	Father	Relatedness	Control	Relatedness
Tasha	Xaver	0.516	Emil	0.035
Tipi	Yeti	0.517	Zambo	0.076
Tweety	Xaver	0.516	Emil	0.035
Undine	Zambo	0.508	Xaver	0.032
Vicky	Beetle	0.500	Adam	0.063
Vivian	Beetle	0.500	Adam	0.063
Zizi	Adrian	0.500	Zambo	0.055
Zoly	Adrian	0.500	Zambo	0.055
Zuby	Adrian	0.500	Zambo	0.055
Zwipsy	Adrian	0.500	Zambo	0.070

Table 11.

Matrilineal Relatedness Between the Female-Father Dyads and Between the Female-Control Male Dyads.

Female	Father	Relatedness	Control	Relatedness
Tasha	Xaver	0.037	Emil	0.016
Tipi	Yeti	0.048	Zambo	0.043
Tweety	Xaver	0.037	Emil	0.016
Undine	Zambo	0.070	Xaver	0.053
Vicky	Beetle	0.000	Adam	0.063
Vivian	Beetle	0.000	Adam	0.063
Zizi	Adrian	0.000	Zambo	0.055
Zoly	Adrian	0.000	Zambo	0.055
Zuby	Adrian	0.000	Zambo	0.055
Zwipsy	Adrian	0.000	Zambo	0.070

Thus we do not expect matrilineal relatedness to have been confounded with patrilineal relatedness. Advertisement calls were recorded from fathers aged 2-8 years (mean=6) and from control males aged 2-9 years (mean=7) at the time of recording. Alarm calls were recorded from fathers aged 5-8 years (mean=6) and from control males aged 6-8 years (mean=8). Mouse lemurs are sexually mature at one year old (Zimmermann & Radespiel, 2007), thus all calls were recorded from adult males. Additionally, because mouse lemurs have been shown not respond differently to calls from lemurs of different ages (Leliveld, Scheumann, & Zimmermann, 2010), we do not expect age to have confounded our results. We used calls from a total of seven males, from which five were fathers and four were unrelated males. Some fathers were also used as unrelated males for other females. Familiarity was controlled in that each female had been housed in the same room as her father and her control male for longer than six months including time during the breeding season when mating calls and alarm calls are frequently heard in the animal rooms. Lemurs in the colony have visual, olfactory, and auditory contact with the other lemurs in their rooms. Three father-daughter dyads and three control-male-female dyads had a few hours of interaction with each other. For two females (one litter: Vicky and Vivian) the father was not removed from the mother's cage until a few hours after the birth was discovered. (Normally the father is removed from the mother's cage several days before birth and is never housed in the same cage as his daughters. Adults are typically caged with 1-3 other adults, and if that is not possible, they are caged alone until a cage-mate is available). Additionally one other father-daughter dyad (Yeti-Tipi) and three control male-female dyads had a few hours of contact with each other when they were briefly put together in the recording chamber when recordings were made for this study or previous studies. Therefore, the number of father-daughter dyads and control male-female dyads that had prior experience with each other was equal and thus balanced. For each of these three father-daughter dyads and three control male-female dyads the maximum total time that they would have had together was a few hours, thus we do not expect this to have influenced the playback results and consider the females be equally familiar with both their fathers and their control males because they have shared a room with both males for more than 6 months and not been in the same cage for more than a few hours. During this study no female heard recordings that were made during a recording session in which she participated. Four control male-female dyads and one father daughter dyads were currently sharing a room at the time of the experiments. It was not possible to standardize when in the females' lives or for how long they shared the room with their fathers and control males because, over the course of their lives, the housing arrangements had always been dependent upon the needs of on-going experiments and the breeding program. We chose the subjects we did to maximize sample size and standardize familiarity as much as possible, given the housing histories and relatedness constraints within the colony. Appendix N provides the details of how familiar each female was with her father and her control male.

Subjects were habituated to the sound attenuated testing chamber though previous experiments and an extra 30 min. habituation session prior to the first session where a stimulus was presented. Each female participated in six testing sessions. Within each session the female heard four stimulus types: a mate advertisement call from her father, a mate advertisement call from her control male, an alarm call series from her father and an alarm call series from her control male. Each female heard novel call exemplars from the same pair of males in each of the six sessions (except for two females, Tasha and

Tweety, from whose father only two advertisement and alarm call sequences could be obtained). Within a session, the stimulus types were played in a randomized order and separated by a minimum rehabituation time of five minutes (previously shown to be an adequate rehabituation time for mouse lemurs (Scheumann & Zimmermann, 2008)). Sessions were conducted within the first three hours of the subjects' active period (dark period of the light cycle). Each session lasted between approximately 30 and 90 min. Subjects participated in only one session per day with a minimum of one day and a maximum of six weeks between sessions. All females' scores for further analyses were medians calculated across the sessions per stimulus type for each behavioral variable.

Each stimulus consisted of one advertisement call (typically 500-600 ms) or an alarm calls series of equal length to the advertisement call of that male (typically 5-8 calls). This stimulus was repeated three times, separated by about 3.6 seconds (mean intercall interval between advertisement calls given by wild mouse lemurs (Scheumann & Zimmermann, 2008)). Total stimulus length was approximately 12 sec. Stimuli were filtered in BatSound Pro 3.31 (low pass: 80 kHz, high pass 5 kHz), prepared in Signal 4.0., and played at 75 ±1 dB at a distance of 80 cm (RMS measurement, Brüel und Kjær Measuring Amplifier Type 2610) while the lemur licked juice from a bottle in a sound-attenuated chamber. The juice bottle guaranteed that the distance between the loudspeaker and the lemur's head was the same across all stimuli presentations, for all sessions, for all subjects. For cage set-up see Figure 13, and for additional technical details of playbacks and video analysis see prior work (Scheumann & Zimmermann, 2008).

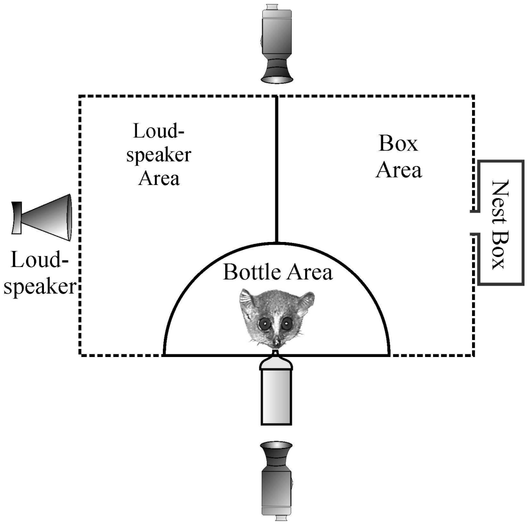

Figure 13. Cage set-up for playback experiments. The close camera is behind the drinking bottle and the wide-angle camera is behind the lemur. Latency to look to the speaker, duration of the look to the speaker, and duration of looking to the box were coded on the close camera. Latency to speaker area, duration in loudspeaker area, duration in bottle area, latency to box area, latency to box, latency to leave bottle area, duration in box area, duration in box were coded on the wide-angle camera. The sound attenuated chamber was 225 cm by 340 cm by 225 cm. The cage was 80 cm by 50 cm by 87 cm. See Appendix O for an ethogram of the scored behavioral variables.

We observed the subjects' behavior from outside the chamber on the camcorder's display screen to avoid influencing the subject. We conducted a frame-by-frame analysis during one min. after the onset of the playback in Interact 8.0.4. (Mangold, Arnstorf, Germany) analyzing 11 behavioral variables. See Appendix O for behavioral ethogram. Videos were muted and assigned random numbers before scoring, thus, as it was impossible to identify individuals on video, the experimenter was blind, while coding, to both the lemur's identity and to what stimulus was played. When the behavioral measures for the first and last sessions were compared, no habituation effects were found (Wilcoxon matched pairs tests on each of the four stimulus types, P>0.05). Intra-observer reliability was confirmed by reanalyzing 20 videos (17%); each pair of observations for each variable were not significantly different (Bonferroni corrected paired T-test, test-wide alpha>0.05) and were significantly correlated (Bonferroni corrected Spearman correlation, rho≥0.73, test-wide alpha<0.05).We ran principal components analysis on the behavioral data of the advertisement calls and the alarm calls (advertisement calls: PROC FACTOR, method=principal, SAS, Cary, USA; alarm calls: Factor analysis, principal components method, SPSS 20).We used a principal components analysis because it enabled us to simultaneously consider several behavioral responses which were coded as separate variables but are different measurements of the same underlying "latent" variable (Field, 2009). This is important because not all of the animals show the same behavioral responses. For example, one might run into the speaker area while another might look towards the speaker but not go over to it. Both demonstrate heightened attention to the speaker, and thus are considered measurements of the underlying latent variable 'Attention to Speaker.'

For each call type we analyzed the 11 behavioral variables and obtained a set of three principal components. These components explained 77% and 77% of the variation in the behavioral responses to advertisement calls and alarm calls, respectively. We conducted Bonferroni corrected Wilcoxon matched pairs tests on the component scores for each component, testing for differences between responses to fathers and unrelated males for each call type (SPSS 20, Chicago, USA). Test-wide alpha per call type was set at 0.05.

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CHAPTER 5

DISCUSSION

Summary

The main findings of this dissertation are that gray mouse lemurs show 1) patrilineal kin signatures and patrilineal kin recognition via the mating call, 2) no patrilineal signatures and a lack of patrilineal kin recognition via the alarm call, and 3) weak matrilineal signatures and a lack of evidence for matrilineal kin recognition via the agonistic call. This is the first study of kin recognition in a solitary foraging primate (see General Introduction) and as such, has far reaching implications for the evolution of primate social complexity.

This discussion has several sections: a discussion of the selective forces which produce varying degrees of kin recognition in each of these calls in mouse lemurs, the implications for current models of evolution of sociality, the need to for future work to simultaneously evaluate selection at multiple levels (i.e., individual, kin, species, etc), evaluation of conservation applications, and recommendations for future research.

Selective Forces Producing Variation in Kin Recognition

At first glance, the absence of matrilineal kin recognition and the finding of paternal kin recognition are surprising. In mammals, matrilineal kin recognition through learned familiarity with the mother (and, through her, possibly with other matrilineal kin) is expected to occur widely, due to the obligate relationship with the mother during lactation (Rendall, 2004). In contrast, paternal kin recognition is generally believed to occur through phenotype matching (sensu (Widdig, 2007): matching an unknown individual either to oneself or to known kin). While familiarity may be a possible mechanism for group-living species with high male reproductive skew where same age cohort mates are likely to be paternal half-siblings of the alpha male (Widdig, 2013), in a promiscuously mating solitary forager with no paternal care and multiple paternities in litters, like the gray mouse lemur (Eberle & Kappeler, 2004a, 2004b, 2006; Radespiel et al., 1998; Radespiel et al., 2002; Radespiel, Sarikaya et al., 2001), familiarity is not likely to be reliable. These different mechanisms produce predictable differences in how widespread vocal recognition of maternal and paternal kin is. Matrilineal kin recognition via vocalizations has been widely documented in social mammals (i.e., primates (Cheney & Seyfarth, 1980; Nunn, 2000; Rendall, 2004; Rendall et al., 2009; Rendall et al., 1996; Seyfarth & Cheney, 2003), hyenas (Holekamp et al., 1999), elephants (McComb et al., 2000; McComb et al., 2003), pinnipeds (Insley et al., 2003), goats (Briefer & McElligott, 2011; Briefer et al., 2012), bats (Balcombe, 1990; Knoernschild & Von Helversen, 2008)). Far less work has been done on vocal recognition of maternal kin in less social species, though recognition is often inferred via other cues (i.e., (Eberle & Kappeler, 2006; Stoen et al., 2005). In contrast, while long-term field studies suggest that social mammals often behave as if they recognize paternal kin (i.e., baboons: (Buchan et al., 2003), hyenas: (Van Horn et al., 2004; Wahaj et al., 2004), reviews: (Silk, 2009; Widdig, 2007)), far less is known about the mechanisms involved. Studies investigating the cues have shown that macaques use vocalizations for paternal kin recognition (Pfefferle et al.,

2014) and that laboratory rodents use olfaction (i.e., (Kruczek & Golas, 2003; Todrank et al., 2005), review: (Widdig, 2007)).

Given this prevalence of maternal kin recognition and rarity of evidence for paternal kin recognition via vocalizations (citations above), at first glance our results are surprising. However, they can be understood as being a result of the different selective pressures on the different call types due to call function and call acoustics. Since paternal kin recognition was found ((Kessler et al., 2012), Chapter 4), I do not expect the lack of maternal kin recognition to be due to a cognitive inability to recognize maternal kin. Instead, I expect that the lack of matrilineal kin recognition is due to the call type tested.

The mating call is a long-distance, frequency modulated, harmonic call with a complex acoustic structure that is well suited to displaying individual and patriline signatures though the patterning of the modulations (Leliveld et al., 2011; Zimmermann & Lerch, 1993). These signatures and their recognition are likely to be integral to the call's function for long-distance mate recruitment and inbreeding avoidance (Kessler et al., 2012; Leliveld et al., 2011; Zimmermann & Lerch, 1993). As such, the paternal kin recognition I observed is likely to be a crucial element of the dispersed social networks of gray mouse lemurs ((Kessler et al., 2012), Chapter 4).

The alarm call is a long-distance, largely non-frequency modulated harmonic call with individual signatures but no signatures for patriline (Leliveld et al., 2011). The less complex acoustic structure, relative to the mating call (Leliveld et al., 2011), may also make this call less suited for displaying kin signatures ((Kessler et al., 2012), Chapter 4). This call is given in disturbance situations, including when mobbing predators (Eberle &

Kappeler, 2008; Leliveld et al., 2011). Mobbing behavior is not restricted to situations benefitting kin (Eberle & Kappeler, 2008) and I did not find evidence of paternal kin recognition based on this call ((Kessler et al., 2012), Chapter 4).

The agonistic call is a short-distance, frequency modulated call that is harmonic, but noisier than the mating call and the alarm call (Leliveld et al., 2011). The acoustic structure is more modulated than the alarm call and it has signatures for individual and weak signatures for matriline ((Kessler et al., 2014; Leliveld et al., 2011), Chapter 2). Though the agonistic call is a high amplitude call, it is given during conflicts with conspecifics that are within close range ((Kessler et al., 2014; Leliveld et al., 2011), Chapter 2). In contrast to findings in monkeys and hyenas (i.e., (Cheney & Seyfarth, 1980, 1999; Fischer, 2004; Fugate et al., 2008; Holekamp et al., 1999; Wittig et al., 2007)), mouse lemurs do not appear to use agonistic calls to monitor agonistic interactions involving kin (Chapter 3). Therefore, though this is a high amplitude call which should be audible to out-of-sight conspecifics, it does not appear to facilitate kin selection over the dispersed social networks via the recruitment of support from maternal kin (Chapter 3).

There are two contrasting, but not necessarily mutually exclusive theories regarding the selective pressures produced by the distance at which a social call is typically given. The first suggests that stronger individuality is expected in long distance calls which are given when the listener is likely to be far away and therefore must be identified without the assistance of visual and olfactory cues (Leliveld et al., 2011; Mitani et al., 1996). In contrast other researchers suggest that the pairing of vocal signatures (i.e., individual signatures) with an individuals' behavior (i.e., aggressive chasing, attacking) serves to establish a lasting relationship between the caller and listener (i.e., a dominance hierarchy) in which that vocal signature will be associated with the fear induced by the prior aggression or coalitionary behavior with kin (Owren & Rendall, 1997, 2001). Given that I found stronger kin recognition based on the mating call (long distance social cohesion call) than in the agonistic call (short distance, non-cohesive call) ((Kessler et al., 2012), Chapters 3-4), our data support the former theory (Leliveld et al., 2011; Mitani et al., 1996). Since mouse lemurs are solitary foragers who compete largely by scramble, not contest competition (Dammhahn & Kappeler, 2009, 2010; Eberle & Kappeler, 2002, 2004a, 2004b; Kappeler & van Schaik, 2002; Radespiel, Ehresmann et al., 2001; Thoren et al., 2011), conditioning a fear response into subordinates is likely to be less important in mouse lemurs relative to group-living species (Chapais, 1995; Owren & Rendall, 1997, 2001; Silk, 2002, 2007b; Silk et al., 2004).

