

Trachypithecus delacouri (Primates: Cercopithecidae)

LEE E. HARDING

SciWrite Environmental Sciences Ltd., 2339 Sumpter Drive, Coquitlam, British Columbia V3J 6Y3, Canada; harding@SciWrite.ca

Abstract: *Trachypithecus delacouri* (Osgood, 1932), commonly called Delacour's langur or lutung, is a black and white lutung (leaf monkey) endemic to northern Vietnam. It is a diurnal and primarily arboreal species, but spends more time on the ground than other species of *Trachypithecus*. *T. delacouri* lives among limestone cliffs and consumes the leaves of a broad spectrum of plant species but its choice of food items tends to be based on the chemical makeup of the plant phenophases with protein content the strongest predictor of leaf selection. Territorial, but with overlapping territories, it usually lives in single-male–multifemale groups of 5–30, although 2 adult males may be present. With a declining population perhaps as low as 200 individuals in 17 or fewer isolated populations, it is 1 of the world's most endangered primates.

Key words: Delacour's langur, leaf monkey, lutung, *Trachypithecus francoisi*, *Trachypithecus laotum*, *Trachypithecus leucocephalus*, *Trachypithecus poliocephalus*

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Trachypithecus delacouri (Osgood, 1932) Delacour's Langur

Pithecus delacouri Osgood, 1932:205, and plate X facing p. 208. Type locality “Hoi Xuan, northeastern Annam.” Osgood (1932:197) further described it as “a locality near the coast in Annam and just below the border of Tonkin.” This locality is now in northern Vietnam. *Pithecus* was suppressed by the International Commission on Zoological Nomenclature, Opinion 114 (International Commission on Zoological Nomenclature 1929).

Presbytis (?) *francoisi delacouri*: Ellerman and Morrison-Scott, 1951:211. Name combination.

Semnopithecus delacouri: Brandon-Jones, 1984a:398. Name combination.

Trachypithecus (*Trachypithecus*) *delacouri*: Rowe, 1996:188. First use of current name combination.

Trachypithecus francoisi delacouri: Fooden, 1996:846. Name combination.

CONTEXT AND CONTENT. Order Primates, superfamily Cercopithecoidea, family Cercopithecidae, subfamily Colobinae, and tribe Presbytini. In addition to *Trachypithecus*, this subfamily includes the genera *Colobus*, *Nasalis*, *Ptilocolobus*, *Presbytis*, *Procolobus*, *Pygathrix*, *Rhinopithecus*, *Semnopithecus*, and *Simias*. The genus *Trachypithecus* includes 17, 18, 19, or 20 species in 4 phylogenetic groups: *T. francoisi* group: *T. francoisi*, *T. delacouri*, *T. laotum*, *T. (l.) hatinhensis*, *T. poliocephalus*, *T. (p.) leucocephalus*, and *T. (l. or h.) ebenus*; *T. pileatus* group: *T. pileatus*, *T. geei*, and *T.*

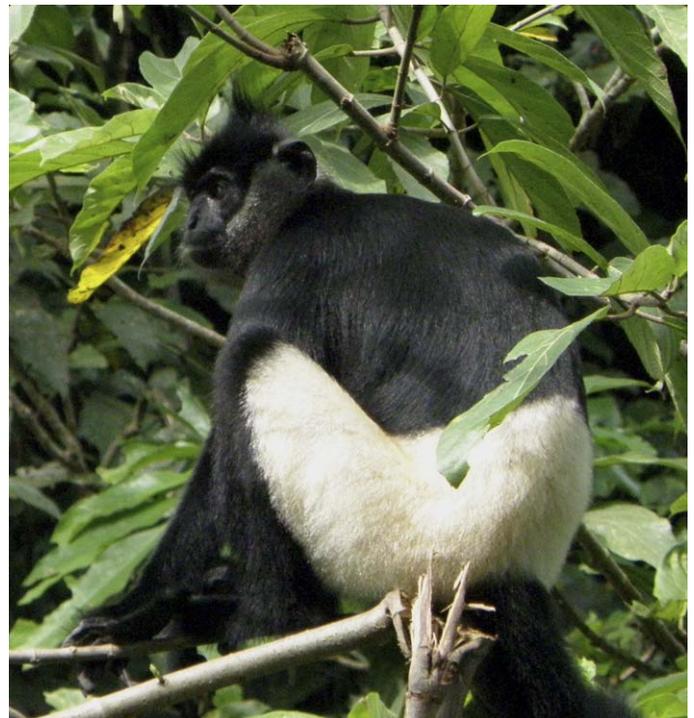


Fig. 1.—An adult *Trachypithecus delacouri* photographed at the Endangered Primate Rescue Center, Vietnam. Photograph by Bui Duc Tien used with permission.

