

Unexpected diversity of slow lorises (*Nycticebus* spp.) within the Javan pet trade: implications for slow loris taxonomy

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Key words: Indonesia, Java, slow loris, pet trade, morphological variability, taxonomy, conservation

Abstract

Since the 1950s, Sundaland (Borneo, Java, Sumatra and their surrounding islands) was thought to be inhabited by a single slow loris species, the greater slow loris *Nycticebus coucang*. Early taxonomies as well as recent morphological and genetic studies, however, point to at least three species native to this region: *N. coucang*, *N. menagensis*, and *N. javanicus*. In the light of this taxonomy, all Sundaland slow lorises, previously considered Least Threatened, have been listed as Vulnerable or Endangered. Of particular concern is the fact that slow lorises are the most common protected primate species in the rampant South-east Asian pet trade, resulting in their recent transferral to CITES Appendix I precluding all international commercial trade. Due to lack of knowledge regarding morphological differences between the three species, they are still managed as one, with potential serious affects to wild populations, as hard-release of individuals of unknown geographic origin is common. This paper examines morphological variability of 34 live slow lorises, all of which were rescued from the wildlife trade in Java, Indonesia. Morphometric data and diagnostic images were collected, various species descriptions were considered and statistical analyses were conducted and compared with other taxonomists' classifications. A discriminant function analysis provided support for four distinct groupings: *Nycticebus coucang* and *N. javanicus*, as well as evidence for two new taxa that correspond closely to *N. hilleri* and *N. ornatus*. The morphological traits that varied significantly and the external characteristic trends described in this study that contributed to these groupings might provide a baseline to classify *Nycticebus* taxa. This information is pertinent for appropriate captive management and specific designation of rescued individuals and for designing proper *in-situ* and *ex-situ* conservation strategies.

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Introduction

Until recently, the cryptic appearance and lifestyles of nocturnal primates concealed an abundance of species within taxonomic groups including Tarsiiformes, Lemuriformes, Galaginae, and Aoutidae (Bearder, 1999). Long-term and detailed studies of the behaviour, ecology, morphology and genetics of these groups revealed that the real number of species was highly underestimated and have led to a wide-spread acceptance of new speciose taxonomic arrangements, (Masters, 1988; Zimmermann *et al.*, 1988; Martin, 1995; Bearder, *et al.*, 1995; Hafen *et al.*, 1998; Nietsch, 1999; Pastorini *et al.*, 2003). Many of these new species, formerly thought to have a broad distribution, are now known to inhabit highly restricted ranges, increasing threat via habitat loss or other stochastic events (Ganzhorn *et al.*, 1997).

It is not surprising, then, that similar trends might be found amongst the Lorisinae, the lorises of Asia, in particular the slow lorises (*Nycticebus*) which range from Northern India to the Philippines (Nekaris and Bearder, 2007). Historically, taxonomists recognized at least nine species within the genus *Nycticebus* (Table 1). In 1953, these taxa were consolidated to a single species, *N. coucang* (Osman Hill, 1953). Later, Groves (1971, 1998) argued that *N. pygmaeus* was consistently different enough from *N. coucang* to be a species in its own right. Captive slow lorises from that point were managed as two distinct species, despite enormous variation in body size and different management needs (Fitch-Snyder and Schulze, 2000). In the last few years, an accumulating number of studies pointed to genetic, morphological and behavioural variability within the lorises (Duckworth, 1994; Ravoosa, 1998; Groves, 1998; Supriatna and Hendras, 2000; Fitch-Snyder and Ehrlich, 2003; Roos, 2003; Miehs and Nekaris, 2005; Chen, *et al.*, 2006; Groves and Maryanto, in press). Five species are now generally recognized and have been independently assessed

Table 1. A historical review of species and subspecies of *Nycticebus* that have been identified with their authorities (Osman Hill, 1953; Groves, 2001).

<i>Nycticebus coucang</i> (Boddaert, 1784)	<i>Nycticebus menagensis</i> (Lydekker, 1893)	<i>Nycticebus bengalensis</i> (Lacépède, 1800)	<i>Nycticebus javanicus</i> (E. Geoffroy, 1812)	<i>Nycticebus pygmaeus</i> (Bonhote, 1907)
<i>Tardigradus coucang</i> • Boddaert, 1784	<i>Lemur menagensis</i> • Lydekker, 1893	<i>Loris bengalensis</i> • Lacépède, 1800	<i>Bradylemur tardigradus</i> • Lesson, 1840	<i>Nycticebus intermedius</i> • Dao, 1960
<i>Lemur tardigradus</i> • Raffles, 1821	<i>N. borneanus</i> • Lyon, 1906	<i>N. cinereus</i> • Milne-Edwards, 1867	<i>N. ornatus</i> • Thomas, 1921	
<i>Stenops tardigradus</i> • Van der Hoeven, 1844	<i>N. bancanus</i> • Lyon, 1906	<i>N. tenasserimensis</i> • Elliot, 1913	<i>N. tardigradus javanicus</i> • Lydekker, 1904	
<i>N. sumatrensis</i> • Ludeking, 1867	<i>N. philippinus</i> • Cabrera, 1908	<i>N. incanus</i> • Thomas, 1921		
<i>N. tardigradus</i> • Anderson, 1881		<i>N. tardigradus typicus</i> • Lydekker, 1905		
<i>N. coucang hilleri</i> • Stone and Rehn, 1902				
<i>N. c. buku</i> • Robinson, 1917				
<i>N. c. brachycephalus</i> • Sody, 1949				

