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Olfactory Communication

and

Sexual Selection in Strepsirrhines

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Olfactory Communication

and

Sexual Selection in Strepsirrhines

by

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Report

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Dedication

To my family.

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Abstract

Olfactory Communication

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Sexual Selection in Strepsirrhines

by

Carl Joshua Toborowsky, M.A.

The University of Texas at Austin, 2009

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Although most strepsirrhines do not exhibit apparent physical signs of sexually selected traits, researchers have suggested that olfactory communication is sexually selected. The goal of this thesis is to (1) review sexual selection theory with an emphasis on sensory communication, and (2) test whether olfactory communication is sexually selected in strepsirrhines. I examined the relationships between primate mating systems and several measures of olfactory communication in 22 species: scent marking rates, the number of scent marking methods, and the volume of the main and accessory olfactory bulbs. I also evaluated qualitative data on olfactory communication in three lemur species to determine whether they meet the criteria of a sexually selected trait. Polygynandrous and monogamous species did not significantly differ from each other in scent marking rates, scent glands, or volume of the main and accessory olfactory bulbs. Three species of strepsirrhine met all criteria of having sexually selected olfactory traits, suggesting that polygynandrous lemurs are subject to sexual selection on several levels of olfactory communication.

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Introduction

Secondary sexual traits that increase reproductive success are considered sexually selected (Darwin 1871). Sexual selection manifests itself in two forms: intrasexual selection and intersexual selection, or mate choice (Darwin 1871; Bradbury and Andersson 1987). Since Darwin (1871), others have expanded upon sexual selection theory (Bateman 1948; Tinbergen 1951; Fisher 1958; Parker 1970; Trivers 1972; Zahavi 1975; Zahavi 1977; Clutton-Brock 1991; Andersson 1994; Penn and Potts 1999). For example, Trivers (1972) argued that asymmetries in parental investment are the source of sex differences in ornaments and weaponry in organisms. Emlen and Oring (1977) suggested that the limits of accessibility to mating partners determines the intensity of sexual selection: the stronger the limitation, the greater the degree of sexual selection.

A form of natural selection, sexual selection takes place when differences exist in the ability to attract and compete for members of the opposite sex (Trivers 1972; Emlen and Oring 1977). Intrasexual selection is a form of sexual selection whereby members of the same sex compete for access to mates (Darwin 1871; Fisher 1958). As in other mammals, in primates, intrasexual selection most often occurs among males (Jannett Jr 1986; Plavcan et al. 1995; Kappeler and van Schaik 2002; Setchell and Kappeler 2003a; Lawler et al. 2005; Thoren et al. 2006). Intersexual selection, wherein potential mates prefer certain traits in members of the opposite sex (Darwin 1871), is more difficult to demonstrate in primates, but some empirical evidence exists in support of mate choice in some taxa (cf Fisher et al. 2003a,b).

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Intrasexual Selection

Intrasexually selected traits and displays function to intimidate rivals (Hingston 1933; Tinbergen 1951; Guthrie 1970). Zahavi (1975; 1977) proposed that displays serve as a mechanism for individuals to assess the competitive ability of their rivals, a process that may result in the avoidance of fighting in instances where they are physically outmatched. Intrasexually selected traits may be physical armaments or visual adornments, such as large antlers (Clutton-Brock 1982), large canines (Plavcan et al. 1995; Thoren et al. 2006), large body size (Searcy 1979) or coloration (Crook 1972; Setchell and Dixson 2001). For example, males of many primate species have canines that are twice as large as those of females (Plavcan and van Schaik 1992), which are used to intimidate rivals (Harvey et al. 1978).

Intrasexually selected characteristics are not always obvious visual signals, however, and may manifest as behavioral traits (*e.g.*, scent-marking behavior: Ralls 1971; mate-guarding: Clutton-Brock 1989; Eberle and Kappeler 2002), internal morphological traits (*e.g*., olfactory bulb size and olfactory sensitivity: Peretto et al. 2001; Dorries et al. 1995), or differences in auditory (Pollock 1986; Clark 1988) and olfactory communication (Epple et al. 1988; Hagelin 2007; Scordato and Drea 2007; Charpentier et al. 2008a). For example, male mouse lemurs (*Microcebus* sp.) often remain close to recently inseminated females (mate guarding) to keep rivals away (Radespiel 2000). An individual's sperm may also function as an intrasexually selected trait (Parker 1970; Harcourt et al. 1995). Males of many primate species engage in sperm competition (Dixson 1995; Parga 2003; Eberle et al. 2007a), wherein sperm from multiple individuals

compete to inseminate ova (Parker 1970).

Species that experience high levels of intrasexual competition for mates are expected to be subjected to sexual selection (Emlen and Oring 1977), and the intensity of intrasexual competition is contingent upon how well males can monopolize access to mates (Orians 1969; Selander 1972; Jarman 1974; Le Boeuf 1974; Emlen and Oring 1977; Berry and Shine 1980; Wittenberger 1983). Different reproductive strategies affect the mating system of a species (Clutton-Brock 1989), which then influences reproductive success (Clutton-Brock and Vincent 1991; Mass et al. 2009). Monogamous species exhibit little sexual dimorphism or competition for mates (Emlen and Oring 1977; Krebs and Davies 1993). A monogamous male may obtain a limited number of mating opportunities, and therefore traits that promote survival have greater adaptive value than those that are sexually selected (Selander 1965). Polygynandrous species, however, experience a higher rate of intrasexual competition for mates (Emlen and Oring 1977; Kappeler 1997b), and should exhibit a greater degree of sexual dimorphism and characters that are under intense sexual selection (Trivers 1972; Andersson 1994; Kappeler 1997b; Setchell and Kappeler 2003b; Mass et al. 2009).

Additionally, because mate monopolization depends on the spatial distribution of receptive females (Emlen and Oring 1977; Ims 1990) and subsequently, mating system (Emlen and Oring 1977), male home range size will have an effect on the degree of mate monopolization, scramble competition for mates (Radespiel 2000; Eberle and Kappeler 2002; Eberle and Kappeler 2004b) and degree of intrasexual selection.

However, more than one mating system may occur in the same species (Dixson

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1998). Additionally, a mating system is not necessarily the same for each species. For example, monogamy in the potto (*Perodicticus potto;* Pimley et al. 2005) may differ from monogamy in fat-tailed dwarf lemurs (*Cheirogaleus medius*; Fietz et al. 2000), as extra-pair copulations are not uncommon in *C. medius*.

Intersexual Selection

In addition to advertising state of physical fitness to potential opponents as a way to minimize fighting, a signal may serve as the basis for mate choice (Kodric-Brown and Brown 1984; Andersson 1994). The choosy sex is usually the sex which invests most in offspring (Trivers 1972; Clutton-Brock and Parker 1992), which is almost always the female in primates (Kleiman 1977). Several hypotheses have been proposed to explain why mate discrimination is adaptive (for review: Setchell et al. 2001; Setchell and Kappeler 2003b). First, careful mate selection may benefit the choosy sex in terms of material goods (bowerbirds: Borgia 1985; Borgia 1995; Borgia and Presgraves 1998; Uy and Borgia 2000), food (Janson 1984; 1994; Engqvist and Sauer 2001), or in terms of parental care (Strassmann 1981; Keddy-Hector et al. 1989; Price 1990; van Schaik and Paul 1996; Tardiff and Bales 1997; Iwasa and Harada 1998; Bercovitch and Ziegler 2002; Heymann 2003). For example, female chimpanzees and bonobos occasionally copulate with males that offer to share food (Stanford 1999). Vervet monkey females often choose to mate with males that are friendly towards offspring (Keddy-Hector et al. 1989; Keddy-Hector 1992).

