10
Predator Defense by Slender Lorises and Pottos

K. Anne-Isola Nekaris, Elizabeth R. Pimley, and Kelly M. Ablard

Introduction

Crypsis is argued to be the most widely used anti-predator strategy amongst nocturnal primates, wrought in its extreme form amongst the Asian lorises (Lorisinae: *Loris* and *Nycticebus*) and African pottos (Perodicticinae: *Arctocebus* and *Perodicticus*) (van Schaik & van Hoof, 1983; Terborgh & Janson, 1986; Cheney & Wrangham, 1987; Stanford, 2002; Wiens, 2002). Lorises and pottos are classically characterized by relatively slow, non-saltatory locomotion (Walker, 1969; Sellers, 1996). Silent movement, combined with cryptic coloration, small group size, discrete use of vocalizations, and increased olfactory communication are said to camouflage these primates (Petter & Hladik, 1970; Charles-Dominique, 1977). Much support for these notions has been offered by past studies of lorises and pottos.

The most compelling evidence of cryptic adaptations is provided by the unusual morphological adaptations of lorises and pottos, particularly their locomotor anatomy. Charles-Dominique (1977) contended that silent locomotion without abrupt transition, as seen in both lorises and pottos, is the ultimate behavioral adaptation to evade visually and auditorally directed predators (Petter & Hladik, 1970; Wiens, 2002). Morphological specializations of the post cranial anatomy of pottos and lorises allow them to remain still until a potential threat has passed (Rasmussen & Nekaris, 1998); this is exhibited by pottos and angwantibos in Gabon (Charles-Dominique, 1990). Though some captive settings yield freezing in *Nycticebus* and *Loris* (Fitch-Snyder & Schulze, 2001), the only comparable behavior exhibited by wild animals (*L. l. lydekkerianus*) occurred before they were observed crossing open ground (Bearder et al., 2002).

In addition to specializations that may aid lorises and pottos in escaping localization by predators, these animals also have evolved morphological strategies for coping with any predators they may encounter. Pottos are equipped with a scapular shield covered by thick skin and bristles of sensory hair, which they use to engage in active combat (Fig. 10.1); ultimately, a potto may escape by falling to the ground under conditions of extreme danger (Charles-Dominique, 1977). Although

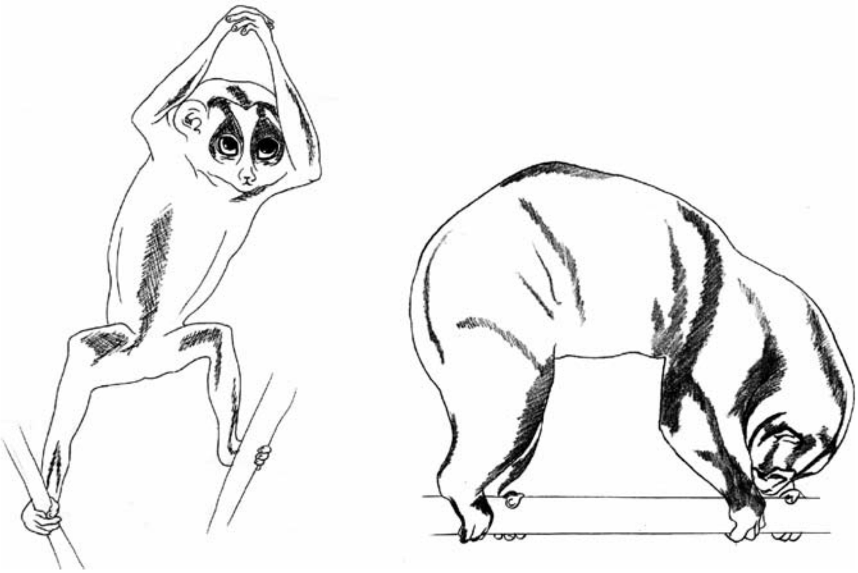

FIGURE 10.1. Two ways in which lorises may defend against predators after being detected: a grey slender loris in a cobra-like pose (drawn from video); a potto assuming a head-butting posture (drawn from a photograph from Charles-Dominique, 1977)

slender lorises have thickened skin in their nuchal area (Schulze & Meier, 1995), they have not been seen to combat potential predators in a way comparable to pottos (Bearder et al., 2002). Instead, slender lorises may ward off or startle predators with a form of mimicry that imitates a cobra (Fig. 10.1). By raising its slender arms near its ears or above its head, swaying its body in a serpentine fashion, and emitting a cobra-like hiss, the slender loris has been seen to ward off a cat (Still, 1905) and to challenge conspecifics (Schulze & Meier, 1995).

Differing strategies of concealment are revealed when observers examine the degree to which pottos and slender lorises use vocal advertisement. Charles-Dominique (1977) found that pottos (*P. potto edwardsi)* and angwantibos (*A. aureus*) not only used vocalizations discretely throughout the night (if at all), but also remained virtually silent in the face of predators, only on occasion omitting a barely audible “wheet.” Mysore slender lorises (*L. l. lydekkerianus*), to the contrary, made loud calls throughout the night, with a rate of calling similar to or greater than other nocturnal primates (e.g., lesser bushbabies (*Galago moholi*), fork marked lemurs (*Phaner furcifer*), and spectral tarsiers (*Tarsius spectrum*)) (Schülke, 2001; Bearder et al., 2002; Gursky, 2003). Furthermore, on some occasions, they whistled or screamed when face to face with a potential predator (Bearder et al., 2006). A similar pattern is currently being revealed amongst red slender lorises (*L. t. tardigradus*) (Bernede & Nekaris, unpub. data).

Olfactory communication via scent marking, common amongst both pottos and lorises (Schilling, 1979; Fisher et al., 2003a), has been described as discrete in the extreme (Charles-Dominique, 1974, 1977). It has also been argued that most arboreal predators, including raptors and carnivores, rely on visual and auditory cues for hunting their prey (Charles-Dominique, 1990). However, the olfactory processing capabilities of predators are now known to be profound (Perrot-Sinal, 1999; Shivik, 1999; Gutzke, 2001; Koivula et al., 1997; Koivula & Korpimaki, 2001; Roberts & Gosling, 2001; Wyatt, 2003). Furthermore, strong evidence argues that chemo-communication, rather than being the ultimate form of crypsis, may instead play an important role in anti-predatory strategies (e.g., Jackson et al., 1990; Alterman, 1995; Chivers, 1995; Banks et al., 2000; Rohr & Madison, 2001; Banks et al., 2002; Hagey et al., 2006).

The above précis suggests that rather than being wholly cryptic, lorises and pottos use combined strategies of advertisement and active combat to varying degrees to cope with potential predators. In this contribution we provide information from two new field studies regarding the ways in which slender lorises (*L. l. nordicus* and *L. tardigradus tardigradus*) and pottos (*P. p. edwardsi*) confront actual and potential predators. As is common with studies of predation (Hill & Dunbar, 1998), few observations of actual attack were observed. Thus, we describe the degree to which lorises and pottos use vocal communication when faced with predators, describe how they modify behavior in the face of potential predators, and explore the function of olfactory behavior. We then reassess the anti-predator strategies of these primates.

