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

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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).

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 lorisis, 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 exudativeres, 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. iberanus* 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 Lorisinae is necessary, but difficult without baseline ethological data for the species in question. Considering the many changes to lorisid 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* (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.

<table>
<thead>
<tr>
<th>Angola</th>
<th>Cameroon</th>
<th>Nigeria</th>
<th>Kenya</th>
<th>Rwanda</th>
<th>Uganda</th>
</tr>
</thead>
<tbody>
<tr>
<td>KuF</td>
<td>NS</td>
<td>M-N</td>
<td>IK</td>
<td>RF</td>
<td>CRNP</td>
</tr>
<tr>
<td>Coordinates</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>11°09'S</td>
<td>8°40'S</td>
<td>4°55'E</td>
<td>8°56'E</td>
<td>5°13'E</td>
<td>5°25'E</td>
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<tr>
<td>14°17'E</td>
<td>14°31'E</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Average annual rainfall (mm) (monthly range)</td>
<td></td>
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</tr>
<tr>
<td>741</td>
<td>880</td>
<td>2496</td>
<td>2439</td>
<td>2218</td>
<td>2438</td>
</tr>
<tr>
<td>Average annual temperature (°C) (monthly range)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>22.1</td>
<td>23.9</td>
<td>26.6</td>
<td>25.8</td>
<td>24.9</td>
<td>25.8</td>
</tr>
<tr>
<td>Level of disturbance</td>
<td>Unprotected</td>
<td>Unprotected</td>
<td>Forest-farm mosaic</td>
<td>Forest-farm mosaic</td>
<td>Protected</td>
</tr>
<tr>
<td>Habitat type</td>
<td>moist, tall forest, mostly secondary</td>
<td>primary &amp; secondary</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>Perodicticus edwardsi</td>
<td>Perodicticus ibeanus</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of individuals observed</td>
<td>8</td>
<td>9</td>
<td>7</td>
<td>17</td>
<td>7</td>
</tr>
<tr>
<td>Median height (m) (range)</td>
<td>18</td>
<td>18</td>
<td>10</td>
<td>9.5</td>
<td>17</td>
</tr>
<tr>
<td>Field station available</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
<td>Research accommodation</td>
</tr>
<tr>
<td>Ease of access</td>
<td>Roads and cut paths</td>
<td>No formal trail system</td>
<td>Roads and cut paths</td>
<td>Formal trail system</td>
<td>Roads and cut paths</td>
</tr>
<tr>
<td>Radio tracking logistically feasible</td>
<td>High</td>
<td>Medium</td>
<td>High</td>
<td>High</td>
<td>Medium</td>
</tr>
</tbody>
</table>

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; BINP = Bwindi Impenetrable NP.
Table 2. Ethogram modified from an ethogram created for captive lorisids by Fitch-Snyder and Schulze (2001).

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

General behaviour

We observed 42 of 50 behaviours at least once; 30 of 50 for *P. edwardsi* and 39 of 50 for *P. iberus*. 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. iberus* 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. iberus* 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. iberus* open its mouth and emit a series of loud, long whistles lasting several seconds. Although ‘Whistle’ is described on the generalised lorisid 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. iberus* 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, Clasping, 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 lorisids. 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.

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