Secondly, mate choice may yield indirect benefits for offspring, such as attractiveness of offspring to future mates (Fisher 1958; Lande 1981; Kirkpatrick 1982)

or immunocompetence and parasite resistance (Hamilton and Zuk 1982; Folstad and Karter 1992; Penn and Potts 1998; Penn and Potts 1999; Schwensow et al. 2008). Mating indiscriminately may be detrimental for offspring in terms of parasite load and genetic heterozygosity (Charpentier et al. 2008b). For example, ring-tailed lemurs in captivity who suffer inbreeding depression exhibit significantly high levels of blood parasites and die from disease earlier than more heterozygous individuals (Charpentier et al. 2008b).

Lastly, Ryan and colleagues (Ryan 1990a; Ryan 1990b; Ryan et al. 1990; Ryan and Rand 1990; Ryan and Keddy-Hector 1992) hypothesized that mate choice is based not on direct or indirect benefits, but on pre-existing sensory biases preferred by the choosing sex (sexual selection for sensory exploitation hypothesis). In the sensory exploitation model, the choosing sex mates with that member of the opposite sex that can best exploit its sensory biases. Recent research on primate color vision lends support to the pre-existing sensory bias hypothesis (Fernandez and Morris 2007).

Olfaction

Olfactory signaling is common in mammals (Ralls 1971; Goodrich and Mykytowycz 1972; Mykytowycz 1972; Brown 1979) and serves as a method of communication within and between social groups (Eisenberg and Kleiman 1972; Brown and Macdonald 1985). Olfactory signals can communicate a signaler's identity (Shorey 1976; Schilling 1979), species (Epple et al. 1982), social status (Huck and Banks 1982), reproductive condition (Coblentz 1976; Belcher et al. 1988; Epple et al. 1988; Converse et al. 1995; Smith and Abbott 1998) and parasite load (Clayton 1991; Kavaliers and Colwell 1995; Penn and Potts 1998). Olfactory signals are costly to maintain (Rich and Hurst 1999; Johansson

and Jones 2007) and are considered honest signals of overall genetic quality, health and competitive ability (Faivre et al. 2003; López et al. 2006; McGlothlin et al. 2008).

Mammals with little sexual dimorphism in size may be sexually dimorphic in olfactory morphology and signaling (Blaustein 1981). Blaustein (1981) suggested that in small mammals, scents represent functional equivalents to secondary sex traits subject to sexual selection to the same degree as visual traits. Because the secretions of scent glands come into action through their application to the environment (*i.e*., through scent marking), Blaustein's argument should also apply to scent marking behavior (e.g., Ralls 1971). Scent marking refers to the secretion of non-volatile odorants from either a gland on the body or in the form of saliva, urine or feces, and the subsequent placement of the odorant onto a substrate (Ralls 1971). Like those of other mammals, primate olfactory signals can originate from skin and scent glands (Wislocki 1930; Mykytowycz 1972; Manley 1976; Epple et al. 1993; Brumloop et al. 1995), urine (Andrew and Klopman 1976; Epple et al. 1987; Palagi et al. 2005), feces (Perret 1995a; Whitten and Russell 1996; Irwin et al. 2004), saliva (Epple 1970; Perret 1995a; Powzyk 1997; Heymann 1998), and vaginal secretions (Keverne and Michael 1971; Wildt et al. 1977; Cerda-Molina et al. 2006).

Primate scent marks serve many purposes (Lewis 2005; 2006; Drea and Scordato 2008; Johnston 2008; Palagi and Norscia 2008), including territory demarcation (Pochron et al. 2005; Palagi and Norscia 2008) and signaling reproductive condition (Schilling and Perret 1987). Among primates, most often platyrrhines and strepsirrhines utilize olfactory signaling in the form of scent marking (Schilling 1979; Dixson 1998; Heymann 2003).

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As strepsirrhines are, for the most part, sexually monomorphic (Kappeler 1991), they do not exhibit apparent or obvious sexually dimorphic physical traits seen in catarrhines (e.g., large canines, large body size differences), and to a lesser extent, in platyrrhines (Ford 1994). Members of the genus *Eulemur*, however, are sexually dichromatic (Tattersall 1982), and some species of *Propithecus* exhibit patterns of male bimorphism (Patel 2006; Lewis and van Schaik 2007; Lewis 2009).

Depending on the context, olfactory signals can be sociosexual or ecological (Ralls 1971). Olfaction plays an important role in mate selection (Heymann 1998; Penn and Potts 1999), advertising rank, and reproductive state (Eisenberg and Kleiman 1972; Mykytowycz and Goodrich 1974), particularly for platyrrhines (Epple 1986; Heymann 2003) and strepsirrhines (Schilling 1979). Dominance may be linked to olfactory signals as well (Kappeler 1990; Fornasieri and Roeder 1992). In general, dominant male lemurs scent mark at higher rates than subordinates (Kappeler 1990; Fornasieri and Roeder 1992; Kappeler 1998; Kraus et al. 1999; Lewis and van Schaik 2007). Setchell and Kappeler (2003) expect female primates to mate with males of high status, as dominance may signal high genetic quality and the ability to secure resources. Janson (1984) has shown that during the estrus period, female capuchins solicit only the dominant male for copulations, and solicit subordinate males only during periods of less fertility. As a result, one might expect individuals that scent mark most frequently to increase their probability of mating and reproductive success. In mouse lemurs (*Microcebus murinus*), for example, dominant males have both the highest rates of scent marking and highest mating and reproductive success (Perret 1995; Andres et al. 2001; Radespiel et al. 2002; Eberle et al.

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2007). In addition to serving as various sociosexual cues, primates use olfaction to perceive environmental and ecological phenomena, such as location and quality of food items (Bolen and Green 1997; Dominy et al. 2001; Bicca-Marques and Garber 2004) and predators (Caine and Weldon 1989; Nolte et al. 1994; Apfelbach et al. 2005; Sündermann et al. 2008).

The different types of olfactory signals are mediated in most non-aquatic mammals by two distinct olfactory systems (Smith and Rossie 2006): the main olfactory system (MOS) and the accessory olfactory system (AOS). All primates have a functional MOS, but the AOS is present and functional only in prosimians and platyrrhines (Stephan et al. 1982; Baron et al. 1983; Smith and Rossie 2006). Although the two olfactory systems are responsible for the transduction of olfactory signals (Scalia and Winans 1975), the manners in which the MOS and the AOS operate are different. The MOS receives volatile odorant molecules from the environment during respiration, and the main olfactory bulb (MOB) relays that sensory information to various parts of the cerebrum (Scalia and Winans 1975).