in the IUCN Red List (Nekaris and Nijman, 2007), yet many researchers, zoological collections managers, and rescue centre workers still operate in accordance with the 1971 taxonomy (Supriatna *et al.*, 2001; Molur *et al.*, 2003; Schulze and Groves, 2004; Perez, *et al.*, 2005; Shapiro, 2007).

One factor more than any other demands clarification of slow loris taxonomy. Slow lorises are repeatedly found to be the most common protected primate species represented in Southeast Asian animal markets (Malone *et al.*, 2003; Harris, 2003; Webber and Nekaris, 2004; McGreal, 2007), and in some cases, the most common protected animal species in these markets (Shepherd *et al.*, 2004). The extent of this trade led to a successful proposal by Cambodia to transfer all members of the genus from CITES (Convention on International Trade in Endangered Species) II to I (Nekaris and Nijman, 2007). The illegal wildlife trade not only contributes to the loss of wild populations (Hunyh, 1998; Ratajszczak, 1998; Fitch-Snyder and Thanh, 2002), but also leads to arbitrary release of animals to forested areas without consideration of their geographic origin (Schulze and Groves, 2004). Confiscated animals of different species housed together may hybridise causing further complications (*pers. obs.*). Most animals, however, die due to lack of specialised knowledge for keeping slow lorises, or due to complications of health problems acquired whilst in transit or in animals markets (Streicher, 2004; den Haas and Sanchez, *pers. comm.*).

In Indonesia, trade of slow lorises is illegal, and possession of a loris by buyers or traders is punishable by law. None of the previous studies of slow lorises in Indonesian markets identified the animals at the species or subspecies level, classing them all as *N. coucang*. If Indonesian trade laws are enforced and animals are not transported between islands, one would hypothesise that animals in markets and in confiscations should come from the island on which they are traded or confiscated (but see Schulze and Groves, 2004). In this study, we had access to 34 slow lorises confiscated in the Javan animal trade, and predicted that all animals should be in accordance with *N. javanicus*. We provide a detailed analysis of variation within this group of confiscated slow lorises in order to address a number of issues relating to loris conservation. Are multiple taxa present in the Javan trade? If so, which ones? Are these taxa identifiable? What features can be used to discern Indonesian slow loris taxa in order to manage their rescue and rehabilitation?

Methods

Thirty-four live *Nycticebus* specimens of unknown origin, all rescued from the illegal wildlife trade in Java, Indonesia, were maintained at the Schmutzer Primate Centre, Jakarta, Indonesia. In May 2006, the animals were measured for 32 morphological and pelage-related characters using templates specifically designed for

Table 2. Characters used in the current study; figures showing precise measurements and scores for facial pattern are available in Schulze *et al.* (2007).

General	
1. Sex	2. Weight
Pelage Characteristics	
Face	Body
3. Facial markings scored	9. Colour of dorsal hair, general
4. Colour of dark facial markings	10. Frosting on back present or absent
5. Colour of forehead	11. Colour of ventral hair, superficially
6. Colour of median facial stripe	12. Ventral hair base colour
7. Colour of preauricular hair	13. Throat hair base colour
8. Skin pigmentation	14. Girth measurement of zone with dark dorsal hair, measured as a percent of girth circumference
	15. Dorsal stripe enclosed by light lateral stripe, zone, light neck?
	16. Dorsal stripe extends to the more caudal part of trunk? (long vs short)
	17. Hair quality: woolly? Amount of stiff guard hair? Wavy or curly?
	18. Hair length [mm] on back
Measurements (mm)	
19. Chest girth circumference	27. Head and body length
20. Tail length from hind edge of anus	28. Maximum length of head
21. Upper arm (humerus) length	29. Muzzle length
22. Forearm (radius) length	30. Head breadth
23. Thigh (femur) length	31. Face breadth
24. Leg (tibia) length	32. Ear length
25. Hand span	
26. Foot span	

Nycticebus spp. (Fitch-Snyder and Schulze, 2000) (Table 2). We used a large number of pelage-related characters for two reasons. Firstly, accumulating evidence suggests that the markings of nocturnal animals may play an important role in species recognition systems (Bearder, 1999; Bearder, *et al.*, 2006). Secondly, because animals were not anaesthetised, visual assessment with the aid of a colour chart allowed for rapid collection of many characters with limited stress to the animal. All morphometric measurements were taken with digital callipers, and with a Pesola 1000 g spring scale. Hair samples were taken from the thoracic region of the dorsum at the root and measured for length with a digital microscope; the average of ten hairs for each individual was used in analysis. Diagnostic photos were taken of each individual. Later, measurements and images were collected of specimens from the Natural History Museum London, Zoological Museum Amsterdam and Naturalis Leiden for subsequent species comparison of 'trade' animals of unknown origin with museum specimens of known origin to ascribe the individuals to a known taxon.

