

Conservation implications of low encounter rates of five nocturnal primate species (*Nycticebus* spp.) in Asia

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Abstract Five species of slow lorises were once considered to comprise a single strongly polymorphic species, *Nycticebus coucang*, ranging throughout South and Southeast Asia. The cryptic nature of these nocturnal primates has led to a lack of understanding of their distribution patterns and abundance. In short surveys, often few if any lorises are detected, meaning that the few available density estimates are from long-term studies. Based on new research in Sebangau National Park, Borneo, and compilation of survey data from other areas, we provide the first comparative abundance estimates for all five slow loris species: *N. coucang* occurred in significantly higher abundances (median encounter rate 0.80/km: $n = 15$), than *N. bengalensis* (0.26/km; $n = 12$), or *N. javanicus* (0.11/km: $n = 2$), *N. menagensis* (0.02/km: $n = 3$), and *N. pygmaeus* (0.13/km: $n = 4$). Abundance estimates in Sebangau (0.19/km) did not increase with increasing survey effort, but for all species and studies combined, study duration was positively correlated with abundance estimates. We did not find a relation between abundance and body mass, nor between abundance and latitude. Long-term studies are more likely to be conducted at sites where the species of interest is particularly plentiful. The data suggest that slow lorises occur at low abundances throughout much of their range, and some in larger social groups than previously assumed. We recommend taking into account the species' heterogeneous distribution (potentially requiring larger survey effort), their social structure, the use of red lights as opposed to white lights whilst surveying, and to make use of their vocalisations when surveying slow lorises.

Keywords Central Kalimantan · Cryptic species · Lorisidae · *Nycticebus menagensis* · Slow loris · Sebangau · Strepsirrhini

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Introduction

Slow lorises (*Nycticebus* spp.) are relatively small Asian nocturnal primates, cryptic in both their behaviour and appearance. Until recently, only two species were recognised: the slow loris *N. coucang*, considered at Low Risk throughout a large range stretching from Northern India to the Philippines, and the more threatened lesser slow loris *N. pygmaeus*, confined to Laos, Cambodia, Vietnam and China (Brandon-Jones et al. 2004). Extreme diversity within *Nycticebus* in terms of cranial morphology, genetic variation, body size, facial markings, dentition, and pelage colouration has sparked major taxonomic revision, with five species (*N. bengalensis*, *N. coucang*, *N. javanicus*, *N. menagensis*, *N. pygmaeus*) currently recognised (Groves 1971, 1998; Roos 2003; Chen et al. 2006; Groves and Maryanto in press) with further unexplained variability within this taxonomic arrangement (Nekaris and Jaffe 2007).

The five-species approach has had a dramatic impact on the conservation status of *Nycticebus* (Table 1). All taxa are now classified as Endangered or Vulnerable mainly due to habitat loss and unsustainable levels of harvesting for traditional medicines and pets (Ratajszczak 1998; Nekaris and Nijman 2007). Unfortunately, few published field data document the density or detail the distribution of the different taxa. Many of the records available regarding loris presence come from local informants (Chivers and Burton 1988; Choudhury 1998, 1999; Nijman and van Balen 1998; Indrawan and Rangkuti 2001; Koenig et al. 2004) or are based on presence of lorises in the trade (Hunyh 1998; Schulze and Groves 2004). Researchers who have sought lorises in the field have often encountered few, and usually attribute this to short duration of study or poor survey technique rather than low loris abundance (Barrett 1981; Duckworth 1994; Fitch-Snyder and Vu 2002; but see Evans et al. 2000; Rhadakrishna and Sinha 2004).

Belonging to the Sundaland Biodiversity hotspot, Indonesia is not only floristically-rich, but also arguably boasts the world's greatest primate diversity, including three slow loris species (Table 1) (Brooks et al. 2000; Supriatna et al. 2001). Despite an impressive amount of research on primates, including the nocturnal tarsiers (e.g. Chivers 1992; Gursky 1998; van Schaik et al. 2003; Geissmann et al. 2005; Merker et al. 2005; Nijman 2006), virtually nothing is known about Indonesian lorises. Unpublished studies from Java and Sumatra found few to no lorises during line transect searches (Arisona, Gursky and Miehs, pers. comm.; Nekaris and Nijman, unpub. data), and no published density estimates are known to us. Intriguingly, slow lorises are often the most common protected primate species recorded in markets (Malone et al. 2002; Shepherd et al. 2005; Webber and Nekaris, 2004).