shortridgei; *T. obscurus* group: *T. obscurus*, *T. phayrei*, *T. crepusculus*, and *T. barbei*; and *T. cristatus* group: *T. cristatus*, *T. margarita*, *T. auratus*, *T. mauritius*, and *T. germaini* (Harding 2010). *Trachypithecus* is exclusively South and Southeast Asian except for *T. shortridgei*, *T. phayrei*, *T. poliocephalus leucocephalus*, and *T. francoisi*, which also occur in southern and southeastern China.

NOMENCLATURE NOTES. de Pousargues (1898:319) 1st described *T. francoisi*, François's lutung or langur, as "*Semnopithecus francoisi*." Elliot (1913) placed *T. francoisi* (and some other *Trachypithecus* species) into a subgenus, *Lophopithecus*, as *Pygathrix francoisi*. Pocock (1928) grouped *Semnopithecus* and *Trachypithecus* into *Presbytis* and later (Pocock 1934) separated *Trachypithecus* from *Presbytis* and *Semnopithecus* based on infant color, although his 1939 paper did not mention any of the *francoisi*-group species. Ellerman and Morrison-Scott (1951) placed them, with a query, as subspecies under *Presbytis francoisi* and subsequent authors (e.g., Đào 1977; Khajuria 1955; Lekagul and McNeely 1988; Napier and Napier 1967; Weitzel and Groves 1985) used *Presbytis* as the senior synonym for *Trachypithecus* and *Semnopithecus*. Brandon-Jones (1984a) included *T. delacouri* in the subgenus *Trachypithecus* under *Semnopithecus*, although in a different edition of the same book (Brandon-Jones 1984b) he described 10 species of *Trachypithecus* including *T. delacouri*, as full species under the genus *Trachypithecus*. He later (Brandon-Jones 1996) combined *Trachypithecus* into *Semnopithecus* while continuing to recognize *francoisi*, *delacouri*, and *leucocephalus* as full species. Groves (1989) separated *Trachypithecus* from *Semnopithecus* and considered all *francoisi*-group species to be conspecific with *T. francoisi*, but later (Groves 2001) followed Nadler (1994) in recognizing *T. delacouri*. DNA analysis confirms the species status of *T. delacouri* (Roos 2004; Roos et al. 2007) and the monophyly of *Trachypithecus* vis-à-vis *Semnopithecus* and *Presbytis* (Khajuria 1956; Md. Zain et al. 2008, 2010; Osterholz et al. 2008).

Although some have classified the white-headed lutung as a subspecies of *T. francoisi*, *T. f. leucocephalus* (Ding et al. 2000; Wang et al. 1999), Brandon-Jones et al. (2004) referred it to a subspecies of Cat Ba or golden-headed lutung, *T. poliocephalus*: *T. p. leucocephalus*. Since Roos et al. (2007) provided further evidence of this, *T. p. leucocephalus* is used herein. The status of *T. ebenus* is unclear: phylogenetically, it clusters with *T. (laotum) hatinhensis*, Hatinh or black lutung, which itself may be a full species or a subspecies of or conspecific with *T. laotum*, Lao lutung (Roos et al. 2007).

Trachypithecus is from the Greek *trachys*, rough, and *pithekos*, ape. The species is named for the collector of the type specimen, the prominent French ornithologist, Jean Delacour (Osgood 1932). Its name is vooc mong trang in Vietnamese.

Groves (2001) and others used the common name leaf monkey for *Presbytis* species and langur for *Trachypithecus* species; however, langur is a Hindi word applied to species of *Semnopithecus* of India and Sri Lanka, a genus that no longer includes *Trachypithecus*; hence, the Malay word lutung is more appropriate for *Trachypithecus* as surili is for *Presbytis* (Bernstein 1968; Brotoisworo 1979; Geissmann et al. 2004; Weitzel and Groves 1985). Leaf monkey remains a useful term for all 3 genera (Pocock 1939).