SPSS 12.0 was used for all statistical analyses. Discriminant analyses were conducted to test the validity of grouping of animals based on their close similarity

to museum specimens. Non-parametric statistical tests were used for group and pair-wise comparisons due to small sample size, with probability set at the 0.10 level (Zar, 1999).

Results

Four morphotypes of slow loris were distinguished in the sample when comparing to museum specimens, principally using their characteristic facial masks (including inter-ocular stripe, preauricular hair pattern, circumocular patch shape, and shape and diffusion of crown) (Fig. 1): a greyish small Sumatran form (n=16), a large rufescent Sumatran form (n=9), a short-coated small Javan form (n=6), and a long-coated larger Javan form (n=3). Although more research needs to be conducted comparing these animals with type specimens, they correspond closely to the following taxa: *N. cf. coucang*, *N. cf. hilleri*, *N. cf. javanicus*, and *N. cf. ornatus*. For ease of discussion, the species names are referred to in the rest of this paper, but it should be noted that more research is required with a larger sample size to explore the taxonomic status of these species further.

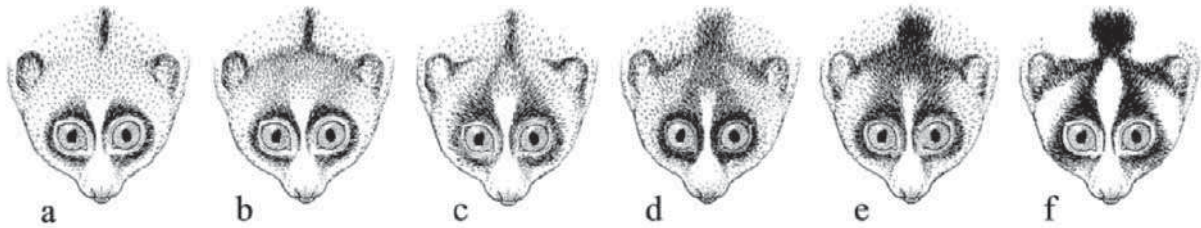


Fig. 1. Key used for assigning facial markings to the lorises in this study, drawn by H. Schulze. Individuals in this study corresponded to c (*coucang*), d (*hilleri*), or f (*javanicus/ornatus*).

When all taxa and all characters were included in a single discriminant function analysis, the percentage of correct classifications obtained was 100%, and groups were clearly discriminated on the basis of two functions (Fig. 2). The first function significantly explained 89.7% of the variance between the four taxa and was dependent on overall colour and facial pattern (Wilks' Lambda: $\chi^2 = 174.5$, $df = 90$, $p < 0.0001$). The second function significantly explained 7.5% of the variance and was dependent on overall size (Wilks' Lambda: $\chi^2 = 85.4$, $df = 58$, $p < 0.01$). A second analysis was run on the same data combining the Javan forms due to small sample size of *ornatus*. In this case, the percentage of correct classifications obtained was 100%, and groups were still clearly discriminated on the basis of two functions. The first function significantly explained 98.7% of the variance between the four taxa and was dependent on overall colour and facial pattern (Wilks' Lambda: $\chi^2 = 175.7$, $df = 62$, $p < 0.0001$). The second function significantly, dependent on size, explained 1.3% of the variance (Wilks' Lambda: $\chi^2 = 53.6$, $df = 30$, $p < 0.01$).

As facial pattern was the main character used to classify the animals based on museum specimens, a

second analysis was run excluding this character, still grouping the Javan forms. The classification remained at 100% for the three groups (Fig. 3). The variance explained significantly by the first function, still relating to colour pattern, reduced to 90.5% (Wilks' Lambda: $\chi^2 = 168.8$, $df = 87$, $p < 0.0001$), whereas variation as explained by size rose to 7.8% (Wilks' Lambda: $\chi^2 = 78.6$, $df = 56$, $p < 0.03$).

Table 3 summarises the morphometric measures of each taxon, showing relatively (but not significantly) larger (*N. javanicus* and *N. hilleri*) and relatively smaller (*N. ornatus* and *N. coucang*) forms on each island. Table 5 highlights pelage characteristics that differ significantly amongst the groups. General size and colour patterns in 12 different characters differentiate these groups of lorises, despite the small sample size (Fig. 4).