Methods

Slender Lorises

Nekaris in Sri Lanka carried out fieldwork on slender lorises; details of the study sites and data collection methodology are provided elsewhere (Nekaris, 2001, 2003; Nekaris & Jayewardene 2003, 2004). Terminology for vocalizations follows Schulze & Meier (1995) and for olfactory behavior follows Osman Hill (1938), Ilse (1955), Andrew & Klopman (1974), Manley (1974), Ehrlich & Musicant (1977), and Rasmussen (1986). Data on the northern Ceylon grey slender loris (*L. l. nordicus*), hereafter grey loris, were collected over two field seasons from 2001–2002 at Polonnaruwa and Minneriya-Giritale Sanctuary yielding approximately 190 hrs of direct observation over 446 hrs of nocturnal field effort; additional information regarding predation comes from the sites of Trincomalee, Mihintale, Ritigala, and Anuradhapura. The Southwestern Ceylon red slender loris (*L. tardigradus tardigradus*), hereafter red loris, was studied over six field seasons from 2001–2004 at Masmullah Proposed Forest Reserve; additional information comes from Kanneliya Forest Reserve, Kakanadura Forest Reserve, Bangamukande Estate, and Dandeniya Forest Reserve, yielding 210 hrs of observation over a period covering 519 hrs of nocturnal field effort. All data were entered into SPSS v11.0; the analyses presented here are descriptive statistics.

Pottos

Fieldwork on Milne-Edwards' potto (*P. potto edwardsi*), hereafter potto, was carried out by Pimley from February 1998 to December 2000 at WWF Mount Kupe Forest Reserve in Bakossiland, southwestern Cameroon (Pimley et al., 2005a,b; Pimley & Bearder, in press). During radio tracking of 11 individuals a form of instantaneous point sampling was used (Altman, 1974) whereby the observer recorded whether a behavior occurred or not at the end of each 5-minute sample point. Continuous recording was used for detailed accounts of complex behavioral sequences (Pimley et al., 2005a). Only point samples related to vocalizations and olfaction are presented here (for others, see Pimley, 2002; Pimley et al., 2005a,b). Vocalization terminology follows Bearder et al. (1995) and Ambrose (1999, 2003). Olfactory behavior is divided into smelling and scent marking with genital glands or urine (Evans & Schilling, 1995). "Scent marking" was defined as marking a substrate or conspecifics with scent glands or urine. "Sniffing" involved the nose in contact with or near a substrate or conspecifics or having the head raised while the nose moved. For the purpose of describing olfactory behavior, "substrates" include all non-animal elements of the environment: branches, lianes, climbers, vines, ground and air. "Signaling" involved marking conspecifics or substrates with scent gland or genital secretions, while "receiving" refers to olfactory investigation of a conspecific or substrate.

Data from behavioral observations (consisting of 5-min sample intervals) were not normally distributed, so they were transformed by the arcsine square-root (percentages) and square-root (association indices) to normalize the data distribution (Kolmogorov-Smirmov test, $p > 0.1$), enabling the data to be analyzed with parametric statistics (Motulsky, 1995). T-tests were used to compare transformed data sets for adult males and females. All tests were two-tailed with a significance level of $p \leq 0.05$.

Results

Vocalizations and Displays: Slender Lorises

Both red and grey lorises made calls in proximity to potential predators. A grey loris emitted four sequential single whistles in the direction of a ring-tailed civet (*Viverricula indica majori*) moving on the ground. Another loris emitted a series of single whistles when a fishing cat (*Felis viverrinas*) passed on the ground. On only one occasion did lorises whistle near their sleeping site: A group of red lorises whistled singly six times while a golden palm civet (*Paradoxurus zeylonensis*) was in the vicinity; whistles ceased when the civet moved away.

Reactions to being caught by the researcher may lend a clue as to how lorises would behave when seized by an actual predator (Charles-Dominique, 1977).

Adult and juvenile grey and red lorises growled at observers while twisting their body around the researcher's wrist to bite the opposite side of the hand. One adult and one juvenile loris (both males) engaged in a cobra imitation. The adult engaged in this behavior on a tree branch, while the juvenile stood on the palm of the researcher's hand. Both raised their arms over their heads in the form of a cobra's hood, and made typical growling vocalizations with intermittent spits (Fig. 10.1).

Noisy displays were observed on 38 occasions. An estrous female who was being pursued by males not only whistled loudly, but also loudly thrashed branches at her pursuers. On twelve occasions when males were observed to follow estrous females, they were observed to abandon fluid locomotion for noisy branch scrambling. On 26 different occasions, lorises were observed to "self-play." This behavior involved shaking branches, as well as tumbling and twisting over them while making a play face. On three occasions the researcher detected the loris by hearing the noise it was making.

Vocalizations and Displays: Pottos

In the field no vocalizations were heard between a potto and a predator or between pottos, even when two animals were together. On two occasions pottos temporarily housed together called to one another. Three males housed together whistled to each other when one animal came too close (<1 m) to another. When the researcher entered the enclosure within 50 cm of a potto, three males whistled at a higher frequency than before. One male potto in temporary captivity made a grunting and hissing noise followed by simulated bites when the researcher attempted to pick the animal up. Pottos growled when trapped, suggesting this vocalization may be used towards an enemy.

Evading Predators by Freezing or Fleeing: Slender Lorises

Slender lorises frequently moved near potential predators without showing any sign of fear. The only predator that elicited immobility in the lorises was an Indian krait (*Bangarus caeruleus*). An adult female red loris that was foraging 7 m from her parked juvenile abruptly rejoined it; they entered a dense tangle and both stared down at the ground where the snake was passing, moving into the foliage and were no longer visible to observers. Carnivores and birds were encountered many times and yielded limited behavioral responses from lorises (Table 10.1). Despite the lorises seeming ambivalence to felids, Department of Wildlife officials reported that feral cats and jungle cats catch and kill the animals.

Evading Predators by Freezing or Fleeing: Pottos

Potential carnivore predators on Mt. Kupe included the serviline genet (*Genetta servilina*), African palm civet (*Nandina binotata*), African civet (*Civetticus civetta*), and West African linsang (*Poiana leightoni*). Infrequent sightings of the

Table 10.1.