Whereas the MOS is responsible for the transduction of volatile molecules, the AOS converts both volatile and non-volatile, or liquid odorants into sensory information (Evans and Schilling 1995), sending information to the accessory olfactory bulb (AOB) and then to the amygdala and hypothalamus (Scalia and Winans 1975). The most commonly studied chemosensory substances are pheromones, which are related to sociosexual behaviors (Michael and Keverne 1968; Cowley and Brooksbank 1991; Stockhorst and Pietrowsky 2004; Zufall and Leinders-Zufall 2007). Secreted pheromones

often elicit behavioral reactions in other individuals of the same species (Stockhorst and Pietrowsky 2004). The vomeronasal organ (VNO), which is part of the AOS, is responsible for the transduction of pheromones (but see Wang et al. 2007) and other non-volatile sensory information in the brain (Scalia and Winans 1975; Stephan et al. 1982; Evans 2006). Primates have two different kinds of pheromones: (1) primer pheromones, which elicit long-term hormonal and physiological changes (e.g., estrogen levels), and (2) releaser pheromones, which elicit more immediate behavioral responses (e.g., aggression, mating) (Meredith 1991).

Although catarrhines lack an AOB and a functional VNO (Liman and Innan 2003; Zhang and Webb 2003), the catarrhine MOS recognizes and processes some pheromones (McClintock 1971; Stern and McClintock 1998; Keverne 1999; Jacob and McClintock 2000; Alport 2004; Wysocki and Preti 2004). Some studies suggest that olfaction plays a role in catarrhine mating (Keverne and Michael 1971; Feistner 1991; Cerda-Molina et al. 2006) and food acquisition (Chauvin and Thierry 2005). Both male and female mandrills (*Mandrillus sphinx*) use their sternal gland to scent mark, but adult males scent mark most often and have the largest glands, suggesting a possible role in sexual selection (Feistner 1991; Dixson 1998). In a series of studies on rhesus macaques, Michael and colleagues (Michael et al. 1967; Michael and Keverne 1968; Keverne and Michael 1971; Michael et al. 1976) determined that male macaques are sexually stimulated by female pheromones emanating from vaginal secretions, demonstrating the use of olfactory communication in macaque mating (but see Goldfoot 1981).

Studies have shown that callitrichid olfactory morphology and signaling behavior

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is sexually selected (Heymann 2003; Snowdon 2004). Studies of strepsirrhine behavior often suggest that olfactory communication is sexually selected (e.g. Kappeler 1988; Andrés et al. 2001; Gould and Overdorff 2002), but few authors have experimentally tested this hypothesis (but see Fisher et al. 2003ab). One problem is that demonstrating whether a trait is the result of sexual selection, or perhaps some other adaptive mechanism, is difficult to test.

Outside of primates, studies show that dominant males scent mark most frequently (Ralls 1971; Adams 1976; Allen et al. 1999; Gosling and Roberts 2001) and have larger scent glands (Ralls 1971; Mykytowycz 1972; Mykytowycz and Goodrich 1974). These intrasexual differences may influence female mating decisions. For example, Huck and Banks (1982) show that female lemmings prefer the odors of dominant males to that of defeated males when odors of both males are presented at the same time. Female beavers (Rosell and Schulte 2004), capybaras (Herrera 1992), klipspringers (Roberts and Dunbar 2000), and some cichlid fish (Plenderleith et al. 2005) preferentially mate with males based on sexually selected olfactory cues.

It is difficult to draw similarities between primates and non-primate mammals in terms of olfactory signaling and mate choice, because female primates generally know their potential mates from regular interactions as a result of long-term association in groups (Kappeler and van Schaik 2002). A female primate who has spent several years in association with a particular male is already familiar with him, and olfactory signaling alone may not influence her mating decisions (Setchell and Kappeler 2003). A combination of behavioral and sensory signaling cues in addition to past interactions

likely persuades her (Kappeler 2002; Setchell and Kappeler 2003; Kappeler and van Schaik 2004). Additionally, what is a good mate choice for one female may be bad for another (Brown 1997). Genetic compatibility ("good genes") may have to do more with MHC dissimilarities, not just overall genetic quality (Knapp et al. 2006; Charpentier et al. 2008a; Schwensow et al. 2008).

Snowdon's Criteria

Snowdon (2004) has put forth a set of criteria that must be met in order for a trait to be considered sexually selected. First, a trait must be sexually dimorphic (Fisher 1958; Zahavi 1975; Snowdon 2004), and the sex that invests less in offspring is predicted to be the sex upon which sexual selection is acting (Trivers 1972; Emlen and Oring 1977; Kleiman and Malcolm 1981). For example, genital marking in *Lemur catta* is performed more by females than males (Kappeler 1990, 1998), but males investigate scent marks more often than females (Gould and Overdorff 2002; Palagi and Dapporto 2006). In pigs, olfactory sensitivity to certain pheromones is sexually dimorphic and may be sexually selected (Dorries et al. 1995), meeting Snowdon's (2004) first criterion.

Second, traits must also vary within the same sex to be sexually selected (Darwin 1871; Snowdon 2004). For example, male orangutans exhibit bimaturism, in which adults with established territories have developed cheek flanges and large bodies, and other males are smaller and lack flanges (Utami Atmoko and van Hooff 2004). Body size and canine size is a result of sexual selection in many primate species (Plavcan and van Schaik 1992; Kappeler 1996; Thoren et al. 2006). Leg shape in male *Propithecus verreauxi* varies among individuals, suggesting locomotor performance is a sexually

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selected trait (Lawler et al. 2005). Antler size in some species of cervid (Kodric-Brown and Brown 1984) and red deer (Kruuk et al. 2002) is sexually selected.

Third, a trait cannot be considered to be sexually selected unless members of the same species can distinguish between variations in the trait, such as identity, group identity, parasite load, overall good genes and health, and reproductive state (Bateman 1948; Zahavi 1975; Snowdon 2004). For example, callitrichids can discriminate between groups, sexes and individuals based on scent signatures (Epple et al. 1988; Smith et al. 1997). Female rhesus macaques (*Macaca mulatta*) show a preference for males with very red faces (Waitt et al. 2003), which is a sign of a hormonal change during the mating season. Discrimination of differences in traits among individuals, however, does not necessarily make a characteristic sexually selected (Snowdon 2004).

Finally, discrimination of trait differences must attract mates or repel rivals, and the results of such discrimination must yield differential mating and reproductive success (Snowdon 2004). In catarrhines, for example, exaggerated female sexual swellings serve to attract males, and the ability of males to discern optimal mating time based on the size of the swelling is a sexually selected characteristic (Burt 1992; Pagel 1994; Nunn 1999; Domb and Pagel 2001; Nunn et al. 2001; Zinner et al. 2004). In Soay sheep, male horn length, body size and testes volume positively influence mating and reproductive success (Preston et al. 2003). In lions, West and Packer (2002) have demonstrated that dominant males have the longest and darkest manes, which plays a role in both inter- and intra-sexual selection: the long manes both intimidate potential rivals and attract females.