Pairwise comparisons were then run amongst significant traits to examine differences between groups. The only ordinal character that distinguished the two Javan taxa was hair length (Mann-Whitney U: $U = 0$, $p < 0.03$). Sumatran taxa were distinguished by head breadth (Mann-Whitney U: $U = 36$, $p < 0.05$) and brachial index (Mann-Whitney U: $U = 42$, $p < 0.09$). They were further distinguished by several categorical traits:

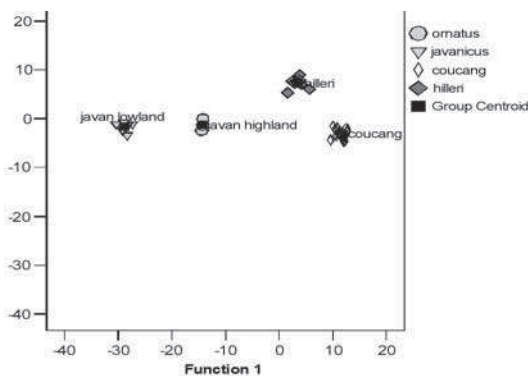


Fig. 2. Discriminant Function Analysis based on 32 characters predicting group membership for all four morphotypes.

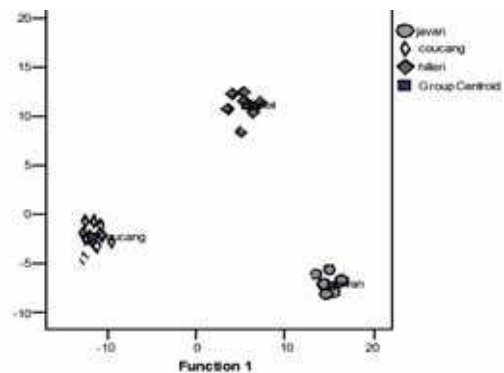


Fig. 3. Discriminant function analysis based on three morphotypes, based on 31 characters, excluding facial mask.

Table 3. Morphometric parameters for the four morphs of slow lorises classified in this study, based on 34 individuals; weights are in grams and lengths are in mm. Characters with an asterisk (* = <0.10, ** = <0.05, *** = <0.01) are significantly different in a Kruskal-Wallis ANOVA. Characters with plusses (+ = <0.10, ++ = <0.05, +++ = <0.01, ++++ = <0.001) differed in pairwise comparisons of Javan (*javanicus* and *ornatus*) and Sumatran (*hilleri* and *coucang*) lorises.

Character (g or mm)	Average \pm standard deviation			
	<i>N. javanicus</i> (n = 6)	<i>N. ornatus</i> (n = 3)	<i>N. hilleri</i> (n = 9)	<i>N. coucang</i> (n = 16)
Weight	670.0 \pm 140.0	572.0 \pm 51.3	688.6 \pm 156.4	594.2 \pm 111.5
Head length	59.2 \pm 7.4	59.3 \pm 0.9	60.6 \pm 4.9	61.7 \pm 4.2
Muzzle length++	19.9 \pm 3.4	19.5 \pm 1.8	20.9 \pm 5.5	23.3 \pm 4.2
Head breadth*	43.6 \pm 4.5	42.1 \pm 0.9	38.6 \pm 2.7	45.4 \pm 10.7
Body length**, ++++	250.8 \pm 11.6	245.0 \pm 5.0	238.2 \pm 15.2	229.8 \pm 23.3
HBL	293.1 \pm 13.3	284.8 \pm 4.2	277.9 \pm 14.1	268.2 \pm 24.6
Chest girth	190.8 \pm 17.7	180.0 \pm 8.7	191.1 \pm 11.9	181.8 \pm 24.2
Dark % girth***, ++++	48.0 \pm 10.9	40.8 \pm 2.7	58.4 \pm 10.0	54.3 \pm 10.2
Neck circumference, ++	136.7 \pm 12.1	130 \pm 10.0	145.6 \pm 10.1	146.3 \pm 14.9
Tail length	20.4 \pm 4.1	21.7 \pm 4.8	20.5 \pm 5.8	19.7 \pm 4.5
Humerus length	67.2 \pm 8.4	74.9 \pm 5.7	71.6 \pm 6.8	73.6 \pm 7.6
Radius length	71.8 \pm 7.4	70.9 \pm 2.2	69.6 \pm 4.8	66.4 \pm 5.3
Femur length	83.2 \pm 7.7	77.5 \pm 11.5	77.4 \pm 8.5	76.8 \pm 12.4
Tibia length, +	85.9 \pm 5.0	85.2 \pm 7.0	82.5 \pm 5.8	79.4 \pm 8.3
Hand span**, ++	59.1 \pm 10.1	56.8 \pm 2.4	50.8 \pm 11.1	54.2 \pm 6.3
Foot span	70.3 \pm 2.2	70.3 \pm 4.5	68.2 \pm 8.0	67.5 \pm 5.7
Ear length	16.8 \pm 2.6	18.8 \pm 1.4	18.1 \pm 4.5	17.0 \pm 2.6
Intermembral index	82.1 \pm 6.4	90.38 \pm 9.1	88.5 \pm 3.3	90.9 \pm 14.2
Humeral femoral index	80.8 \pm 7.39	97.7 \pm 9.1	93.1 \pm 9.1	100.6 \pm 32.8
Brachial index*, ++	107.9 \pm 15.0	95.2 \pm 10.3	97.7 \pm 9.2	90.9 \pm 10.2
Crural index	104.1 \pm 13.5	110.8 \pm 7.7	107.3 \pm 10.1	107.5 \pm 29.9
Average hair length***, ++++	22.4 \pm 0.9	26.8 \pm 3.2	20.1 \pm 2.4	20.2 \pm 3.3

Table 4. Pelage characteristics distinguishing the four morphotypes using a chi-square cross-tabulation (* = <0.10, ** = <0.05, *** = <0.01, **** = <0.0001).