Species	Potential Predator	Predator Behavior	Loris Reaction
grey	ring-tailed civet (*Vivericula indica majori*)	vocalizing in same tree as loris	travel past and ignore
grey	ring-tailed civet (*V. i. majori*)	move on ground within 10 m	ignore
grey	ring-tailed civet (*V. i. majori*)	move within 1.5–15 m, licks lips	forage for 15 minutes in close proximity whilst carrying twins, as low as 1 m
grey	ring-tailed civet (*V. i. majori*)	move within 2 m without stopping or looking	adult female walked past while carrying singleton
grey	ring-tailed civet (*V. i. majori*)	within <1–15 m	forage for 25 minutes in close proximity
red	ring-tailed civet (*V. i. majori*)	civet travels 4 m underneath a loris in tree	ignore and travel
grey	Indian palm cat (*Paradoxurus h. hermaphroditus*)	move within 10 m in tree	ignore while grooming, continually wiping hands and arms over face
grey	Indian palm cat (*P. h. hermaphroditus*)	move within 15 m in tree	seemed to detect civet and descended into undergrowth
grey	Indian palm cat (*P. h. hermaphroditus*)	lie draped over branch 20 m away	ignore and forage
red	Indian palm cat (*P. h. hermaphroditus*)	move within 5 m	ignore and travel
red	Indian palm cat (*P. h. hermaphroditus*)	leaping and traveling	stop and stare in the direction of traveling cat
red	golden palm civet (*Paradoxurus zeylonensis*)	move within 20 m	foraging without hesitation
grey	fishing cat (*Felis viverrinas*)	move on ground within 5 m on five separate occasions	forage; ignore cat; meet with social partner for grooming; forage; ignore
grey	jungle cat (*Felis chaus kelaarti*)	move on ground within 5 m and stare	female carrying twins ignores cat
grey	rusty spotted cat (*Pronailurus rubignosa*)	move on ground within 4 m	female and parked juvenile ignore cat
red	serpent eagle (*Spilornis cheela)*	called near loris	moved to dense lianes
red	brown fish owl (*Ketupa zeylonensis)*	called near loris on 18 occasions	continued with normal behavior
grey	barn owl (*Tyto alba*)	landed in same tree	whistled and moved to cover

golden cat (*Profelis aurata*), leopard (*Panthera pardus*), and black-legged mongoose (*Bdeogale nigripes*) have been reported.

Although no active hunting by the 2–3.5-kg *N. binotata* was observed, strong evidence supports that these viverrids are a primary predator of pottos. A sub-adult male potto and his radio collar were eaten by an adult palm civet. Initial evidence for this came from the altered ranging patterns and change in frequency of the collar, indicating that it was inside another animal. Prior to its being eaten by the civet, the potto appeared to be in healthy condition, suggesting it was a predatory rather than a scavenging event. On occasions when palm civets entered an area of forest inhabited by a potto, the potto would either move away from the civet or hide inside dense vegetation until the palm civet had moved on ($n = 5$).

No encounters were observed between pottos and any other potential predators. The arboreal *G. servilina* at 1–2 kg may have some difficulty tackling a similarly sized adult potto, but it would be able to catch a young one. *Bdeogala nigripes*, although predominantly terrestrial, was once seen moving rapidly through the trees, and is a known predator of pottos at another site (Charles-Dominique, 1977). At 2–3.5 kg, this carnivore would be capable of dealing with an adult potto. Terrestrial carnivores such as *Panthera pardus* (50–60 kg), *Profelis aurata* (5.5–18 kg), and domestic dogs would all be capable of surprising a potto on the ground.

Like the slender loris, the potto showed defensive reactions to its human captors. When highly alarmed, a potto would repeatedly bite the substrate in front of it in between hissing and grunts before lunging at the potential attacker.

Chemical Communication: Slender Lorises

Dense rainforest conditions made it impossible to quantify slender loris olfactory communication. Qualitative observations still provide an insight into this behavior. Slender lorises used both direct (urine is directly deposited by the genitalia) and indirect (urine is deposited on a substrate with aid of another body part) modes of urine marking, and they also marked with scent glands. Odors produced were pungent and were often used by researchers to locate animals in the forest. Rhythmic micturition was the most common direct scent marking method for both taxa, occurring during traveling, foraging, and social interactions, and occurring on branches of all sizes and orientations, and during all activities other than resting. Intra-group countermarking of branches at the center of the group range was observed; scents were often inspected by the countermarker with the tongue (with and without Flehmen) before rhythmic micturition took place. Females often used concentrated rhythmic micturition at single prominent points, coating a small surface with a thick layer of urine, keeping one leg raised. Urine marking was observed in proximity to a sleeping site on only one occasion by a grey loris.

Urine washing was common, and seen most often in relation to consumption of noxious food items. Both loris taxa urine-washed before catching and/or after consuming unpalatable prey or when stung by an insect. Urine washing was also conducted before grooming of infants, which were to be parked for the night (grey lorises) or for a period of 2–3 hrs (red lorises).

Olfactory behavior in a social context was pronounced. Passing-over occurred during grooming bouts between red and grey loris males and females. Anogenital sniffing almost always began a grooming bout in both taxa, but usually was directed by males to females. Naso-muzzle sniffing occurred in both taxa when the female accepted the male. It was also directed by the male to infants clinging to the mother. Bouts of grooming sometimes were interrupted by naso-muzzle sniffing.

The specialized brachial gland of *Loris* was used in both taxa. During allogrooming, it was licked and rubbed mainly over the face, but also over the body. Both red and grey males were seen to press their brachial glands against a female, particularly if she rejected a grooming attempt. Mothers were seen to rub this gland over infants during normal grooming sessions. When animals were caught, the brachial gland exuded a pungent sticky substance. Although *Loris* lacks the specialized genital glands of pottos, two grey loris females exhibited a secretion from their vulva. Two male red lorises exhibited a thick pungent secretion on their testes.

Chemical Communication: Pottos

Pottos engaged in either indirect or direct modes of olfactory communication 162 times, or an average of 25.06% (±0.06) of observations. The relative frequencies of behavior associated with olfaction, namely smelling and/or scent marking conspecifics and/or substrates, are illustrated in Figure 10.2. Pottos spent significantly more time in direct olfactory communication than indirect forms of olfactory behavior (paired t test: $t = 10.43, p = 0.001, \mathrm{df} = 9$). Substrates were both smelled and scent-marked significantly more frequently than conspecifics were either smelled or scent-marked (paired t test: $t = -9.76$, $p = 0.001$, $\mathrm{df} = 9$. No significant difference was found in the amount of sample points spent by females and males in scent-marking (independent t test: $t = -0.94, p = 0.38, \mathrm{df} = 7$, NS). Olfactory behaviors tended to be more common in males than females, although this difference was not significant (independent t test: $t = 1.04, p = 0.34, \mathrm{df} = 7$, NS). No significant difference was found between the number of sample points the sexes smelled and scent-marked conspecifics (independent t test $= 2.70, p = 0.80, \mathrm{df} = 7$, NS) or substrates (independent t test: $\mathrm{t} = 0.37, p = 0.72, \mathrm{df} = 7$, NS).