Table 1 Taxonomy, average body weight, conservation status and distribution of *Nycticebus*

Species	Common name	Body weight (grams)	Conservation status	Distribution
<i>N. bengalensis</i>	Bengal slow loris	1134–1605	VU A2acd + 3cd + 4acd	Cambodia; China; India; Laos; Myanmar; Thailand; Vietnam
<i>N. coucang</i>	Greater slow loris	599–685	EN A2cd	Indonesia (Sumatra); Malaysia (West); Singapore; Thailand
<i>N. javanicus</i>	Javan slow loris	565–687	EN A2cd	Indonesia (Java)
<i>N. menagensis</i>	Bornean slow loris	265–300	VU A2cd	Brunei; Indonesia (Kalimantan); Malaysia (Sabah and Sarawak); Philippines (southernmost)
<i>N. pygmaeus</i>	Lesser or pygmy slow loris	418–422	VU A2cd	Cambodia, China, Laos, Vietnam

The Bornean slow loris *N. menagensis* is currently considered amongst the least threatened of the lorises, classified as Vulnerable (IUCN 2007). The smallest of all slow lorises (Table 1), it cannot only be distinguished from the others genetically, but also by its pale golden to red fur, light marks on its head, and the consistent lack of a second upper incisor (Groves 1998; Ravosa 1998; Chen et al. 2006). No surveys or behavioural studies have targeted this species, but, based on data collected from researchers in the field and historic specimens from museum collections, Meijaard et al. (2005) suggested it to be common. As loris ‘presence’ is usually not determined first-hand (Chivers and Burton 1988; Choudhury 1998; Nijman and van Balen 1998; Indrawan and Rangkuti 2001), it cannot be presumed that lorises still occur in areas from where they were once collected. Indeed, studies of slender lorises (*Loris tardigradus* and *L. lydekkerianus*) in Sri Lanka showed they were often absent (Nekaris and Jayewardene 2004).

In light of the current lack of information and the threats of habitat destruction and wildlife trade, it is vital that surveys are undertaken to ascertain the situation of wild populations (Supriatna et al. 2001; Molur et al. 2003). Until now, the only published studies that have provided detailed density estimates were conducted at pre-selected sites where lorises were particularly abundant (Barrett 1981; Wiens 2002). From other areas, and mainly based on short-term surveys, we merely have *indications* of how common or rare the animals are. This suggests that (1) the species are abundant in some areas but genuinely rare at others, or (2) that the species are more common but it takes time for surveyors to learn how to survey lorises properly, or alternatively, it takes time for the lorises to adapt to the presence of surveyors. Although not mutually exclusive, if (1) is true we expect no relation between survey effort and abundance, whereas if (2) is true we expect estimates of abundance to increase with increasing survey effort. We tested these hypotheses in two ways: by conducting an intensive survey on *N. menagensis*; and by compiling data on abundance and survey effort in all other slow loris taxa.

Methods

Bornean slow loris survey

Study area

We selected Sebangau National Park (also known as Sabangau) in Central Kalimantan, Indonesia, as our study area (Fig. 1). This site consists of 5680 km² of peat swamp forest, and has been claimed to harbour the largest population of both Bornean orang-utans (*Pongo pygmaeus*) and white-bearded gibbons (*Hylobates albibarbis*) (Morrogh-Bernard et al. 2003; Buckley et al. 2006).

This study was based at the Setia Alam Field Station, (2°20′42″ S–114°2′11″ E). The site is described in detail elsewhere (Morrogh-Bernard 2003; Buckley et al. 2006). The area is an old logging concession and was selectively logged for thirty years up until 1996. The study was conducted in three different forest types with pre-existing transect systems. The majority of the survey took place in mixed peat swamp forest. This study area is overlaid with a 2 km² grid system containing 17 major transects, which were marked at 25 m intervals with flagging tape. Two excursions were also made to low interior and tall interior forests, characterised by transect systems marked at 50 m intervals, measuring 5.2 km² and 5.5 km², respectively.