Character	Distinguishes four types	Distinguishes Sumatran/Javan
Facial pattern (Fig. 1)	****	****
Dorsal stripe enclosed by lateral stripe	****	****
Dorsal stripe ending at caudal, thoracic or lumbar region	**	**
Dorsal stripe colour (red vs brown variations)	*	***
Preauricular hair colour (white/grey vs red vs brown variations)	*	*
Forehead colour		**

facial mask ($\chi^2 = 21.1$, $df = 1$, $p < 0.0001$), dorsal stripe length ($\chi^2 = 6.8$, $df = 2$, $p < 0.03$) and preauricular hair colour ($\chi^2 = 6.2$, $df = 3$, $p < 0.10$).

Finally, pairwise comparisons were run on these same traits grouping all Javan lorises and all Sumatran lorises. Eight ordinal characters distinguish these groups as well as well as six characters relating to pelage (Tables 3 and 4).

Discussion

Two species are clearly discernible in the Javan trade – *N. coucang* and *N. javanicus*. Indeed, nearly two

thirds of the sample in this study was from Sumatra, where trade in slow lorises is known to be high (Shepherd *et al.*, 2004). Variability within these groups aside, the high proportion of Sumatran lorises in this sample was similar to that seen in the trade in orang-utans and gibbons on Java (Nijman 2005), suggesting that inter-island trade is poorly enforced. Slow lorises are wholly protected in Indonesia. Although fines and jail sentences should be imposed on those trading or owning lorises, and indeed other protected wildlife, effective law enforcement with respect to wildlife protection laws is all but non-existent in Indonesia (Nijman 2006).

Furthermore, Javan slow lorises are considered Endangered, and trade has been identified as a consider-

N. hilleri

- Rich, reddish-brown in colour, including the dorsal stripe and facial markings
- Nuchal region reddish brown
- Crown is diffused with rounded forks above the eyes
- Dorsal stripe does not generally extend to the caudal region
- Red body colour extends to the belly, with a more red ventral region
- Pre-auricular hair can be reddish

N. coucang

- Brownish with brown crown and dark dorsal stripe enclosed by darker line
- Nuchal region frosted
- Head forks meet circumocular patch to form points
- Brown body colour covers less percentage of the body, with a lighter ventral region.
- Dorsal stripe continues to caudal region
- Pre-auricular hair white or grey

Fig. 4. Pelage characters that distinguish the four loris morphotypes (all photos by Nekaris, continued on p. 193).

able threat. Non-systematic surveys by International Animal Rescue, an organisation that does discern between the Javan and Sumatran forms, noted a marked decrease of Javan forms in the markets over the last few years (den Haas and Sanchez, pers. comm.; Jaffe, 2005). As demand for slow lorises is still high, and numbers of Javan animals has decreased, trade could be a direct indicator of decrease of these animals in the wild. Similar trends have been identified in Vietnam and Cambodia, where lorises have become both increasingly difficult to observe in both the wild and the trade (Streicher and Nadler, 2003; Starr, pers. comm.).

The analyses performed in this study clearly distinguished Sumatran lorises from Javan lorises. *Nycticebus javanicus* was first recognised as a distinct taxon in 2000 (Supriatna and Hendras, 2000). A subsequent molecular study relied on only a single specimen from Java, and this taxon could not be discerned from this small sample size (Chen *et al.*, 2006). In a more detailed craniometric study, Groves and Maryanto (in press) decided that Javan lorises, based on a sample of

25 skulls, were consistently distinct enough, especially when combined with pelage characters, to merit separation as a distinct species. This study provides further evidence, using a set of characters used to distinguish other nocturnal mammals (Masters and Spencer, 1989), that *N. javanicus* warrants distinction as a species.

Earlier studies also pointed to great variation within *Nycticebus* from Sumatra and Borneo (Groves, 1971; McPhee and Jacobs, 1986; Ravosa, 1998). Indeed, in 1904, Lydekker (p. 346) noted “the marked distinction between the grey Malay phase and the rufous Sumatran phase of the species (Fig. 5).” The small sample size in this study clearly distinguished two Sumatran forms, in accordance with *N. coucang* and *N. hilleri*. Two Javan forms were also distinguished, but mainly on hair length, perhaps indicating altitudinal differences. These differences were enough, however, for them earlier to be distinguished as *N. javanicus* and *N. ornatus* (Osman Hill, 1953). In the case of Sumatran species, the red form fetches higher prices in markets and is said to be more rare (Dwi, pers. comm.). *Nycticebus menagen-*

