

**COMPARATIVE ECOLOGY AND BEHAVIOUR OF EASTERN
POTTO *PERODICTICUS IBEANUS* AND CENTRAL POTTO
P. EDWARDSI IN ANGOLA, CAMEROON, KENYA, NIGERIA,
RWANDA AND UGANDA**

Averee M. Luhrs, Magdalena S. Svensson & K. Anne-Isola Nekaris
Nocturnal Primate Research Group, Oxford Brookes University
Headington, Oxford, OX3 0BP, UK
averee.luhrs@utsa.edu; m.svensson@brookes.ac.uk; anekaris@brookes.ac.uk

ABSTRACT

Comparative behavioural research reveals both intra- and inter-species diversity among primates. Few long-term behavioural studies have been conducted on African nocturnal primates. Here we describe and compare behavioural and ecological observations on two species of pottos (*Perodicticus ibeanus* and *P. edwardsi*) across ten sites. We observed a total of 51 *P. edwardsi* and 28 *P. ibeanus*. We recorded all 21 postures within an established lorisid ethogram, as well as 42 of 50 behaviours. Eating, locomotion, freezing, resting and sniffing were the most common behaviours. We recorded behaviours not previously described for perodicticines, including bark chewing and unique vocalisations. Three species of pottos are now recognised, with potentially more species to be revealed within this cryptic and nocturnal genus. Although there are similarities among potto species, we show that unique ecological adaptations and behaviours may further elucidate their diversity.

Keywords: Behaviour, nocturnal, Lorisidae, Perodicticinae, *Perodicticus*, taxonomy

INTRODUCTION

In primates, comparative ethological research has uncovered differences in behaviour and habitat use between and among similar species living in sympatry or within the same species living in different faunal communities (Charles-Dominique *et al.*, 1980; Garber & Leigh, 1988; McGraw, 1988; Gebo & Chapman, 1995). Research comparing the behaviour of wild robust chimpanzees *Pan troglodytes* (Blumenbach, 1775) has revealed variation in feeding ecology among populations in different habitats (Hockings & Sousa, 2012), while studies comparing wild orangutan *Pongo* spp. populations (Whiten *et al.*, 1999) and robust chimpanzee populations (van Schaik *et al.*, 2003) revealed 'cultural' differences in tool use. Comparative research has also highlighted the habitat flexibility of primates, uncovering differential responses to habitat or faunal community change as a result of anthropogenic influences (Tan, 1999; Reed & Bidner, 2004).

From the 1960s through the 1980s, Jewell and Oates (1969), Bearder and Doyle (1974), Charles-Dominique (1971, 1974, 1977), Charles-Dominique and Bearder (1979)

and Oates (1984) laid a foundation for research on Lorisiformes (Galagidae and Lorisidae, the latter comprising Perodicticinae and Lorisinae). Since that time, few field studies on these taxa have lasted for more than a year. An increasing body of behavioural research on Asian lorises has revealed a diverse array of previously unrecognised species and unique traits, including the use of venom in the slow lorises *Nycticebus* spp. (Nekaris *et al.*, 2013). Such studies initially relied on a single ethogram created for all lorises, based largely on observations of captive lorises (Fitch-Snyder & Schulze, 2001). Field research showed that many behaviours were either unique to Asian lorises (slow or slender lorises *Loris* spp.) or were not displayed (Nekaris, 2001; Rode-Margono *et al.*, 2014; Poindexter & Nekaris, 2017). For example, slender lorises are extreme insectivores whereas slow lorises are obligate exudativores, with respective feeding strategies associated with unique behaviours, postures and digestion. This research revealed that in captivity these species were fed inappropriate foods leading to illness (Cabana & Nekaris, 2015; Williams *et al.*, 2015).

Since Perodicticinae and Lorisinae diverged roughly 40 million years ago, a range of unique behaviours occur among taxa (Pozzi *et al.*, 2015; Svensson *et al.* 2018). Molecular and morphological data have not resolved whether the Perodicticinae (pottos and angwantibos *Arctocebus* spp.) are more closely related to the Lorisinae or to the Galagidae, the family comprised of the vocal, fast-moving, galagos (Yoder *et al.*, 2001; Pozzi *et al.*, 2015). Understanding behavioural similarities and differences to other lorisiforms may help resolve this evolutionary puzzle. Yoder *et al.* (2001) suggest that the Perodicticinae and Lorisinae are either the result of extremely rapid evolution of specialised adaptations, or represent one of the most spectacular examples of parallel evolution amongst primates.

Although some recent literature (Pimley & Bearder, 2013) refers to only one species of potto - *Perodicticus potto* (Müller, 1776), most authorities now recognise three species (western potto *P. potto*, eastern potto *P. ibeanus* Thomas 1910, and central potto *P. edwardsi* Bouvier, 1879), with most authors mentioning the potential for additional taxa (figure 1) (Groves, 2001; Stump, 2005; Butynski & de Jong, 2007, 2017; Oates, 2011; Pozzi *et al.*, 2015). Here we follow the taxonomy used by Nekaris (2013) and IUCN (2018).

Charles-Dominique (1974) described wild pottos as strictly arboreal slow climbers and graspers, preferring secondary vegetation. Pottos were thought to be vocally silent, though perhaps communicating in the ultrasonic range (Heffner *et al.*, 1969). Pottos communicate with conspecifics through scent-marking, urine-washing and various glandular secretions (Manley, 1974; Oates, 1984; Pimley *et al.*, 2005a,b).

Morphologically, pottos are robust, with a wide, barrel-like body. Perhaps because of this, several of their positional behaviours are slightly different from those of the Lorisinae (figure 2). Traits unique to pottos include a shield on the shoulder blades thought to be a defence against predators (Charles-Dominique, 1977; Oates, 2011; Svensson *et al.*, 2018), and adapted pincer-like hands and feet exhibiting the most pronounced degree of hallucal adduction among lorisiforms (Jolly, 1972). Pottos share with slow lorises the unique trait of having a uni-male uni-female social organisation (Bearder *et al.*, 2003; Pimley *et al.*, 2005a). They appear to lack, however, the specialised slow loris traits of being venomous and consuming a diet primarily of gums (Nekaris *et al.*, 2013, but see Burrows, *et al.*, 2015). Pottos are especially reliant on olfactory cues when searching for food, with movement described as 'nose-down foraging' (Oates, 1984; Pimley *et al.*, 2005a) (figure 2d).