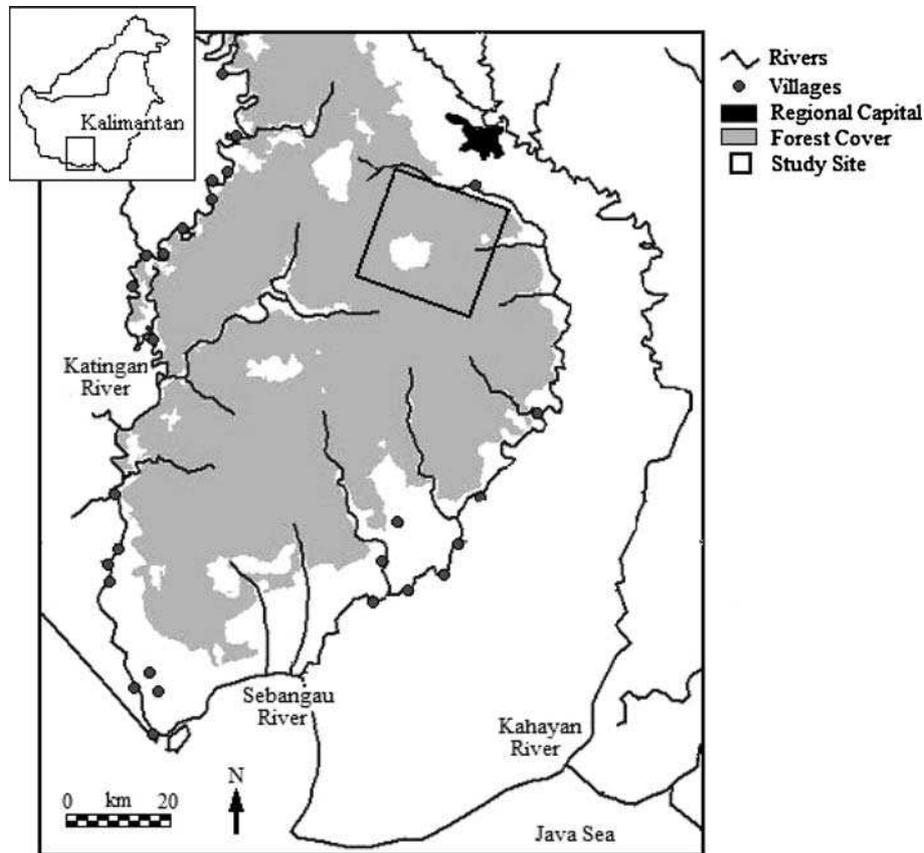


Fig. 1 Map showing the location of the study site within the Sebangau National Park, Borneo

Survey techniques

Line transect surveys were carried out by Blackham from 20 May 2005 to 5 Aug 2005 using the pre-existing transect system. In loris studies based on all-night follows, the animals were active throughout the night (Nekaris 2003; Wiens and Zitzmann 2003). Thus surveys began from 1800 to 1900 and finished between 2230 and 0300. A selection of transects were walked each night and were randomly selected to avoid bias (White and Edwards 2000). Apart from one transect in the low interior forest that was walked only once, all were walked twice at a speed of 400 m/h by a group of two people to minimise disturbance to the animals (Charles-Dominique and Bearder 1979). Although a lone person creates even less disturbance (Duckworth et al. 1994), for safety reasons, a team size of two was desirable. All levels of the vegetation were scanned using Petzl 4.5 V headlamps with a combination of red and white filters (Nekaris 2003). The following data were collected for each sighting: transect length, perpendicular distance of an animal from transect, number of individuals, height in tree, activity when first detected, and tree species (Nekaris and Jayawardene 2004).

Intra-generic comparison

Data on slow loris sightings were gathered from the literature and from our own observations. Studies were used only if they contained the following information: study duration, effort on transects in kilometres or hours, and number of encounters or index of abundance. Because we were interested in analysing data at the specific level, studies that did not identify species in regions where two species occur sympatrically also were excluded. Although it is possible that three taxa of slow loris occur in Laos (Evans et al. 2000), only two (*N. bengalensis* and *N. pygmaeus*) have been confirmed; slow lorises other than *N. pygmaeus* were thus considered *N. bengalensis*. Studies yielding zero sightings were excluded. A study is defined as being conducted in one area and by one (team of) researcher(s); when different strata are sampled within an area, one study may yield multiple estimates of abundance. Study duration is the total number of days included in the study. Survey effort refers to total distance or total number of hours walked or motored. All data were transformed into linear estimates (animals/km) for comparability, using data provided in the studies. Based on this and other loris studies, we assumed that the effective strip half width was between 10 and 25 m, the average speed walked was between 400 m and 1.5 km per hour, and the average survey effort was six hours per night, unless data in the paper indicated otherwise.

Statistical analyses

For the survey, an index of abundance was calculated using linear animal encounter rate along each transect, following Sutherland (2002) and studies of other loris taxa (Barrett 1984; Nekaris and Jayewardene 2004; Rhadakrishna et al. 2006). Because data were not normally distributed, non-parametric tests were used; Yates' correction for continuity was applied to χ^2 tests where appropriate. Tests were two-tailed, with *P* set at the 0.05 level (Zar 1999).

Results

Bornean survey

A total of 12 lorises were seen over the 75-day study period (Table 2). The median distance of a loris from the transect line was 12.6 m (range 6.6–28.3 m) and all were seen at heights of 15–20 m in the trees. All detections were made visually, either by detecting the loris' reflective *tapetum lucidum* or when an animal directly crossed over the path. No vocalisations were heard.