Pottos marked the substrates with urine by gently lowering the penis or clitoris onto the substrate during locomotion (rhythmic micturition). Genital secretions of pottos were deposited by the female wiping her vulval glands and the male his scrotal glands along the substrate. Scent-marking of conspecifics was another form of indirect communication and was observed between paired male and female pottos, during allogrooming and copulation. A male and female potto would rub their genital glands and then touch the fur of the conspecific, thereby transferring scent, termed genital-scratching marking. One male potto was observed wiping his scrotal gland on his female partner and straddling her and passing-over. Pottos engaged in marking their bodies with their own odors, and were observed

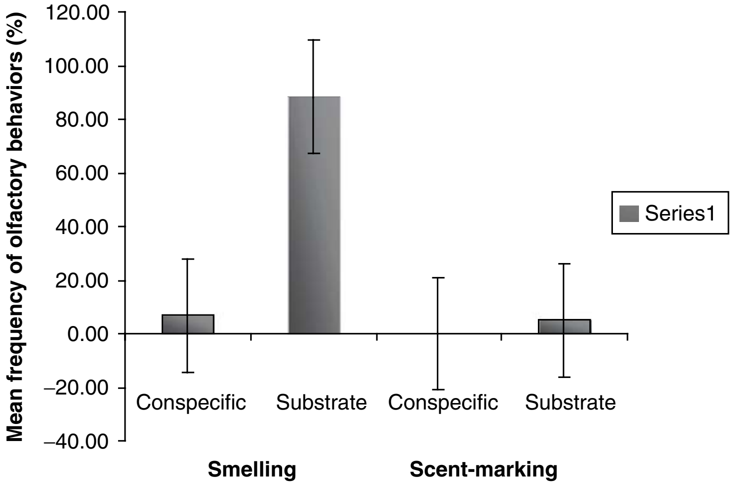

FIGURE 10.2. Mean percentage frequency of olfactory behaviors used by pottos on Mt Kupe, Cameroon. Smelling substrates includes branches, lianes, leaves, ground and air. Scent-marking includes marking with urine, genital glands, passing-over, genital-scratching and rhythmic micturition

marking themselves with genital grand secretions during autogrooming by genital-scratching marking.

Direct modes of olfactory communication were witnessed in pottos when two familiar individuals met. This occurred between paired males and females, and between an adult and a sub-adult male. The two animals faced each other and grasped the shoulders of the conspecific, then sniffed the cheeks and muzzle of each other in turn. Grooming of the head, neck, and shoulder region for several minutes normally followed. When the meeting preceded copulation, the male initiated olfactory investigation of the female's genital region.

Pottos were commonly observed to travel with their noses close to the substrate (nose-down searching). A male potto, after smelling the branch he was on, which was in the home range of another female, engaged in Flehmen, where he opened his mouth, rolled back his lips and raised his nose to sniff the air. Pottos often paused during locomotion to sniff the air or the surrounding substrates.

Discussion

Reactions to potential predators varied between slender lorises and pottos in this study. The most profound difference between the taxa is the common use of vocal communication by lorises, but virtually none pottos. Although all taxa engage in noisy displays, these are more common amongst the lorises. Pottos were seen face to face with predators less often than lorises, which in general ignored them. The greatest similarity amongst the taxa was their profuse use of olfactory communication; whether or not this communication mode is "discrete in the extreme" is discussed further here.

Slender lorises were much more vocal than pottos. In addition to the array of whistles discussed here, lorises frequently utter social "chitters," "kriks," and soft squeaks when engaged in social interactions (Nekaris & Jayewardene, 2003), suggesting that vocal communication is an important aspect of the behavioral repertoire of both taxa. Slender lorises in India were found to be similarly vocal (Bearder et al., 2002). Interestingly, slender lorises are relatively silent with regard to whistles in the captive setting, despite their using milder social calls here (Schulze & Meier, 1995), suggesting that loud whistles provide long distance messages that are less useful in captivity (Zimmerman, 1985, 1995).

Whistles are probably used in many contexts, including contact, spacing, aggression, and appeasement (Schulze & Meier, 1995; Bearder et al., 2002). Our data show that the whistle may also serve a predatory warning function. Both taxa emitted single whistles in the face of potential predators. This short whistle may serve as a quick warning to conspecifics that a predator is in the area (Hersek & Owings, 1993) or may serve as a pursuit deterrence signal, alerting the predator that it has been spotted (Woodland et al., 1980; Hasson, 1991).

A previous study showed that red lorises produced more multi-syllabic calls than grey lorises, with their calls characterized by greater frequency modulation than those of grey lorises (Coultas, 2002). Frequency modulation may function to minimize interference caused by dense vegetation; as vegetation absorbs and scatters sound, multi-syllabic calls may provide an advantage to red slender lorises living in dense rain forest (Wiley & Richards, 1978). Another possibility is that narrow frequency range and long duration of whistles means that no matter how many are emitted, predators would have difficulty localizing them (Daschbach et al. 1981). An ongoing study of red loris vocalizations will, it is hoped, shed additional light on the function of loris calls (Bernede, unpub. data).

Pottos in this study were only heard to vocalize in the presence of potentially threatening humans, accompanied by audible biting of branches. Similar observations were made of the same taxon in Gabon (Charles-Dominique, 1977). When attacked by a palm civet, a potto produced a strident vocalization ("groan" or "heee"), while audibly striking its jaw against a branch. This display had the effect of driving the palm civet away. At the same study site, pottos infrequently made a tsic contact call and a distress wheet call (Charles-Dominique, 1977). Such threat calls were also observed infrequently in the sympatric perodicticine, *Arctocebus aureus*. This relative silence coincides with the classic description of perodicticines as cryptic.

Silence also is a feature meant to characterize the locomotion of lorises and pottos. Charles-Dominique (1977) described discrete locomotion as the primary predator defense of pottos. In general, both lorises and pottos moved silently through their environment. Slender lorises, however, engaged in loud displays with branches. Such displays, lasting as long as 3 hrs, have also been seen in wild *L. l. lydekkerianus* and captive *L. l. nordicus* during self-play, and during social interactions where twig rattling may be part of a dominance display or a sign of stress (Schulze & Meier, 1995; Nekaris, 2001). The benefits of noisy displays are more obvious in a mating context (Lima & Dill, 1990; Andersson, 1994); the function of noisy self-play remains unclear.

Freezing or taking cover in the presence of potential predators was more applicable to pottos than to slender lorises. Lorises rarely modified their behavior in the face of a potential predator, concurring with observations of Mysore slender lorises (Bearder et al., 2002). The most noticeable reaction was freezing in the presence of a snake. A reticulated python consumed a greater slow loris (*N. coucang*) in Malaysia (Wiens & Zitzmann, 1999), and snakes are known to kill other nocturnal primates (Gursky, 2002). Slow lorises also made no reaction when owls or palm civets passed in close proximity, and were most cautious on the ground (Wiens, 2002), again mirroring Mysore slender lorises (Nekaris, 2001). It is possible that lorises are unpalatable to some predators and, thus, are avoided by them (see below).

Viverrids were, however, confirmed predators to pottos; in this study a palm civet consumed a potto, and pottos took cover when civets were present in their range. These viverrids were also a threat to Milne-Edwards' pottos in Gabon. When a palm civet attempted to attack an adult potto, the potto assumed the defense posture, thrusting at the civet with its scapular shield and striking at it by moving its body forward with teeth exposed. The potto remained immobile after this episode, until a second civet approached it, which the potto succeeded in knocking off the branch (Charles-Dominique, 1977). The black-legged mongoose was also identified as a potential predator at Mt. Kupe. In Gabon this mongoose launched an attack on a potto; the potto escaped by moving into impenetrable foliage, a behavior also exhibited by animals in our study. A dog was seen to kill a potto moving on the ground. Both a dead snake and genet experimentally presented to pottos elicited such fear that the animals fell to the ground to evade the danger (Charles-Dominique, 1974). These numerous examples indeed suggest that pottos may be at a higher predation risk than lorises if detected, and thus masterful silence may be of greater benefit to them.