Our findings also suggest that source filter theory (i.e., Ey et al., 2007; Fant, 1960; Fant et al., 2000; Fitch, 1997, 2010; Fitch & Hauser, 1995; Hauser et al., 1993; Owren & Linker, 1995; Owren & Rendall, 1997, 2001; Rendall et al., 2005) is not as relevant for the ultrasonic/high frequency calls of mouse lemurs as it is for larger bodied species (Ehret, 2006; Leliveld et al., 2011). In contrast to larger bodied species like baboons, macaques or humans, for which formant frequencies and format dispersion is often highly important for producing acoustic signatures (Fitch, 1997; Fitch & Fritz, 2006; Fitch & Hauser, 1995; Owren & Rendall, 1997, 2001; Rendall et al., 2005), in these mouse lemur calls the harmonics are too widely spaced to produce strong formants

(Leliveld et al., 2011). Their signatures appear to be produced by the contour of the fundamental frequency (Ehret, 2006; Leliveld et al., 2011). Given that mouse lemurs have been proposed to call in the high frequency/ultrasonic range as a predator defense against owls which do not hear such high frequencies, coding signature information in the frequency contour may be a result of selection to convey signature information without lowering the calls' frequencies and breaking crypsis (Zimmermann, 1995a). It is important to realize that none of these theories are mutually exclusive and, given that each has some support in the literature (see citations above), each has likely contributed to shaping the evolution of vocal communication. However, it is also clear that the selective forces acting upon the vocalizations of large-bodied, highly social species may be different than those acting upon small-bodied, solitary or solitary foraging species (Zimmermann, 1995a).

Furthermore, while playback experiments deliberately isolate only one type of cue, that of the vocalization, in the wild, communication is highly multi-modal including potentially visual, olfactory, and/or spatial information. Therefore, it may not be necessary for perfect discrimination to occur based solely upon acoustic cues. Given that, the perception of pheromones is expected to be highly important for mouse lemurs, (Hohenbrink, Mundy, Zimmermann, & Radespiel, 2013; Hohenbrink, Radespiel, & Mundy, 2012; Yoder et al., 2014), olfactory signals are expected to be rich in complementary information. Furthermore, mouse lemurs have been shown to have spatial memories for food resources (Joly & Zimmermann, 2007; Lührs, Dammhahn, Kappeler, & Fichtel, 2009), therefore it is not difficult to image that they could also use these abilities to remember the location of each neighbor's range. A combination of imperfect information from all of these channels of information may be sufficient to produce reliable enough information for kin recognition and selection to occur.

Implications for the Evolution of Sociality

There are two contrasting, though not necessarily mutually exclusive, possibilities for the role of kin recognition in the evolution of mammalian social complexity and I will consider to what extent the data presented in this dissertation supports or does not support each.

The first is the cryptic kin selection model (Hatchwell, 2010) which predicts that kin-biased sociality could evolve in a population where kin are spatially clustered when animals behave altruistically towards their neighbors (who will then, on average, be kin). This model does not require any kin recognition more precise than recognition based on spatial cues (Hatchwell, 2010). Thus recognition based upon familiarity or upon phenotype matching is not required (sensu (Widdig, 2007)). In contrast, the social network model predicts that the social networks of solitary foragers provided the foundation for the evolution of more complex forms of sociality (Müller & Thalmann, 2000). It follows from this model, that if solitary foragers were able to use these social networks to recognize kin, that these social networks may have then facilitated the kin selection that drove the evolution of kin based social groups (Kessler et al., 2014; Kessler et al., 2012). The social network model is compatible with evidence suggesting that the neurophysiological structures involved in mammalian mother-infant recognition and bonding were the evolutionary basis from which other forms of mammalian social bonding evolved, including the various forms of primate social complexity (Broad, Curley, & Keverne, 2006; Müller & Thalmann, 2000) and with models arguing that gregarious sociality evolved via kin recognition and nepotism in the philopatric sex (i.e., (Perrin & Lehmann, 2001; Waser & Jones, 1983).

I conclude that our data offer tentative support for the social network model, but do not definitively reject the cryptic kin selection model (Hatchwell, 2010; Kessler et al., 2014; Kessler et al., 2012; Müller & Thalmann, 2000). That patrilineal kin recognition was found via the mating call supports the social network theory ((Kessler et al., 2012), Chapter 4). Given that females are the philopatric sex (Radespiel et al., 2003; Schliehe-Diecks et al., 2012), basing mate choice solely upon what males they encountered in their ranges would put them at a high risk for mating with fathers and paternal brothers. Thus, the cryptic kin selection model would seem to have significant disadvantages for the recognition of patrilineal kin in the typical mammalian social system with male dispersal.

However, the social networks model was also not supported by our findings showing a lack of kin recognition based on the alarm and agonistic calls ((Kessler et al., 2012), Chapters 3-4). The lack of kin recognition using these call types suggests that the function of these calls within the social networks is not to facilitate kin selection via alarm calls to/from kin or via coalitionary behavior with kin as would be expected by the social network model (Müller & Thalmann, 2000). Thus, the lack of kin biased behavior via these calls underscores the differences in the degree of kin-biased behavior in social species and solitary foraging species (Chapais & Berman, 2004; Kappeler, 2008; Perrin & Lehmann, 2001; Silk, 2007b, 2009; Waser & Jones, 1983).

At first glance, it would appear that the lack of kin recognition based on the alarm and agonistic calls supports the cryptic kin selection model ((Hatchwell, 2010; Kessler et al., 2014; Kessler et al., 2012), Chapters 3-4). The lack of kin recognition based on the alarm call is consistent with previous work invoking cryptic kin selection as an explanation for when two mouse lemurs, after hearing vocalizations from an unrelated conspecific caught by a snake, approached and cooperatively attacked a snake until it released the conspecific (Eberle & Kappeler, 2008). Similarly, I found that, in contrast to socially complex monkeys and hyenas (Cheney & Seyfarth, 1980, 1999; Holekamp et al., 1999) mouse lemurs do not use agonistic calls to recognize their kin (Chapter 3). Had they done so, it would have suggested that the social networks of solitary foragers may facilitate the evolution of kin recruitment via agonistic calls. However, our data do not support this scenario. Instead, perhaps a lack of discrimination fosters social tolerance. Social tolerance has been suggested to facilitate high density populations, leading to increasing levels of home-range overlap and interaction among individuals, and thus increasing levels of sociality (Maher, 2009a, 2009b; Meshriy et al., 2011; Messier et al., 2012; Silk, 2007a). Therefore, if animals are not able to recognize their kin, it may inhibit aggression among neighbors, and thus, in a social system where kin were spatially clustered landscape, facilitate social tolerance among kin. (But see (Hurst & Barnard, 1995) an example where a lack of kin recognition created social intolerance).

However, the cryptic kin selection model predicts that kin selection occurs even when kin recognition based on cues other than spatial cues does not occur (Hatchwell, 2010). While our data showed that kin recognition did not occur based on the alarm and agonistic calls ((Kessler et al., 2012), Chapters 3-4)), it does not show that kin selection occurred despite of this lack of kin recognition. In order for the model to be supported, data are needed showing that kin selection is occurring based on these calls, even though kin recognition did not occur (Hatchwell, 2010). For example, cryptic kin selection might be supported if further studies show that mouse lemurs' alarm calls routinely benefit kin based on the spatial proximity of listening kin. While this does not seem unlikely, further studies would be necessary to decisively demonstrate it.

Similarly, cryptic kin selection via the agonistic call would be supported if future studies were to show that despite a lack of kin recognition, females use the agonistic call to recruit other females to support them during conflicts and that, due to spatial proximity, females are more likely to intervene on behalf of related females (recruitment during agonistic conflicts has not, to our knowledge, been shown in this species). Therefore, for both the alarm calls and agonistic calls, further work is necessary to fully test the cryptic kin selection model.

An additional, but important limitation of our data is that it is not able to differentiate between different models predicting *which forms* of gregarious sociality evolved first in primates. Various models include 1) the socio-ecological model which has been predicted to produce an 'unstructured' model in which all transitions are equally likely (i.e., pairs to multi-male, to harems), and are produced by individual reactions to resource availability (Eberle & Kappeler, 2002; Kappeler & van Schaik, 2002; Shultz et al., 2011; Sterck, Watts, & van Schaik, 1997) or 2) various step-wise models which argue that certain transitions are more likely than others (i.e., (Müller & Thalmann, 2000; Shultz et al., 2011)). Though our data cannot support one pattern of evolutionary transitions over others, our finding of patrilineal kin recognition via mating vocalizations, in combination with previous work suggesting non-acoustic recognition of maternal kin (recognition of own infants in the nest by mouse lemur mothers (Eberle & Kappeler, 2006)), suggests that whatever the pattern of transitions was, it was probably structured, at least in part, by kin relations. I say ‘at least in part’ because transitions from nocturnality to diurnality and the corresponding changes in predator avoidance are also believed to have been pivotal (Müller & Thalmann, 2000; Shultz et al., 2011). However, I suggest that activity period models are not necessarily mutually exclusive with models arguing for the importance of kin relations and dispersal patterns (i.e., (Perrin & Lehmann, 2001; Waser & Jones, 1983)).

Levels of Selection

An additional question that is highly relevant to understanding how social complexity evolved, is the question of on which level selection is primarily acting (Grafen, 1990; Rendall, 2004; Tang-Martinez, 2001). The presence of kin group signatures and evidence that animals use these cues to bias their behavior in favor of kin, does not necessarily mean that selection is acting upon that cue type to facilitate this kin recognition (Grafen, 1990; Rendall, 2004; Tang-Martinez, 2001). Though several theorists have raised this issue (Grafen, 1990; Rendall, 2004; Tang-Martinez, 2001), it has not received wide-spread attention. These authors each question whether the existence of a signature, which may then be used for recognition, is really a result of selection at that level (Grafen, 1990; Rendall, 2004; Tang-Martinez, 2001). They question whether it could be a result of selection for individual distinctiveness or species specific vocalizations (Grafen, 1990; Rendall, 2004; Tang-Martinez, 2001). Under this model, kin signatures may still occur and even facilitate kin selection, but this still may be just a side-effect of selection at a different level (Grafen, 1990; Rendall, 2004; Tang-Martinez, 2001). Significant possibilities are that selection may occur at the level of species specific calls, i.e., mating calls as part of mate recognition systems, or at the level of individually distinctive calls as a way of facilitating social systems with long-lasting, complex relationships between individuals (Grafen, 1990; Rendall, 2004; Tang-Martinez, 2001). To make the question even more complicated, selection at each of these levels is not likely to be mutually exclusive with the others, thus selection for distinctiveness and recognition could occur at the level of the individual, the kin group, and the species simultaneously with varying degrees of strength that could change over time.

In order to deal with this problem we need a framework with which we can test hypotheses of selection at these different levels against each other. I would propose that when selection is targeting one level stronger than the other, that differentiation should be more pronounced at that level. I would recommend testing this in three ways. The first is to run the discriminant function tests on as many levels as possible, i.e., on both kin groups to determine classification accuracy by kin group and on individuals, to determine classification accuracy by individual. Classification should be more accurate at the level where selection is acting the most strongly. The second is to use a ratio of acoustic distances between calls at the different levels. Doing so would enable researchers to compare the relative distances within and between one level (i.e., individuals), to within and between another level (i.e., kin groups) (examples of distance measures and their usages: (Gasc et al., 2013; Kastein et al., 2013; Kessler et al., 2014; Kessler et al., 2012; Pröhl, Hagemann, Karsch, & Hobel, 2007; Pröhl, Koshy, Mueller, Rand, & Ryan, 2006). The relative sizes of these ratios should be highly informative. Third, recognition should be tested at the different levels (i.e., (Rendall et al., 1996)). The null hypothesis is that the strength of recognition should be related to the strength of the signature at that level. However, what we as scientists measure is not always what the animals themselves find to be biologically relevant (i.e., (Fugate et al., 2008)). Therefore, performing playback studies should also be made a priority.

Only when we begin to have a picture of how distinctiveness and recognition varies at these different levels within and across species will be able to examine whether signatures at these different levels are evolving independently and doing so will tell us a great amount about the evolution of acoustic signatures and their relative significances for the evolution of sociality (Grafen, 1990; Rendall, 2004; Tang-Martinez, 2001).

Conservation Implications

A current trend in applied acoustics is the non-invasive, relatively inexpensive technique of acoustic monitoring. Previous research has advocated using vocalizations to conduct inexpensive, non-invasive censuses of species diversity (bats: (Fukui, Agetsuma, & Hill, 2004; Hourigan, Catterall, Jones, & Rhodes, 2008; MacSwiney, Clarke, & Racey, 2008; Papadatou, Butlin, & Altringham, 2008; Preatoni et al., 2005; Russo & Jones, 2003; Rydell, Arita, Santos, & Granados, 2002; Vaughan, Jones, & Harris, 1997), sportive lemurs: (Mendez-Cardenas et al., 2008), frogs: (Bridges & Dorcas, 2000)), population density (primates: (Aldrich, Molleson, & Nekaris, 2008; Buckley, Nekaris, & Husson, 2006; Estrada, Luecke, Van Belle, Barrueta, & Meda, 2004; Geissmann & Nijman, 2006)), and population distribution (underwater seals and porpoises: (Van Parijs, Lydersen, & Kovacs, 2003; Wilson, Benjamins, & Elliott, 2014)). One of the goals of this dissertation was to investigate the feasibility of using vocalizations to inexpensively and non-invasively census kin groups. Though high frequencies are very vulnerable to degradation via attenuation and reverberation (Marten & Marler, 1977; Marten, Quine, & Marler, 1977; Masters, 1991; Mitani & Stuht, 1998; Richards & Wiley, 1980; Wiley & Richards, 1978, 1982), the success of acoustic surveys using bat calls is well documented (Fukui et al., 2004; Hourigan et al., 2008; MacSwiney et al., 2008; Papadatou et al., 2008; Preatoni et al., 2005; Russo & Jones, 2003; Rydell et al., 2002; Vaughan et al., 1997). Thus, I had hoped that monitoring in multiple locations might be able to provide an estimate of the number of female sleeping groups or male patrilines in the population. Such a monitoring program would have the advantage of inexpensively monitoring baseline population structure and tracking changes could alert researchers to a population breakdown requiring immediate conservation action.

Unfortunately, I do not see this as being very feasible with the gray mouse lemur population and suspect that these findings would probably generalize to other mouse lemur species. I do not expect acoustic monitoring of kin groups to be highly successful due to 1) relatively low classification rates by kin group using differing call types and 2) the high frequency/ultrasonic calls do not carry well enough over long distances (Marten & Marler, 1977; Marten et al., 1977; Richards & Wiley, 1980; Wiley & Richards, 1978, 1982), and 3) low calling rates in this cryptic species.

Because the rates of successful classification by kin group are noticeably lower than that of classification by individual (79% of mating calls correctly classified by patriline, 45% for alarm calls by patriline, and 47% for agonistic calls by matriline (Kessler et al., 2014; Kessler et al., 2012), Chapters 2 and 4)), I suggest that kin groups may not be the most practical unit for such monitoring. Prior work has shown that classification by individual is more accurate (89% for mating calls, 63% for alarm calls, 62% for agonistic calls ((Leliveld et al., 2011), see also (Zimmermann & Lerch, 1993)). In addition, given that some vocalizations (i.e., mating calls) have been shown to be species specific, even among closely related sympatric species (Braune et al., 2008), classification by species or individual using these vocalizations is likely to be more reliable.