Although data on scent marking rates or other olfactory behaviors are not

available for all primates to evaluate under Snowdon's criteria (Snowdon 2004), many studies strongly suggest that strepsirrhine and platyrrhine olfactory communication is sexually selected (Converse et al. 1995; Aujard 1997; Heymann 1998; Kappeler 1998; Fisher et al. 2003a; Fisher et al. 2003b; Heymann 2003; Hayes et al. 2004; Pochron et al. 2005; Hayes et al. 2006; Heymann 2006; MacDonald et al. 2008). For example, pygmy marmoset (*Cebuella pygmaea*) females convey reproductive information to males, while simultaneously suppressing reproduction in other females through a combination of anogenital scent marks and other sexual behaviors (Converse et al. 1995). Converse and colleagues (1995) demonstrate that pygmy marmoset olfactory behavior is very likely sexually selected, as all of Snowdon's criteria (2004) are met (sexual dimorphism in the signal, intrasexual variation, ability of individuals to discriminate the variances in the trait, and differential reproductive success based on the trait). In another study, pygmy loris females (*Nycticebus pygmaeus*) preferentially mated with males whose scent was most familiar (Fisher et al. 2003b). In the case of the pygmy loris, the intrasexual competition between males is a form of scramble competition, whereby the male who scent marks the most gains the opportunity to mate (Fisher et al. 2003a,b).

The goal of this study was to investigate the interspecific relationships among primate mating systems, anatomical structures, and olfactory behaviors to test the hypothesis that sexual selection influences olfaction in strepsirrhines. Previous publications have reviewed olfactory communication in relation to primate social structures (Barton 2006), but not in relation to mating system. If olfactory communication is sexually selected in primates, mating system exerts stronger selection pressure than

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social system. I also examine intraspecific variation in olfactory traits in strepsirrhines in order to demonstrate differences between sexes that may be sexually selected. Lastly, I evaluate strepsirrhine taxa and explore which species fit Snowdon's (2004) model of sexually selected olfactory communication. Since monogamous species, by definition, experience little to no competition for mates (Wittenberger and Tilson 1980; van Schaik and Kappeler 2003), I expected monogamous strepsirrhines to exhibit lower scent marking rates, less sexual dimorphism in number of scent glands and methods of scent marking (e.g., anogenital, throat, salivary, brachial), and smaller MOBs and AOBs than polygynandrous species. Additionally, I predicted sexual dimorphism to be present in strepsirrhine olfactory signals and anatomy: signaling frequency, scent gland number, and modes of scent marking. The composition and concentration of odorants is expected to differ according to sex. I expected polygynandrous males to exhibit the highest rates of scent marking, mating and reproductive success in species that use olfactory communication as a sexually selected trait (Snowdon 2004).

Methods

Strepsirrhine main and accessory olfactory bulb measurements were collected from Stephan and colleagues (Stephan et al. 1982; Baron et al. 1983). Mating system data were collected from the primate literature (Pollock 1975a; Dominique 1977; Pollock 1979; Ganzhorn et al. 1985; Kappeler 1988, 1993, 1997; Merenlender 1993; Hemingway 1995; Sterling and Richard 1995; Dixson 1997; Brockman 1999; Tan 1999; Fietz et al. 2000; Zinner et al. 2003; Eberle and Kappeler 2004a; Schülke et al. 2004; Schülke and Ostner 2005; Dunham 2008). In species for which there were multiple types of mating systems

reported, I gave priority to wild over captive studies and longer studies over shorter studies. Monogamous species were defined as adult males and females having only one mating partner (Emlen and Oring 1977). Species that are classified as monogamous but exhibit extra-pair copulations (e.g., *Cheirogaleus*, *Phaner*) were classified as monogamous. If both males and females of a species have multiple mating partners, I classified that species as polygynandrous. I gathered data on olfactory behaviors (i.e., scent-marking, scent marking glands and methods) from both wild and captive studies (Table 1).

Table 1. Taxa, behavioral and morphological data used in analyses of olfactory communication.

Species	MS	BM	SM♂	Meth♂	Meth♀	HR	AOB	MOB
Family Cheirogaleidae								
Cheirogaleus major	M	374	-	3	3	4.4	4.04	158
C. medius	P	156	-	2	2	4	2.66	102
Microcebus murinus	P	68	0.4	3	3	3.2	1.62	43
Phaner furcifer	M	330	-	2	1	5.01	-	-
Family Lemuridae								
Eulemur coronatus	P	1690	0.86	3	2	11	-	-
E. fulvus rufus	P	2295	3.7	6	5	100	3.21	207
E. mongoz	M	1630	-	-	-	5	-	-
E. rubriventer	M	1980	0.51	-	-	19	-	-
Lemur catta	P	2210	2.45	5	4	20	-	-
Varecia variegata	P	3470	-	2	1	90	5.27	369

Table 1 Cont.

Species	MS	BM	SM♂	Meth♂	Meth♀	HR	AOB	MOB
Family Indriidae								
Indri indri	M	6545	1.22	2	2	37	2.32	168
Propithecus diadema	P	5940	5.55	2	1	37	-	-
P. edwardsi	P	5870	0.95	2	1	400	-	-
P. verreauxi	P	3090	3.15	2	1	6.5	3.39	147
Family Daubentoniidae								
Daubentonia madagascariensis	P	2621	-	4	4	170.3	8.31	685
Family Lorisidae								
Arctocebus calabarensis	P		-	1	1	-	-	-
Perodicticus potto	M	830	-	1	1	-	2.74	310
Loris tardigradus	P	192	-	1	1	-	2.3	85.8

Table 1 Cont.

Species	MS	BM	SM♂	Meth♂	Meth♀	HR	AOB	MOB
Nycticebus coucang	M	679	-	-	-	-	4.28	159
Galago senegalensis	P	227	-	4	4	-	2.58	79.2
Galagoides demidovii	P	63	-	4	4	-	1.26	83.1
Otolemur crassicaudatus	P	1190	-	4	4	-	2.52	166

MS: mating system; BM: body mass (g); SM♂: male scent marking rates (#/hour); Meth: scent marking methods; HR: home range (ha);AOB: accessory olfactory bulb volume (mm^3); MOB: main olfactory bulb volume (mm^3); P=polygynandrous; M=monogamous.

Sources: (Hill 1953; Montagna and Ellis 1959; Montagna and Ellis 1960; Montagna et al. 1961; Yasuda et al. 1961; Montagna and Yun 1962a; Petter 1962; Jolly 1966; Machida et al. 1966; Montagna et al. 1966; Doyle and Bearder 1970; Pollock 1975b; Schilling 1979; Charles-Dominique and Petter 1980; Hladik et al. 1980; Katsir and Crewe 1980; Stephan et al. 1982; Baron et al. 1983; Rasmussen 1986; Kappeler 1988; Morland 1991; Merenlender 1993; Overdorff 1993; Sterling 1993; Ancrenaz et al. 1994; Hemingway 1995; Freed 1996; Kappeler 1997a; Powzyk 1997; Buesching et al. 1998; Curtis et al. 1999; Fietz 1999a; Fietz 1999b; Nekaris 2000; Radespiel 2000; Gould and Overdorff 2002; Richard et al. 2002; Palagi et al. 2003; Schülke and Kappeler 2003; Wiens and Zitzmann 2003; Schülke et al. 2004; Lehman et al. 2005; Pimley et al. 2005; Pochron et al. 2005; Hayes et al. 2006; Lewis 2006; Mertl-Millhollen 2006; Overdorff and Tecot 2006; Gupta 2007; Lahann 2007).