This study further elucidates the vital importance of olfactory communication to slender lorises and pottos. Slender lorises and pottos employ complex social networks that are maintained by olfactory communication to varying degrees (Seitz, 1969; Charles-Dominique, 1977; Schilling, 1979; Fisher et al., 2003a; Wiens & Zitzmann, 2003). Pottos display well-developed anogenital glands, lack brachial glands, and do not urine wash, whereas slender lorises urine wash, have brachial glands, and lack anogenital glands (Schilling, 1979; Rasmussen & Nekaris, 1998). These anatomical differences may confer different functions in terms of both social and anti-predator behavior.

As in the present study, Charles-Dominique (1974, 1978) found that gregariousness amongst pottos occurs primarily via urine marking and/or secretions from their anogenital glands. Females produce a vaginal discharge which is mixed with urine during marking at the time of estrous, inducing a strong attraction for males, informing them of her reproductive status while simultaneously arousing sexual behavior (Epple, 1974).

These chemo-signals can elicit a response in conspecifics and are certainly used in various social contexts (Schilling, 1979; Perret, 1995; Palagi et al., 2002). Odors produced by conspecifics may convey information such as sex, species, social status, or reproductive state (Clark, 1982a, 1982b; Petrulis, et al. 2000). Scent marks from anogenital glands have been found to convey subsets of information, such as intersexual communication, self-advertisement, territorial demarcation, and to incite male-male competition (Heymann, 2000; Heymann, 2001; Smith & Gordon, 2002; Wolff et al., 2002; Lewis, 2004; Braune et al., 2005). Although pottos forage near to one another, they rarely move cohesively (Pimley et al., 2005a); thus, chemo-signals may form a social bridge between individuals who rarely encounter each other (Epple, 1974; Johnston, 1999). The information non-gregarious mammals relay via scent-marking has also been observed in species that live commensally (Kotenkova & Naidenko, 1999; Solomon, 1999; Humphries et al., 2001), reiterating the importance of scent in the social lives of pottos.

The social functions of olfactory behavior cited are also applicable to slender lorises. *Loris*, however, may more actively use chemical communication in antipredatory behavior by using a pheromone to ward off predators or announce them to conspecifics, as in the case of *Nycticebus* (Nekaris, 2002; Hagey et al., this volume). Both *Loris* and *Nycticebus* emit an oily secretion from their brachial glands when confronted with similar physiological stressors (Alterman, 1995). This exudate, when mixed with saliva, has been determined to be highly volatile and it releases a pungent odor, suggesting that it may function as an alarm pheromone (Schilling, 1979; Alberts, 1992; Hagey et al., this volume). Alarm pheromones are relatively ubiquitous, predominantly not species-specific, and are emitted when a predator is detected, possibly to repel it (Mathis et al., 1995; Wyatt, 2003). Pheromones can elicit a flight or fight response and may contain compounds that can make flesh unpalatable or toxic (Wyatt, 2003). Conspecifics who detect an alarm pheromone may decrease their activity (Chivers, 1995).

This chemical might function in *Loris* in several ways. First, during the cobra imitation lorises were seen to rub their arms on the head, perhaps transferring chemicals from their brachial gland to a vulnerable part of their body. A similar behavior by *Nycticebus* results in the secretion drying and crystallizing on the top of the head (Hagey et al., this volume). In this solid form, the odors are prolonged and can also be detected visually by conspecifics, serving as a potential alarm (Gosling & Roberts, 2001; Roberts & Gosling, 2001). As has been suggested for *Nycticebus* and *Perodicticus* (Alterman, 1995), urine washing in combination with grooming of infants may serve as an additional effective olfactory barrier from predators via a pungent odor (e.g., an alert signal), a perilous chemical signal (e.g., an alarm pheromone), or as a form of predator mimicry (Wyatt, 2003).

Mimicry may also be used by lorises in another manner. During this and previous studies, urine washing was frequent before and after eating or being stung by noxious insects (Nekaris, 2001; Nekaris & Rasmussen, 2003). Such insects form a large part of the loris dietary repertoire and may serve as an exogenous source of a toxic substance that may later be secreted by lorises during urine washing (Darst et al., 2005). Urine washing before capture of toxic insects may be indicative of a self-defense mechanism by the way it mimics the scents of prey items to facilitate their capture without triggering alarm responses (Caldwell, 1996). Urine washing did also occur in other contexts and might serve additional purposes, such as enhancing the grip, as it does in galagos (Welker, 1973; Harcourt, 1981).

Finally, numerous studies point to the ability of potential predators to detect olfactory signals, suggesting that this form of communication may not be cryptic. Scent-marking with glands, urine, or feces containing pheromones such as kairomones, allomones, and allelochemicals can be utilized by predators to either mimic pheromones of prey or to deceive prey (Watson et al., 1999; Heymann, 2000; Wyatt, 2003). Predators can eavesdrop on pheromone trails, which can help them predict the location and movement of prey, thereby enhancing their hunting strategy (Gosling & Roberts, 2001). Predators of lorisines not only employ their ability to analyze chemicals with their vomeronasal organs (e.g., Alterman, 1995), but some avian predators can detect and follow the pheromone trails or marks of prey that are visible as ultraviolet light (Wyatt, 2003). Fisher et al. (2003b) have shown that the urine of *Nycticebus pygmaeus* has UV properties; the pungent odor of slender loris urine indicating that it contains molecules of low volatility suggests it is similar, and again suggests strategies of advertisement that are different from pottos. Further studies should consider patterns of scent-marking amongst the taxa and how these might be used to confound predators (Gosling, 1982).

Conclusions

This study has shown that although in many ways lorises and pottos are adapted to avoid predator detection they differ greatly in other behavioral mechanisms that usually fall under the category of crypsis. Pottos are less vocal, less gregarious, and more cautious in the face of potential predators than slender lorises. Both pottos and slender lorises have evolved independent means to contend with predators upon detection—the potto with its defensive shield and the loris with loud vocalizations, and potentially with the use of alarm pheromones. Olfactory communication is of vital importance to both of these lorisiforms, and its role in predator avoidance and defense should be considered in future studies. This study further elucidates that despite similar anatomical adaptations for slow climbing quadrupedalism, the behavioral repertoire of lorises and pottos is characterized by more variability than previously acknowledged.

Acknowledgments. K.A.I. Nekaris and K.M. Ablard would like to thank the Ball family of Hen Dafarn, Gelliwen, Wales, for making the writing of this paper possible. R. Swaisgood and H. Schulze provided incredibly insightful reviews.

L. Birkett drew the images for this paper. T. Wyatt provided invaluable information and resources regarding olfactory communication.