In the peat swamp forest, four sightings of lorises occurred, yielding nine individuals: a single adult, a female and her dependent young, three adults, and a sighting of three adult-sized animals, one of which was larger than the other two. Tree species (and their local names) on which the animals were observed were: *Combretocarpus rotundatus* (tumi), *Palaquium leiocarpum* (hankang), *Callophylum hosei* (bintangor), and *Syzygium cf. nigricans*

Table 2 Summary of survey effort and encounter rates with Bornean slow lorises *N. menagensis* in peat swamp and interior forests in Sebangau National Park, Central Kalimantan, Indonesia

	Effort (km)	Animals seen	Encounter rate (km ⁻¹)
Peat swamp forest	50.85	9	0.19
Low and tall interior forests	9.00	3	0.33

(jambu burung kecil). Of the two three-loris sightings, one occurred on *C. hosei* and the other on *S. nigricans*, both of which were fruiting. These animals clearly fed together affiliatively and in close proximity; the food source could not be identified. Two sightings of lorises yielding three individuals occurred in the interior forest. A pair of adults was observed only 50 m from a lone animal in a hankang tree, raising the possibility that they were part of the same social group (Schülke and Kappeler 2003; Wiens and Zitzmann 2003).

As no difference was found between encounter rate in different forest types ($\chi^2 = 0.55$, $df = 1$, $P > 0.40$), giving equal weight to all transects, an overall encounter rate of 0.19 lorises/km was calculated. Encounter rates decreased over time from 0.37/km during the first 25 days, to 0.26/km for the first 50 days, to 0.19/km after 75 days; the difference between the first and the latter two approaching significance ($\chi^2 = 3.67$, $df = 1$, $P = 0.06$).

Intrageneric comparison

We selected 15 studies yielding 36 estimates of abundance (Table 3). Minimum and maximum abundant estimates differed by approximately one-fifth with a high correlation between them (Pearson's rank correlation coefficient $r = 0.85$, $n = 36$, $P < 0.0001$); only the maxima are analysed here. A median estimate of abundance of 0.26/km was calculated, with median study duration of 10 days. Study duration was not homogeneously distributed across the taxa (Kruskal–Wallis analysis of variance $H = 14.0$, $df = 4$, $P < 0.01$). Pair-wise comparisons revealed that studies of *N. coucang* were significantly longer in duration than those of *N. bengalensis* and *N. pygmaeus* (Mann–Whitney $U = 33.5$, $n_1 = 12$, $n_2 = 15$, $P < 0.005$ and $U = 8$, $n_1 = 15$, $n_2 = 4$, $P < 0.05$, for *N. bengalensis* and *N. pygmaeus*, respectively); the median study duration for *N. coucang* was 10 days, 6.5 days for *N. bengalensis* and 7 days for *N. pygmaeus*. A significant positive correlation was found between study duration and maximum abundance estimate (Pearson's rank correlation coefficient $r = 0.48$, $n = 36$, $P < 0.005$). When the two long-term studies of *N. coucang* at pre-selected sites of high density were excluded, the correlation was no longer significant ($r = -0.11$, $n = 31$, $P = 0.55$). When comparing abundance estimates, a significant difference was found among taxa ($H = 16.8$, $df = 4$, $P = 0.002$). Abundance estimates for *N. coucang* (median = 0.80/km) were higher than for *N. bengalensis* (median = 0.26/km) ($U = 37.5$, $n_1 = 15$, $n_2 = 12$, $P < 0.01$), *N. menagensis* (median = 0.02/km) ($U = 1.5$, $n_1 = 15$, $n_2 = 3$, $P < 0.01$), and *N. pygmaeus* (median = 0.13) ($U = 5$, $n_1 = 15$, $n_2 = 4$, $P < 0.01$). Furthermore, abundance estimates for *N. bengalensis* were significantly higher than those for *N. menagensis* ($U = 3$, $n_1 = 12$, $n_2 = 3$, $P < 0.03$).

Slow lorises occur in seasonal forest as far north as northeastern India to the ever-wet tropical rainforest on the equator, and body weight ranges from 1.6 kg for *N. bengalensis* to a mere 300 grams in *N. menagensis* (Table 1). Yet, no relationship was found between latitude and average estimate of abundance per species per study site ($r = 0.20$, $n = 21$, $P = 0.40$), or between species' body mass and average species abundance ($r = 0.01$, $n = 5$, $P = 0.98$).