I used non-parametric statistics to examine the relationship between mating system and the relative volume of the MOB and AOB in strepsirrhines. I corrected for body mass by using the published olfactory bulb volumes as a per mille measure of total brain volume (Stephan et al. 1982; Baron et al. 1983). I used non-parametric tests to evaluate whether mating system has an effect on scent marking rates (monogamous n=2, polygynandrous n=7; Table 1). Although in most strepsirrhines the dominant males sire the most offspring and scent mark most frequently (Dugmore et al. 1984; Kappeler 1990; Fornasieri and Roeder 1992), I examined median marking rates of all males during the mating season in polygynandrous species, because those data are most readily available. I did not examine female scent marking rates for either mating system type. If authors did not provide scent marking rates but did publish raw data, I calculated rates by dividing the number of scent marks by the number of observation hours.

Because home range size may influence olfactory communication intensity (Gould and Overdorff 2002), I used correlation tests to examine the relationship between home range and scent marking rates. Home range size was corrected for body mass by using the residuals of a linear regression of body mass and home range.

Lastly, I used non-parametric statistics to examine the effect of mating system on the number of scent marking methods in both sexes (Fig. 1). I collected data on scent glands and marking methods from the primate literature (Hill 1953; Montagna and Ellis 1959; Montagna and Ellis 1960; Montagna et al. 1961; Yasuda et al. 1961; Montagna and Yun 1962a; 1962c; Montagna et al. 1966; Clark 1975; Crewe et al. 1979; Schilling 1979; Dixson 1998; Rasmussen and Nekaris 1998). I did not include lorises and galagos in the

scent marking analyses because I could not find any published data on scent marking

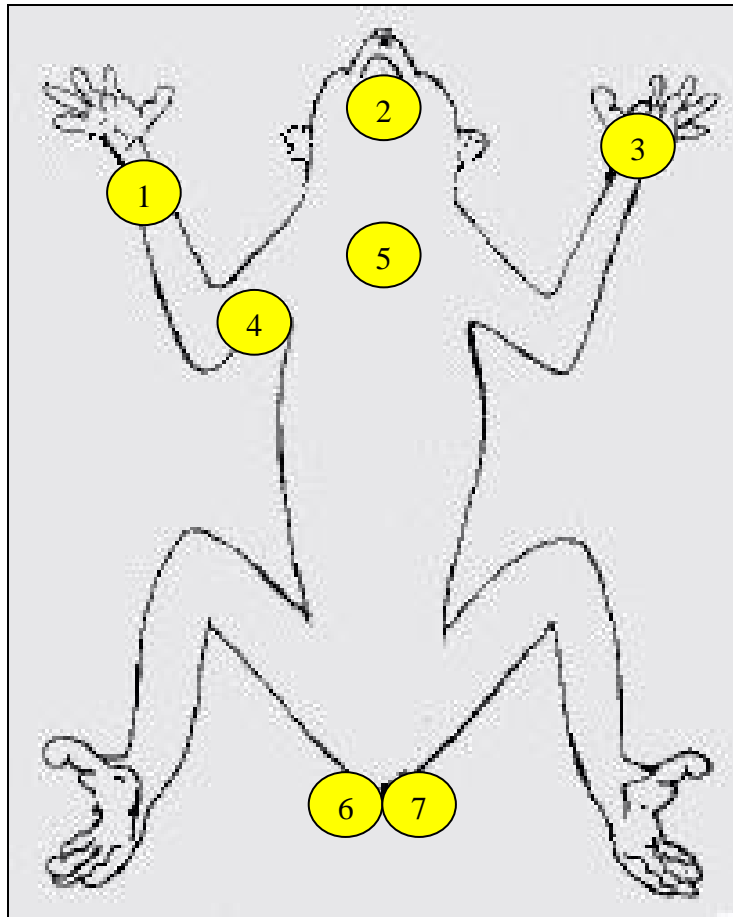rates. I analyzed all data in R and set the significance level at $p<0.05$.

Figure 1. Locations of scent glands and bodily secretions used in olfactory communication. Redrawn from Rasmussen and Nekaris (1998). (1): antebrachial gland; (2): saliva, buccal or facial marking; (3): palmar gland; (4): brachial gland; (5) sternal gland; (6) anogenital gland; (7): urine/fecal marking.

Results

Scent Marking Rates

Monogamous strepsirrhine males do not scent mark significantly less frequently than polygynandrous males (Fig. 2; One-Tailed Mann-Whitney U Test; $n_1=7$, $n_2=2$, U=10, p=0.5). However, scent mark rate data were available only for two monogamous species. Monogamous species ranged from 0.51 (*E. rubriventer*) to 1.22 marks per hour (*I. indri*), with a median of 0.87 marks per hour. Polygynandrous species ranged from 0.40 (*M. murinus*) to 5.55 marks per hour (*P. diadema*), with a median of 2.45 marks per hour. After correcting for body mass, home range was not correlated with scent marking rates (Spearman Test, S = 144, $r^2 = 0.04$, p=0.61).
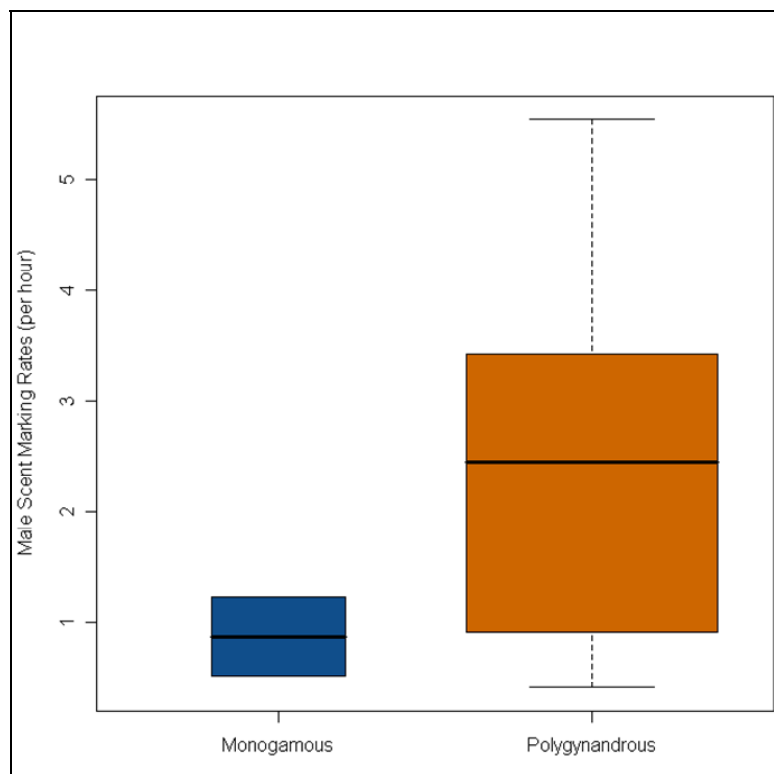

Figure 2. Comparison of male scent marking rates and mating systems. Bold lines indicate median value, whiskers indicate interquartile values.