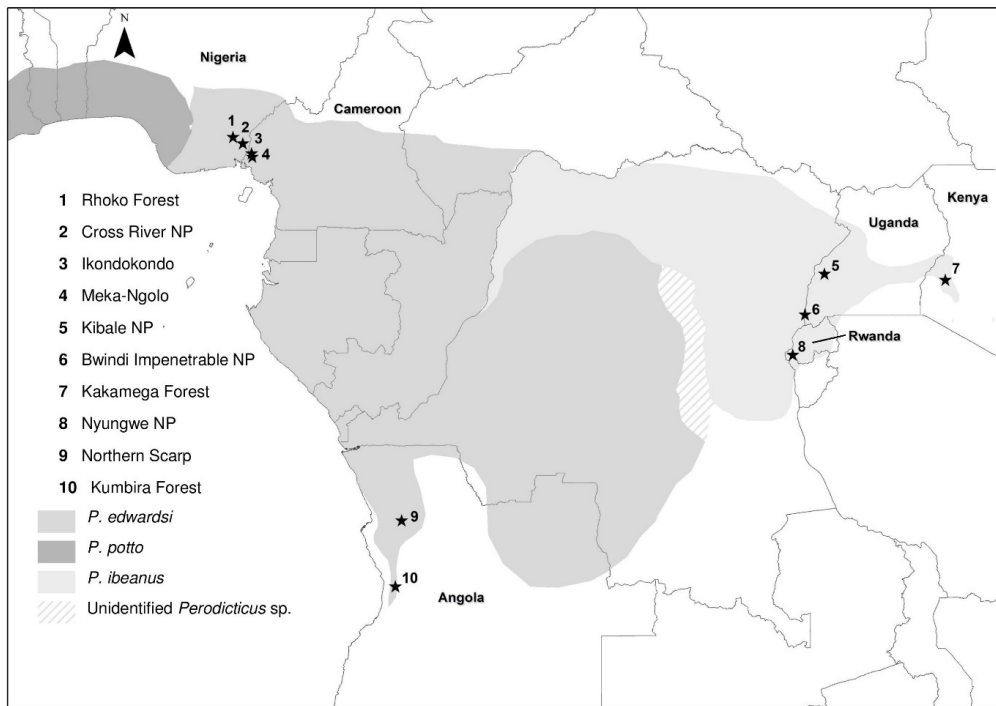


Figure 1. Range of *Perodicticus* spp. and locations of study sites. Map modified from IUCN shape files (IUCN, 2018).

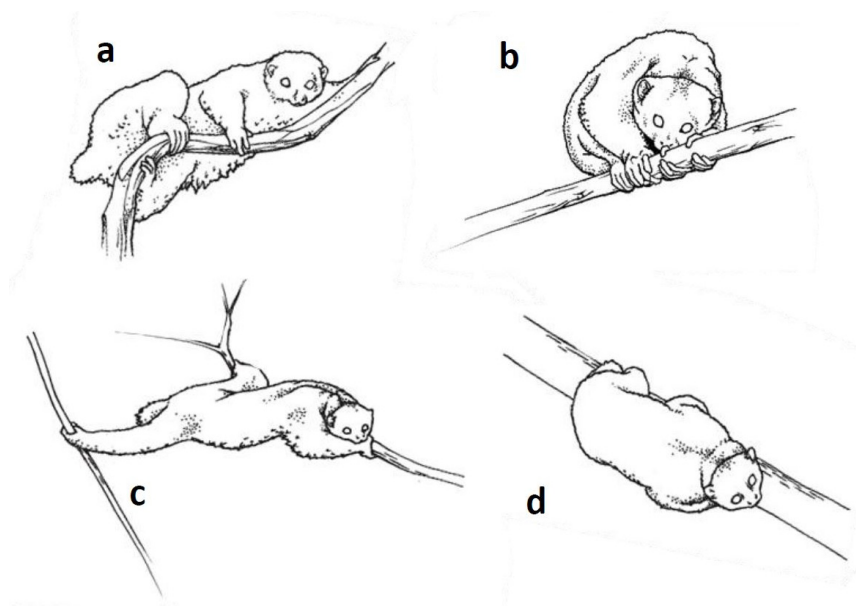


Figure 2a–d. Positional behaviours and nose-down foraging in *Perodicticus*. Illustrations by M. Fusco.

More research uncovering the degree of ecological and behavioural similarity between Perodicticinae and Lorisiae is necessary, but difficult without baseline ethological data for the species in question. Considering the many changes to lorid taxonomy, evidence of species-specific behaviour would help to justify and clarify such changes. We aim to create a baseline for a comprehensive comparison of behaviour across pottos to highlight the diversity exhibited by this wide-ranging genus. We compiled a series of observations on two species of potto covering a wide geographic range. We aimed to identify similarities and differences in general, and positional and social behaviour using observations of pottos *in situ*. We then utilised this research to identify gaps in our knowledge of these species, highlight the discrepancies that arise among perodicticines, and identify key areas of focus for future research.