An additional significant challenge to such an acoustic remote monitoring system is the likelihood of false negatives. Because many of the most frequent mouse lemur calls (mating calls, alarm calls, agonistic calls (Leliveld et al., 2011)) are high frequency or ultrasonic calls, they are very vulnerable to degradation via attenuation and reverberation

(Marten & Marler, 1977; Marten et al., 1977; Richards & Wiley, 1980; Wiley & Richards, 1978, 1982), thus they do not travel well over long distances. In addition, because mouse lemurs primary defense against predators is crypsis ((Zimmermann, 1995a, 1995b), the number of individuals estimated in the population via acoustic monitoring must be regarded as a minimum number and that the actual number may be significantly higher.

In conclusion, given these challenges, it is difficult to say whether the rate of false negatives would be so high as to make it too inefficient to be cost effective. Before widespread implementation, this technique should be tested in a population of known density during the breeding season when the likelihood of recording the highly species and individually distinctive mating calls is highest. This could be tested as follows: 1) sound pressure tests of diffusion rates through the habitat (during different weather conditions) would need to be done to estimate what the spatial coverage of one recording device would have, so that no “holes” were left unrecorded. Ideally, an animal calling between two recorders should be recorded on both recorders and they should be synchronized so that researchers could identify the animal as the same individual. This would provide evidence that the entire area had sufficient coverage. Then if the estimates of the density of the population were sufficiently close to the known density, this would validate the accuracy of the technique. Then additional tests could be done outside the mating season to determine whether this technique would also achieve accurate measures of population size during seasons when the animals are less vocal. Given that my experience suggests that not all lemurs vocalize each night, a scaling factor would need to be developed so that the minimum number of vocalizing individuals could be calculated and then from that number, scaled up to give an approximate number of animals present in the habitat.

However, this has several serious drawbacks. It is based on several important assumptions (i.e., that enough individuals will vocalize in any given night and that this minimum number of vocalizing individuals could be reliably scaled up to produce an accurate estimate of population size) which would need to be tested in populations of known densities. Furthermore, the cost (i.e., recording equipment) and effort required to set up, test, and validate such a monitoring method is significantly higher than that of conducting a few nights of trapping or census walks, especially when this species can be very reliably trapped. Therefore, such an acoustic monitoring system is only likely to be valuable for situations where trapping and census walks are not possible. That said, acoustic monitoring of species, individuals and kin groups may be more practical in species that are more vocal and give lower frequency calls which would then carry further (Marten & Marler, 1977; Marten et al., 1977; Richards & Wiley, 1980; Wiley & Richards, 1978, 1982), thus requiring fewer recording devices in the environment (i.e., guereza colobus (Schel & Zuberbühler, 2012) or indri (Giacoma, Sorrentino, Rabarivola, & Gamba, 2010), in which many groups frequently chorus).

Methodological Issues and Recommendations for Future Research

My original methodology for this dissertation was to use the gathering calls, which, like the mate advertisement calls, have a highly modulated trill structure and are sometimes given when groups are gathering at sleeping sites at dawn (SEK, pers. obs. 2011). In a closely related species, *M. ravelobensis,* these gathering calls have been found to be distinctive by social group (Braune et al., 2005).

During the first half of the first season of fieldwork (May-July of 2010) and briefly during the beginning of the second season (May, 2011) I attempted to record these gathering calls. I sat, often from 12am to 6 am, near the sleeping sites and attempted to record vocalizations when the mouse lemurs entered their sleeping sites. Unfortunately, it was extremely difficult to get recordings of calls. In 2010, many of the lemurs were only occasionally observed to sleep in groups (unpublished data). When they slept alone, they did not vocalize upon approaching the sleeping site. I also frequently found that when I sat quietly and waited by a frequently used sleeping site, on the nights when I was there, either the lemurs did not come or only one lemur came. I attempted to follow the lemurs to their sleeping sites, but found that the noise of me moving through the forest 1) made the lemur run quickly away from me without vocalizing and 2) made so much background noise that high quality recordings would not have been possible even if the lemurs had vocalized. A few times I did manage to be at the sleeping site waiting silently when the lemurs came and did hear a few calls but I was 1) unable to identify the caller and 2) unable to obtain high quality recordings. The caller could not be identified because 1) only one of the lemurs in the group had a collar, 2) the lemurs were running through the treetops in the dark, and 3) high frequency calls are difficult to localize (Marten & Marler, 1977; Marten et al., 1977; Richards & Wiley, 1980; Wiley & Richards, 1978, 1982), thus it is necessary to see the caller's mouth or abdomen move during calling.

Furthermore, the calls that I did record had a very low signal to noise ratio and were not suitable for further usage. Because high frequency calls do not transmit well over distances (Marten & Marler, 1977; Marten et al., 1977; Richards & Wiley, 1980; Wiley & Richards, 1978, 1982), obtaining a high signal to noise ratio is very difficult from a distance of even a few meters. I also attempted to record gathering calls from females housed together in temporary captivity, but I found that no gathering calls were given, even when the females co-slept. As gathering calls are believed to be used for communication with conspecifics who are out of visual contact (Braune et al., 2005), individuals may not be motivated to vocalize to conspecifics with whom they are sharing a cage.

These experiences suggest that for researchers wishing to record gathering calls, it would be necessary to provide the lemurs with high quality sleeping sites which they will use with a high site fidelity and pre-install recording equipment in those sleeping sites. This may be possible using pre-installed nest boxes and adapting the field procedure used in Kirindy (Eberle & Kappeler, 2006) or in captivity using similar methods. Under these conditions, identifying callers would only be possible if 1) video cameras were also installed remotely and synchronized with the recording equipment or 2) the sleeping boxes contained microchip readers inside them which were then synchronized with the recording equipment. Future playback studies using gathering calls should then be conducted at or near the sleeping sites at dawn.

For such playback studies, it may be advantageous to modify the feeding platform paradigm used in this dissertation. I found that during the dry season, banana is a very highly valued resource for the lemurs and as such, they were strongly motivated to continue eating, regardless of whether they heard an agonistic call from a stranger or kin. This makes it difficult to distinguish whether they were unable to recognize their kin or whether they recognized kin, but were not motivated to react differently to kin and nonkin. This study built upon a large history of studies which have successfully used looking time as response variables with which to determine individual/kin/species recognition (i.e., (Cheney & Seyfarth, 1980, 1999)). However, given that female mouse lemurs are strongly motivated to continue eating, especially at the end of the dry season when they are all potentially pregnant (SEK, pers. obs.), I would recommend measuring alternative behavioral variables. I would recommend conducting playback experiments at a feeding platform combined with multiple artificial sleeping boxes set-up with pre-installed cameras/microchip readers in them. The sleeping boxes should be arranged in different directions equi-distance from the platform but out of sight (i.e., one to the north, south, east and west of the platform). The sleeping boxes should be installed several months in advance so that the lemurs can find and use the sleeping boxes. Then, when these are recognized sites, I would play gathering calls from kin or nonkin from the different boxes to a lemur while she eats at the platform shortly before dawn. I would hypothesize that after finishing eating the banana, she would be more likely to approach and look inside the nest box from which a kin call was played relative to the other available nest boxes. I would hypothesize that she would be less likely to approach and look inside the nest box from which a nonkin call was played, relative to the other available nest boxes.

This set-up could be used in the field or adapted for the lab; however, looking time may still be a useful variable to measure in the lab since females would be under significantly less nutritional stress. While wild females may be under strong pressure to continue feeding unless their own survival is immediately at risk, captive females may be better able to spare the energy to give more attention to, and thus show behavior distinguishing between, the kin and nonkin callers.

An additional avenue for future research is to investigate differences in kin recognition within mouse lemurs. Given that these species show great differences in their degrees and type of sociality (i.e., (Dammhahn & Kappeler, 2005; Eberle & Kappeler, 2006; Radespiel, 2000; Radespiel et al., 1998; Radespiel et al., 2009; Radespiel, Sarikaya et al., 2001; Weidt et al., 2004)), this provides an excellent way to relate differences in social systems to differences in kin recognition. While very little is known about the social systems for many of the newly discovered species, future studies of those that are known would be highly informative. For example, *M. ravelobensis* also forms daytime sleeping groups, but these groups are more often mixed sex sleeping groups than in *M. murinus* (Eberle & Kappeler, 2006; Radespiel et al., 2009; Radespiel, Sarikaya et al., 2001; Weidt et al., 2004). Furthermore, *M. berthae* forms less stable sleeping groups, with individuals often sleeping alone, though unlike *M. murinus* and *M. ravelobensis* all male sleeping groups have been observed (Dammhahn & Kappeler, 2005). Based on the results presented in this dissertation, I would predict that across mouse lemur species, maternal kin recognition (proximate mechanism of familiarity (Rendall, 2004)) should correlate with the level of sociality among maternal kin (of both sexes) while paternal kin recognition (proximate mechanism of phenotype matching (Widdig, 2007)) should be relatively similar across species because all species will need to avoid inbreeding. If the comparative sample were then expanded beyond *Microcebus* to include the pair-living *Cheirogaleus* and *Phaner* (Fietz, 1999; Fietz & Dausmann, 2003; Fietz, Zischler, & Schwiegk, 2000; Schülke, 2005; Schülke & Kappeler, 2003; Schülke, Kappeler, & Zischler, 2004; Schülke & Ostner, 2005), I would then expect paternal kin recognition to occur through both familiarity and phenotype matching. I would expect that social fathers/offspring would recognize each other as kin even if they are not genetically related (for information on extra-pair paternities: (Fietz et al., 2000; Schülke et al., 2004)). Furthermore, if individuals recognize paternal kin via phenotype matching similarly to the gray mouse lemur ((Kessler et al., 2012), Chapter 4), then I would expect inbreeding avoidance among paternal kin of extra-pair paternities even if they do not share a nest. More data is urgently needed on *Mirza* (Kappeler, Rasoloarison, Razafimanantsoa, Walter, & Roos, 2005; Kappeler, 1997b; Rode et al., 2013; Schülke & Ostner, 2005) and *Allocebus* (Biebouw, 2009; Biebouw, Bearder, & Nekaris, 2009), which appear to show flexible sleeping patterns. As more becomes known about these species, comparisons should be highly informative.

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APPENDIX A

THE 25%, 50%, AND 75% QUARTILE OF THE ACOUSTIC PARAMETERS INCLUDED IN THE PRINCIPAL COMPONENT ANALYSIS FOR EACH FEMALE AND FOR EACH KIN GROUP

K	**Ind**	**F_0S (Hz)**			**F_0Peak (Hz)**			**F_0E (Hz)**			**Start Bandwidth (Hz)**			**Call Duration (ms)**			**Time to Peak (ms)**			**Inter-call Interval (ms)**		
		25%	**50%**	**75%**	**25%**	**50%**	**75%**	**25%**	**50%**	**75%**	**25%**	**50%**	**75%**	**25 %**	**50 %**	**75 %**	**25 %**	**50 %**	**75 %**	**25 %**	**50 %**	**75 %**
1	06-09	8008	10352	11133	11670	11719	12354	11035	11817	12207	3036	3326	3590	25	29	33	21	23	28	129	160	294
	19-10	8496	8984	9375	12451	13477	14453	9180	9668	10156	3141	3590	3986	31	33	41	17	20	22	77	82	95
	41-11	10156	10352	12012	13818	14648	15430	10938	11231	11866	3643	4065	4646	31	36	43	17	20	24	110	140	174
	Grp 1	**8789**	**10156**	**10596**	**12012**	**13379**	**14502**	**9961**	**10938**	**11768**	**3274**	**3590**	**4145**	**29**	**33**	**40**	**19**	**21**	**23**	**91**	**125**	**167**
2	51-10	9766	12402	12549	20117	22461	24072	12745	13575	14648	2904	3485	4488	39	41	47	19	21	26	123	227	275
	58-10	10547	11621	12207	12695	13672	14112	11670	12402	13086	3274	4013	4435	37	40	41	20	22	23	145	199	225
	11-11	12988	13477	13916	14649	15235	16455	12988	13477	14112	3276	3878	4665	33	35	47	15	17	18	55	75	113
	Grp 2	**11279**	**12500**	**13135**	**14014**	**15235**	**20459**	**12305**	**13184**	**13721**	**3247**	**3696**	**4435**	**36**	**40**	**42**	**17**	**20**	**22**	**109**	**141**	**225**
3	10-10	9521	9766	10742	12012	12989	15186	9717	10156	11036	2614	2904	4488	43	53	60	26	27	33	104	156	236
	112-10	7727	7983	8459	9119	10474	11206	8936	9229	10180	2872	3041	4055	43	46	51	27	29	32	184	274	314
	Grp 3	**7947**	**9082**	**9766**	**10364**	**11280**	**13037**	**9155**	**9888**	**10657**	**2772**	**3041**	**4055**	**43**	**50**	**56**	**26**	**29**	**32**	**147**	**208**	**283**
4	45-10	10156	11133	11133	12451	12793	13916	9961	11036	11328	2772	3696	4118	38	40	41	16	17	18	202	215	227
	101-10	10693	11426	11523	11865	12695	13379	10742	11036	11377	3115	3485	3907	42	49	50	26	28	30	153	165	189
	Grp 4	**10596**	**11133**	**11475**	**12354**	**12695**	**13672**	**10596**	**11036**	**11328**	**3089**	**3643**	**3907**	**39**	**42**	**49**	**17**	**21**	**28**	**161**	**201**	**218**
5	113-10	10156	10449	10547	10889	11914	12109	9570	9961	10254	2904	4752	5148	37	53	62	16	19	28	138	145	208
	52-11	11719	11914	12207	13184	13575	15039	11670	12500	14258	3722	4963	5887	39	61	69	18	26	30	112	153	162
	Grp 5	**10400**	**11426**	**11914**	**11914**	**12598**	**13623**	**9864**	**10742**	**12500**	**3564**	**4805**	**5649**	**38**	**57**	**64**	**17**	**22**	**29**	**137**	**152**	**175**

	28-09	11279	11328	12207	17529	18848	20898	11133	11133	11621	4066	4419	5006	38	40	43	15	17	18	81	116	147
	17-10	11475	11523	12354	18067	19336	19531	16846	18946	19385	2688	3145	5084	12	17	19	11	14	14	162	175	184
6	36-11	13672	14746	17041	19238	20703	21973	13721	14746	15772	5913	8659	15259	19	22	25	11	13	15	52	60	74
	46-11	9912	10938	11768	12451	12793	12891	8984	9668	11914	2851	3274	4277	27	64	68	16	22	22	71	93	115
	Grp 6	**11182**	**11621**	**13232**	**14063**	**18848**	**20459**	**11133**	**12500**	**16699**	**3089**	**4298**	**6151**	**18**	**25**	**42**	**13**	**15**	**18**	**71**	**104**	**162**

Note. Values are calculated across all calls for all individuals in that kin group. Kin group values are bolded. “K” is kin group. “Ind” is the individual.

APPENDIX B

PERCENTAGES OF EACH INDIVIDUAL’S CALLS THAT WERE CORRECTLY AND INCORRECTLY CLASSIFIED INTO THE DIFFERENT KIN GROUPS USING PCA1 AND PCA2 IN A NONPERMUTATED DISCRIMINANT FUNCTION ANALYSIS

Kin Group	Individual	Percent Classified into Kin Groups					
		1	2	3	4	5	6
1	41-11	**60**	10	0	0	10	20
	19-10	**90**	0	0	0	10	0
	06-09	**70**	10	20	0	0	0
	Mean	**73.3**	6.7	6.7	0.0	6.7	6.7
2	11-11	0	**0**	0	0	0	100
	51-10	30	**0**	0	0	0	70
	58-10	70	**30**	0	0	0	0
	Mean	33.3	**10.0**	0.0	0.0	0.0	56.7
3	112-10	20	0	**80**	0	0	0
	10-10	30	0	**10**	0	60	0
	Mean	25.0	0.0	**45.0**	0.0	30.0	0.0
4	101-10	60	0	0	**0**	40	0
	45-10	100	0	0	**0**	0	0
	Mean	80.0	0.0	0.0	**0.0**	20.0	0.0
5	52-11	0	20	0	0	**60**	20
	113-10	50	0	0	0	**50**	0
	Mean	25.0	10.0	0.0	0.0	**55.0**	10.0
6	17-10	0	0	0	0	0	**100**
	28-09	10	40	0	0	0	**50**
	46-11	0	30	0	0	70	**0**
	36-11	0	0	0	0	0	**100**
	Mean	2.5	17.5	0.0	0.0	17.5	**62.5**

Note. Correct classifications are bolded.