Scent Marking Methods

Polygynandrous species do not differ significantly from monogamous species in the number of scent marking methods (Fig. 3; One-Tailed Mann-Whitney U Test; $n_1=15$, $n_2=4$, U=40, p=0.17). Monogamous and polygynandrous females do not differ significantly (One-Tailed Mann-Whitney U Test; $n_1=15$, $n_2=4$, U=38.5, p=0.21), and monogamous and polygynandrous males do not differ significantly in number of scent marking methods (One-Tailed Mann-Whitney U Test; $n_1=15$, $n_2=4$, U=42, p=0.13). Polygynandrous species ranged between 1 and 6 marking methods, with a mean value of 3.17 for males (median = 3) and 2.58 for females (median = 2). Monogamous species ranged between 1 and 3 marking methods, with a mean value of 2 for males (median = 2) and 1.8 for females (median = 2).
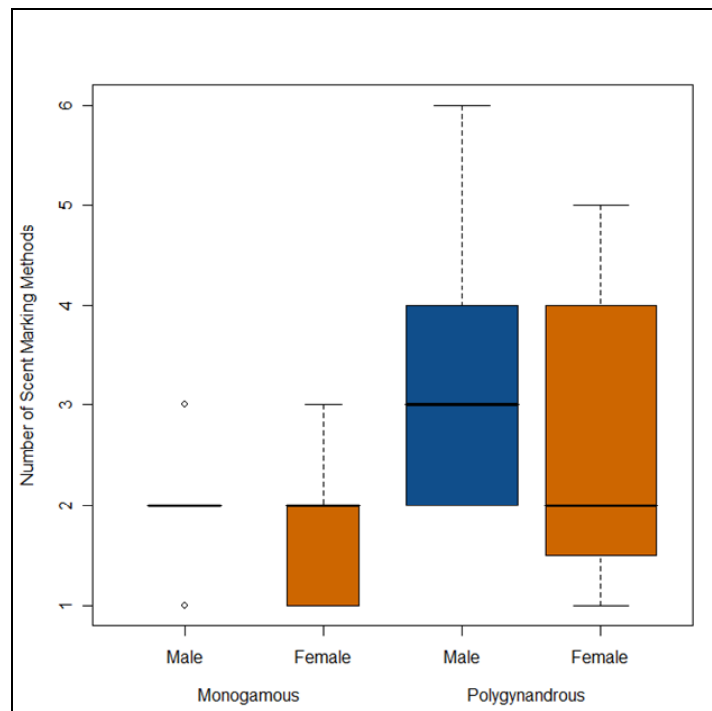

Figure 3. Comparison of scent marking methods in strepsirrhines. Bold lines indicate median value, whiskers indicate interquartile values.

Olfactory Bulb Volume

Strepsirrhines of different mating systems do not significantly differ in the relative volume of the accessory olfactory bulb (Fig. 4a; One-Tailed Mann-Whitney U Test; n_1=17, n_2=12, U=108, p=0.41) or the main olfactory bulb (Fig. 4b; One-Tailed Mann-Whitney U Test; n_1=17, n_2=12, U=102, p=0.51). Polygynandrous species relative AOB size ranged from 0.13 (*P. verreauxi*) to 0.97 (*M. murinus*) per mille total brain volume, with a mean value of 0.36 per mille total brain volume. Polygynandrous relative MOB size ranged from 5.9 (*P. verreauxi*) to 26 (*M. murinus*) per mille total brain volume, with a mean value of 16.02 per mille total brain volume. Monogamous species relative AOB ranged from 0.06 (*I. indri*) to 0.9 (*C. medius*) per mille total brain volume, with a mean of 0.39 per mille total brain volume. Monogamous relative MOB ranged from 4.6 (*I. indri*) to 34 (*C. medius*) per mille total brain volume, with a mean of 16.65 per mille total brain volume.
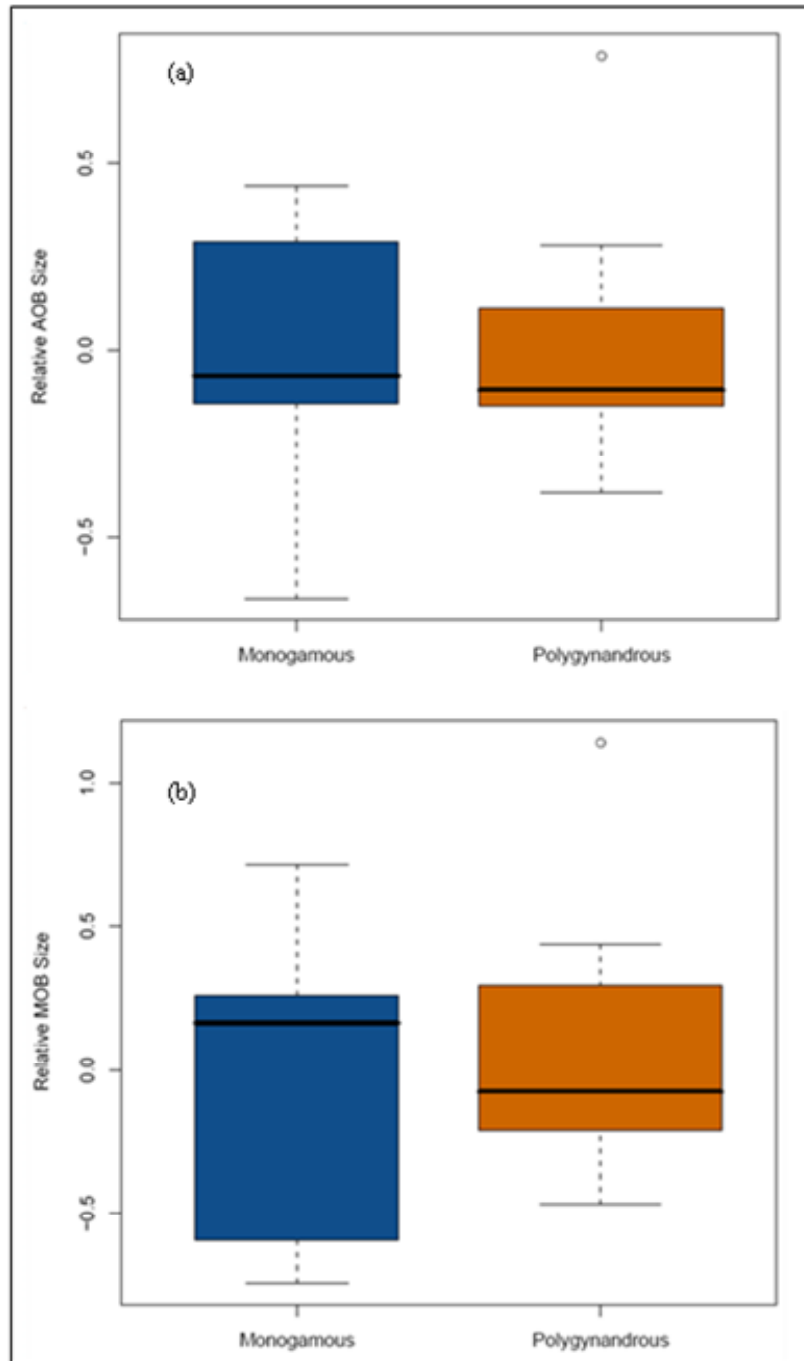
Figure 4. Differences in relative AOB size (a) and relative MOB size (b) of 29 strepsirrhine species. Bold lines indicate median values, whiskers indicate interquartile values. Brain volume data are from Stephan et al. (1982) and Baron et al. (1983).