Discussion

Abundance of lorises and recommendations for surveys

The outdated view that nocturnal primates are completely solitary has been shown to be invalid (Charles-Dominique 1977; Schülke and Kappeler 2003; Nekaris 2006). In the case

Table 3 Summary of studies of slow loris population assessments that included measures of abundance via nocturnal field observations; all abundance estimates are transformed into linear measures; all measures are approximate

Species name	Study site	Habitat type	Abundance estimate	Study duration	
<i>N. bengalensis</i>	Nambor Forests, Assam, India ^a	Highly logged, disturbed forest	0.05/km	15 nights	
	Gibbon Wildlife Sanctuary, Assam, India ^a	Mildly logged forest with unknown disturbance	0.03/km	12 nights	
	Bherjan Wildlife Sanctuary, Assam, India ^a	Mildly logged forest with unknown disturbance	0.25/km	3 nights	
	Lumding Reserve Forest, Assam, India ^a	Mildly logged forest with unknown disturbance	0.33/km	4 nights	
	Phou Xang He, Central Laos ^b	Semi-evergreen forest	~0.30–0.65/km	7 nights	
	Nakay-Nam Theun, Central Laos ^c	Seasonally dry and wet evergreen forest	0.04–0.08/km	16 nights	
	Xe Piang, Central Laos ^d	Semi-evergreen forest	0.13–0.27/km	14 nights	
	Muang Hom, Central Laos ^e	Semi-evergreen forest and shrub	0.10–0.21/km	6 nights	
	Nam Kading, Central Laos ^e	Semi-evergreen forest and shrub	0.10–0.22/km	7 nights	
	Nam Ao, Central Laos ^e	Semi-evergreen forest	0.14–0.30/km	4 nights	
	Bang Navang, Central Laos ^e	Semi-evergreen forest	0.09–0.20/km	2 nights	
	Xe Namoy, South Laos ^e	Semi-evergreen forest	0.40–0.87/km	4 nights	
	<i>N. coucang</i>	Pasoh Forest Reserve, Negri Sembilan, Malaysia ^f	Primary disturbed	~0.01–0.02/km	74 nights
		Manjung District, Perak, Malaysia ^g	Unlogged primary forest	80/km ²	100 radio tracking nights*
Manjung District, Perak, Malaysia ^g		Logged forest, swamp forest, secondary savannah	20/ km ²	100 radio tracking nights*	
Petalang Jaya, Selangor, Malaysia ^h		Secondary forest	~0.4–1.0/km	10 nights	
Tekam Forest Reserve, Pahang, Malaysia ^f		Logged primary forest	~0.40/km	53 nights*	
Tekam Forest Reserve, Pahang, Malaysia ^f		Unlogged primary forest	~0.8/km	53 nights	
Tekam Forest Reserve, Pahang, Malaysia ⁱ		Primary forest	22.4/km ²	175 nights	
Tekam Forest Reserve, Pahang, Malaysia ⁱ		Logged primary forest	~1.0/km	15 nights	
Tekam Forest Reserve, Pahang, Malaysia ⁱ		Logged primary forest	6/km ²	15 nights	
Tekam Forest Reserve, Pahang, Malaysia ⁱ		Logged primary forest	~0.30/km	10 nights	
Tekam Forest Reserve, Pahang, Malaysia ⁱ	Logged primary forest	26/km ²	10 nights		
Tekam Forest Reserve, Pahang, Malaysia ⁱ	Logged primary forest	~1.28/km	10 nights		
Tekam Forest Reserve, Pahang, Malaysia ⁱ	Logged primary forest	5/km ²	10 nights		
			~0.25/km		

Table 3 continued

Species name	Study site	Habitat type	Abundance estimate	Study duration
	Tekam Forest Reserve, Pahang, Malaysia ⁱ	Logged primary forest	10/km ² ~0.49/km	10 nights
	Tekam Forest Reserve, Pahang, Malaysia ⁱ	Logged primary forest	4/km ² ~0.20/km	10 nights
	Tekam Forest Reserve, Pahang, Malaysia ⁱ	Logged primary forest	33/km ² ~1.63/km	10 nights
	Tekam Forest Reserve, Pahang, Malaysia ⁱ	Logged primary forest	23/km ² ~1.14/km	10 nights
	Tekam Forest Reserve, Pahang, Malaysia ⁱ	Logged primary forest	13/km ² ~0.64/km	10 nights
	Tekam Forest Reserve, Pahang, Malaysia ⁱ	Logged primary forest	10/km ² ~0.49/km	10 nights
	Tekam Forest Reserve, Pahang, Malaysia ⁱ	Logged primary forest	4/km ² ~0.20/km	10 nights
	Tekam Forest Reserve, Pahang, Malaysia ⁱ	Logged primary forest	33/km ² ~1.63/km	10 nights
	Tekam Forest Reserve, Pahang, Malaysia ⁱ	Logged primary forest	23/km ² ~1.14/km	10 nights
	Tekam Forest Reserve, Pahang, Malaysia ⁱ	Logged primary forest	13/km ² ~0.64/km	10 nights
<i>N. javanicus</i>	Gunung Gede Pangrango National Park, West Java, Indonesia ^l	Submontane and montane forest	~0.02/km	21 nights
	Gunung Gede Pangrango National Park, West Java, Indonesia ^k	Submontane and montane forest	~0.20/km	2 nights
<i>N. menagensis</i>	Sebangau National Park, Central Kalimantan, Indonesia ^l	Peat swamp and tall interior forest	0.36/km	75 nights
	Ulu Segama, Sabah, Malaysia ^m	Primary forest	0.02/km	25 nights
	Ulu Segama, Sabah, Malaysia ⁿ	Primary and logged forest	0.01/km	29 nights
<i>N. pygmaeus</i>	Ben En National Park, Thanh Hoa, Vietnam ^o	Hardwood forest and bamboo	~0.05–0.10/km	11 nights
	Nam Kading, Central Laos ^e	Semi-evergreen forest and shrub	~0.06–0.13/km	7 nights
	Xe Namnoy, South Laos ^e	Semi-evergreen forest	~0.10–0.22/km	4 nights
	Phou Xang He, Central Laos ^b	Semi-evergreen forest	~0.05–0.10/km	7 nights