K.A.I. Nekaris thanks the Department of Wildlife Conservation and Forest Department of Sri Lanka for authorizing this study. Logistical aid and/or field assistance for slender loris studies was provided by M. Abare, D. Coultas, W. Dittus, S. Gamage, A. Gunawardene, K. Hart, J. Jayewardene, E. Leavitt, W. Liyanage, A. Perera, C. Perera, R. Perera, V. Perera, H. Schulze, J. Stokes, and S. Wimalasuriya. Loris studies were funded by grants to Nekaris from Margot Marsh Primate Biodiversity Fund, Columbus Zoological Park and Aquarium, Primate Conservation, Inc., People's Trust for Endangered Species, One with Nature of the Philadelphia Zoo, Petzl Headlamp Company, and the School of Social Sciences and Law of Oxford Brookes University. E.R. Pimley thanks her research assistants: G. Ngole, G. Ekwe, P. Mesumbe, A. Ekinde, O. Mokoko, M. Etube, A. Ekwoge, H. Enongene, O. Mesumbe, and D. Menze for their invaluable support with fieldwork. She also acknowledges the staff of WWF Cameroon and members of the Sub-Department of Animal Behaviour, Departments of Zoology and Biological Anthropology, University of Cambridge, for logistical support and advice. Support for the field study of pottos came from the UK Medical Research Council.

References

Alberts, A.C. (1992). Constraints on the design of chemical communication systems in terrestrial vertebrates. *The American Naturalist*, 139: S62–S69.

Alterman, L. (1995). Toxins and toothcombs: Potential allospecific chemical defenses in *Nycticebus* and *Perodicticus*. In L. Alterman, G.A. Doyle, and M.K. Izard (Eds.), *Creatures of the dark: The nocturnal prosimians* (pp. 413–424). New York: Plenum Press.

Altman, J. (1974). Observational study of behavior: Sampling methods. *Behavior*, 49: 227–265.

Ambrose, L. (1999). Species diversity in West and Central African galagos (Primates, Galagonidae): The use of acoustic analysis. Doctoral thesis. Oxford Brookes University, Oxford.

Ambrose, L. (2003). Three acoustic forms of Allen's galagos (Primates; Galagonidae) in the Central African region. *Primates*, 44: 25–39.

Andersson, M. (1994). *Sexual selection*. Princeton, NJ: Princeton Univ. Press.

Andrew, R.J., and Klopman, R.B. (1974). Urine-washing: Comparative notes. In R.D. Martin, G.A. Doyle, and A.C. Walker (Eds.), *Prosimian biology* (pp. 303–312). London: Duckworth.

Banks, P.B., Norrdahl, K., and Korpimäki, E. (2000). Nonlinearity in the predation risk of prey mobility. *Proceedings of the Royal Society Biological Sciences Series B*, 267: 1621–1625.

Banks, P.B., Norrdahl, K., and Korpimäki, E. (2002). Mobility decisions and the predation risks of reintroduction. *Biological Conservation*, 103: 133–138.

Bearder, S.K., Honess, P.E., and Ambrose, L. (1995). Species diversity among galagos with special reference to mate recognition. In L. Alterman, G. Doyle, and M.K. Izard (Eds.), *Creatures of the dark: The nocturnal prosimians* (pp. 331–352). New York: Plenum Press.

Bearder, S.K., Nekaris, K.A.I., and Buzzell, C.A. (2002). Dangers of the night: Are some primates afraid of the dark? In L.E. Miller (Ed.), *Eat or be eaten: Predator sensitive foraging in primates* (pp. 21–43). Cambridge: Cambridge Univ. Press.

Bearder, S.K., Nekaris, K.A.I., and Curtis, D.J. (2006). A re-evaluation of the role of vision in the activity and communication of nocturnal primates. *Folia Primatologica*, 77 (1–2): 50–71.

Braune, P., Schmidt, S., and Zimmermann, E. (2005). Spacing and group coordination in a nocturnal primate, the golden brown mouse lemur (*Microcebus ravelobensis*). *Behavioural Ecology and Sociobiology*, 58(6): 587–596.

Caldwell, J. (1996). The evolution of myrmecophagy and its correlates in poison frogs (Family: Dendrobatidae). *Journal of Zoology*, 240: 75–100.

Charles-Dominique, P. (1974). Vie sociale de *Perodicticus potto* (Primates: Lorisides). Étude de terrain en forêt equatorial de l'ouest africain au Gabon. *Mammalia*, 38: 355–379.

Charles-Dominique, P. (1977). *Ecology and behaviour of nocturnal primates*. London: Duckworth.

Charles-Dominique, P. (1978). Solitary and gregarious prosimians: Evolution of social structures in primates. In D.J. Chivers and K.A. Joysey (Eds.), *Recent advances in primatology*, Volume 3 (pp. 139–149). New York: Academic Press.

Charles-Dominique, P. (1990). Ecological adaptations related to locomotion in primates: An introduction. In F.K. Jouffroy, M.H. Stack, and C. Niemitz (Eds.), *Gravity, posture and locomotion in primates* (pp. 19–31). Sedicesimo: Editrice II.

Cheney, D., and Wrangham, R.W. (1987). Predation. In B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, and T.T. Struhsaker (Eds.), *Primate societies* (pp. 227–239). Chicago: Univ. of Chicago Press.

Chivers, D.P., Brown, G.E., and Smith, J.F. (1995). Chemical alarm signals: Predator deterrents or predator attractants? *The American Naturalist*, 145: 994–105.

Clark, A.B. (1982a). Scent marks as social signals in *Galago crassicaudatus*. I. Sex and reproductive status as factors in signals and responses. *Journal of Chemical Ecology*, 8(8): 1133–1151.

Clark, A.B. (1982b). Scent marks as social signals in *Galago crassicaudatus*. II. Discrimination between individuals by scent. *Journal of Chemical Ecology*, 8(8): 1153–1165.

Coultas, D.S. (2002). Bioacoustic analysis of the loud call of two species of slender loris (*Loris tardigradus* and *L. lydekkerianus nordicus)* from Sri Lanka. MSc thesis. Oxford Brookes University, Oxford.

Darst, C.R., Menéndez-Guerrero, P.A., Coloma, L.A., and Cannatella, D.C. (2005). Evolution of dietary specialization and chemical defense in poison frogs (Dendrobatidae): A comparative analysis. *The American Naturalist*, 165: 56.

Daschbach, N.J., Schein, M.W., and Haines, D.E. (1981). Vocalizations of the slow loris, *Nycticebus coucang* (Primates, Lorisidae). *Inter. Jour. of Primatol.*, 2, 71–80.

Ehrlich, A., and Musicant, A. (1977). Social and individual behaviors in captive slow lorises (*Nycticebus coucang*). *Behaviour*, 60: 195–220.

Epple, G. (1974). Primate pheromones. In M.C. Birch (Ed.) *Pheromones* (pp. 366–385). New York: Elsevier.

Evans, C., and Schilling, A. (1995). The accessory (vomeronasal) chemoreceptor system in some prosimians. In L. Alterman, G.A. Doyle, and M.K. Izard (Eds.), *Creatures of the dark: The nocturnal prosimians* (pp. 393–411). New York: Plenum Press.

Fisher, H.S., Swaisgood, R.R., and Fitch-Snyder, H. (2003a). Odor familiarity and female preferences for males in a threatened primate, the pygmy loris *Nycticebus* *pygmaeus*: Applications for genetic management of small populations. *Naturwissenschaften*, 90(11): 509–512.

Fisher, H.S., Swaisgood, R.R., and Fitch-Snyder, H. (2003b). Countermarking by male pygmy lorises (*Nycticebus pygmaeus*): Do females use odor cues to select mates with high competitive ability? *Behav. Ecol. and Sociobiol.*, 53(2): 123–130.