APPENDIX C

SUMMARY OF THE DATA USED TO FORM THE KIN (K), NEIGHBOR (N), CAGE-MATE (C), AND STRANGER (S) DYADS

Listener	Caller	R	Mt: L/C	Co-sleep	Listener captured	Caller captured	LMM	K vs. N	K vs. C	K vs. S	N vs. S
10-10	112-10	0.41[a]	H6/H6	Y	DVII,DVI,EVI	DVII,CVII	K	Y	Y	Y	
11-11	51-10	0.34[c]	H6/H6	Y	EVII,DVI,CVI	EW,FW,EVIII,FVIII,DVIII,GW	K	Y	Y		
11-11	58-10	0.62[a]	H6/H6	Y	EVII,DVI,CVI	FW,EW	K	Y			
101-10	45-10	0.51[a]	H3/H3	Y	GVI,FVI	GVI	K	Y			
17-10	28-09	0.52[a]	H4/H4	Y	FI,GI,GII-GI,GE	GE-GI,GE,GI	K		Y	Y	
17-10	46-11	0.44[a]	H4/H4	Y	FI,GI,GII-GI,GE	EII,FII	K			Y	
17-10	36-11	0.49[a]	H4/H4	Y	FI,GI,GII-GI,GE	GI,FI	K			Y	
19-10	41-11	0.44[a]	??/H6	Y	DVIII,DW,DVIII-EVIII	CW,CVIII,BW	K	Y	Y	Y	
28-09	17-10	0.52[a]	H4/H4	Y	GE-GI,GE,GI	FI,GI,GII-GI,GE	K	Y		Y	
36-11	17-10	0.49[a]	H4/H4	Y	GI,FI	FI,GI,GII-GI,GE	K			Y	
36-11	28-09	0.23[b]	H4/H4	?	GI,FI	GE-GI,GE,GI	K			Y	
36-11	46-11	0.38[a]	H4/H4	Y	GI,FI	EII,FII	K			Y	
41-11	19-10	0.44[a]	H6/??	Y	CW,CVIII,BW	DVIII,DW,DVIII-EVIII	K	Y	Y	Y	
46-11	17-10	0.44[a]	H4/H4	Y	EII,FII	FI,GI,GII-GI,GE	K		Y	Y	
46-11	36-11	0.38[a]	H4/H4	Y	EII,FII	GI,FI	K		Y	Y	
46-11	28-09	0.17[b]	H4/H4	?	EII,FII	GE-GI,GE,GI	K			Y	
51-10	58-10	0.29[b]	H6/H6	Y	EW,FW,EVIII,FVIII,DVIII,GW	FW,EW	K	Y	Y	Y	
51-10	11-11	0.34[c]	H6/H6	Y	EW,FW,EVIII,FVIII,DVIII,GW	EVII,DVI,CVI	K	Y			
52-11	113-10	0.36[a]	H3/H3	No	FIII,GIII,GII	GIV,GIII,SIII,SII	K	Y		Y	
06-09	21-09	0.06	H6/H6	No	CVIII,BW,CW,BVIII,AVIII,AW	NVIII, AVIII, AW, NW	N	Y			Y
113-10	17-10	-0.05	H3/H4	No	GIV,GIII,SIII,SII	FI,GI,GII-GI,GE	N	Y			Y
113-10	36-11	0.01	H3/H4	No	GIV,GIII,SIII,SII	GI,FI	N	Y			
17-10	113-10	-0.05	H4/H3	No	FI,GI,GII-GI,GE	GIV,GIII,SIII,SII	N	Y			Y
21-09	06-09	0.06	H6/H6	No	NVIII, AVIII, AW, NW	CVIII,BW,CW,BVIII,AVIII,AW	N	Y			Y
36-11	113-10	0.01	H4/H3	No	GI,FI	GIV,GIII,SIII,SII	N	Y			Y
46-11	113-10	0.11	H4/H3	No	EII,FII	GIV,GIII,SIII,SII	N	Y			Y

01-11	04-11	-0.06	H5/H1	No	NVIII	AE,NE,CI,DII,AII,NII,BI,BE	C			
04-11	11-11	-0.12	H1/H6	No	AE,NE,CI,DII,AII,NII,BI,BE	EVII,DVI,CVI	C			
04-11	01-11	-0.06	H1/H5	No	AE,NE,CI,DII,AII,NII,BI,BE	NVIII	C			
10-10	51-10	-0.02	H6/H6	No	DVII,DVI,EVI	EW,FW,EVIII,FVIII,DVIII,GW	C	Y		
11-11	41-11	-0.03	H6/H6	No	EVII,DVI,CVI	CW,CVIII,BW	C	Y		
17-10	21-09	0.16	H4/H6	No	FI,GI,GII-GI,GE	NVIII, AVIII, AW, NW	C	Y		
19-10	67-08	0.02	??/H7	No	DVIII,DW,DVIII-EVIII	SW,SVIII	C	Y		
41-11	46-11	0.03	H6/H4	No	CW,CVIII,BW	EII,FII	C	Y		
46-11	67-08	0.10	H4/H7	No	EII,FII	SW,SVIII	C	Y		
46-11	41-11	0.03	H4/H6	No	EII,FII	CW,CVIII,BW	C	Y		
51-10	10-10	-0.02	H6/H6	No	EW,FW,EVIII,FVIII,DVIII,GW	DVII,DVI,EVI	C	Y		
01-11	56-10	0.02	H5/H4	No	NVIII	BI,CI	S			
04-11	67-08	0.08	H1/H7	No	AE,NE,CI,DII,AII,NII,BI,BE	SW,SVIII	S			
06-09	14-09	-0.21	H6/H6	No	CVIII,BW,CW,BVIII,AVIII,AW	GVIII,GW	S			Y
10-10	56-10	0.18	H6/H4	No	DVII,DVI,EVI	BI,CI	S		Y	
113-10	06-09	-0.15	H3/H6	No	GIV,GIII,SIII,SII	CVIII,BW,CW,BVIII,AVIII,AW	S			Y
17-10	10-10	-0.15	H4/H6	No	FI,GI,GII-GI,GE	DVII,DVI,EVI	S		Y	Y
17-10	06-09	-0.17	H4/H6	No	FI,GI,GII-GI,GE	CVIII,BW,CW,BVIII,AVIII,AW	S		Y	
17-10	67-08	0.05	H4/H7	No	FI,GI,GII-GI,GE	SW,SVIII	S		Y	
19-10	17-10	-0.28	??/H4	No	DVIII,DW,DVIII-EVIII	FI,GI,GII-GI,GE	S		Y	
21-09	56-10	-0.13	H6/H4	No	NVIII, AVIII, AW, NW	BI,CI	S			Y
28-09	10-10	-0.03	H4/H6	No	GE-GI,GE,GI	DVII,DVI,EVI	S		Y	
36-11	21-09	-0.04	H4/H6	No	GI,FI	NVIII, AVIII, AW, NW	S		Y	Y
36-11	06-09	-0.20	H4/H6	No	GI,FI	CVIII,BW,CW,BVIII,AVIII,AW	S		Y	
36-11	10-10	-0.09	H4/H6	No	GI,FI	DVII,DVI,EVI	S		Y	
41-11	113-10	0.19	H6/H3	No	CW,CVIII,BW	GIV,GIII,SIII,SII	S		Y	
46-11	06-09	0.05	H4/H6	No	EII,FII	CVIII,BW,CW,BVIII,AVIII,AW	S		Y	Y
46-11	21-09	-0.04	H4/H6	No	EII,FII	NVIII, AVIII, AW, NW	S		Y	

46-11	10-10	0.00	H4/H6	No	EII,FII	DVII,DVI,EVI	S	Y
51-10	17-10	-0.05	H6/H4	No	EW,FW,EVIII,FVIII,DVIII,GW	FI,GI,GII-GI,GE	S	Y
52-11	06-09	-0.14	H3/H6	No	FIII,GIII,GII	CVIII,BW,CW,BVIII,AVIII,AW	S	Y

[a] $P<0.001$, Likelihood ratio > 37.02, Type II error <0.77

[b] $P<0.01$, Likelihood ratio > 11.95, Type II error <0.59

[c] $P<0.05$, Likelihood ratio > 3.31, Type II error <0.36.

Note. Listener is the animal to whom the playback stimulus was played. Caller is the animal that produced the stimulus. R is the pairwise relatedness of the dyad (Queller & Goodnight, 1989). Mt L/C is the mitochondrial haplotype of the listener followed by that of the caller. Co-Sleep is whether the dyad shared a sleeping site in the wild (not while in temporary captivity during recording). Listener captured and Caller captured are the capture sites of the respective members of that dyad (see also Fig. 3). LMM is the type of dyad (kin, neighbor, cage-mate, or stranger) for the linear mixed model analysis. The last four columns show in which pairwise tests this dyad was included. y=yes. K vs. N is the Mann Whitney U test for differences in reactions to kin (N=10) and neighbors (N=7). K vs. C, K vs. S, and N vs. S are the Wilcoxon Matched Pairs Tests for differences between reactions to kin and cage-mates (N=8 pairs), kin and strangers (N=15), and strangers and neighbors (N=6), respectively. Dyads not included in any of the pairwise tests were still included in the LMM (N=57 dyads: 19 kin, 7 neighbor, 11 cage-mate, 20 stranger).

APPENDIX D

TEST STATISTICS AND P-VALUES FROM THE MANN WHITNEY U TESTS COMPARING REACTIONS TO KIN VS. NEIGHBORS AND FROM THE WILCOXON MATCHED PAIRS TESTS COMPARING REACTIONS TO KIN VS. CAGE-MATES, KIN VS. STRANGERS, AND NEIGHBORS VS. STRANGERS

	Kin vs Neighbors											
Time	Duration Feed		Duration Look		Duration Vigilant		Latency Look		Latency Vigilant		Latency Stop Feed	
	Statistic	P-value	Statistic	P-value	Statistic	P-value	Statistic	P-value	Statistic	P-value	Statistic	P-value
1.00	29.00	0.55	24.50	0.28	32.00	0.66	26.50	0.38	34.00	0.88	30.50	0.65
1.50	31.50	0.73	30.50	0.64	32.00	0.66	26.50	0.38	34.00	0.88	30.50	0.65
2.00	32.50	0.80	30.50	0.64	32.50	0.76	26.50	0.38	34.50	0.95	30.50	0.65
2.50	31.50	0.73	31.50	0.72	28.00	0.42	26.50	0.38	32.00	0.73	30.50	0.65
3.00	32.50	0.80	29.50	0.58	24.00	0.23	24.00	0.27	29.50	0.55	29.00	0.55
3.50	30.00	0.62	29.00	0.54	21.00	0.14	24.00	0.27	27.00	0.40	29.00	0.55
4.00	32.00	0.77	27.00	0.42	21.00	0.14	24.00	0.27	27.00	0.40	29.00	0.55
4.50	30.00	0.62	26.00	0.36	17.50	0.07	24.00	0.27	24.50	0.28	30.00	0.62
5.00	30.50	0.66	26.00	0.36	16.50	0.06	24.00	0.27	24.50	0.28	30.00	0.62
5.50	31.00	0.69	26.00	0.37	16.50	0.06	25.00	0.32	24.50	0.28	30.00	0.62
6.00	31.00	0.69	27.00	0.42	18.50	0.09	25.00	0.32	24.50	0.28	30.00	0.62
6.50	30.00	0.62	27.50	0.45	19.50	0.11	25.00	0.32	24.50	0.28	30.00	0.62
7.00	30.00	0.62	27.50	0.45	20.50	0.14	25.00	0.32	24.50	0.28	30.00	0.62
7.50	30.00	0.62	27.50	0.45	20.50	0.14	25.00	0.32	24.50	0.28	30.00	0.62
8.00	30.00	0.62	27.50	0.45	20.50	0.14	25.00	0.32	24.50	0.28	30.00	0.62
8.50	30.00	0.62	28.50	0.52	21.50	0.16	25.00	0.32	24.50	0.28	30.00	0.62
9.00	30.00	0.62	28.50	0.52	21.50	0.16	25.00	0.32	24.50	0.28	30.00	0.62
9.50	29.00	0.56	28.50	0.52	21.50	0.16	25.00	0.32	24.50	0.28	30.00	0.62
10.00	29.00	0.56	29.50	0.58	21.50	0.16	25.00	0.32	24.50	0.28	30.00	0.62
10.50	29.00	0.56	29.50	0.58	22.50	0.20	25.00	0.32	24.50	0.28	30.00	0.62
11.00	29.00	0.56	29.50	0.58	22.50	0.20	25.00	0.32	24.50	0.28	30.00	0.62

11.50	29.00	0.56	29.50	0.58	22.50	0.20	25.00	0.32	24.50	0.28	30.00	0.62
11.96	27.00	0.43	29.50	0.58	22.50	0.20	25.00	0.32	24.50	0.28	30.00	0.62

	Kin vs Neighbors											
Time	Duration Feed		Duration Look		Duration Vigilant		Latency Look		Latency Vigilant		Latency Stop Feed	
	Statistic	P-value	Statistic	P-value	Statistic	P-value	Statistic	P-value	Statistic	P-value	Statistic	P-value
1.00	-0.52	0.60	-0.31	0.75	-0.45	0.65	-0.31	0.75	-0.45	0.65	-0.52	0.60
1.50	-0.52	0.60	-0.52	0.60	-0.45	0.65	-0.31	0.75	-0.45	0.65	-0.52	0.60
2.00	-0.73	0.46	-0.94	0.35	-1.08	0.28	-0.31	0.75	-0.54	0.59	-0.52	0.60
2.50	-0.94	0.35	-0.84	0.40	-1.21	0.22	-0.31	0.75	-0.67	0.50	-0.73	0.46
3.00	-0.73	0.46	-0.63	0.53	-1.76	0.08	-0.31	0.75	-0.67	0.50	-0.73	0.46
3.50	-0.68	0.50	-0.63	0.53	-1.36	0.17	-0.31	0.75	-0.73	0.46	-0.73	0.46
4.00	-0.68	0.50	-0.34	0.73	-0.85	0.40	-0.17	0.87	-0.68	0.50	-0.51	0.61
4.50	-0.51	0.61	-0.51	0.61	-0.85	0.40	-0.17	0.87	-0.68	0.50	-0.51	0.61
5.00	0.00	1.00	-0.34	0.74	-0.68	0.50	-0.17	0.87	-0.68	0.50	-0.34	0.74
5.50	-0.34	0.74	0.00	1.00	-0.51	0.61	0.00	1.00	-0.68	0.50	-0.34	0.74
6.00	-0.34	0.74	0.00	1.00	-0.34	0.74	-0.34	0.74	-0.85	0.40	-0.34	0.74
6.50	-0.28	0.78	0.00	1.00	-0.42	0.67	-0.34	0.74	-0.84	0.40	-0.56	0.58
7.00	-0.28	0.78	0.00	1.00	-0.63	0.53	-0.34	0.74	-0.98	0.33	-0.56	0.58
7.50	-0.28	0.78	0.00	1.00	-0.70	0.48	-0.34	0.74	-0.98	0.33	-0.56	0.58
8.00	-0.35	0.73	0.00	1.00	-0.70	0.48	-0.34	0.74	-1.12	0.26	-0.70	0.48
8.50	-0.21	0.83	0.00	1.00	-0.70	0.48	-0.34	0.74	-1.12	0.26	-0.70	0.48
9.00	-0.21	0.83	0.00	1.00	-0.77	0.44	-0.34	0.74	-1.12	0.26	-0.70	0.48
9.50	-0.14	0.89	-0.51	0.61	-0.91	0.36	-0.34	0.74	-1.12	0.26	-0.70	0.48
10.00	-0.14	0.89	-0.68	0.50	-1.19	0.23	-0.34	0.74	-1.05	0.29	-0.70	0.48