^a Rhadakrishna and Sinha (2004); ^b Duckworth (1994); ^c Duckworth (1998a); ^d Duckworth et al. (1994); ^e Evans et al. (2000); ^f Barret (1984); ^g Wiens and Zitzmann (2003); ^h Shepherd and Nijman (unpub. data); ⁱ Johns (1983); ^j Gursky and Arisona (pers. comm.); ^k Arisona and Nekarlis, (unpub. data); ^l this study; ^m Grieser-Johns (pers. comm.—data collected from 1980–1993); ⁿ Haydon (1994) and in Duckworth (1997); ^o Fitch-Snyder and Vu (2002)

of slow lorises, social behaviour seems to vary across species, with some species described as monogamous and solitary (*N. coucang*—Wiens and Zitzmann 2003) or polygynous, with a propensity towards gregariousness (*N. bengalensis*, *N. coucang* and *N. pygmaeus*—Elliot and Elliot 1967; Rasmussen 1986; Dixson 1998; Streicher 2004). Regardless of social organisation, multiple studies have encountered more than one loris, including observations of social feeding and sexual behaviour (Duckworth 1994; Collins 2007; S. Hogg, pers. comm.; Nekaris and Nijman, unpub. data). Five of the six sightings during our Sebangau study were of multiple lorises. From these data, we suggest that when surveying for lorises, researchers should pay attention for other group members in order to estimate densities more accurately.

The abundance estimate of 0.19 lorises/km in the Sebangau National Park calculated in this study allies closely to figures generated by most other studies of *Nycticebus*, but is slightly below the median of abundance estimates reviewed here. Abundance estimates of *Nycticebus* show no relation with latitude nor with body mass of the species. These results in part substantiate the notion that *Nycticebus* is abundant in some areas but genuinely rare in others (see also Table 4). Although the definition of rarity may differ between researchers, for most taxa in most areas, over a dozen kilometres have to be surveyed before encountering a single loris, which we constitute as rare (Nekaris and Nijman 2007). Despite their data generally not yielding high density estimates (Table 3), Evans et al. (2000) and Duckworth et al. (1994) regarded slow lorises amongst the most common nocturnal mammal in Laos, which merely suggests that other nocturnal mammals are even less abundant. In our dataset, a (positive) relationship between survey effort and abundance was only apparent when the two intensive studies on *N. coucang* in West Malaysia were included. These studies did yield much higher densities, and this might be explained in several ways.

The estimations made by Wiens and Zitzmann (2003) might be due to an unjustified extrapolation of home range sizes from radio-collared individuals to indicate abundance over the entire protected area, of which their study site was only a small part. Many nocturnal primates, including bushbabies, slender lorises and tarsiers, are not spaced evenly across a habitat; rather, one may see many, and then walk for hours or days without encountering another animal. This distribution may be accounted for by habitat selectivity or sensitivity to disturbance, but in all cases, animals were not homogeneously distributed (Jewell and Oates 1969; Bearder and Doyle 1974; Nekaris and Jayewardene 2004; Merker 2006). In the case of *Nycticebus*, heterogeneous densities of both *N. pygmaeus* and *N. bengalensis* were observed in Laos. Even at sites yielding high numbers of lorises, they were largely absent from deciduous areas, and contact frequencies were notably scarcer above 500 m, yielding a pattern similar to those described for other nocturnal primates (Evans et al. 2000; Duckworth, pers. comm.).