N. javanicus

- Brown to reddish in colour
- Nuchal region white
- Dorsal stripe enclosed by whitish lateral stripe
- Distinct white diamond between the eyes extending to forehead
- Circumocular patches extend to the cheeks
- dorsal stripe extends to the lumbar or thoracic region
- brown body colour covers more percentage of the body than highland, making ventral region darker
- short woolly hair with small ear tufts
- long silky hair with more tufted ears

sis, Sumatran *N. coucang* and *N. javanicus* have been isolated on their respected islands since the Holocene or postglacial period, and within their islands are also isolated due to river and mountain boundaries (van den Bergh *et al.*, 2001). Therefore, the results shown here and the suggestion that these taxa are distinctive on the species or subspecies level are not surprising. Also, the two Javan forms found within this sample coincide with the notion of altitudinal variation; a common factor classifying Indonesian primate subspecies (Brandon-Jones *et al.*, 2004).

Ravosa (1998), looking at craniometric variables, found high variability within this group, but suggested that the differences within 'coucang' were clinal. What he and other authors studying *Nycticebus* skeletal morphology did not consider is that in many other nocturnal primate species, mate recognition systems depend on vocal and olfactory signals as well as contrasting facial patterns (Mayr, 1963; Bearder, *et al.*, 1995). Thus animals that are almost identical skeletally are often in fact distinct species (Masters and Bragg, 2000). Mayr

N. ornatus

- Light brown in colour
- Nuchal region white
- Dorsal stripe enclosed by whitish lateral stripe
- Distinct white diamond between the eyes extending to forehead
- Circumocular patches extend to the cheeks
- dorsal stripe extends to the lumbar or thoracic region
- brown body colour covers less percentage of the body than lowland, making ventral region lighter

(1942) argued that a taxon is a valid subspecies if it can be distinguished on 75% of its traits; from this sample, such is the case with *N. c. hilleri*. Separation of this taxon from *N. coucang coucang* might help to explain considerable variability and low percent discrimination of individuals into this taxon within Sumatran *N. coucang* observed in previous studies (Ravosa, 1998; Groves and Maryanto, in press). Further morphological, behavioural and genetic studies are required to understand variability within *Nycticebus* keeping this taxonomic arrangement in mind.

Whether or not taxonomic arrangements of the Sunda slow lorises should be altered, identification of the morphotypes is essential for rescue and release programmes. Trade is so great that numbers of lorises coming into rescue centres exceed their capacity (den Haas and Sanchez, pers. comm.). Reduced populations in the wild, combined with mounting evidence for both national and international trade, have resulted in transferral of the genus *Nycticebus* to CITES I – the first transferral of a primate species since 1989 (Nekaris



Fig. 5. A drawing from 1904 from Lydekker distinguishing *coucang* (left) from *hilleri* (right).

and Nijman, 2007). Specialist needs of these species also mean that they perish quickly in captivity (Fitch-Snyder and Schulze, 2000); thus oftentimes immediate re-release is considered as preferable (Wiek, 2007). This means that in countless cases, animals are reintroduced without regard to their health status, their behavioural needs, or their geographic origin (Schulze and Groves, 2004; Streicher, 2004). In the single reintroduction programme conducted ethically and systematically, one third of the released animals perished despite following all IUCN protocol (Streicher and Nadler, 2003). The results for hard released animals are probably far direr.

These cases illustrate that it is essential that rescue centres and confiscation authorities are able to identify animals in order to release them to an appropriate locality (Streicher and Nadler, 2003; Schulze and Groves, 2004). As cryptic species, physical differences amongst the slow lorises are subtle. We hope that information provided in this study will be useful in developing further identification keys for individuals confiscating or rehabilitating lorises and for better understanding speciation amongst *Nycticebus*.

Acknowledgements

We thank The Schmutzer Primate Centre and International Animal Rescue Indonesia for allowing us access to the lorises in their care and for accommodation; in particular we thank Femke den Haas, Pramudya Harzani, and Alphonz. Doug Brandon-

Jones, Colin Groves, Karmele Sanchez, Helga Schulze, Carly Starr and Jon Wells helped with various aspects of the analysis; Schulze also provided the figure. Two reviewers, Simon Bearder and Colin Groves improved the quality of this manuscript through helpful comments. We thank the following individuals for access to and help with their zoological collections: Hein van Grouw (Naturalis Leiden), Daphne Hill and Paula Jenkins (Natural History Museum London), Vincent Nijman (Zoological Museum Amsterdam), and Malgosia Nowak-Kemp (Natural History Museum Oxford). Funding was provided to Nekaris by Oxford Brookes University Research Strategy Fund and SYNTHESIS (NL-TAF-3491).