10.50	-0.14	0.89	-0.68	0.50	-1.33	0.18	-0.34	0.74	-1.12	0.26	-0.70	0.48
11.00	0.00	1.00	-0.68	0.50	-1.47	0.14	-0.34	0.74	-1.12	0.26	-0.70	0.48
11.50	0.00	1.00	-0.68	0.50	-1.47	0.14	-0.34	0.74	-1.12	0.26	-0.56	0.58
11.96	-0.14	0.89	-0.68	0.50	-1.54	0.12	-0.34	0.74	-1.12	0.26	-0.56	0.58

	Kin vs. Stranger											
Time	Duration Feed		Duration Look		Duration Vigilant		Latency Look		Latency Vigilant		Latency Stop Feed	
	Statistic	P-value	Statistic	P-value	Statistic	P-value	Statistic	P-value	Statistic	P-value	Statistic	P-value
1.00	-0.73	0.46	-1.38	0.17	-0.70	0.48	-1.38	0.17	-0.21	0.83	-0.73	0.46
1.50	-0.56	0.58	-1.48	0.14	-0.98	0.33	-1.38	0.17	-0.70	0.48	-0.59	0.55
2.00	-0.59	0.56	-1.73	0.08	-0.65	0.51	-1.38	0.17	-0.53	0.59	-0.59	0.55
2.50	-0.14	0.89	-2.05	0.04	-0.87	0.39	-1.60	0.11	-0.26	0.80	-0.66	0.51
3.00	-0.16	0.88	-2.05	0.04	-0.80	0.42	-1.60	0.11	0.00	1.00	-0.66	0.51
3.50	-0.59	0.55	-2.05	0.04	-0.63	0.53	-1.60	0.11	-0.24	0.81	-0.66	0.51
4.00	-0.63	0.53	-2.13	0.03	-0.41	0.68	-1.60	0.11	-0.28	0.78	-0.41	0.68
4.50	-0.85	0.40	-2.13	0.03	-0.16	0.88	-1.60	0.11	-0.35	0.73	-0.28	0.78
5.00	-0.82	0.41	-2.13	0.03	-0.19	0.85	-1.60	0.11	-0.31	0.75	-0.28	0.78
5.50	-0.79	0.43	-2.12	0.03	-0.13	0.90	-1.73	0.08	-0.31	0.75	-0.28	0.78
6.00	-0.53	0.59	-1.84	0.07	-0.19	0.85	-1.80	0.07	-0.31	0.75	-0.28	0.78
6.50	-0.28	0.78	-1.65	0.10	-0.13	0.90	-1.80	0.07	-0.19	0.85	-0.35	0.73
7.00	-0.25	0.80	-1.45	0.15	-0.13	0.90	-1.80	0.07	-0.19	0.85	-0.35	0.73
7.50	-0.22	0.83	-1.41	0.16	-0.09	0.92	-1.80	0.07	-0.19	0.85	-0.35	0.73
8.00	-0.16	0.88	-1.18	0.24	-0.03	0.97	-1.80	0.07	-0.19	0.85	-0.35	0.73
8.50	-0.03	0.97	-1.02	0.31	-0.03	0.97	-1.80	0.07	-0.19	0.85	-0.35	0.73
9.00	-0.16	0.88	-0.87	0.38	-0.03	0.97	-1.64	0.10	-0.25	0.80	-0.35	0.73
9.50	-0.22	0.83	-0.73	0.46	-0.03	0.97	-1.64	0.10	-0.25	0.80	-0.28	0.78
10.00	-0.35	0.73	-0.80	0.42	-0.03	0.97	-1.64	0.10	-0.31	0.75	-0.28	0.78

10.50	-0.53	0.59	-0.70	0.48	-0.09	0.92	-1.64	0.10	-0.31	0.75	-0.28	0.78
11.00	-0.53	0.59	-0.77	0.44	-0.22	0.83	-1.64	0.10	-0.31	0.75	-0.28	0.78
11.50	-0.41	0.68	-0.77	0.44	-0.22	0.83	-1.64	0.10	-0.31	0.75	-0.28	0.78
11.96	-0.35	0.73	-0.77	0.44	-0.22	0.83	-1.60	0.11	-0.31	0.75	-0.28	0.78

	Neighbor vs. Stranger											
Time	Duration Feed		Duration Look		Duration Vigilant		Latency Look		Latency Vigilant		Latency Stop Feed	
	Statistic	P-value	Statistic	P-value	Statistic	P-value	Statistic	P-value	Statistic	P-value	Statistic	P-value
1.00	-0.11	0.92	-0.63	0.53	-0.92	0.36	-0.84	0.40	-0.73	0.47	-0.11	0.92
1.50	-0.31	0.75	-0.31	0.75	-1.10	0.27	-0.84	0.40	-0.73	0.47	-0.11	0.92
2.00	-0.31	0.75	-0.31	0.75	-0.73	0.47	-0.84	0.40	-0.73	0.47	-0.11	0.92
2.50	-0.52	0.60	-0.11	0.92	-0.73	0.47	-0.84	0.40	-0.73	0.47	-0.11	0.92
3.00	-0.42	0.67	-0.11	0.92	-0.73	0.47	-0.84	0.40	-0.73	0.47	-0.11	0.92
3.50	-0.42	0.67	-0.11	0.92	-0.73	0.47	-0.84	0.40	-0.73	0.47	-0.11	0.92
4.00	-0.42	0.67	-0.11	0.92	-0.73	0.47	-0.84	0.40	-0.73	0.47	-0.11	0.92
4.50	-0.31	0.75	-0.11	0.92	-0.73	0.47	-0.84	0.40	-0.73	0.47	-0.11	0.92
5.00	-0.31	0.75	-0.11	0.92	-0.94	0.35	-0.84	0.40	-0.94	0.35	-0.11	0.92
5.50	-0.52	0.60	-0.31	0.75	-0.94	0.35	-0.84	0.40	-0.94	0.35	-0.11	0.92
6.00	-0.31	0.75	-0.31	0.75	-0.67	0.50	-0.84	0.40	-0.94	0.35	-0.11	0.92
6.50	-0.31	0.75	-0.31	0.75	-0.41	0.69	-0.84	0.40	-0.94	0.35	-0.11	0.92
7.00	-0.52	0.60	-0.52	0.60	-0.14	0.89	-0.84	0.40	-0.94	0.35	-0.11	0.92
7.50	-0.52	0.60	-0.52	0.60	-0.41	0.69	-0.84	0.40	-0.94	0.35	-0.11	0.92
8.00	-0.52	0.60	-0.52	0.60	-0.41	0.69	-0.84	0.40	-0.94	0.35	-0.11	0.92
8.50	-0.52	0.60	-0.52	0.60	-0.67	0.50	-0.84	0.40	-0.94	0.35	-0.11	0.92
9.00	-0.52	0.60	-0.52	0.60	-0.67	0.50	-0.84	0.40	-0.94	0.35	-0.11	0.92
9.50	-0.52	0.60	-0.52	0.60	-0.67	0.50	-0.84	0.40	-0.94	0.35	-0.11	0.92

10.00	-0.52	0.60	-0.52	0.60	-0.94	0.35	-0.84	0.40	-0.94	0.35	-0.11	0.92
10.50	-0.52	0.60	-0.52	0.60	-0.94	0.35	-0.84	0.40	-0.94	0.35	-0.11	0.92
11.00	-0.52	0.60	-0.52	0.60	-0.94	0.35	-0.84	0.40	-0.94	0.35	-0.11	0.92
11.50	-0.52	0.60	-0.52	0.60	-0.94	0.35	-0.84	0.40	-0.94	0.35	-0.11	0.92
11.96	-0.52	0.60	-0.52	0.60	-0.94	0.35	-0.84	0.40	-0.94	0.35	-0.11	0.92

Note. These tests were performed at half second intervals. Yellow and green mark tests that show trends and significant results, respectively, before a Bonferroni correction. Samples sizes were 10 kin and 7 neighbor dyads for kin vs. neighbors, 8 pairs of dyads for kin vs. cage-mates, 15 matched pairs for kin vs. strangers, and 6 matched pairs for neighbors vs. strangers.

APPENDIX E

SUMMARY OF THE RESULTS FROM THE LINEAR MIXED MODELS

3 Seconds					
Variable	Source	Numerator df	Denominator df	F	P
Feed	Intercept	1.00	56.98	17.24	<0.001
	Order	1.00	54.55	7.27	0.009[a]
	Call type	1.00	44.14	0.02	0.897
Look	Intercept	1.00	57.00	21.16	<0.001
	Order	1.00	57.00	4.63	0.036[b]
	Call type	1.00	57.00	2.28	0.137
Vigilant	Intercept	1.00	57.00	1.49	0.228
	Order	1.00	57.00	0.33	0.570
	Call type	1.00	57.00	1.20	0.278
Latency Look	Intercept	1.00	56.36	4.03	0.049
	Order	1.00	44.75	5.94	0.019[a]
	Call type	1.00	50.16	2.05	0.158
Latency Vigilant	Intercept	1.00	57.00	36.00	<0.001
	Order	1.00	57.00	0.84	0.364
	Call type	1.00	57.00	0.72	0.399
Latency Stop Feed	Intercept	1.00	56.80	3.18	0.080
	Order	1.00	56.99	12.05	0.001[a]
	Call type	1.00	43.82	0.01	0.917
Reaction Index	Intercept	1.00	56.46	34.31	<0.001
	Order	1.00	45.10	9.62	0.003[b]
	Call type	1.00	42.42	0.37	0.549
PCA Look	Intercept	1.00	57.00	9.57	0.003
	Order	1.00	57.00	5.57	0.022[a]
	Call type	1.00	57.00	2.41	0.126

		5.5 Seconds			
Feed	Intercept	1.00	56.60	24.71	<0.001
	Order	1.00	47.81	5.15	0.028[a]
	Call type	1.00	45.84	0.13	0.724
Look	Intercept	1.00	57.00	21.54	<0.001
	Order	1.00	57.00	4.29	0.043[b]
	Call type	1.00	57.00	2.59	0.113
Vigilant	Intercept	1.00	56.62	4.84	0.032
	Order	1.00	48.59	0.46	0.501
	Call type	1.00	48.59	0.07	0.799
Latency Look	Intercept	1.00	57.00	1.41	0.239
	Order	1.00	57.00	7.41	0.009[a]
	Call type	1.00	57.00	2.61	0.112
Latency Vigilant	Intercept	1.00	57.00	18.07	<0.001
	Order	1.00	57.00	1.19	0.280
	Call type	1.00	57.00	0.07	0.795
Latency Stop Feed	Intercept	1.00	56.96	1.31	0.256
	Order	1.00	56.62	13.41	0.001[a]
	Call type	1.00	44.75	0.00	0.965
Reaction Index	Intercept	1.00	56.46	44.82	<0.001
	Order	1.00	45.75	12.73	0.001[b]
	Call type	1.00	46.58	0.47	0.498
PCA Look	Intercept	1.00	57.00	7.80	0.007
	Order	1.00	57.00	6.46	0.014[a]
	Call type	1.00	57.00	3.04	0.087[a]

		11.96 Seconds			
Feed	Intercept	1.00	57.00	57.29	<0.001
	Order	1.00	57.00	1.89	0.175
	Call type	1.00	57.00	0.56	0.459
Look	Intercept	1.00	56.92	13.79	<0.001
	Order	1.00	56.87	4.88	0.031[b]
	Call type	1.00	45.85	0.28	0.597
Vigilant	Intercept	1.00	56.62	5.26	0.026
	Order	1.00	48.48	0.28	0.602
	Call type	1.00	48.79	0.14	0.710
Latency Look	Intercept	1.00	56.50	0.23	0.632
	Order	1.00	46.70	8.92	0.004[a]
	Call type	1.00	49.02	3.21	0.080[a]
Latency Vigilant	Intercept	1.00	57.00	7.91	0.007
	Order	1.00	57.00	2.65	0.109
	Call type	1.00	57.00	0.08	0.783
Latency Stop Feed	Intercept	1.00	56.99	0.25	0.618
	Order	1.00	55.01	15.60	<0.001[a]
	Call type	1.00	45.75	0.00	0.989
Reaction Index	Intercept	1.00	56.90	49.54	<0.001
	Order	1.00	53.21	11.26	0.001[b]
	Call type	1.00	46.82	0.15	0.698
PCA Look	Intercept	1.00	56.98	3.77	0.057
	Order	1.00	54.68	8.16	0.006[a]
	Call type	1.00	45.90	1.78	0.189

[a] Indicates positive slope

[b] Indicates negative slope

Note. df is degrees of freedom. Source is the source of variation. Call type is whether the subject heard a call from kin, a neighbor, a cage-mate, or a stranger. Order is the number of times each individual was tested. See Appendix F for information on the slopes of each parameter. Order or call type effects that are significant after and before a Bonferroni correction are highlighted in green and yellow, respectively.

APPENDIX F

ESTIMATED INTERCEPTS AND SLOPES FOR THE PARAMETERS IN THE LINEAR MIXED MODELS AND THEIR ASSOCIATED TESTS OF SIGNIFICANCE AND 95% CONFIDENCE LIMITS

3 Seconds

Variable	Parameter	Estimate	Std. Error	df	t	P	95% Confidence Interval	
							Lower Bound	Upper Bound
Feed	Intercept	1.39	0.33	56.98	4.15	<0.001	0.72	2.06
	Order	0.11	0.04	54.55	2.70	0.009	0.03	0.19
	Call Type	0.01	0.10	44.14	0.13	0.897	-0.18	0.21
Look	Intercept	1.23	0.27	57.00	4.60	<0.001	0.70	1.77
	Order	-0.07	0.03	57.00	-2.15	0.036	-0.13	0.00
	Call Type	-0.12	0.08	57.00	-1.51	0.137	-0.28	0.04
Vigilant	Intercept	0.26	0.21	57.00	1.22	0.228	-0.17	0.68
	Order	-0.01	0.02	57.00	-0.57	0.570	-0.06	0.03
	Call Type	0.07	0.06	57.00	1.09	0.278	-0.06	0.19
Latency Look	Intercept	0.84	0.42	56.36	2.01	0.049	0.00	1.68
	Order	0.12	0.05	44.75	2.44	0.019	0.02	0.22
	Call Type	0.18	0.12	50.16	1.43	0.158	-0.07	0.43
Latency Vigilant	Intercept	2.25	0.38	57.00	6.00	<0.001	1.50	3.01
	Order	0.04	0.04	57.00	0.92	0.364	-0.05	0.13
	Call Type	-0.09	0.11	57.00	-0.85	0.399	-0.32	0.13
Latency Stop Feed	Intercept	0.71	0.40	56.80	1.78	0.080	-0.09	1.51
	Order	0.17	0.05	56.99	3.47	0.001	0.07	0.26
	Call Type	0.01	0.11	43.82	0.10	0.917	-0.21	0.23
Reaction Index	Intercept	1.87	0.32	56.46	5.86	<0.001	1.23	2.51
	Order	-0.12	0.04	45.10	-3.10	0.003	-0.19	-0.04
	Call Type	-0.06	0.09	42.42	-0.60	0.549	-0.24	0.13
PCA Look	Intercept	-0.55	0.18	57.00	-3.09	0.003	-0.90	-0.19
	Order	0.05	0.02	57.00	2.36	0.022	0.01	0.09
	Call Type	0.08	0.05	57.00	1.55	0.126	-0.02	0.19
5.5 Seconds								
Feed	Intercept	2.82	0.57	56.60	4.97	<0.001	1.68	3.96
	Order	0.15	0.07	47.81	2.27	0.028	0.02	0.29
	Call Type	0.06	0.17	45.84	0.36	0.724	-0.27	0.39