In regards to the second study yielding high abundances, Barrett (1984, p. 188) states that he selected his study site precisely because of the high abundance of lorises. During his surveys of eight other sites, slow lorises were only detected at two (Table 4). A number of factors could account for why a species that is generally sparsely distributed may find itself at high abundance in a particular habitat type. In the case of lorises, which do not leap, the extensive canopy continuity found in early stage secondary growth forest may not only provide excellent substrates, but also may be associated with increased density of insects (Singh et al. 1999; Nekaris et al. 2005). The unstable nature of this habitat may also mean that these populations are only temporarily large; this can be illustrated by Johns' (1986) research (Table 3), whereby numbers of *N. coucang* increased immediately after logging, but then fluctuated over the next 12 years.

Table 4 Indications of abundance of slow lorises

Species	Location	Comment on abundance	Source	Year
<i>N. bengalensis</i>	Vietnam	3 spotted during different surveys in different habitats	Ratajszcak	1998
	Thung Yai Naresuan Wildlife Sanctuary, Thailand ^a	Interviews with local people suggest that 76.4% of the population remains	Steinmetz et al.	2006
	China (Jinping, Luchun, Pingbian, Hekou)	Very rare; slow locomotion lends to hunting; extirpated due to deforestation; no more than a few hundred left	Zhang et al.	1992
	Dibru-Saikhowa Sanctuary, Assam, India	Noted as rare based on past capture records	Choudhury	1998
<i>N. coucang</i>	Gumti Wildlife Sanctuary, Tripura, India	eight groups in primary forest and six in secondary forests based not on sightings but on interviews with local people and forest staff	Gupta	1994
	Genting Sempah, N of Kuala Lumpur, Selangor Malaysia	3 captures in 7 months over 29,289 trap nights in evergreen rain forest	Rudd and Stevens	1992–94
	West Malaysia (Ayer Hitam*, Kepong, Kampong Penderas, Lima Belas*, Petaling Jaya, Gunong Telapa Buruk, Ulu Gombak, Ulu Langat)	Loris presence recorded at 2* (one primary forest, one old logged forest) out of 8 sites with total of 34.7 km effort	Barrett	1984
	Penang Island, Malaysia	1 shot in 11 nights mixed vegetation regenerating forest; noted as uncommon	Liat et al.	1971
<i>N. menagensis</i>	West Malaysia	Collected for medical research from 30 localities across the country; rare in secondary forest, abundant in primary forest	Liat	1969
	Kinabalu National Park, Sabah, Malaysia	Present but rarely seen	Jenkins	1971
	Kinabalu National Park, Sabah, Malaysia	1 capture and 2 recaptures in 46,000 trap nights in primary rain forest	Wells et al.	2004 and pers. comm. (2007)
	Bunguran Besar, Natuna Islands, Indonesia	Seen in selectively logged forests; well-known to local communities	Indrawan and Rangkuti	2001
<i>N. pygmaeus</i>	Similajau National Park, Sarawak, Malaysia	No lorises recorded in 77 hours of nocturnal walks; seem to be rarer than in Indochina	Duckworth	1995
	Vietnam	16 spotted during different surveys in different habitats	Ratajszcak	1998
	China (Wenshan, Mengzi, Maguan, Dawieshan, Pingbian)	5 captures in 1986, one at each site; the species is very rare	Zhang et al.	1992
<i>Nycticebus</i> sp. (unidentified)	Cardamom Mountains, Cambodia	Considered 'present' and not a conservation priority as one seen as a pet nearby, and the carcass of a smoked loris was offered for sale; not seen in the wild	Momberg and Weiler	1999

^a Species identification for this study is based on the location of the sanctuary, which should fall in the range of *N. bengalensis*

It is also possible that through experience gained during these long-term studies, the researchers at sites of high abundance encountered lorises at higher rates simply due to expertise. This notion can be challenged by our data in two ways. Firstly, if experience increases the probability of detection, we would expect estimates of abundance to increase with increasing survey effort. This was not the case in our study area in Sebangau, where animal detection actually decreased over the second and the third month of the study. Secondly, thirteen out of the fifteen studies in Table 3 had, as a member of the research team, an individual who either had extensive experience with lorises or with nocturnal mammals. It is thus probable that if densities of lorises were indeed higher, this should be reflected in the results.

The two trapping studies included in Table 4 are also illustrative in planning future studies of slow lorises. Despite numerous rare mammals being captured and recaptured in general mammal traps, *N. coucang* and *N. menagensis* were amongst the rarest mammals trapped in both studies. Wells (pers. comm.) also detected few lorises visually and stated that he certainly could not classify *N. menagensis* at his study site as 'common'. Similar poor trapping rates were obtained by Wiens and Zitzmann (2003) using loris-specific traps, despite their site having amongst the highest density generated for slow lorises. These contrary findings suggest that trapping is not the best method to determine loris density.