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Snowdon's Criteria

Only three taxa met all of the criteria for sexually selected olfactory communication. *Lemur catta*, *Propithecus verreauxi*, and *Microcebus murinus* all exhibit sexual dimorphism in olfactory behavior, and they all demonstrate intrasexual differences in marking behaviors and composition of secretions. All three taxa exhibit preferential mating with males that either scent-mark most frequently, have the greatest MHC diversity, or have the most complex chemical composition of secretions. The preferential mating success in these species is a reflection of reproductive success.

Lemur catta

Olfactory communication in *L. catta* meets the criteria of a sexually selected trait (Snowdon 2004). First, males and females differ in the number of scent glands (Hill 1953; Kappeler 1998). Both sexes have anogenital glands, chest glands, antebrachial (carpal) glands, and palmar glands (Hill 1953; Schilling 1979), all of which secrete odoriferous substances and are used to deposit scents on various substrates. Only males, however, have brachial glands (Hill 1953; Montagna and Yun 1962b). Additionally, the carpal glands on males are characterized by having a large, keratinized spur, a feature lacking in females (Hill 1953; Montagna and Yun 1962b; Jolly 1966). In addition to meeting the first criterion of exhibiting sexually dimorphic physical traits, *L. catta* males and females differ in olfactory behavior: males scent mark at significantly higher rates than females (Kappeler 1990; Kappeler 1998; Gould and Overdorff 2002). Olfactory signaling in *L. catta* meets the criterion of intrasexual variation. The most dominant males have the highest rates of counter-marking (Kappeler 1998), or depositing a scent

on top of the scent of another individual (Johnston 2008), but the effect of dominance on overall scent marking rates is not yet clear. Ramsay and Giller (1996) found that high ranking males scent mark at the highest rates, but those findings have not yet been corroborated by other studies (*e.g.*, Gould and Overdorff 2002). However, dominant males show a greater increase in testes volume than subordinates during the mating season (Cavigelli and Pereira 2000), which may influence scent marking rates (cf. Dixson 1998; Lewis 2009).

The scent marks of *L. catta* vary not only on an *inter*-individual basis (Palagi and Dapporto 2006; Palagi and Dapporto 2007; Scordato and Drea 2007; Scordato et al. 2007; Drea and Scordato 2008), but also on an *intra*-individual level (Dapporto 2008). Individuals can recognize and discriminate individuals by their chemical profiles (Palagi and Dapporto 2006), meeting Snowdon's (2004) third standard, but each particular gland has its own chemical signature (Dapporto 2008). In a study on *L. catta* brachial glands, Dapporto (2008) found that the left and right glands are chemically unique, and that the chemical differences persist throughout time.

Lastly, there is evidence in *L. catta* that females preferentially mate with males based on their olfactory signatures (Charpentier et al. 2008). Charpentier et al. (2008) identify scrotal olfactory cues as honest indicators of male quality. Olfactory information about the overall genetic quality of *L. catta* is apparent only during the mating season, during which there is a drop in chemical diversity in scent marks, signaling the inability of less fit males to sustain production or expression of varied olfactory signals during times of stress. Charpentier et al. (2008) show that the genetically heterozygous (in both

MHC and overall genetic variation) lemurs can better maintain high complexity of olfactory signals during the mating season. The most genetically diverse male lemurs were able to maintain the production of complex chemicals in their secretions, whereas the less genetically diverse males could produce only simple chemical signals during the mating season (Charpentier et al. 2008).

Propithecus verreauxi

P. verreauxi olfactory communication meets the criteria of a sexually selected trait (Snowdon 2004). Like *L. catta*, *P. verreauxi* is sexually dimorphic in scent glands (Hill 1953). Both males and females have anogenital glands (Schilling 1979), and both sexes utilize urine to mark substrates (Jolly 1966; Schilling 1979). Only males, however, have a chest gland that exudes a sticky, odorous substance (Hill 1953; Lewis and van Schaik 2007). Olfactory behaviors are sexually dimorphic in *P. verreauxi*, as males scent mark at higher rates than females (Lewis 2006; but see Brockman 1999). There is considerable intrasexual variation in *P. verreauxi*, as adult males exhibit two different morphs: stained-chested and clean-chested (Lewis and van Schaik 2007). Males with stained chests use their chest glands to scent mark substrates and other individuals significantly more than those with clean chests (Lewis and van Schaik 2007; Lewis 2009). Kraus and colleagues (1999) posit that the dominant males suppress reproductive behaviors in subordinate males, suggesting that olfaction in *P. verreauxi* may be intrasexually selected.

Male *P. verreauxi* scent marking is highly correlated with mating success (Norscia et al. 2009), but not necessarily with reproductive success. At Berenty Reserve, Norscia and colleagues (2009) found that although males that countermarked female

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scents at the highest rates mated first, those males that groomed the most mated most often. At Kirindy Forest in Madagascar, however, dominant males, who scent mark most often (Kraus et al. 1999; Lewis and van Schaik 2007), sired more than 90% of offspring (Kappeler and Schäffler 2008; Mass et al. 2009). At Beza Mahafaly Special Reserve, fertilizations by extra-group males occurs frequently (Lawler 2007), suggesting population differences in mating strategies. Snowdon's (2004) criterion of variation in a trait yielding differential mating and reproductive success is met by some, but not all populations of *P. verreauxi*.

Microcebus murinus

M. murinus olfactory communication meets the criteria of a sexually selected trait (Snowdon 2004). *M. murinus* is not sexually dimorphic in scent gland number, as both sexes utilize anogenital marking, salivary/buccal marking, and urine marking (Schilling 1979; Buesching et al. 1998). Males scent mark more often than females (Schilling 1979; Perret 1995b), demonstrating intersexual differences in olfactory behavior. Among males, the most dominant individuals scent mark at the highest rates (Perret 1995b; Andrés et al. 2001; Radespiel et al. 2002), investigate female scents more than subordinates (Andrés et al. 2001), and mate most often (Perret 1995b; Andrés et al. 2001). Additionally, there are qualitative differences in the urinary odors of dominant and subordinate males of *M. murinus* (Schilling and Perret 1987), and these urinary odors and scent marks of dominant males play a role in reproductive suppression of subordinate males (Schilling et al. 1984). Information other than reproductive state and individual rank, such as overall genetic health and immunocompetence can be transmitted via olfactory signals (Penn and

Potts 1998; Penn and Potts 1999). For instance, at Kirindy forest in Madagascar, Schwensow et al. (2008) demonstrated that female *M. murinus* chose to mate with males whose major histocompatability complex (MHC) proteins are more different than their own than expected by chance.

Females of *M. murinus* tend to mate with most available males (Eberle and Kappeler 2004a; Eberle et al. 2007b), but mating success does not necessarily lead to reproductive success. For example, in a captive study of *M. murinus*, Andres and colleagues (2001) found that the highest ranking male sired 16 of 17 offspring in the study. In another captive study, the dominant male mated most frequently, but fertilized only half of the offspring (Radespiel et al. 2002). Lastly, Eberle and colleagues (Eberle and Kappeler 2004a; Eberle and Kappeler 2004b; Eberle et al. 2007b) found that males who mate early, but not necessarily first, are most likely to sire offspring. The males that scent mark most often have the highest reproductive success in some *M. murinus* populations, demonstrating that olfactory communication is a sexually selected trait.