Fitch-Snyder, H., and Schulze, H. (2001). *Management of lorises in captivity: A husbandry manual for Asian lorisines*. San Diego: Zoological Society of San Diego, Center for Reproduction of Endangered Species Press.

Gosling, L.M. (1982). A reassessment of the function of scent marking in territories. *Zeitschrift für Tierpsychologie*, 60: 89–118.

Gosling, L.M., and Roberts, S. (2001). Scent-marking by male mammals: Cheat-proof signals to competitors and mates. *Advances in the Study of Behavior*, 30: 169–217.

Gursky, S. (2002). Predation on a wild spectral tarsier (*Tarsius spectrum*) by a snake. *Folia Primatol.*, 73: 60–62.

Gursky, S. (2003). Predation experiments on infant spectral tarsiers (*Tarsius spectrum*). *Folia Primatol.*, 74(5–6): 272–284.

Gutzke, W.H.N. (2001). Field observations confirm laboratory reports of defense responses by snakes to the odors of predatory snakes. In A. Marchlewska-Koj, J. Lepri, and D. Muller-Schwarze (Eds.), *Chemical signals in vertebrates* (9th ed.). (pp. 285–288). New York: Kluwer Academic/Plenum Publishers.

Hagey, L.R., Fry, B.G., and Snyder, H. (2006). Talking defensively: A dual use for the brachial gland exudate of slow and pygmy lorises. In S. Gursky (Ed.), this volume (pp. xx–yy). New York: Kluwer/Academic Press.

Harcourt, C.S. (1981). An examination of the function of urine washing in *Galago senegalensis*. *Zeitschrift für Tierpsychologie*, 55: 119–128.

Hasson, O. (1991). Pursuit-deterrent signals: Communication between prey and predator. *Trends in Ecology and Evolution*, 6: 325–329.

Hersek, M.J, and Owings, D.H. (1993). Tail flagging by adult California ground squirrels: A tonic signal that serves different functions for males and females. *Animal Behaviour*, 46: 129–138.

Heymann, E.W. (2000). Spatial patterns of scent marking in wild moustached tamarins, *Saguinus mystax*: No evidence for a territorial function. *Animal Behaviour*, 2000: 723–730.

Heymann, E.W. (2001). Interspecific variation of scent-marking behaviour in wild tamarins, *Saguinus mystax* and *Saguinus fuscicollis*. *Folia Primatol.*, 72: 253–267.

Hill, R.A., and Dunbar, R.I.M. (1998). An evaluation of the roles of predation rate and predation risk as selective pressures on primate grouping behaviour. *Behaviour*, 135 (4): 411–430.

Humphries, R.E., Robertson, D.H.L., Nevison, C.M., Beynon, R.J., and Hurst, J.L. (2001). The role of urinary proteins and volatiles in competitive scent marking among male house mice. In A. Marchlewskha-Koj, J. Lepri, and D. Muller-Schwarze (Eds.), *Chemical signals in vertebrates* (9th ed.). (pp. 353–360). New York: Kluwer Academic/Plenum Publishers.

Ilse, D.R. (1955). Olfactory marking of territory in two young male lorises kept in captivity in Poona. *British Jour. of Animal Behav.*, 3: 118–120.

Jackson, B.D., Morgan, E.D., and Billen, J.P.J. (1990). A note on pygidial glands of primitive Australian ants: A new source of odorous chemicals. In A.R. McCaffery and I.D. Wilson (Eds.), *Chromatography and isolation of insect hormones and pheromones* New York: Plenum Press. p. 335–341.

Johnston, R.E. (1999). How do hamsters know whose scent is on top and why should it matter? In R. Johnston, D. Muller-Schwartz, and P. Sorenson (Eds.), *Advances in chemical signals in vertebrates* (pp. 227–238). New York: Kluwer Academic/Plenum Publishers.

Koivula, M., Korpimaki, E. and Viitala, J. (1997). Do Tengmalm's owls see vole scent marks visible in ultraviolet light? *Animal Behaviour*, 54: 873–877.

Kotenkova, E.V., and Naidenko, S.V. (1999). Discrimination of con- and heterospecific odors in different taxa of the *Mus musculus* species group. In R. Johnston, D. Muller-Schwartz, and P. Sorenson (Eds.), *Advances in chemical signals in vertebrates* (pp. 299–208). New York: Kluwer Academic/Plenum Publishers.

Lewis, R.J. (2004). Sex differences in scent-marking in Sifaka: Mating conflict or male services? Unpublished doctoral dissertation. University of Texas at Austin, Texas.

Lima, S. L. and Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, 68: 619–640.

Manley, G. (1974). Functions of the external genital glands of *Perodicticus* and *Arctocebus*. In R.D. Martin, G.A. Doyle, and A.C. Walker (Eds.), *Prosimian biology* (pp. 313–329). London: Duckworth.

Mathis, A., Chivers, D.P., and Smith, J.F. (1995). Chemical alarm signals: Predator deterrents or predator attractants. *The American Naturalist*, 145(6): 994–1005.

Motulsky, H. (1995). *Intuitive biostatistics*. Oxford: Oxford Univ. Press.

Nekaris, K.A.I. (2001). Activity budget and positional behavior of the Mysore slender loris (*Loris tardigradus lydekkarianus*): Implications for "slow climbing" locomotion. *Folia Primatol.*, 72: 228–241.

Nekaris, K.A.I. (2002). Slender in the night. *Natural History*, 2(02): 54–59.

Nekaris, K.A.I. (2003). Observations on mating, birthing and parental care in three taxa of slender loris in India and Sri Lanka (*Loris tardigradus* and *Loris lydekkerianus*). *Folia Primatol.*, 74: 312–336.

Nekaris, K.A.I., and Jayewardene, J. (2003). Pilot study and conservation status of the slender loris (*Loris tardigradus* and *Loris lydekkerianus*) in Sri Lanka. *Primate Conservation*, 19: 83–90.

Nekaris, K.A.I., and Jayewardene, J. (2004). Distribution of slender lorises in four ecological zones in Sri Lanka. *Journal of Zoology*, 262: 1–12.

Nekaris, K.A.I., and Rasmussen, D.T. (2003). Diet of the slender loris. *Inter. Jour. of Primatol.*, 24(1): 33–46.

Osman Hill, W.C. (1938). A curious habit common to lorisoid and platyrrhine monkeys. *Ceylon Journal of Science B*, 21(1): 65.

Palagi, E., Gregorace, A., and Borgognini Tarli, S.M. (2002). Development of olfactory behavior in captive ring-railed lemurs (*Lemur catta*). *Inter. Jour. of Primatol.*, 23(3): 587–599.

Perret, M. (1995). Chemocommunication in the reproduction function of mouse lemurs. In L. Alterman, G.A. Doyle, and M.K. Izard (Eds.), *Creatures of the dark: The nocturnal prosimians* (pp. 372–392). New York: Plenum Press.

Perrot-Sinal, T., Kavaliers, M., and Ossenkopp, P. (1999). Changes in locomotor activity following predator odor exposure are dependent on sex and reproductive status in the meadow vole. In R. Johnston, D. Muller-Schwartz, and P. Sorenson (Eds.), *Advances in chemical signals in vertebrates* (pp. 497–504). New York: Kluwer Academic/Plenum Press.