Irrespective of a researcher's experience, technique still plays an important role in surveying lorises. Charles-Dominique and Bearder (1979) and Nekaris (2003) advocate the use of red lights for observing lorises and pottos. Duckworth (1994), Wiens (2002), and Rhadakrishna et al. (2006), however, chose using white lights, suggesting that either slow lorises were not affected by them, or the advantage of the power of white light over red was so great (especially when other mammals were included in the study) that it was worth the risk to use such lights. The use of powerful (white) search lights may also lead to a larger proportion of sightings of very young parked infants, whose naïveté makes them less fearful of human observers, in relation to adults, as indeed observed by Rhadakrishna and Sinha (2004). In surveys of pottos (*P. potto*), slender lorises (*L. lydekkerianus* and *L. tardigradus*) and slow lorises (*N. javanicus*), Nekaris (unpub. data) found that red light usually yielded more sightings and always yielded lengthier sightings, increasing the chance of recording an animal on the line transect. As arboreal nocturnal animals are more often recorded by their eyeshine than by sighting the full body (Duckworth 1998b), white lights offer no advantage over red in terms of detection of lorises, although they are beneficial for identification. Finally, as lorises are collected throughout their range for the animal trade (Nekaris and Nijman 2007), white rather than red light may lead to torch-shyness as in other nocturnal mammals (Duckworth 1998a, b), yet another reason to opt for the less visible and less disturbing red option.

The distinctive call of slow lorises also should aid in their detection (Zimmermann 1985). Lorises were not heard by Blackham in our study. In all other studies reviewed here the calls are either not mentioned or are reported as not occurring, possibly leading to an underestimation of loris populations. The ability to tune in on this species' high frequency whistle may increase detections; Nekaris, for instance, detected *N. javanicus* within ten minutes after entering a national park in Java. It is possible that due to misconceptions of lorises in the literature, a researcher may not expect a 'cryptic' animal to call, and thus until now have not listened out for them (Nekaris and Bearder 2007). Experience with captive lorises or vocal recordings would be worthwhile before searching for them in the field to familiarise oneself with the call.

Finally, team size can play a role when searching for lorises. With an anti-predator strategy of freezing in dense foliage or covering the face with forearms during situations of extreme alarm, lorises are more likely to take cover when sought by a large team of researchers (Nekaris et al. 2006). Although team size is rarely reported, sightings of lorises (and other animals) increase when group size is small, or ideally one (Duckworth et al. 1994). Team size should definitely be taken into consideration when reporting loris numbers as low. In areas where political unrest or dangerous animals require a large team of usually inexperienced assistants (e.g. Fitch-Snyder and Vu 2002; Rhadakrishna et al. 2006), at the very least, efforts should be made to reduce noise, to increase inter-person distance, or to provide only one torch for every two or three people. Certainly, bright colours, loud chatting and smoking should be avoided (Sutherland 2002) as these are very disruptive to lorises.

Implications for loris conservation

Large flagship species such as orang-utans, elephants and tigers are meant to preserve vast habitats suitable for many other smaller species (Andelman and Fagan 2000). Smaller species, however, might have discrete habitat requirements, such as arboreal continuity with small gaps, terrestrial continuity with heavy undergrowth cover, or abundance of various dietary items (Entwistle and Stephenson 2000). Caro et al. (2004) showed that those animals deemed flagships for an area did not have a relationship with smaller vertebrates, and indeed, smaller animals at the larger spectrum of small might be a better umbrella for the small vertebrate community.

In our study, slow lorises, which have been considered amongst the most common mammals in Borneo, were rare in the Sebangau National Park. In other studies, slow-climbing lorisiforms have been shown to thrive in areas of arboreal continuity of fine branches, where descent to the ground should be rare (Charles-Dominique 1977; Pimley et al. 2005; Nekaris et al. 2005). Often, these areas are tree fall zones or small forest remnants, which by their nature would not support gibbons or orang-utans – the flagship species in Sebangau and in other national parks claiming to harbour large populations of lorises (e.g. Nijman 2003; Meijaard et al. 2005). Thus long-term studies of the behavioural ecology of all *Nycticebus* taxa in different habitat types are needed before assumptions can be made about their distribution across these habitats.

Slow lorises have historically been considered Data Deficient or Least Concern (IUCN 2002), partially due to a misunderstanding of their taxonomy, but principally due to the fact that they are believed to be common throughout their range. It is mainly catastrophic habitat loss in Southeast Asia that has necessitated the upgrade of the conservation status of all these taxa to Endangered or Vulnerable. In this paper we have compiled the first dataset for all species of slow loris, and have shown that rather than being common, that these species are rare and generally sparsely distributed throughout much of their range. We urgently recommend detailed study of all taxa in order to further our understanding of the distribution and conservation status of these unique primates.

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