References

- Bearder SK. 1999. Physical and social diversity among nocturnal primates: a new view based on long-term research. *Primates* 40: 267-282.
- Bearder SK, Honess PE, Ambrose L. 1995. Species diversity among galagos with special reference to mate recognition. Pp 331-352 in Alterman L, Doyle G, Izard MK, editors. *Creatures of the dark: the nocturnal prosimians*. New York: Plenum.
- Bearder SK, Nekaris KAI, Curtis D. 2006. A re-evaluation of the role of vision for the activity rhythms of nocturnal primates. *Folia Primatologica* 77: 50-71.
- Brandon-Jones D, Eudey AA, Geissmann T. 2004. Asian primate classification. *International Journal of Primatology* 25: 97-164.
- Chen JH, Pan D, Groves CP. 2006. Molecular phylogeny of *Nycticebus* inferred from mitochondrial genes. *International Journal of Primatology* 27: 1187-1200.
- Duckworth JW. 1994. Field sighting of the pygmy loris (*Nycticebus pygmaeus*) in Laos. *Folia Primatologica* 63: 99-101.

- Fitch-Snyder H, Ehrlich A. 2003. Mother-infant interactions in slow lorises (*Nycticebus bengalensis*) and pygmy lorises (*Nycticebus pygmaeus*). *Folia Primatologica* 74: 259-271.
- Fitch-Snyder H, Schulze H. 2000. *Husbandry Manual for Asian Lorises* (*Nycticebus and Loris*). San Diego: Center for Reproduction of Endangered Species (CRES) Zoological Society of San Diego.
- Fitch-Snyder H, Thanh VN. 2002. A preliminary survey of lorises (*Nycticebus* spp.) in northern Vietnam. *Asian Primates* 8: 1-3.
- Ganzhorn JU, Rakotosamimanana B, Hannah L. 1997. Priorities for biodiversity conservation in Madagascar. *Primate Report* 48: 1-81.
- Groves CP. 2001. *Primate Taxonomy*. Washington and London: Smithsonian Institution Press.
- Groves CP. 1998. Systematics of tarsiers and lorises. *Primates* 39: 13-27.
- Groves CP. 1971. Systematics of the genus *Nycticebus*. Pp 44-53 in Biegert J, Leutenegger W, editors. *Taxonomy, anatomy, reproduction. Proceedings of the third international congress of primatology, vol 1*. Basel: S Karger.
- Groves C, Maryanto I. In press. Craniometry of slow lorises (Genus *Nycticebus*) of insular Southeast Asia. *Primates of the Oriental Night, Treubia* (Shekelle M, editor).
- Hafen T, Neveu H, Rumpler Y, Wilden I, Zimmermann E. 1998. Acoustically dimorphic advertisement calls separate morphologically and genetically homogenous populations of the grey mouse lemur (*Microcebus murinus*). *Folia Primatologica* 69 (Suppl. 1): 342-356.
- Harris L. 2003. Survey of pet markets in Indonesia: continuing project. MSc Thesis. Oxford, U.K.: Oxford Brookes University.
- Harrison T, Krigbaum J, Manser J. 2006. Primate biogeography and ecology on the Sunda Shelf Islands: a paleontological and zooarchaeological perspective. Pp 331-374 in Lehman SM, Fleagle JG, editors. *Primate Biogeography and Prospects*. New York: Springer.
- Hunyh DH. 1998. Ecology, biology and conservation status of prosimians species in Vietnam. *Folia Primatologica* 69: 101-108.
- Jaffe S. 2005. Designing a project for the reintroduction and rehabilitation of slow lorises in Indonesia. MSc Dissertation. Oxford, UK: Oxford Brookes University.
- Lydekker R. 1904. On two lorises. *Proceedings of the Zoological Society of London* 2: 345-346.
- MacPhee RDE, Jacobs LL. 1986. *Nycticeboides simpsoni* and the morphology, adaptations, and relationships of Miocene Siwalik Lorisidae. Pp 131-161 in Flanagan KM, Lillegraven JA, editors. *Contributions to Zoology, University of Wyoming Special Paper 3*. Laramie, USA: University of Wyoming Press.
- Malone N, Purnama AR, Wedana M, Fuentes A. 2002. Assessment of the sale of primates at Indonesian bird markets. *Asian Primates* 8: 7-11.
- Martin RD. 1995. Prosimians: from obscurity to extinction? Pp 535-563 in Alterman L, Doyle GA, Izard MK, editors. *Creatures of the Dark: The Nocturnal Prosimians*. New York: Plenum Press.
- Masters JC. 1988. Speciation in the greater galagos (Prosimii: Galaginae): A review and synthesis. *Biological Journal of the Linnean Society* 34: 149-174.
- Masters JC, Bragg NP. 2000. Morphological correlations of speciation in bushbabies. *International Journal of Primatology* 21: 793-813.
- Masters JC, Spencer HG. 1989. Why we need a new genetic species concept. *Systematic Zoology* 38: 270-279.
- Mayr E. 1942. *Systematics and the Origin of Species*. New York: Columbia University Press.
- Mayr E. 1963. *Animal Species and Evolution*. Cambridge, MA: Harvard University Press.
- McGreal S. 2007. Loris confiscations highlight need for protection. *IPPL News* 34: 3.
- Miehs A, Nekaris KAI. 2004. A comparison of the captive behaviour and exhibit use of the Bengal slow loris (*Nycticebus bengalensis*) and pygmy loris (*Nycticebus pygmaeus*) at London Zoo. South Australian Museum, Adelaide: Proceedings from the Australasian Primate Society 23rd Annual Conference.
- Molur S, Brandon-Jones D, Dittus W. 2003. *The status of South Asian primates: conservation assessment and management plan (C.A.M.P) workshop report*. Coimbatore: Zoo Outreach Organisation/CBSG-South Asia.
- Nekaris KAI, Bearder SK. 2007. The strepsirrhine primates of Asia and Mainland Africa: diversity shrouded in darkness. Pp 24-45 in Campbell C, Fuentes A, MacKinnon K, Panger M, Bearder SK, editors. *Primates in Perspective*. Oxford: Oxford University Press.
- Nekaris KAI, Nijman V. 2007. CITES proposal highlights threat to nocturnal primates (*Nycticebus*: Lorisidae). *Folia Primatologica* 78: 211-214.
- Nietsch A. 1999. Duet vocalisations among different populations of Sulawesi tarsiers. *International Journal of Primatology* 20: 567-583.
- Nijman V. 2005. *In full swing: an assessment of trade in orangutans and gibbons on Java and Bali, Indonesia*. Petaling Jaya, Selangor, Malaysia: TRAFFIC Southeast Asia.
- Nijman V. 2006. In-Situ and Ex-Situ status of the Javan Gibbon and the role of zoos in conservation of the species. *Contributions to Zoology* 75: 161-168.
- Osman-Hill WC. 1953. *Primates: A Comparative Anatomy and Taxonomy. I - Strepsirhini*. Edinburgh: Edinburgh University Press.
- Pastorini J, Thalmann U, Martin RD. 2003. A molecular approach to comparative phylogeography of extant Malagasy lemurs. *Proceedings of the National Academy of Sciences USA* 100: 5879-5884.
- Perez LE, Czekala NM, Weisenseel KA, Lasley BL. 2005. Excretion of radio labelled estradiol metabolites in the slow loris (*Nycticebus coucang*). *American Journal of Primatology* 16: 321-330.
- Ratajszczak R. 1998. Taxonomy, distribution and status of the lesser slow loris *Nycticebus pygmaeus* and their implications for captive management. *Folia Primatologica* 69 (Suppl 1): 171-174.
- Ravosa MJ. 1998. Cranial allometry and geographic variation in slow lorises (*Nycticebus*). *American Journal of Primatology* 45: 225-243.