Petrulis, A., Peng, M., and Johnston, R.E. (2000). The role of the hippocampal system in social odor discrimination and scent-marking in female golden hamsters (*Mesocricetus auratus*). *Behavioural Neuroscience*, 114(1): 184–195.

Petter, J.J., and Hladik C.M. (1970). Observations sur le domaine vital et la densité de population de *Loris tardigradus* dans les forêts de Ceylon. *Mammalia*, 34: 394–409.

Pimley, E.R. (2002). The behavioural ecology and genetics of the potto (*Perodicticus potto edwardsi*) and Allen's bushbaby (*Galago alleni cameronensis*). Doctoral thesis. University of Cambridge, Cambridge.

Pimley, E.R., and Bearder, S.K. (In press). Potto (*Perodicticus*). In J. Kingdon, D. Happold, and T. Butysnki (Eds.), *Mammals of Africa*, Vol. 1. (pp. xx–yy). Cambridge: Cambridge Univ. Press.

Pimley, E.R., Bearder, S.K., and Dixson, A.F. (2005a) Examining the social organization of the Milne-Edwards' potto *Perodicticus potto edwardsi*. *Amer. Jour. of Primatol.*, 66(4): 317–330.

Pimley, E.R., Bearder, S.K., and Dixson, A.F. (2005b). Home range analysis of *Perodicticus potto edwardsi* and *Sciurocheirus cameronensis*. *Inter. Jour. of Primatol.*, 26(1): 191–206.

Rasmussen, D.T. (1986). Life history and behavior of slow lorises and slender lorises. Doctoral thesis. Duke University, Durham, NC.

Rasmussen, D.T., and Nekaris, K.A.I. (1998). Evolutionary history of the lorisiform primates. *Folia Primatol.*, 69: 250–285.

Roberts, S.C., and Gosling, L.M. (2001). The economic consequences of advertising scent mark location on territories. In A. Marchlewsha-Koj, J. Lepri, and D. Schwarze (Eds.), *Chemical signals in vertebrates* (9th ed.). (pp. 11–17). New York: Kluwer Academic/Plenum Press, New York.

Rohr, J.R., and Madison, D.M. (2001). A chemically mediated trade-off between predation risk and mate search in newts. *Animal Behaviour*, 62: 863–869.

Schilling, A. (1979). Olfactory communication in prosimians. In G.A. Doyle and R.D. Martin (Eds.), *The study of prosimian behaviour* (pp. 461–542). London: Academic Press, Inc.

Schülke, O.(2001). Social anti-predator behaviour in a nocturnal lemur. *Folia Primatologica*, 72(6): 332–334.

Schulze, H., and Meier, B. (1995). Behaviour of captive *Loris tardigradus nordicus*: A qualitative description including some information about morphological bases of behavior. In L. Alterman, M. Doyle, and M.K. Izard (Eds.), *Creatures of the dark: The nocturnal prosimians* (pp. 221–250). New York: Kluwer Academic/Plenum Publishers.

Seitz, E. (1969). Die Bedeutung gerüchlicher Orientierung beim Plumplori *Nycticebus coucang* Boddaert 1785 (Prosimii, Lorisidae). *Zeitschrift für Tierpsychologie*, 26: 73–103.

Sellers, W. (1996). A biomechanical investigation into the absence of leaping in the locomotor repertoire of the slender loris (*Loris tardigradus*). *Folia Primatol.*, 67: 1–14.

Shivik, J.A., and Clark, L. (1999). The development of chemosensory attractants for brown tree snakes. In R. Johnston, D. Muller-Schwartz, and P. Sorsenson (Eds.), *Advances in chemical signals in vertebrates* (pp. 649–654). New York: Kluwer Academic/Plenum Publishers.

Smith, E.T., and Gordon, J.S. (2002). Sex differences in olfactory communication in *Saguinus labiatus*. *Inter. Jour. of Primatol.*, 23(2): 429–441.

Solomon, N.G. (1999). The functional significance of olfactory cues in the pine vole (*Microtus pinetorum*). In R. Johnston, D. Muller-Schwartz, and P. Sorsenson (Eds.), *Advances in chemical signals in vertebrates* (pp. 407–419). New York: Kluwer Academic/Plenum Publishers.

Stanford, C. (2002). Avoiding predators: Expectations and evidence in primate antipredator behavior. *Inter. Jour. of Primatol.*, 23(4): 741–757.

Still, J. (1905). On the loris in captivity. *Spolia Zeylanica*, 3: 155–157.

Terborgh, J., and Janson, C. (1986). Socioecology of primate groups. *Annual Review of Ecological Systematics*, 17: 111–135.

van Schaik, C., and van Hoof, J. (1983). On the ultimate causes of primate social systems. *Behaviour*, 5: 91–117.

Walker, A.C. (1969). The locomotion of the lorises, with special reference to the potto. *East African Wildlife Journal*, 7: 1–5.

Watson, S.L., Ward, J.P., David, K.B., and Stavisky, R.C. (1999). Scent-marking and cortisol response in the small-eared bushbaby (*Otolemur garnettii*). *Physiology & Behavior*, 66(4): 695–699.

Welker, C. (1973). Ethological significance of the urine washing by *Galago crassicaudatus* E. Geoffroy, 1812 (Lorisiformes: Galagidae). *Folia Primatol.*, 20: 429–452.

Wiens, F. and Zitzmann, A. (1999). Predation on a wild slow loris (*Nycticebus coucang*) by a reticulated python (*Python reticulatus*). *Folia Primatol.*, 70: 362–364.

Wiens, F. (2002). Behavior and ecology of wild slow lorises (Nycticebus coucang): Social organisation, infant care system and diet. Doctoral thesis. Bayreuth University, Bayreuth (Germany).

Wiens, F., and Zitzmann, A. (2003). Social structure of the solitary slow loris *Nycticebus coucang* (Lorisidae). *Journal of Zoology*, 261(1): 35–46.

Wiley, R.H., and Richards, D.G. (1978). Physical constraints on acoustic communication in the atmosphere: Implications for the evolution of animal vocalizations. *Behav. Ecol. and Sociobiol.*, 3: 69–94.

Wolff, J.O., Mech, S.G., and Thomas, S.A. (2002). Scent marking in female prairie voles: A test of alternative hypotheses. *Ethology*, 108: 483–494.

Woodland, D.J., Jaafar, Z., and Knight, M.-L. (1980). The "pursuit deterrent" function of alarm signals. *American Naturalist*, 115: 748–753.

Wyatt, T.D. (2003). *Pheromones and animal behavior: Communication by smell and taste*. Cambridge: Cambridge Univ. Press.

Zimmerman, E. (1985). Vocalisations and associated behaviours in adult slow loris (*Nycticebus coucang*). *Folia Primatol.*, 44: 52–64.

Zimmermann, E. (1995). Acoustic communication in nocturnal prosimians. In: Alterman, L., Doyle, G. A. and Izard, M. K. (eds.), *Creatures of the Dark: The nocturnal prosimians* (pp. 311–330). New York: Plenum Press.