MATERIAL AND METHODS

Study sites

We observed *P. ibeanus* in Kakamega Forest Reserve (FR) in Kenya (K.A.I. Nekaris, July 2006), in Bwindi Impenetrable National Park (NP) (M.S. Svensson, June 2011) and in Kibale NP (A.M. Luhrs, May–July 2015; K.A.I. Nekaris, June 2006) in Uganda, and in Nyungwe NP in Rwanda (M.S. Svensson, July 2017) (figure 1; table 1). We observed *P. edwardsi* in Kumbira Forest and Northern Scarp (M.S. Svensson, September 2013) in Angola, where observations all occurred outside the previously known range of *P. edwardsi* (figure 1) (Bersacola *et al.*, 2015). We also observed *P. edwardsi* in Meka-Ngolo and Ikondokondo (resettlement) (A.M. Luhrs, May–July 2016) in Cameroon, and in Rhoko Forest, Cross River in Nigeria (A.M. Luhrs, February–April 2017) (figure 1; table 1).

Data collection

We walked existing trails in all forest systems from dusk (~18:30 h) until the trails ended or 02:00–03:00 h. When we detected pottos, we recorded the following information: height of animal above ground, support type (branch, terminal twigs, vines, ground), support orientation (vertical, horizontal, oblique) and behaviour of the animal upon first contact. If the animal used branch supports, branch size was recorded as small (<6 cm circumference), medium (6–25 cm circumference) and large (>25 cm circumference) (*cf.* Gebo & Chapman, 1995).

We qualitatively annotated the focal animal's behaviour, focussing on recording the diversity of behaviours. We referenced behaviours using a modified version of an ethogram by Fitch-Snyder and Schulze (2001). The ethogram provides a list of 62 behaviours in five categories: Individual, Social, Agonistic & Response, Mother-Infant Behaviours and Vocalisations (that are largely specific to Asian lorises). Of the 62 behaviours, we selected 50 to measure. Selection was based on relevancy for wild observations (for example we excluded the behaviour "Explore Cage"). We adapted the behavioural categories from those provided by Fitch-Snyder and Schulze (2001), creating the categories 'General Behaviour', 'General Social Behaviour', 'Mother-Infant Interactions' and 'Agonistic & Response'. We used the terminology of Poindexter and Nekaris (2017) for positional behaviours (table 2).

RESULTS

We observed 51 *P. edwardsi* and 28 *P. ibeanus* at ten locations (table 1). Observations lasted 1–120 minutes.

Table 1. Study site characteristics and suitability of each site for future studies of *Perodicticus*.

	Angola		Cameroon		Nigeria		Kenya	Rwanda	Uganda	
	KuF	NS	M-N	IK	RF	CRNP	KaFR	NNP	KNP	BNP
Coordinates	11°09'S 14°17'E	8°40'S 14°31'E	4°55'N 8°56'E	5°03'N 8°55'E	5°40'N 8°13'E	5°25'N 8°35'E	0°19'N 34°52'E	2°29'S 29°10'E	0°33'N 30°21'E	0°59'S 29°37'E
Average annual rainfall (mm) (monthly range)	741 (0–152)	880 (0–195)	2496 (25–411)	2439 (17–401)	2218 (14–353)	2438 (17–401)	1803 (80–233)	1482 (22–186)	1236 (49–167)	1065 (39–132)
Average annual temperature (°C) (monthly range)	22.1 (19.2–23.9)	23.9 (20.9–25.7)	26.6 (25.1–28.2)	25.8 (24.3–27.4)	26.4 (24.9–28.3)	25.8 (24.3–27.4)	22.1 (21.1–23.1)	18.3 (17.8–18.8)	22.4 (21.8–23.5)	22.1 (21.7–22.8)
Level of disturbance	Medium	High	High	High	Medium	Low	Medium	Low	Medium	Low
Habitat type	Unprotected moist forest, mostly secondary	Unprotected moist forest, primary & secondary	Forest-farm mosaic	Forest-farm mosaic	Unprotected disturbed forest	Protected secondary forest	Protected secondary forest	Protected forest	Protected secondary forest & forest fragments	Protected forest
Species	<i>Perodicticus edwardsi</i>		<i>Perodicticus edwardsi</i>		<i>Perodicticus ibeanus</i>		<i>Perodicticus ibeanus</i>		<i>Perodicticus ibeanus</i>	
Number of individuals observed	8	9	7	17	7	3	11	4	12	1
Median height (m) (range)	18 (10–25)	18 (3–38)	10 (3–13)	9.5 (0–13)	17 (8–25)	11 (9–13)	5 (3–16)	15 (9–20)	5.5 (3–10)	15 (15)
Altitude of observations	860–900	460–710	166–249	116–148	124–162	131–143	1500–1650	1930–2330	1200	1480
Field station available	No	No	No	No	Yes	Research accommodation	Yes	Yes	Yes	Yes
Ease of access	Roads and cut paths	Roads and cut paths	No formal trail system	Roads and cut paths	Formal trail system	Roads and cut paths	Formal trail system	Tourist paths	Formal trail system	Roads and cut paths
Radio tracking logistically feasible	High	Medium	High	High	High	Medium	High	Low	Medium	Medium
Other nocturnal primates encountered	<i>Gd. kumbirensis</i> , <i>O. crassicaudatus</i>	<i>Gd. kumbirensis</i> , <i>Gd. demidovii</i>	<i>S.a. cameroonensis</i> , <i>Galagoides</i> spp.	<i>S.a. cameroonensis</i> , <i>cameroonensis</i> , <i>Galagoides</i> spp.	<i>A. calabarensis</i> , <i>Gd. demidovii</i> , <i>Gd. thomasi</i> , <i>E. pallidus</i> , <i>S.a. cameroonensis</i>	<i>A. calabarensis</i> , <i>Gd. demidovii</i> , <i>Gd. thomasi</i> , <i>E. pallidus</i> , <i>S.a. cameroonensis</i>	Unknown	<i>Gd. thomasi</i> , <i>G. matschiei</i> , <i>Galago</i> sp.	<i>Gd. thomasi</i> , <i>G. matschiei</i>	<i>Gd. thomasi</i> , <i>Gd. demidovii</i> , <i>G. matschiei</i>

Rainfall and temperature refer to data from 1991–2015 (www.worldbank.org/climateportal). KuF = Kumbira Forest; NS = Northern Scarp; M-N = Meka-Ngolo; IK = Ikondokondo; RF = Rhoko Forest; CRNP = Cross River NP; KaFR = Kakamega Forest Reserve; NNP = Nyungwe NP; KNP = Kibale NP; BNP = Bwindi Impenetrable NP.