Look	Intercept	1.74	0.37	57.00	4.64	<0.001	0.99	2.49
	Order	-0.09	0.04	57.00	-2.07	0.043	-0.18	0.00
	Call Type	-0.18	0.11	57.00	-1.61	0.113	-0.40	0.04
Vigilant	Intercept	0.74	0.34	56.62	2.20	0.032	0.07	1.42
	Order	-0.03	0.04	48.59	-0.68	0.501	-0.11	0.05
	Call Type	0.03	0.10	48.59	0.26	0.799	-0.17	0.22
Latency Look	Intercept	0.95	0.80	57.00	1.19	0.239	-0.65	2.54
	Order	0.25	0.09	57.00	2.72	0.009	0.07	0.44
	Call Type	0.38	0.24	57.00	1.61	0.112	-0.09	0.86
Latency Vigilant	Intercept	3.14	0.74	57.00	4.25	<0.001	1.66	4.62
	Order	0.09	0.09	57.00	1.09	0.280	-0.08	0.26
	Call Type	-0.06	0.22	57.00	-0.26	0.795	-0.50	0.38
Latency Stop Feed	Intercept	0.84	0.73	56.96	1.15	0.256	-0.62	2.30
	Order	0.32	0.09	56.62	3.66	0.001	0.15	0.50
	Call Type	0.01	0.21	44.75	0.04	0.965	-0.40	0.42
Reaction Index	Intercept	2.02	0.30	56.46	6.69	<0.001	1.42	2.63
	Order	-0.13	0.04	45.75	-3.57	0.001	-0.20	-0.06
	Call Type	-0.06	0.09	46.58	-0.68	0.498	-0.24	0.12
PCA Look	Intercept	-0.76	0.27	57.00	-2.79	0.007	-1.30	-0.21
	Order	0.08	0.03	57.00	2.54	0.014	0.02	0.14
	Call Type	0.14	0.08	57.00	1.74	0.087	-0.02	0.30
11.96 Seconds								
Feed	Intercept	8.31	1.10	57.00	7.57	<0.001	6.11	10.51
	Order	0.17	0.13	57.00	1.37	0.175	-0.08	0.43
	Call Type	-0.24	0.33	57.00	-0.75	0.459	-0.89	0.41
Look	Intercept	2.07	0.56	56.92	3.71	<0.001	0.95	3.19
	Order	-0.15	0.07	56.87	-2.21	0.031	-0.29	-0.01
	Call Type	-0.08	0.16	45.85	-0.53	0.597	-0.40	0.23
Vigilant	Intercept	1.40	0.61	56.62	2.29	0.026	0.18	2.62
	Order	-0.04	0.07	48.48	-0.53	0.602	-0.18	0.11
	Call Type	0.07	0.18	48.79	0.37	0.710	-0.29	0.43
Latency Look	Intercept	0.84	1.74	56.50	0.48	0.632	-2.65	4.33
	Order	0.61	0.20	46.70	2.99	0.004	0.20	1.02
	Call Type	0.92	0.51	49.02	1.79	0.080	-0.11	1.95

Latency Vigilant	Intercept	4.66	1.66	57.00	2.81	0.007	1.34	7.98
	Order	0.31	0.19	57.00	1.63	0.109	-0.07	0.70
	Call Type	-0.14	0.49	57.00	-0.28	0.783	-1.12	0.85
Latency Stop Feed	Intercept	0.75	1.49	56.99	0.50	0.618	-2.24	3.73
	Order	0.71	0.18	55.01	3.95	<0.001	0.35	1.07
	Call Type	-0.01	0.43	45.75	-0.01	0.989	-0.86	0.85
Reaction Index	Intercept	1.97	0.28	56.90	7.04	<0.001	1.41	2.53
	Order	-0.11	0.03	53.21	-3.36	0.001	-0.18	-0.05
	Call Type	-0.03	0.08	46.82	-0.39	0.698	-0.19	0.13
PCA Look	Intercept	-0.94	0.48	56.98	-1.94	0.057	-1.91	0.03
	Order	0.17	0.06	54.68	2.86	0.006	0.05	0.28
	Call Type	0.18	0.14	45.90	1.33	0.189	-0.09	0.46

APPENDIX G

DESCRIPTIVE STATISTICS FOR THE BEHAVIORAL VARIABLES AND PRINCIPAL COMPONENT LOOK AT 3 SECONDS, 5.5 SECONDS, AND 11.96 SECONDS

3 seconds									
		N	Range	Min.	Max.	Mean	Std. Error	Std. Dev.	Variance
Feed	Kin	19	2.84	0.16	3.00	1.77	0.24	1.03	1.05
	Neighbor	7	2.44	0.56	3.00	2.05	0.36	0.97	0.93
	Cage-mate	11	2.88	0.12	3.00	2.01	0.38	1.25	1.57
	Stranger	20	2.68	0.32	3.00	1.81	0.22	0.96	0.93
Look	Kin	19	2.68	0.00	2.68	0.80	0.21	0.93	0.86
	Neighbor	7	2.16	0.00	2.16	0.77	0.32	0.84	0.70
	Cage-mate	11	2.08	0.00	2.08	0.50	0.20	0.68	0.46
	Stranger	20	2.60	0.00	2.60	0.47	0.17	0.78	0.61
Vigilant	Kin	19	1.60	0.00	1.60	0.36	0.12	0.54	0.29
	Neighbor	7	0.64	0.00	0.64	0.11	0.09	0.24	0.06
	Cage-mate	11	0.68	0.00	0.68	0.19	0.09	0.30	0.09
	Stranger	20	2.60	0.00	2.60	0.57	0.19	0.83	0.69
Latency Look	Kin	19	2.80	0.20	3.00	1.61	0.29	1.27	1.62
	Neighbor	7	2.80	0.20	3.00	1.45	0.52	1.37	1.88
	Cage-mate	11	2.84	0.16	3.00	1.98	0.39	1.29	1.66
	Stranger	20	2.88	0.12	3.00	2.09	0.29	1.28	1.64
Latency Vigilant	Kin	19	2.68	0.32	3.00	2.24	0.25	1.08	1.17
	Neighbor	7	2.72	0.28	3.00	2.44	0.40	1.05	1.11
	Cage-mate	11	2.44	0.56	3.00	2.43	0.27	0.89	0.80
	Stranger	20	2.80	0.20	3.00	1.93	0.27	1.23	1.51
Latency Stop Feed	Kin	19	2.80	0.20	3.00	1.31	0.28	1.24	1.54
	Neighbor	7	2.80	0.20	3.00	1.42	0.53	1.40	1.96
	Cage-mate	11	2.84	0.16	3.00	1.91	0.40	1.31	1.72
	Stranger	20	2.88	0.12	3.00	1.24	0.27	1.21	1.45
PCA Look	Kin	19	1.62	-1.28	0.34	-0.23	0.13	0.58	0.34
	Neighbor	7	1.41	-1.06	0.34	-0.24	0.21	0.56	0.32
	Cage-mate	11	1.37	-1.03	0.34	-0.04	0.15	0.49	0.24
	Stranger	20	1.61	-1.27	0.34	-0.01	0.12	0.53	0.29

5.5 seconds									
		N	Range	Min.	Max.	Mean	Std. Error	Std. Dev.	Var.
Feed	Kin	19	5.34	0.16	5.50	3.48	0.40	1.73	2.99
	Neighbor	7	3.46	2.04	5.50	4.10	0.49	1.30	1.70
	Cage-mate	11	5.38	0.12	5.50	3.33	0.71	2.34	5.48
	Stranger	20	4.66	0.84	5.50	3.78	0.33	1.47	2.15
Look	Kin	19	4.16	0.00	4.16	1.08	0.30	1.32	1.75
	Neighbor	7	2.96	0.00	2.96	1.18	0.44	1.18	1.38
	Cage-mate	11	3.30	0.00	3.30	0.89	0.36	1.20	1.43
	Stranger	20	2.74	0.00	2.74	0.56	0.20	0.88	0.78
Vigilant	Kin	19	2.86	0.00	2.86	0.84	0.22	0.96	0.93
	Neighbor	7	0.64	0.00	0.64	0.13	0.09	0.25	0.06
	Cage-mate	11	2.08	0.00	2.08	0.48	0.22	0.72	0.51
	Stranger	20	4.30	0.00	4.30	0.86	0.27	1.20	1.45
Latency Look	Kin	19	5.30	0.20	5.50	2.66	0.58	2.51	6.29
	Neighbor	7	5.30	0.20	5.50	2.17	0.92	2.44	5.94
	Cage-mate	11	5.34	0.16	5.50	3.19	0.74	2.44	5.96
	Stranger	20	5.38	0.12	5.50	3.72	0.56	2.50	6.25
Latency Vigilant	Kin	19	5.18	0.32	5.50	3.24	0.46	2.02	4.07
	Neighbor	7	5.22	0.28	5.50	4.23	0.84	2.22	4.93
	Cage-mate	11	4.94	0.56	5.50	3.84	0.62	2.04	4.17
	Stranger	20	5.30	0.20	5.50	3.09	0.52	2.34	5.47
Latency Stop Feed	Kin	19	5.30	0.20	5.50	2.02	0.53	2.32	5.36
	Neighbor	7	5.30	0.20	5.50	2.13	0.93	2.47	6.08
	Cage-mate	11	5.34	0.16	5.50	3.09	0.75	2.49	6.18
	Stranger	20	5.38	0.12	5.50	1.89	0.50	2.26	5.09
PCA Look	Kin	19	2.68	-1.94	0.74	-0.19	0.21	0.91	0.83
	Neighbor	7	2.16	-1.42	0.74	-0.32	0.31	0.81	0.65
	Cage-mate	11	2.10	-1.37	0.74	-0.03	0.26	0.85	0.72
	Stranger	20	2.07	-1.33	0.74	0.21	0.17	0.77	0.59

11.96 seconds									
		N	Range	Min.	Max.	Mean	Std. Error	Std. Dev.	Var.
Feed	Kin	19	7.64	4.32	11.96	8.70	0.57	2.49	6.20
	Neighbor	7	8.52	3.44	11.96	9.83	1.12	2.97	8.82
	Cage-mate	11	11.84	0.12	11.96	7.65	1.27	4.21	17.71
	Stranger	20	11.12	0.84	11.96	8.25	0.75	3.37	11.35
Look	Kin	19	5.16	0.00	5.16	1.47	0.41	1.79	3.21
	Neighbor	7	3.88	0.00	3.88	1.31	0.54	1.43	2.05
	Cage-mate	11	4.28	0.00	4.28	1.45	0.47	1.56	2.44
	Stranger	20	6.40	0.00	6.40	1.21	0.40	1.80	3.22
Vigilant	Kin	19	5.76	0.00	5.76	1.63	0.38	1.64	2.69
	Neighbor	7	4.08	0.00	4.08	0.67	0.57	1.52	2.31
	Cage-mate	11	2.32	0.00	2.32	0.84	0.25	0.84	0.71
	Stranger	20	7.76	0.00	7.76	1.83	0.49	2.21	4.87
Latency Look	Kin	19	11.76	0.20	11.96	5.04	1.27	5.55	30.82
	Neighbor	7	11.76	0.20	11.96	4.01	2.08	5.50	30.24
	Cage-mate	11	11.80	0.16	11.96	5.31	1.52	5.05	25.51
	Stranger	20	11.84	0.12	11.96	7.75	1.25	5.58	31.17
Latency Vigilant	Kin	19	11.64	0.32	11.96	4.97	1.05	4.56	20.80
	Neighbor	7	11.68	0.28	11.96	8.84	2.02	5.35	28.58
	Cage-mate	11	11.40	0.56	11.96	6.88	1.51	5.01	25.07
	Stranger	20	11.76	0.20	11.96	4.74	1.05	4.69	22.00
Latency Stop Feed	Kin	19	11.76	0.20	11.96	3.42	1.10	4.78	22.87
	Neighbor	7	11.76	0.20	11.96	3.98	2.09	5.53	30.53
	Cage-mate	11	11.80	0.16	11.96	5.14	1.53	5.07	25.66
	Stranger	20	11.84	0.12	11.96	3.22	1.05	4.71	22.14
PCA Look	Kin	19	4.10	-2.35	1.75	0.01	0.35	1.53	2.34
	Neighbor	7	3.59	-1.83	1.75	-0.09	0.51	1.35	1.83
	Cage-mate	11	3.45	-1.70	1.75	0.06	0.41	1.35	1.83
	Stranger	20	4.66	-2.91	1.75	0.55	0.36	1.61	2.61

APPENDIX H

SUMMARY OF THE RESULTS FROM THE LINEAR MIXED MODELS WITH AN INTERACTION TERM

3 seconds					
	Source	Numerator df	Denominator df	F	P
Feed	Intercept	1.00	52.32	11.24	0.001
	Order	1.00	45.87	0.87	0.357
	Call Type	1.00	44.59	0.15	0.699
	Order * Call Type	1.00	42.84	0.32	0.572
Look	Intercept	1.00	57.00	5.29	0.025
	Order	1.00	57.00	0.01	0.929
	Call Type	1.00	57.00	0.03	0.865
	Order * Call Type	1.00	57.00	1.66	0.202
Vigilant	Intercept	1.00	57.00	3.06	0.086
	Order	1.00	57.00	1.86	0.178
	Call Type	1.00	57.00	0.14	0.712
	Order * Call Type	1.00	57.00	1.53	0.221
Latency Look	Intercept	1.00	52.83	5.61	0.022
	Order	1.00	51.23	0.00	0.959
	Call Type	1.00	49.62	0.06	0.805
	Order * Call Type	1.00	48.55	1.81	0.185
Latency Vigilant	Intercept	1.00	57.00	12.80	0.001
	Order	1.00	57.00	1.37	0.247
	Call Type	1.00	57.00	0.03	0.853
	Order * Call Type	1.00	57.00	0.69	0.409
Latency Sop Feed	Intercept	1.00	53.86	3.75	0.058
	Order	1.00	45.54	1.19	0.282
	Call Type	1.00	44.72	0.49	0.487
	Order * Call Type	1.00	43.04	0.87	0.355
Reaction Index	Intercept	1.00	50.51	12.04	0.001
	Order	1.00	45.31	0.58	0.452
	Call Type	1.00	43.44	0.19	0.666
	Order * Call Type	1.00	41.60	0.96	0.334

PCA Look	Intercept	1.00	52.49	1.42	0.239
	Order	1.00	51.33	0.00	0.959
	Call Type	1.00	49.53	0.04	0.838
	Order * Call Type	1.00	48.51	1.87	0.178
5.5 Seconds					
Feed	Intercept	1.00	51.48	15.37	0.000
	Order	1.00	47.53	0.41	0.526
	Call Type	1.00	45.78	0.08	0.778
	Order * Call Type	1.00	44.18	0.36	0.553
Look	Intercept	1.00	57.00	5.07	0.028
	Order	1.00	57.00	0.05	0.817
	Call Type	1.00	57.00	0.04	0.836
	Order * Call Type	1.00	57.00	1.99	0.164
Vigilant	Intercept	1.00	52.74	5.42	0.024
	Order	1.00	50.41	1.64	0.206
	Call Type	1.00	48.87	0.55	0.463
	Order * Call Type	1.00	47.66	1.18	0.283
Latency Look	Intercept	1.00	52.67	3.01	0.088
	Order	1.00	51.39	0.05	0.817
	Call Type	1.00	49.67	0.01	0.938
	Order * Call Type	1.00	48.65	1.58	0.215
Latency Vigilant	Intercept	1.00	57.00	5.09	0.028
	Order	1.00	57.00	1.94	0.169
	Call Type	1.00	57.00	0.43	0.516
	Order * Call Type	1.00	57.00	0.97	0.328
Latency Stop Feed	Intercept	1.00	53.36	1.24	0.270
	Order	1.00	46.33	2.49	0.122
	Call Type	1.00	45.35	0.10	0.750
	Order * Call Type	1.00	43.69	0.18	0.674

Reaction Index	Intercept	1.00	51.49	19.77	0.000
	Order	1.00	48.56	2.22	0.143
	Call Type	1.00	46.68	0.02	0.896
	Order * Call Type	1.00	45.22	0.10	0.750
PCA Look	Intercept	1.00	57.00	0.84	0.362
	Order	1.00	57.00	0.00	0.968
	Call Type	1.00	57.00	0.03	0.870
	Order * Call Type	1.00	57.00	2.11	0.151
		11.96 Seconds			
Feed	Intercept	1.00	57.00	25.53	0.000
	Order	1.00	57.00	0.79	0.378
	Call Type	1.00	57.00	0.05	0.830
	Order * Call Type	1.00	57.00	0.07	0.794
Look	Intercept	1.00	53.93	4.86	0.032
	Order	1.00	47.29	0.38	0.543
	Call Type	1.00	46.43	0.06	0.815
	Order * Call Type	1.00	44.90	0.44	0.510
Vigilant	Intercept	1.00	52.53	7.41	0.009
	Order	1.00	50.28	2.51	0.120
	Call Type	1.00	48.65	1.06	0.309
	Order * Call Type	1.00	47.43	2.33	0.134
Latency Look	Intercept	1.00	52.69	0.83	0.367
	Order	1.00	50.66	0.61	0.440
	Call Type	1.00	49.06	0.15	0.702
	Order * Call Type	1.00	47.89	0.65	0.425
Latency Vigilant	Intercept	1.00	57.00	2.73	0.104
	Order	1.00	57.00	1.31	0.258
	Call Type	1.00	57.00	0.03	0.859
	Order * Call Type	1.00	57.00	0.17	0.681

Latency Stop Feed	Intercept	1.00	52.80	0.17	0.679
	Order	1.00	47.34	3.88	0.055
	Call Type	1.00	46.12	0.01	0.938
	Order * Call Type	1.00	44.53	0.01	0.932
Reaction Index	Intercept	1.00	52.74	24.14	0.000
	Order	1.00	48.47	2.75	0.103
	Call Type	1.00	47.14	0.03	0.861
	Order * Call Type	1.00	45.66	0.00	0.952
PCA Look	Intercept	1.00	52.92	0.65	0.423
	Order	1.00	47.61	0.63	0.430
	Call Type	1.00	46.41	0.01	0.915
	Order * Call Type	1.00	44.84	0.67	0.417

Note. df is degrees of freedom. Source is the source of variation. Call type is whether the subject heard a call from kin, a neighbor, a cage-mate, or a stranger. Order is the number of times each individual was tested.