Discussion

Olfactory communication is sexually selected in some strepsirrhine species, which is consistent with the hypothesis that sexually monomorphic species exhibit sexual dimorphism in non-visual traits (Blaustein 1981). This study demonstrates that no clear pattern links mating system to olfaction as a mechanism of sexual selection. Scent marking rates, number of scent glands, and volume of the main and accessory olfactory bulb are not influenced by mating system, suggesting an insignificant role in sexual selection for most of the taxa in this study. However, a qualitative analysis of olfactory

communication in strepsirrhines does suggest that it is sexually selected in at least three species (*L. catta, P. verreauxi*, and *M. murinus*). Small sample size and lack of published data on olfaction imposed constraints on this study and may drive some of the quantitative results in this study. Further investigation is warranted with the availability of new data.

Scent Marking Rates

The scent marking rates of monogamous strepsirrhines are not significantly different from polygynandrous species for several possible reasons. First, sample size is very small. Scent marking rates were available only for two monogamous strepsirrhines. The inclusion of more monogamous species might change the results of this study. Second, marking rates may not be the most informative variable for olfactory communication in strepsirrhines. Chemical signals carry a great deal of information (Ralls 1971), and some researchers suggest that the quality of the signal and the information contained therein may be of greater importance to the receiver than the quantity of signals (Hayes et al. 2004, 2006; Charpentier et al. 2008a; Mass et al. 2009; but see Fisher et al. 2003ab). The chemical composition of lemur scent marks changes seasonally and varies individually, which could imply that the ability to maintain attractive signals or the ability to discern differences in signals is the sexually selected trait, not the capacity for marking the most. Third, some of the scent marking data comes from captive studies. For example, *M. murinus* may exhibit vastly different scent marking behaviors in captivity than in the wild due to spatial constraints, loss of the need to forage for food and mates, and the lack of predators.

Monogamous and polygynandrous non-primate mammals use olfaction as a means of communication (Jarman 1974; Huck and Banks 1982; Gosling and Roberts 2001), but comparisons with primate olfactory communication is difficult. Scent marking rates are not available for most non-primate species, and determining the function of the scent marks is difficult (Roberts and Dunbar 2000; Gosling and Roberts 2001). Whether mating system significantly affects olfactory communication as a sexually selected trait in non-primates remains unanswered.

Home Range

Home range is expected to affect rates of scent marking in mammals (Rosell and Schulte 2004). If one taxon ranges farther than another, the species with a larger home range is expected to encounter more unmarked areas, more intruders, and should increase scent marking rates (Rosell and Schulte 2004). Relative home range size is not correlated with scent marking rates in this study. However, since the home range data in this study were for species groups, and no female scent marking rates were analyzed, a more inclusive analysis may yield different results.

Scent Marking Methods

The number of scent marking methods does not significantly differ between monogamous and polygynandrous strepsirrhines. Other mammals that use chemical signaling as a form of sexual selection show variation in scent gland size and number (Thiessen and Rice 1976; Gosling and Roberts 2001), but whether mating system has an effect on marking behavior is undetermined. In this study, the males of all monogamous taxa had the same number of scent marking methods as their female counterpart except

for *Phaner furcifer*, a species which engages in extra-pair copulations (Schülke et al. 2004). Conversely, males had more marking methods than females in seven of the polygynandrous taxa in this study.

The degree of sexual dimorphism in sexually selected physical and visual traits is strongly linked with mating system in catarrhines (Crook 1972), but strepsirrhine olfactory behavior and olfactory traits do not share a similar association with mating system. Although reliable morphometric measures of strepsirrhine scent gland area are not available (but see French and Cleveland 1984), I expect gland size to vary as a function of intersexual, intrasexual, and mating system differences (*sensu* Blaustein 1981; Kappeler 1997b). In capybaras, the volume of male scent glands is significantly correlated with testes mass, high rates of scent marking, and reproductive success (Herrera 1992), which meets Snowdon's (2004) criteria for sexual selection. Similarly, scent gland size and reproductive success are positively associated in hamsters (Zhang et al. 2001) and voles (Wolff et al. 1994). Because gland size fluctuates in non-primate mammals seasonally (Herrera 1992; Zhang et al. 2001; Wolff et al. 1994; Rosell and Schulte 2004), gland size may vary across seasons in strepsirrhines as well, and merits further investigation to determine if gland size falls under sexual selection.

Olfactory Bulb Size

Mating system affects neither the main nor the accessory bulb size in strepsirrhines. Barton (2006) came to a similar conclusion using the same morphometric data, and found no correlation between strepsirrhine social system and olfactory bulb size. Barton (2006) did not make a distinction between mating and social system, but the alternate

classification in this study yielded the same results. Other studies have shown that the mammalian accessory olfactory bulb is sexually dimorphic and exhibits degrees of plasticity (Pomeroy et al. 1990; Peretto et al. 2001). No sexual dimorphism in the size of either olfactory bulb occurs in primates (Stephan et al. 1982; Baron et al. 1983). In rats, however, the AOB changes over time due to constant rearrangement of neural circuits in the brain (Pomeroy et al. 1990). Subsequently, the conclusions from this study may change with more sophisticated studies on fluctuations of olfactory bulbs over time.

Qualitative Analysis

Studies of strepsirrhines have shown that many taxa may exhibit sexually selected olfactory communication (e.g., Kappeler 1998; Fisher et al. 2003a), but very few studies investigate all of the criteria suggested by Snowdon (2004). Although the qualitative results of this study demonstrate that olfactory communication is sexually selected in three species, some data spuriously suggest olfactory communication is sexually selected in other taxa. For example, the red-fronted brown lemur (*Eulemur fulvus rufus*) shows sexual dimorphism in the number of scent marking methods (males use brachial glands to scent mark), and can identify individual sex and identity from scent marks (Harrington 1974, 1976a,b, 1977). However, *E. f. rufus* scent marking behavior does not differ between mating and non-mating seasons, suggesting that there is no significant change in the signal (Gould and Overdorff 2002). In another example, the thick-tailed galago (*Otolemur crassicaudatus*) is sexually dimorphic in gland size (males have larger sternal glands), can discriminate age, sex, and identity by scent alone, but males cannot discern female reproductive condition from scent marks (Clark 1982a,b).

Conclusions

This study attempted to elucidate the relationships between mating system and olfactory communication as a sexually selected trait in strepsirrhines. The interspecific analyses did not suggest that olfactory communication is sexually selected, but intraspecific analyses demonstrated that olfactory communication is sexually selected in some polygynandrous strepsirrhines. While quantitative analyses did not yield significant results, caution is warranted in their interpretation due to the difficulties in assigning a mating system for each taxon. In three polygynandrous species, data support the hypothesis that olfactory communication is sexually selected. As more data are available on olfactory investigation rates, scent marking rate comparisons across seasons, and differential reproductive success, researchers will be better able to conduct inter- and intra-specific studies on sexual selection and olfactory communication.

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This report was typed by the author.