Table 2. Ethogram modified from an ethogram created for captive lorises by Fitch-Snyder and Schulze (2001).

General Behaviour	General Social Behaviour	Mother-Infant Interactions	Agnostic & Response
Eat / Feed	Play	Ventral-ventral	Attack
Drink	Aggressive	Huddle	Manual defensive threat
Rest	Allo-groom	Attempt ventral	Threat
Locomote	Leave	Grasp	Aggressive pursuit
Auto-groom	Follow	Climb on	Assertion
Sniff	Proximity	Ventral-dorsal	Submissive posture
Urine mark	Aggressive approach	Head block	Flight
Vocalise	Approach	Inverted holding	
Freeze	Incomplete approach	Park	
Sleep	Approach-pass		
Crouch	Depart		
Self-scratching	Contact		
Arm-rubbing	Social explore		
Facial-rubbing	Social play		
	Play-solicit		
	Solicit		
	Clasp		
	Sniff/Lick		
	Mount attempt		
	Copulation		

General behaviour

We observed 42 of 50 behaviours at least once; 30 of 50 for *P. edwardsi* and 39 of 50 for *P. ibeanus*. The latter species was seen more often in social contact. We most commonly recorded Eating, Locomotion, Freezing, Resting and Sniffing. We never observed Drinking, Play, Play-Solicit, Mount Attempt, Copulation, Assertion or Submissive Posture.

We recorded several behaviours not present on our ethogram. In Kibale NP, a juvenile *P. ibeanus* grasped a medium oblique branch in a crouch position and, with its posterior pressed against a vertical branch fork, tucked its head underneath its body so only the nose emerged from the ventral region. It then rubbed its posterior back-and-forth against the branch for about 5 seconds in what appeared to be scent-marking.

We observed *P. ibeanus* vocalising both in Kibale NP and Kakamega FR. In Kibale NP, we heard a raspy whistle preceding and during an aggressive interaction between two adult males. This vocalisation best matched the context of a 'Krik' or 'Pant'. In Kakamega FR, we observed a solitary *P. ibeanus* open its mouth and emit a series of loud, long whistles lasting several seconds. Although 'Whistle' is described on the generalised loriseid ethogram, the whistle of this individual bore no resemblance to a slow or slender loris whistle. When either of these genera whistle, they do not, evidently, open their mouth (K.A.I. Nekaris, pers. obs.).

We observed chewing on large tree branches by *P. edwardsi* in Meka-Ngolo, and by *P. ibeanus* in Nyungwe NP. While grasping a large branch with both hands, these individuals bit the branch and carefully moved the head side-to-side, seemingly with great effort. This behaviour could be a method to extract insects or exudates (*cf.* Oates, 1984).

Social behaviour

Of the 29 social behaviours listed in the ethogram, we observed 16 in *P. edwardsi* and 21 in *P. ibeanus*. Both species were observed alone and in groups of up to three individuals.

In Cameroon, we observed adult *P. edwardsi* feeding near one another in the same tree, as well as engaged in an agonistic chase followed by the flight of one individual. In Kibale NP, we witnessed one agonistic interaction between two adults.

We observed juveniles only twice and only for *P. ibeanus*, distinguishing them by their silvery coat. Both were only marginally smaller than the mother (*cf.* Oates, 2011). In Nyungwe NP we observed an adult and a juvenile moving together downwards on a large tree trunk. In Kibale NP, a mother and juvenile engaged in a bout of social interaction. Of the nine mother-infant behaviours, all but three (Head-Block, Inverted Holding, Park) occurred at least once. Juveniles were accompanied by their (presumed) mother three times and observed alone twice. When with its mother, the juvenile rarely broke contact. Social behaviours included Allo-Grooming, Sniffing, Licking, Rubbing, Claspings, General Contact, and Ventral-Ventral and Ventral-Dorsal Clinging. Juveniles climbed in a spiral pattern around branches, or engaged in Prey-Catching in the Bipedal Hang posture. Juveniles displayed more behaviours than adults, which were more often stationary and cautious, or in motion, using a single series of movements (*e.g.* Quadrupedal Walk).

Postures, support and habitat use

Of 21 postures, we recorded all at least once. For *P. edwardsi* we observed all postures except Horizontal Suspension with One Foot, and for *P. ibeanus* all but Vertical Suspension with Two Feet. Both species use a range of support types at various heights and orientations (table 1). At the ten sites they used vines at five sites, fine terminal branches at seven sites, medium branches at eight sites, and large trunks and branches at all sites. They were observed on the ground at only three sites. These observations show that both *P. edwardsi* and *P. ibeanus* use secondary forest habitats.

Perodicticus edwardsi in Angola and Nigeria were observed at higher median heights (17–18 m) than in the other locations (table 1). Twice in Ikondokondo, *P. edwardsi* travelled on the ground. This species was described by farmers in Cameroon as occurring more often in cocoa *Theobroma cacao* Linnaeus, 1753 plantations, and was said to be a pest in banana *Musa* spp. plantations and in bush mango *Irvingia gabonensis* (Aubry-Lecomte ex O'Rorke) Baill. Though *P. edwardsi* was viewed on bush mango, we never observed fruit-eating. In Kumbira Forest and Northern Scarp, *P. edwardsi* was found in forests with medium to high levels of disturbance, often in proximity to human settlements.