APPENDIX I

QUARTILES OF THE ACOUSTIC PARAMETERS MEASURED FROM THE ADVERTISEMENT CALLS AND THEIR LOADINGS ON THE PRINCIPAL COMPONENTS

Acoustic Parameter	Quartiles			Component Loadings	
	25	50	75	Component 1	Component 2
Frequency range of modulation six	11428.00	13143.00	14286.00	0.858	0.096
Frequency range of modulation five	11066.00	12653.00	14286.00	0.852	-0.053
Max. frequency of third modulation from end	19518.50	21633.00	23306.00	0.845	-0.266
Max. frequency of the modulation before the end	15918.00	17714.00	20000.00	0.843	-0.373
Max. frequency of the second modulation from the end	17193.00	19429.00	21857.00	0.835	-0.371
Frequency range of modulation four	10235.50	12000.00	13714.25	0.823	-0.151
Frequency range of modulation seven	11228.00	13265.50	14694.00	0.800	0.197
Max. frequency of end modulation	14286.00	15510.00	16612.00	0.799	-0.246
Frequency range of the third modulation from the end	5714.75	7975.00	10428.00	0.762	-0.438
Fundamental frequency of the end	11719.00	13086.00	14697.00	0.750	-0.093
Frequency range of the third modulation	8421.00	10857.00	13143.00	0.733	-0.372
Duration of third modulation from the end	8.00	10.00	13.00	0.718	-0.037
Frequency range of the second modulation from the end	4543.25	6216.50	9316.50	0.711	-0.551
Fundamental frequency of the start	20325.00	23499.00	24853.75	0.704	0.572
Duration of the modulation before the end	7.00	9.00	13.00	0.687	-0.211
Duration of the second modulation before the end	7.75	10.00	12.00	0.682	-0.177
Frequency range of the modulation before the end	3265.75	4905.00	8164.00	0.676	-0.575
Duration of modulation four	11.00	13.00	14.00	0.669	-0.153
Duration of the end modulation	5.00	10.00	13.00	0.652	-0.452
Duration of modulation six	12.00	13.00	15.00	0.620	-0.031
Number of modulations	18.00	20.00	23.00	-0.620	0.057
Frequency range of the end modulation	2844.50	3844.00	6129.00	0.613	-0.584
Duration of modulation five	11.75	13.00	14.25	0.596	-0.148
Time until the turning point	36.00	42.00	53.25	-0.561	0.021
Frequency range of modulation two	6939.00	8496.00	11275.75	0.553	-0.513
Duration of modulation seven	12.00	13.00	15.00	0.541	0.094
Duration of modulation three	11.00	12.00	13.00	0.536	-0.074
Duration of modulation two	10.00	11.50	13.00	0.519	-0.440
Time until the call's maximum	68.75	78.50	89.25	-0.434	-0.127
Call duration	594.75	656.50	734.75	-0.406	-0.133
Duration of modulation one	8.00	10.00	11.00	0.252	-0.070

Peak frequency of the end	12219.50	13513.50	15997.25	0.250	0.107
Max. frequency of modulation three	27551.00	31143.00	33917.25	0.399	0.886
Max. frequency of modulation two	29478.00	32571.00	35714.00	0.407	0.868
Max. frequency of modulation four	26639.00	29959.00	32245.00	0.481	0.835
Max. frequency of modulation five	26286.00	29714.00	31020.00	0.548	0.779
Fundamental frequency of the turning point	21851.00	24078.50	26739.25	0.345	0.756
Max. frequency of modulation one	31358.75	34286.00	37143.00	0.546	0.752
Max. frequency of modulation six	26046.50	28775.50	30367.50	0.583	0.746
Max. frequency of modulation seven	25410.00	28367.00	29592.00	0.574	0.739
Fundamental frequency of the maximum	27466.00	31372.00	34081.75	0.505	0.737
Peak frequency of the maximum	27881.00	31787.00	34668.00	0.128	0.622
Peak frequency of the turning point	21851.00	24373.50	27197.00	0.281	0.561
Peak frequency of the start	20508.00	24292.00	28284.00	0.120	0.458
Frequency range of modulation one	4571.00	5714.00	7194.00	0.301	-0.391

Note. Frequency is measured in Herz and time is milliseconds. Components 1 and 2 are 37% and 22% of the variation, respectively.

APPENDIX J

QUARTILES OF THE ACOUSTIC PARAMETERS MEASURED FROM THE ALARM CALLS AND THEIR LOADINGS ON THE PRINCIPAL COMPONENTS

Acoustic Variable	Quartiles			Component Loadings	
	25	50	75	Component 1	Component 2
Fundamental frequency of the start	11220.29	12207.01	13085.94	0.942	0.151
Max. frequency of the start	11781.40	12841.50	13797.83	0.917	0.153
Min. frequency of the start	10672.15	11748.60	12385.00	0.901	0.180
Max. frequency of the end	12087.00	13324.00	13997.00	0.831	-0.103
Fundamental frequency of the end	11230.00	12305.00	12891.00	0.750	-0.437
Min. frequency of the end	9792.00	11036.00	11979.00	0.681	-0.575
Peak frequency of the start	11230.47	12461.33	13525.39	0.630	0.144
Intersyllable interval	65.66	80.25	95.23	0.391	0.323
Call duration	19.19	21.78	23.95	0.173	0.764
Peak frequency of the end	11475.00	12500.00	13477.00	0.094	0.128

Note. Components 1 and 2 are 48% and 13% of the variation, respectively. Frequency is measured in Hz and time in ms.

APPENDIX K

QUARTILES OF THE BEHAVIORAL RESPONSES TO ALARM CALLS AND THEIR LOADINGS ON THE PRINCIPAL COMPONENTS

Behavior	Quartiles			Component Loadings		
	25%	50%	75%	Component 1	Component 2	Component 3
Duration in bottle area	296.00	534.50	758.75	0.932	0.056	-0.199
Latency to box area	117.38	305.25	715.50	0.930	0.092	-0.217
Latency to leave bottle area	108.88	171.25	531.25	0.886	-0.018	-0.048
Latency to box	143.00	679.75	1491.50	0.773	0.366	-0.119
Duration in speaker area	3.25	92.50	254.63	-0.464	0.800	-0.177
Duration in box	8.50	203.00	355.25	-0.527	-0.757	0.096
Duration in box area	168.63	286.50	421.25	-0.182	0.720	0.413
Latency to speaker area	843.75	1199.75	1476.25	0.527	-0.661	0.353
Duration look speaker	6.75	22.25	40.75	0.531	-0.018	0.726
Duration look box	0.00	13.00	38.63	-0.204	0.083	0.681
Latency look speaker	5.25	130.50	1033.13	-0.234	-0.319	-0.566

Note. Components 1, 2, and 3 are 39%, 22%, and 16% of the variation, respectively. Frequency is measured in Hz and time is in frames (resolution of 25 frames/s).

APPENDIX L

DEFINITIONS AND FORMULAS OF THE ACOUSTIC PARAMETERS MEASURED/CALCULATED FROM THE ADVERTISEMENT CALLS FOR THE PATRILINE SIGNATURE ANALYSIS

Measured Parameters	**Definition**	**Measurement**	**Source**
Min. frequency of modulations 1-7, e-3 to e	Minimum frequency of the first seven (1-7) and last four (e-3-e) modulations of F0 (Hz)	F0 at min1, min2, etc.	Spectrogram
Time at min. frequency of modulations 1-7, e-3 to e	Time at minimum frequency of first seven (1 to 7) and last four (e-3 to e) modulations of F0 (ms)	Time at min1, min2, etc.	Spectrogram
Max. frequency of modulations 1-7, e-3 to e	Maximum frequency of first seven (1 to 7) and last four (e-3 to e) modulations of F0 (Hz)	F0 at min1, min2, etc.	Spectrogram
Time at max. frequency of modulations 1-7, e-3 to e	Time at the maximum frequency of first seven (1 to 7) and last four (e-3 to e) modulations of F0 (ms)	Time at min1, min2, etc.	Spectrogram
Frequency range of modulations 1-7, e-3 to e	Frequency range of each of the first seven (1 to 7) and last four (e-3 to e) modulations of F0 (Hz)	max1-min1, max2-min2, etc.	Spectrogram
Time duration of modulations 1-7, e-3 to e	Duration between the respective minimums and maximums for modulations 1 to 7 and e-3 to e (ms)	Time at max1-Time at min1,etc.	Spectrogram
Peak frequency at the start	Frequency with the highest amplitude at start (S) (Hz)	peak at S	Power Spectrum
Peak frequency at the turning point	Frequency with the highest amplitude at turning point (T) (Hz)	peak at T	Power Spectrum
Peak frequency at the maximum	Frequency with the highest amplitude at maximum (M) (Hz)	peak at M	Power Spectrum
Peak frequency at the end	Frequency with the highest amplitude at the end (E) (Hz)	peak at E	Power Spectrum
Fundamental frequency of the start	Frequency of the start of F0 (Hz)	F0 at S	Power Spectrum
Fundamental frequency of the turning point	Frequency of the turning point of F0 (Hz)	F0 at T	Power Spectrum
Fundamental frequency of the maximum	Frequency of the maximum of F0 (Hz)	F0 at M	Power Spectrum
Fundamental frequency of the end	Frequency of the end of F0 (Hz)	F0 at E	Power Spectrum
Number of modulations	Total number of modulations		Spectrogram
Time at start	Time at the start of F0 (ms)	Time at S	Oscillogram
Time at turning point	Time at turning point of F0 (ms)	Time at T	Spectrogram

Time at maximum	Time at maximum of F0 (ms)	Time at M	Spectrogram
Time at end	Time at end of F0 (ms)	Time at E	Oscillogram

Calculated Parameters	**Definition**	**Calculation**	**Source**
Time until the turning point	Time between the start and the turning point (ms)	Time at T - Time at S	Measured parameters
Time until the call's maximum	Time between the start and the maximum (ms)	Time at M - Time at S	Measured parameters
Call duration	Time between the start and end (ms)	Time at E - Time at S	Measured parameters

APPENDIX M

DEFINITIONS AND FORMULAS OF THE ACOUSTIC PARAMETERS MEASURED /CALCULATED FROM THE ALARM CALLS FOR THE PATRILINE SIGNATURE ANALYSIS

Measured Parameters	**Definition**	**Measurement**	**Source**
Fundamental frequency of the start	Frequency of the start of F0 (Hz)	F0 at S	Power Spectrum
Max. frequency of the start	Maximum frequency of F0 at the start (Hz)	Max. of F0 at S	Spectrogram
Min. frequency of the start	Minimum frequency of F0 at the start (Hz)	Min. of F0 at S	Spectrogram
Fundamental frequency of the end	Frequency of the end of F0 (Hz)	F0 at E	Power Spectrum
Max. frequency of the end	Maximum frequency of F0 at the end (Hz)	Max. of F0 at E	Spectrogram
Min. frequency of the end	Minimum frequency of F0 at the end (Hz)	Min. of Fo at E	Spectrogram
Peak frequency at the start	Frequency with the highest amplitude at start (S) (Hz)	peak at S	Power Spectrum
Peak frequency at the end	Frequency with the highest amplitude at the end (E) (Hz)	peak at E	Power Spectrum
Time at S	Time at start of F0 (ms)	Time at S	Oscillogram
Time at E	Time at end of F0 (ms)	Time at E	Oscillogram
Time at N	Time at start the next call's F0 (ms)	Time at N	Spectrogram
Calculated Parameters	**Definition**	**Calculation**	**Source**
Intersyllable interval	Time between the end of one call (E) and the start of the next (N) (ms)	Time at N - Time at E	Measured parameters
Call duration	Time between the start (S) and end (E) of the call (ms)	Time at E - Time at S	Measured parameters

APPENDIX N

HOUSING HISTORIES OF THE FEMALE-FATHER AND FEMALE-CONTROL DYADS

Subject	**Father**	**Same Cage with Father?**	**Same Room with Father**	**Same Room with Father During Experiments?**	**Control**	**Same Cage with Control?**	**Same Room with Control**	**Same Room with Control During Experiments?**
Tasha	Xaver	No	19 months	No	Emil	No	7 months	No
Tipi	Yeti	A few hours for recording vocalizations	11 months	Yes	Zambo	A few hours for recording vocalizations	11 months	Yes
Tweety	Xaver	No	19 months	No	Emil	No	7 months	No
Undine	Zambo	No	7 months	No	Xaver	No	2 years	No
Vicky	Beetle	A few hours until the birth was discovered	7 months	No	Adam	No	7 months	No
Vivian	Beetle	A few hours until the birth was discovered	7 months	No	Adam	No	7 months	No
Zizi	Adrian	No	3 years	No	Zambo	A few hours for recording vocalizations	5 years	Yes
Zoly	Adrian	No	3 years	No	Zambo	No	5 years	Yes
Zuby	Adrian	No	3 years	No	Zambo	No	17 months	No
Zwipsy	Adrian	No	3 years	No	Zambo	A few hours for recording vocalizations	5 years	Yes

APPENDIX O

ETHOGRAM FOR VIDEO ANALYSIS

Name	Camera	Definition
Duration look to speaker	Close	**Start:** Head has been turned 45 degrees to the loudspeaker. **End:** Head has been turned 45 degrees away from the loudspeaker.
Duration look to box	Close	**Start:** Head has been turned 45 degrees to the box. **End:** Head has been turned 45 degrees away from the box.
Latency to look to loudspeaker	Close	**Start:** First playback starts. **End:** Head is turned 45 degrees towards the loudspeaker.
Duration in loudspeaker area	Wide	**Start:** Front half of lemur’s body is over the line into speaker area. **End:** Front half of lemur’s body is over the line into another area.
Duration in box area	Wide	**Start:** Front half of lemur’s body is over the line into box area. **End:** Front half of lemur’s body is over the line into another area.
Duration in box	Wide	**Start:** Head is fully in the box. **End:** Front half of lemur’s body is outside the box.
Latency to speaker area	Wide	**Start:** First playback starts. **End:** Front half of lemur’s body is over the line into the speaker area
Latency to box area	Wide	**Start:** First playback starts. **End:** Front half of lemur’s body is over the line into the box area.
Latency to box	Wide	**Start:** First playback starts. **End:** Head is fully in the box.
Duration in bottle area	Wide	**Start:** When the first playback starts or lemur re-enters bottle area by crossing the line with the front half of her body. **End:** Front half of lemur’s body is over the line into another area.
Latency to leave bottle area	Wide	**Start:** First playback starts. **End:** Front half of lemur’s body is over the line into another area.