- Roos C. 2003. Molekulare Phylogenie der Halbaffen, Schlangaffen, und Gibbons. Dissertation, München, Germany: Technischen Universität.
- Shapiro LJ. 2007. Morphological and functional differentiation in the lumbar spine of lorises and galagids. *American Journal of Primatology* 69: 86-102.
- Shepherd CR, Sukumaran J, Wich SA. 2005. *Open season: an analysis of the pet trade in Medan, North Sumatra, 1997-2001*. Petaling Jaya, Selangor, Malaysia: TRAFFIC Southeast Asia.
- Schulze H. 2007. Conservation database for lorises and pottos. Available at: <http://www.loris-conservation.org>.
- Schulze H, Groves CP. 2004. Asian lorises: taxonomic problems caused by illegal trade. Pp 33-36 in Nadler T, Streicher U, Thang Long H, editors. *Conservation of Primates in Vietnam*. Frankfurt: Frankfurt Zoological Society.
- Streicher U. 2004. Aspects of the ecology and conservation of the pygmy loris *Nycticebus pygmaeus* in Vietnam. Dissertation. Germany: Ludwig-Maximilians Universität.
- Streicher U, Nadler T. 2003. Re-introduction of pygmy lorises in Vietnam. *Reintroduction News* 23: 37-40.
- Supriatna J, Hendras Wahyono E. 2000 *Panduan Lapangan Primata Indonesia*. Jakarta Indonesia: Yayasan Obor Indonesia.
- Supriatna J, Manansang J, Tumbelaka L. 2001. *Conservation assessment and management plan for the primates of Indonesia*. Apple Valley, MN: IUCN/SSC Conservation Breeding Specialist Group.
- van den Bergh GD, de Vos J, Sondaar PY. 2001. The Late Quaternary palaeogeography of mammal evolution in the Indonesian Archipelago. *Palaeogeography, Palaeoclimatology, Palaeoecology* 171: 385-408.
- Webber C, Nekaris KAI. 2004. Survey of primates and other mammals in markets of Indonesia, with an analysis of conditions and health of the animals. *Folia Primatologica* 75: 60.
- Wiek E. 2007. Loris injuries rise with an alarming rate. Available at <http://www.wfft.org/>.
- Zar JH. 1999. *Biostatistical Analysis*. New Jersey: Prentice Hall.
- Zimmermann E, Bearder SK, Doyle GA, Anderson AB. 1988. Variations in vocal patterns of Senegal and South African lesser bushbabies and their implications for taxonomic relationships. *Folia Primatologica* 51: 87-105.

Received: 18 June 2007

Accepted: 2 July 2007