In Kibale NP and Bwindi Impenetrable NP, *P. ibeanus* was found almost exclusively in the disturbed forest patches near the field site buildings and roads. In Kakamega FR, *P. ibeanus* was observed on six trails in an established grid trail system, as well as within 20 m of camp, though this area was subject to only minor human disturbance. The research station in Kibale NP is bordered by both secondary forest and undisturbed primary forest. Despite occupancy monitoring in these areas, *P. ibeanus* was only observed near camp. In Nyungwe NP, *P. ibeanus* was observed in proximity to roads. We observed *P. ibeanus* in Kibale NP in areas that could have only been reached by ground travel. These areas were different from those in Cameroon in that they were not farmed and were not fragmented from the main forest. In Ikondokondo, habitat was fragmented, characterised by fruit trees, such as plum *Dacryodes edulis* (G. Don) H.J. Lam, bush mango, banana, and cocoa, as well as cassava *Manihot esculenta* Crantz. Here connectivity was high within the undergrowth of some forest patches, but extremely low among patches.

DISCUSSION

Although a limited number of observations, these data exemplify the diversity of potto behaviour and habitat use. The range of behaviours, heights, supports and habitat types occupied by *P. edwardsi* and *P. ibeanus* in this study suggest a high degree of behavioural and habitat-use flexibility.

Both *P. edwardsi* and *P. ibeanus* exhibited active and postural behaviours similar to other lorises. The most unique behaviours related to olfactory marking and vocal communication. In terms of olfaction, we confirm Oates' (1984) observations of rubbing and scent marking, which make pottos unique from Asian lorises. Although pottos are considered relatively silent (Oates, 1984; Bearder *et al.*, 2003; Nekaris *et al.*, 2007; Pimley & Bearder, 2013), we observed audible vocal behaviour in *P. ibeanus*. Although pottos vocalise in captivity (Cowgill, 1969; Buckanoff *et al.*, 2006), we found no equivalent in the literature of the 'Whistle'. Slender lorises emit a variety of whistles, while slow lorises make series of 'Kriks', 'Pants', and high-pitched 'Whistles' (Nekaris & Bearder, 2011). Vocalisations can be useful for discerning among species, as has been done with morphologically cryptic species of galagines (Courtenay & Bearder, 1989; Anderson *et al.*, 2000; Ambrose, 2003; Schneiderová *et al.*, 2016; Svensson *et al.*, 2017). Future studies should be alert for vocalisations in pottos and of their potential use in taxonomy.

We provide observations on pottos eating invertebrates and gouging wood for exudates or insects (Charles-Dominique, 1977; Oates, 1984). Despite farmers in Cameroon reporting *P. edwardsi* as a pest in fruiting trees, we did not observe fruit-eating. It is possible that, rather than fruit, pottos are attracted to the large number of insects present at ripe and rotting fruit. The active behaviour of *P. edwardsi* in fruit trees suggests focus on active prey. In Kibale NP, the high density of African cherry *Prunus africana* (Hook.f.) Kalkman near camp may explain the higher density of *P. ibeanus* in the area. Species in this genus possess extrafloral nectaries, or areas that produce sugar outside of the flower (Bentley, 1977). It has been suggested that extrafloral nectaries promote protection from herbivores or larvae by attracting large numbers of ants (Bentley, 1977; Pemberton & Jang-Hoon, 1996), which are a component of the diet of pottos (Charles-Dominique, 1974, 1979; Oates, 1984).

Perodicticus edwardsi and golden angwantibos *Arctocebus aureus* De Winton, 1902 have been described as primarily solitary, with over 95% of time spent alone (Charles-Dominique, 1977). Slow and slender lorises are more social, spending up to a third of their time with a conspecific, and communicating using scent or vocalisations (Nekaris, 2001; Rode-Margono *et al.*, 2014). Pimley *et al.* (2005b) found that spatial proximity (<20 m) between individuals of *P. edwardsi* was quite common, an observation we also made several times in this study. We did not observe *P. edwardsi* socially in Nigeria, where fragmentation is minimal and food sources more dispersed. Pimley *et al.* (2005a) hypothesised that the high rate of gregariousness in *P. edwardsi* on Mount Kupe relates to patches of high quality fruit trees with the associated insects. Similarly, Javan slow lorises *Nycticebus javanicus* É. Geoffroy, 1812 in anthropogenic landscapes with discrete nectar and gum patches, are highly gregariousness (Rode-Margono *et al.*, 2014). We thus hypothesise that anthropogenic activity with an associated increase in patches of fruits and insects may facilitate increased social behaviour.

Nearly all data on adult-infant interactions in pottos comes from captive individuals (Cowgill, 1969, 1974; Manley, 1974; Frederick, 1998; Buckanoff *et al.*, 2006). Pottos are difficult to breed in captivity, and infant mortality is high (Fitch-Snyder & Schulze, 2001; Buckanoff *et al.*, 2006; Fuller *et al.*, 2014; MacKinnon *et al.*, 2015). As of 2018, all pottos

in captivity are listed as '*Perodicticus potto sensu lato*'. It is unlikely that all pottos in captivity belong to one species, given the recent changes in the taxonomy of the genus (Butynski & de Jong, 2007, 2017; Pozzi *et al.*, 2015). The consequences of housing different species of potto together are unknown, but this husbandry practice could partly be the reason for poor mating success and high infant mortality.

We found *P. edwardsi* at greater median heights than *P. ibeanus*, which may be a result of niche partitioning. At some sites sampled during this study, *P. edwardsi* is sympatric with up to five other nocturnal primate species, including Calabar angwantibo *Arctocebus calabarensis* (J.A. Smith, 1860), whereas *P. ibeanus* is sympatric with no more than three other nocturnal primates (table 1). Most of the species of nocturnal primates with which *P. edwardsi* is sympatric, Allen's squirrel galago *Sciurocheirus alleni* (Waterhouse, 1838), *A. calabarensis* and Demidoff's dwarf galago *Galagoides demidovii* (G. Fischer, 1808) typically occupy the lower strata and highly connected undergrowth of the forest (Charles-Dominique, 1974; Oates, 2011). Munds *et al.* (2013) found that slow lorises occupy higher levels when they are sympatric with tarsiers *Cephalopachus* spp. Bersacola *et al.* (2015) also found evidence of niche partitioning where *P. edwardsi* is sympatric with large-eared greater galago *Otolemur crassicaudatus* É. Geoffroy, 1812 in Angola. *Perodicticus edwardsi* is sympatric with northern needle-clawed galago *Euoticus pallidus* (Gray, 1863), an exudativore, and may avoid gum-feeding in areas where this species is present (Burrows *et al.*, 2015). *Euoticus pallidus* was not encountered in the forest-farm mosaic in Cameroon where we observed 'tree-chewing' by *P. edwardsi*.