APPENDIX P

PERMISSION TO USE CO-AUTHORED WORK

I, Sharon E. Kessler, state that I have received permission from Dr. Ute Radespiel, Alida Hasiniaina, Dr. Lisette Leliveld, Dr. Leanne T. Nash, and Dr. Elke Zimmermann to use the co-authored paper below in this dissertation (Chapter 2):

Kessler, S. E., Radespiel, U., Hasiniaina, A., Leliveld, L., Nash, L. T., & Zimmermann, E. (2014). Modeling the origins of mammalian sociality: Moderate evidence for matrilineal signatures in mouse lemur vocalizations. *Frontiers in Zoology*, *11*, 14.

and permission from Drs. Marina Scheumann, Leanne T. Nash, and Elke Zimmermann to use the co-authored paper below in this dissertation (Chapter 4):

Kessler, S. E., Scheumann, M., Nash, L. T., & Zimmermann, E. (2012). Paternal kin recognition in the high frequency / ultrasonic range in a solitary foraging mammal. *BMC Ecology*, *12*, 26.

Throughout this dissertation, references to "we" or "our" refers to myself and these co-authors.

As these two papers have already been published under the Creative Commons Attribution License 4.0 at http://www.biomedcentral.com/pdf/Creative_Commons_Attribution_4.0_International_CC_BY_4.0.pdf, they are excluded from the copyright of this dissertation.

APPENDIX Q

ANIMAL CARE AND USE COMMITTEE APROVALS AND RESEARCH PERMITS FROM MADAGASCAR NATIONAL PARKS

Institutional Animal Care and Use Committee (IACUC)
Office of Research Integrity and Assurance
Arizona State University

Tempe, Arizona 85287-1103
(480) 965-2179 FAX: (480) 965-7772

Animal Protocol Review

ASU Protocol Number:	10-1077R
Protocol Title:	Kin Recognition in Mouse Lemurs
Principal Investigator:	Leanne Nash
Date of Action:	08/27/2009

The animal protocol review was considered by the Committee and the following decisions were made:

☒ The original protocol was APPROVED as presented.
☐ The revised protocol was APPROVED as presented.
☐ The protocol was APPROVED with RESTRICTIONS or CHANGES as noted below. The project can only be pursued, subject to your acceptance of these restriction or changes. If you are not agreeable, contact the IACUC Chairperson immediately.
☐ The Committee requests CLARIFICATIONS or CHANGES in the protocol as described in the attached memorandum. The protocol will be reconsidered when these issues are clarified and the revised protocol is submitted.
☐ The protocol was approved, subject to the approval of a WAIVER of provisions of NIH policy as noted below. Waivers require written approval from the granting agencies.
☐ The protocol was DISAPPROVED for reasons outlined in the attached memorandum.
☐ The Committee requests you to contact _______________ to discuss this proposal.
☐ A copy of this correspondence has been sent to the Vice President for Research.
☐ Amendment was approved as presented.

RESTRICTIONS, CHANGES OR WAIVER REQUIREMENT:
Approved # of Animals: 130, 100 **Pain Level:** C **Species:** Grey Mouse Lemurs and Golden Brown Lemurs

Approval Period: 08/27/2009 – 08/26/2012
Sponsor: Leakey Foundation, NSF, Wenner Gren
Title: Kin Recognition in Mouse Lemurs

Signature: ______________________________ Date: 8/29/09
IACUC Chair or Designee

Original: Principal Investigator
cc: IACUC Office
IACUC Chair

Institutional Animal Care and Use Committee (IACUC)
Office of Research Integrity and Assurance
Arizona State University
Tempe, Arizona 85287-1103
Phone: (480) 965-2179 *FAX:* (480) 965-7772

Animal Protocol Review

ASU Protocol Number: **10-1077R**
Protocol Title: **Kin Recognition in Mouse Lemurs**
Principal Investigator: **Leanne Nash**
Date of Action: **5/19/2010**

The animal protocol review was considered by the Committee and the following decisions were made:

☐ The original protocol was APPROVED as presented.
☐ The revised protocol was APPROVED as presented.
☐ The protocol was APPROVED with RESTRICTIONS or CHANGES as noted below. The project can only be pursued, subject to your acceptance of these restriction or changes. If you are not agreeable, contact the IACUC Chairperson immediately.
☐ The Committee requests CLARIFICATIONS or CHANGES in the protocol as described in the attached memorandum. The protocol will be considered when these issues are clarified and the revised protocol is submitted.
☐ The protocol was approved, subject to the approval of a WAIVER of provisions of NIH policy as noted below. Waivers require written approval from the granting agencies.
☐ The protocol was DISAPPROVED for reasons outlined in the attached memorandum.
☐ The Committee requests you to contact ____________________ to discuss this proposal.
☐ A copy of this correspondence has been sent to the Vice President for Research.
☒ Amendment was administratively approved to add 2 completely non-invasive procedures.

RESTRICTIONS, CHANGES OR WAIVER REQUIREMENTS:

Total # of Animals: **130, 100** **Pain Level:** **C** **Species:** **Grey Mouse Lemurs and Golden Brown Lemurs**
Sponsor: **Leakey Foundation, NSF, Wenner Gren**
Title: **Kin Recognition in Mouse Lemurs**
Approval Period: **08/27/2009 – 08/26/2012**

Signature: ______________________________ Date: 5/19/2010
IACUC Chair or Designee

Original: Principal Investigator
Cc: IACUC Office
IACUC Chair

Institutional Animal Care and Use Committee (IACUC)
Office of Research Integrity and Assurance
Arizona State University
Tempe, Arizona 85287-1103
Phone: (480) 965-2179 *FAX:* (480) 965-7772

Animal Protocol Review

ASU Protocol Number:	**10-1077R**
Protocol Title:	**Kin Recognition in Mouse Lemurs**
Principal Investigator:	**Leanne Nash**
Date of Action:	**06/29/2010**

The animal protocol review was considered by the Committee and the following decisions were made:

☐ The original protocol was APPROVED as presented.
☐ The revised protocol was APPROVED as presented.
☐ The protocol was APPROVED with RESTRICTIONS or CHANGES as noted below. The project can only be pursued, subject to your acceptance of these restriction or changes. If you are not agreeable, contact the IACUC Chairperson immediately.
☐ The Committee requests CLARIFICATIONS or CHANGES in the protocol as described in the attached memorandum. The protocol will be considered when these issues are clarified and the revised protocol is submitted.
☐ The protocol was approved, subject to the approval of a WAIVER of provisions of NIH policy as noted below. Waivers require written approval from the granting agencies.
☐ The protocol was DISAPPROVED for reasons outlined in the attached memorandum.
☐ The Committee requests you to contact ____________________ to discuss this proposal.
☐ A copy of this correspondence has been sent to the Vice President for Research.
☒ Amendment was approved under designated review to allow for collaring and noninvasive acoustical experiments with male lemurs as previously approved for females and to increase the number of animals by 10.

RESTRICTIONS, CHANGES OR WAIVER REQUIREMENTS:
Total # of Animals: **130 - 110** **Pain Level: C**
Species: **Grey Mouse Lemurs**
Golden Brown Lemurs

Approval: **06/28/2010**
Expiration: **08/26/2012**

Signature: ______________________ Date: 6/29/10
IACUC Chair or Designee

Original: Principal Investigator
Cc: IACUC Office
IACUC Chair

Institutional Animal Care and Use Committee (IACUC)
Office of Research Integrity and Assurance
Arizona State University
Tempe, Arizona 85287-1103
Phone: (480) 965-2179 *FAX:* (480) 965-7772

Animal Protocol Review

ASU Protocol Number: **10-1077R**
Protocol Title: **Kin Recognition in Mouse Lemurs**
Principal Investigator: **Leanne Nash**
Date of Action: **11/17/2010**

The animal protocol review was considered by the Committee and the following decisions were made:

☐ The original protocol was APPROVED as presented.
☐ The revised protocol was APPROVED as presented.
☐ The protocol was APPROVED with RESTRICTIONS or CHANGES as noted below. The project can only be pursued, subject to your acceptance of these restriction or changes. If you are not agreeable, contact the IACUC Chairperson immediately.
☐ The Committee requests CLARIFICATIONS or CHANGES in the protocol as described in the attached memorandum. The protocol will be considered when these issues are clarified and the revised protocol is submitted.
☐ The protocol was approved, subject to the approval of a WAIVER of provisions of NIH policy as noted below. Waivers require written approval from the granting agencies.
☐ The protocol was DISAPPROVED for reasons outlined in the attached memorandum.
☐ The Committee requests you to contact ____________________ to discuss this proposal.
☐ A copy of this correspondence has been sent to the Vice President for Research.
☒ Amendment was approved by Designated Review to add an additional procedure and 100 Microcebus Ravelobensis.

RESTRICTIONS, CHANGES OR WAIVER REQUIREMENTS:

Approved # of Animals: **340** **Pain Level: C**
Species: **210 Microcebus Ravelobensis, 130 Microcebus Murinus**
Approval Period: **08/27/2009 – 08/26/2012**
Sponsor: **Leakey Foundation, NSF, Wenner Gren**
Title: **Kin Recognition in Mouse Lemurs**

Signature: ____________________ Date: 11/17/10
IACUC Chair or Designee

Original: Principal Investigator
Cc: IACUC Office
IACUC Chair

Institutional Animal Care and Use Committee (IACUC)
Office of Research Integrity and Assurance
Arizona State University
660 South Mill Avenue, Suite 315
Tempe, Arizona 85287-6111
Phone: (480) 965-4387 *FAX:* (480) 965-7772

Animal Protocol Review

ASU Protocol Number:	**10-1077R**
Protocol Title:	**Kin Recognition in Mouse Lemurs**
Principal Investigator:	**Leanne Nash**
Date of Action:	**3/23/2011**

The animal protocol review was considered by the Committee and the following decisions were made:

☐ The original protocol was APPROVED as presented.
☐ The revised protocol was APPROVED as presented.
☐ The protocol was APPROVED with RESTRICTIONS or CHANGES as noted below. The project can only be pursued, subject to your acceptance of these restriction or changes. If you are not agreeable, contact the IACUC Chairperson immediately.
☐ The Committee requests CLARIFICATIONS or CHANGES in the protocol as described in the attached memorandum. The protocol will be considered when these issues are clarified and the revised protocol is submitted.
☐ The protocol was approved, subject to the approval of a WAIVER of provisions of NIH policy as noted below. Waivers require written approval from the granting agencies.
☐ The protocol was DISAPPROVED for reasons outlined in the attached memorandum.
☐ The Committee requests you to contact ______________________ to discuss this proposal.
☐ A copy of this correspondence has been sent to the Vice President for Research.
☒ Amendment was approved by full committee review to add 450 lemurs to the protocol.

RESTRICTIONS, CHANGES OR WAIVER REQUIREMENTS:

Total # of Animals: 790 **Pain Level: C**

Species:	**510 Microcebus Ravelobensis, 280 Microcebus Murinus**
Sponsor:	**Leakey Foundation, NSF, Wenner Gren**
Title:	**Kin Recognition in Mouse Lemurs**
Approval Period:	**08/27/2009 – 08/26/2012**

Signature: ______________________________ Date: 3/28/2011
IACUC Chair or Designee

Original: Principal Investigator
Cc: IACUC Office
IACUC Chair

REPOBLIKAN'I MADAGASIKARA
Tanindrazana - Fahafahana - Fandrosoana

MINISTERE DE L'ENVIRONNEMENT ET DES FORETS
B.P. 610, Rue Fernand Kasanga – Tsimbazaza ANTANANARIVO – 101-
Tel: (261 20) 22 668 05 – Fax: (261 20) 22 354 10

AUTORISATION DE :

x - RECHERCHE
- ETUDE

N°103 /10 /MEF/SG/DGF/DCB SAP/ SCBSE

NOM KESSLER
PRENOMS Sharon
ADRESSE Faculté des Sciences – Université de Mahajanga
FONCTION Chercheur
ACCOMPAGNE DE : Leanne.T Nash, E. Zimmermann, S. Rasoloharijaona, R. Rakotondravony, un représentant du CAFF/CORE.

ORGANISME TUTELLE : Faculté des Sciences - Université de Mahajanga

EST AUTORISE(E) A FAIRE DES RECHERCHES / ETUDES DANS :
Le P.N Ankarafantsika et la S.F Ampijoroa.

MENTION SPECIALE EVENTUELLE:
Analyse acoustiques : reconnaissance des parents génétiques en utilisant les vocalisations chez *Microcebus murinus*.
Capture avec relâche après prélèvement d'échantillons de poils et tissu de bout d'oreille ; suivis des animaux par radio –tracking observation sur plate forme, observation dans des volières.
Recherche nocturne autorisée.

DUREE : Six (06) mois renouvelable.

N.B La Faculté des Sciences - Université de Mahajanga doit remettre à la Direction du Système des Aires Protégées, en quatre (04) exemplaires EN FRANÇAIS, le rapport préliminaire à la fin de sa mission et le rapport final avec les résultats des recherches au plus tard deux ans après la mission.
Le bénéficiaire de la présente autorisation doit prendre l'autorisation d'entrée dans les Aires Protégées auprès de MNP (Madagascar National Parks) à Ambatobe Antananarivo.

AMPLIATIONS :
- CAFF/CORE
- DREF/ CEF concernees
- MNP
- P.N Ankarafantsika
- DCAI
- Communes concernées
- **« Pour contrôle et suivi »**

- Faculté des Sciences Mahajanga
« Pour le rapport »

Antananarivo, le 14 AVR 2010

LE DIRECTEUR
DU SYSTEME D'AIRES PROTEGEES
P/

10/05/10 _ Reçu n° 0242 08/10

RAZAFIMANDRANTO Solomampionona

REPOBLIKAN'I MADAGASIKARA
Tanindrazana - Fahafahana - Fandrosoana

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Tel: (261 20) 22 668 05 – Fax: (261 20) 22 354 10

AUTORISATION DE :

x - RECHERCHE
- ETUDE

N° ,102/10/MEF/SG/DGF/DCB.SAP/ SCBSE
NOM LELIVELD
PRENOMS Lisette
ADRESSE Faculté des Sciences – Mahajanga
FONCTION Chercheur
ACCOMPAGNE DE : Ute Radespiel, B. Randrianambinina, Alida Hasiniaina, un représentant du CAFF/CORE.

ORGANISME TUTELLE : Faculté des Sciences - Université de Mahajanga

EST AUTORISE(E) A FAIRE DES RECHERCHES / ETUDES DANS :
Le P.N Ankarafantsika et la S.F Ampijoroa.

MENTION SPECIALE EVENTUELLE:
Analyse spaciales chez *Microcebus murinus*
Capture avec relâche après prélèvement d'échantillons de poils et tissu de bout d'oreille ; suivis des animaux par radio –tracking.
Recherche nocturne autorisée.

DUREE : Six (06) mois renouvelable.

N.B La Faculté des Sciences - Université de Mahajanga doit remettre à la Direction du Système des Aires Protégées, en quatre (04) exemplaires EN FRANÇAIS, le rapport préliminaire à la fin de sa mission et le rapport final avec les résultats des recherches au plus tard deux ans après la mission.
Le bénéficiaire de la présente autorisation doit prendre l'autorisation d'entrée dans les Aires Protégées auprès de MNP (Madagascar National Parks) à Ambatobe Antananarivo.

AMPLIATIONS
- CAFF/CORE
- DREF/ CEF concernées
- MNP
- P.N Ankarafantsika
- DCAI
- Communes concernées
- **« Pour contrôle et suivi »**
- Faculté des Sciences Mahajanga
  « Pour le rapport »

Antananarivo, le 14 AVR 2010

LE DIRECTEUR
DU SYSTEME D'AIRES PROTEGEES pi

RALAFIMANDRANTO Solomampionona

10/05/10 _ Reçu n° 086 & 087/10