We observed pottos travelling on the ground only in fragmented habitats (Cameroon and Kibale NP). It is likely that ground travel is related to habitat type, and puts pottos at higher risk of predation. In Indonesia, slow lorises in highly fragmented habitats rarely travel on the ground, and when they do they seldom move >10 m (K.A.I. Nekaris, unpubl. data). Mysore slender lorises *Loris tardigradus lydekkerianus* (Linnaeus, 1758) in *Acacia* scrubland in India only travelled on the ground to move between shrubs (Nekaris, 2001).

Butynski and de Jong (2007, p 125) speculate that "*It may well be that a number of 'cryptic' species and subspecies remain 'hidden' within Perodicticus, and that the total number of taxa is well beyond the currently recognised one species and three subspecies...*" Pottos are characterised by variation in morphological traits, such as the shape of teeth, skull, and vertebrae, as well as by developmental rate, body size, pelage (Groves, 2001; Stump, 2005; Butynski & de Jong, 2007), and genetic variation (Butynski & de Jong, 2007; Pozzi *et al.*, 2015). These data allowed for the elevation of *P. p. edwardsi* and *P. p. ibeanus* to species level. Morphological comparison is often insufficient for differentiating cryptic species and often relies on invasive field research and limited museum specimens (Stump, 2005). Behavioural research is generally lower cost, less invasive, and can highlight both inter- and intra-population variation. It can also highlight differences that may not be apparent through genetic or morphological study, such as unique postures and locomotion, habitat use and partitioning, and olfactory and vocal communication. Long-term behavioural studies on cryptic species are becoming more urgent than ever—especially considering the increasing use of these species in trade (Svensson & Friant, 2014). With a better understanding of their taxonomy, the conservation status of many cryptic primates is likely to change, and behavioural data such as these may support and facilitate taxonomic decisions.

Here we provide information on several sites where pottos can be observed and studied in detail. Of the sites visited, we considered various aspects as important for long-term field studies, including infrastructure, visibility, safety and the potential for radio tracking. Based on these comparisons, we conclude that the best sites for study of *P. ibeanus* are Kakamega

FR and Kibale NP. The best study sites for *P. edwardsi* are Kumbira Forest or one of the Cameroonian sites (table 1). We urge further studies of these observable populations to bring to light more knowledge of one of the least known primate genera. Priority research on pottos involves obtaining a better understanding of: (1) the relationship between ecological factors, density and distribution; (2) reproductive and dietary differences among species; (3) whether habitat type influences social behaviour; and (4) the exploitation of pottos by local people.

ACKNOWLEDGMENTS

We are grateful to the Primate Action Fund (Cameroon and Nigeria), Fredrika Bremer Forbundet and Iris Jonzen Stiftelse (Angola and Rwanda) for financial support. We thank the Nigerian National Parks Service, Nigerian Immigration Service, CERCOPAN, Pandrillus, Korup Rainforest Conservation Society, Cameroon Ministry of Forestry and Wildlife, Cameroon Ministry of Scientific Research & Innovation, Wildlife Conservation Society Rwanda, and Rwanda Development Board for logistical support. M. Fusco, Y. Kolo, E. Fidelis, C. Jost-Robinson, J. Linder, T. Baron, M. Mills, C. McMahon, M. Adonis, M. Solestine, S.K. Bearder, E. Bersacola, M. Cords, M. Meyers, O. Wilberforce and E. Pimley are thanked for their assistance in the field and/or with the manuscript. We thank the two reviewers, Caroline Harcourt and John Oates, for their comments and feedback.

REFERENCES

- Ambrose, L. (2003). Three acoustic forms of Allen's galagos (Primates: Galagonidae) in the Central African Region. *Primates* **44**(1): 25–39.
- Anderson, M.J., L. Ambrose, S.K. Bearder, A.F. Dixson & S. Pullen (2000). Intraspecific variation in the vocalizations and hand pad morphology of southern lesser bush babies (*Galago moholi*): a comparison with *G. senegalensis*. *International Journal of Primatology* **21**(3): 537–555.
- Bearder, S.K. & G.A. Doyle (1974). Field and laboratory studies of social organization in bushbabies (*Galago senegalensis*). *Journal of Human Evolution* **3**(1): 37–50.
- Bearder, S.K., L. Ambrose, C. Harcourt, P. Honess, A. Perkin, E. Pimley, S. Pullen & N. Svoboda (2003). Species-typical patterns of infant contact, sleeping site use, and social cohesion among nocturnal primates in Africa. *Folia Primatologica* **74**: 337–354.
- Bentley, B.L. (1977). Extrafloral nectaries and protection by pugnacious bodyguards. *Annual Review of Ecological Systems* **8**: 407–427.
- Bersacola, E., M.S. Svensson & S.K. Bearder (2015). Niche partitioning and environmental factors affecting abundance of strepsirhines in Angola. *American Journal of Primatology* **77**(11): 1179–1192.
- Buckanoff, H.D., C. Frederick & H. Weston Murphy (2006). Hand-rearing a potto *Perodicticus potto* at Franklin Park Zoo, Boston. *International Zoo Yearbook* **40**(1): 302–312.
- Burrows, A.M., A. Hartstone-Rose & L.T. Nash (2015). Exudativory in the Asian loris, *Nycticebus*: Evolutionary divergence in the toothcomb and M3. *American Journal of Physical Anthropology* **158**(4), 663–672.

- Butynski, T.M. & Y.A. de Jong (2007). Distribution of the potto *Perodicticus potto* (Primates: Lorisidae) in Eastern Africa, with a description of a new subspecies from Mount Kenya. *Journal of East African Natural History* **96**(2): 113–147.
- Butynski, T.M. & Y.A. de Jong (2017). The Mount Kenya potto is a subspecies of the eastern potto *Perodicticus ibeanus*. *Primate Conservation* **31**: 49–52.
- Cabana, F. & K.A.I. Nekaris (2015). Diets high in fruits and low in gum exudates promote the occurrence and development of dental disease in pygmy slow loris (*Nycticebus pygmaeus*). *Zoo Biology* **34**(6): 547–553.
- Charles-Dominique, P. (1971). *Éco-éthologie et Vie Sociale des Prosimiens du Gabon*. PhD Thesis. Faculté des Sciences, University of Paris-Sud, Paris.
- Charles-Dominique, P. (1974). Ecology and feeding behaviour of five sympatric lorises in Gabon. In R.D. Martin, G.A. Doyle & A.C. Walker (eds.), *Prosimian Biology*. Gerald Duckworth & Co. Ltd., London. Pp. 131–150.
- Charles-Dominique, P. (1977). *Ecology and Behaviour of Nocturnal Primates: Prosimians of Equatorial West Africa*. Columbia University Press, New York.
- Charles-Dominique, P. & S.K. Bearder (1979). Field studies of lorisid behaviour: methodological aspects. In G.A. Doyle (ed.), *The Study of Prosimian Behaviour*. Academic Press, Inc, Cambridge, Massachusetts. Pp. 567–627.
- Charles-Dominique P., H.M. Cooper, A. Hladik, C.M. Hladik, E. Pages, G.F. Pariente, A. Petter-Rousseaux, A. Schilling & J.J. Petter (1980). *Nocturnal Malagasy Primates: Ecology, Physiology and Behaviour*. Academic Press, New York.
- Courtenay, D.O. & S.K. Bearder (1989). The taxonomic status and distribution of bushbabies in Malawi with emphasis on the significance of vocalizations. *International Journal of Primatology* **10**(1): 17–34.
- Cowgill, U.M. (1969). Some observations on the prosimian *Perodicticus potto*. *Folia Primatologica* **11**: 144–150.
- Cowgill, U.M. (1974). Co-operative behaviour in *Perodicticus*. In R.D. Martin, G.A. Doyle & A.C. Walker (eds.), *Prosimian Biology*. Gerald Duckworth & Co. Ltd, London. Pp. 261–272.
- Fitch-Snyder, H. & H. Schulze (2001). *Management of Lorises in Captivity. A Husbandry Manual for Asian Lorises*. Center for Reproduction of Endangered Species (CRES) Zoological Society of San Diego, San Diego.
- Frederick, C. (1998). Observations of paternal care in *Perodicticus potto* at the Cincinnati Zoo and Botanical Garden. *Folia Primatologica* **69**(5): 312–317.
- Fuller, G., K.E. Lukas, C. Kuhar & P.M. Dennis (2014). A retrospective review of mortality in lorises and pottos in North American zoos, 1980–2010. *Endangered Species Research* **23**(3): 205–217.
- Garber, P.A. & S.R. Leigh (1988). Patterns of positional behavior in mixed-species troops of *Callimico goeldii*, *Saguinus labiatus*, and *Saguinus fuscicollis* in northwestern Brazil. *American Journal of Primatology* **54**(1): 17–31.
- Gebo, D.L. & C.A. Chapman (1995). Habitat, annual, and seasonal effects on positional behavior in red colobus monkeys. *American Journal of Physical Anthropology* **96**: 73–82.
- Groves, C.P. (2001). *Primate Taxonomy*. Smithsonian Books, Washington D.C.
- Heffner, H.E., E. Thurston & B. Masterton (1969). Hearing in prosimians. *Journal of the Acoustical Society of America* **45**(1): 299.
- Hockings, K.J. & C. Sousa (2012). Differential utilization of cashew—a low-conflict crop—by sympatric humans and chimpanzees. *Oryx* **46**(3): 375–381.

- International Union for Conservation of Nature and Natural Resources (2018). The IUCN Red List of Threatened Species. <http://www.iucnredlist.org/> [Accessed on 04/04/18].
- Jewell, P.A. & J.F. Oates (1969). Ecological observations on the loroid primates of African lowland forest. *Zoologica Africana* **4**: 231–248.
- Jolly, A. (1972). *The Evolution of Primate Behavior*. Macmillan, New York.
- MacKinnon, K.M., M.J. Guilfoyle, W.F. Swanson & M.A. Stoops (2015). Assessment of the reproductive physiology of the potto (*Perodicticus potto*) through fecal hormone metabolite analyses and trans-abdominal ultrasonography. *Zoo Biology* **34**(3): 244–254.
- Manley, G.H. (1974). Functions of the external genital glands of *Perodicticus* and *Arctocebus*. In R.D. Martin, G.A. Doyle & A.C. Walker (eds.), *Prosimian Biology*. Duckworth, London. Pp. 313–329.
- McGraw, W.S. (1998). Comparative locomotion and habitat use of six monkeys in the Tai Forest, Ivory Coast. *American Journal of Physical Anthropology* **105**: 493–510.
- Munds, R.A., R. Ali, V. Nijman, K.A.I. Nekaris & B. Goossens (2013). Living together in the night: abundance and habitat use of sympatric and allopatric populations of slow lorises and tarsiers. *Endangered Species Research* **22**: 269–277.
- Nekaris, K.A.I. (2001). Activity budget and positional behavior of the Mysore slender loris (*Loris tardigradus lydekkerianus*): Implications for slow climbing locomotion. *Folia Primatologica* **72**: 228–241.
- Nekaris, K.A.I. (2013). Family Lorisidae (angwantibos, pottos and lorises). In R.A. Mittermeier, A.B. Rylands & D.E. Wilson (eds.), *Handbook of the Mammals of the World, Vol. 3*. Lynx Edicions, Barcelona. Pp. 210–235.
- Nekaris, K.A.I. & S.K. Bearder (2011). The loriform primates of Asia and mainland Africa: diversity shrouded in darkness. In C.J. Campbell, A. Fuentes, K.C. MacKinnon, S.K. Bearder & R.M. Stumpf (eds.), *Primates in Perspective*. Oxford University Press, Oxford. Pp. 34–54.
- Nekaris, K.A.I., R.S. Moore, E. J. Rode & B.G. Fry (2013). Mad, bad and dangerous to know: the biochemistry, ecology and evolution of slow loris venom. *Journal of Venomous Animals and Toxins including Tropical Diseases* **19**(1): 21.
- Nekaris, K.A.I., E.R. Pimley & K.M. Ablard (2007). Predator defense by slender lorises and pottos. In S. Gursky-Doyen & K.A.I. Nekaris (eds.), *Primate Anti-Predator Strategies*. Springer, New York. Pp. 222–240.
- Oates, J.F. (1984). The niche of the potto. *International Journal of Primatology* **5**(1): 51–61.
- Oates, J.F. (2011). *Primates of West Africa: A Field Guide and Natural History*. Conservation International, Arlington, Virginia.
- Pemberton, R.W. & L. Jang-Hoon (1996). The influence of extrafloral nectaries on parasitism of an insect herbivore. *American Journal of Botany* **83**(9): 1187–1194.
- Pimley, E.R. & S.K. Bearder (2013). *Perodicticus potto* – potto. In T.M. Butynski., J. Kingdon & J. Kalina (eds.), *Mammals of Africa – Volume 2 Primates*. Bloomsbury, London. Pp. 393–399.
- Pimley, E.R., S.K. Bearder & A.F. Dixson (2005a). Social organization of the Milne-Edward's potto. *American Journal of Primatology* **66**(4): 317–330.
- Pimley, E.R., S.K. Bearder & A.F. Dixson (2005b). Home range analysis of *Perodicticus potto edwardsi* and *Sciurocheirus cameronensis*. *International Journal of Primatology* **26**(1): 191–206.
- Poindexter, S.A. & K.A.I. Nekaris (2017). Vertical clingers and gougers: rapid acquisition of adult limb proportions facilitates feeding behaviours in young Javan slow lorises (*Nycticebus javanicus*). *Mammalian Biology* **87**: 40–49.

- Pozzi, L., K.A.I. Nekaris, A. Perkin, S.K. Bearder, E.R. Pimley, H. Schulze, U. Striecher & C. Roos (2015). Remarkable ancient divergences amongst neglected loriform primates. *Zoological Journal of the Linnean Society* **175**(3): 661–674.
- Reed, K.E. & L.R. Bidner (2004). Primate communities: past, present, and possible future. *American Journal of Physical Anthropology* **125**(S39): 2–39.
- Rode-Margono, E.J., V. Nijman, Wirdateti & K.A.I. Nekaris (2014). Ethology of the Critically Endangered Javan slow loris *Nycticebus javanicus* É. Geoffroy Saint-Hilaire in West Java. *Asian Primates Journal* **4**(2): 27–41.
- Schneiderová, I., J. Zouhar, L. Štefanská, B.Č. Bolfíková, S. Lhota & P. Brandl (2016). Vocal activity of lesser galagos (*Galago* spp.) at zoos. *Zoo Biology* **35**(2): 147–156.
- Stump, D.P. (2005). *Taxonomy of the Genus Perodicticus*. PhD thesis, University of Pittsburgh, Pittsburgh.
- Svensson, M.S. & S. Friant (2014). Threats from trading and hunting of pottos and angwantibos in Africa resemble those faced by slow lorises in Asia. *Endangered Species Research* **23**(2): 107–114.
- Svensson, M.S., E. Bersacola, M.S. Mills, R.A. Munds, V. Nijman, A. Perkin, J.C. Masters, S. Couette, K.A.I. Nekaris & S.K. Bearder (2017). A giant among dwarfs: a new species of galago (Primates: Galagidae) from Angola. *American Journal of Physical Anthropology* **163**(1): 30–43.
- Svensson, M. S., K.A.I. Nekaris, S.K. Bearder, C.M. Bettridge, T.M. Butynski, S.M. Cheyne, D. Nabajit, Y.A. de Jong, A.M. Luhrs, L.V. Luncz, S.T. Maddock, A. Perkin, E. Pimley, S.A. Poindexter, K.D. Reinhardt, D. Spaan, D.J. Stark, C.R. Starr & V. Nijman (2018). Sleep patterns, daytime predation and the evolution of diurnal sleep site selection in loriforms. *American Journal of Physical Anthropology* **166**: 563–577.
- Tan, C.L. (1999). Group composition, home range size, and diet of three sympatric bamboo lemur species (genus *Hapalemur*) in Ranomafana National Park, Madagascar. *International Journal of Primatology* **20**(4): 547–566.
- van Schaik, C.P., M. Ancrenaz, G. Borgen, B. Galdikas, C.D. Knott, I. Singleton, A. Suzuki, S.S. Utami & M. Merrill (2003). Orangutan cultures and the evolution of material culture. *Science* **299**(5603): 102–105.
- Whiten, A., J. Goodall, W.C. McGrew, T. Nishida, V. Reynolds, Y. Sugiyama, C.E. Tutin, R.W. Wrangham & C. Boesch (1999). Cultures in chimpanzees. *Nature* **399**(6737): 682–685.
- Williams, E., F. Cabana & K.A.I. Nekaris (2015). Improving diet and activity of insectivorous primates in captivity: Naturalizing the diet of northern Ceylon gray slender loris, *Loris lydekkerianus nordicus*. *Zoo Biology* **34**(5): 473–482.
- Yoder, A.D., J.A. Irwin & B.A. Payseur (2001). Failure of the ILD to determine data combinability for slow loris phylogeny. *Systematic Biology* **50**(3): 408–424.