DIAGNOSIS

"Allied to *P.[T.] francoisi* and *P.[T.] laotum*, but differing strikingly from both in having the rump and outer side of the thighs pure creamy white; white markings on head more restricted than in *laotum*, but more extensive than in *francoisi*. Fur soft and thick; mantle not highly developed; tail heavily haired throughout, individual hairs reaching a length of about 50 mm" (Osgood 1932:205). *Trachypithecus delacouri* (Figs. 1 and 2) is the largest of the "limestone lutungs," total length, 570–735 mm; length of tail, 724–970 mm; length of ear, 40–45 mm; and length of foot, 150–184 mm (see Groves [2001] for comparative measurements). In discriminant analysis of published external measurements of all *francoisi*-group species, *T. delacouri* is separated from all except for a slight overlap with 1 specimen of *T. francoisi* (François's langur—Groves 2007). The tail is thicker (about 10 mm) at the proximal end than other *Trachypithecus* species and more thickly furred (Nadler et al. 2003), but shorter, relative to body length, than in the other *francoisi*-group species (calculations based on measurements by Groves [2001]). Newborns' yellow-orange pelage is brighter than in *T. francoisi* and *T. laotum*; juveniles have a tassel at the end of the tail that is lost at age 3, when the tail takes the adult appearance (Nadler et al. 2003).

GENERAL CHARACTERS

The crest of *Trachypithecus delacouri* is distinctively high and thin (relative to other *francoisi* group species), very upright anteriorly but sloping forward posteriorly, and the ears stand out noticeably from the head (Fig. 1; Groves 2007). Females have an area of unpigmented skin and a pale patch of pubic hair in front of the callosities; the latter is common to all *francoisi* group species (Nadler 2010a; Nadler et al. 2003).

Nadler et al. (2003) gave the following average measurements: length of head and body—males 570–620 mm, average 595 mm ($n = 5$), females 570–590 mm, average 580 mm ($n = 2$); length of tail—males 820–880 mm, females 840–860 mm, average 855 mm ($n = 2$); and body mass—males 7.5–10.5 kg, average 8.6 kg ($n = 9$), females 6.2–9.2 kg, average 7.8 kg ($n = 5$).



Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of the type specimen of *Trachypithecus delacouri*, an adult male, Natural History Museum catalogue reference no. 32.4.19 (Natural History Museum, London, United Kingdom) from type locality Hoi Xuan. Maximum skull length (premaxillary to supraoccipital crest) is 102 mm. Photograph by Phil Hurst, Natural History Museum, used with permission.

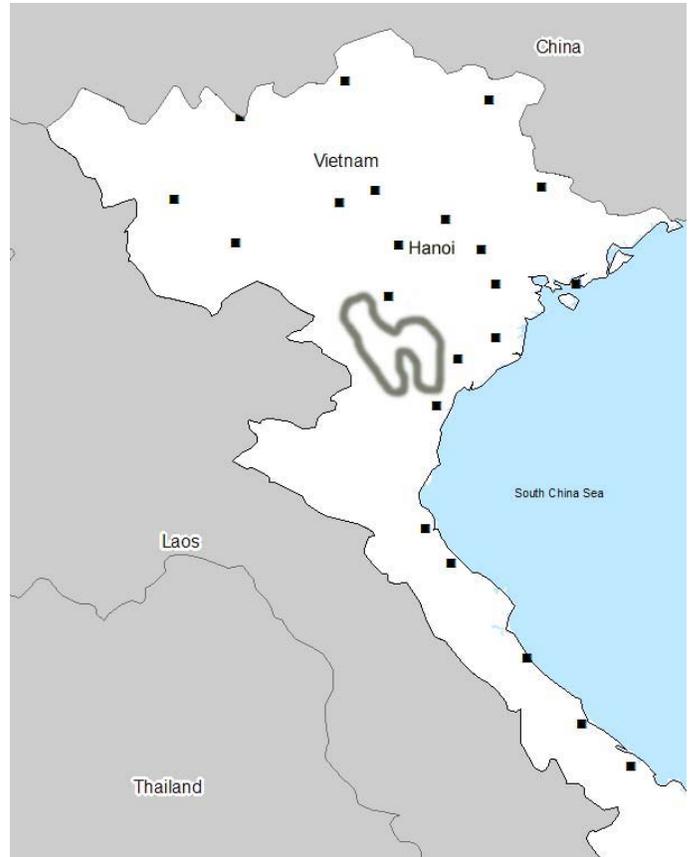


Fig. 3.—Distribution of *Trachypithecus delacouri* is restricted to the Annam Mountains, south of Hanoi, Vietnam (adapted from International Union for Conservation of Nature and Natural Resources, www.iucnredlist.org, accessed 18 January 2009).

On the basis of taxonomic, ecological, and geological data, Đào (1989) theorized that the ancestral form of the *T. francoisi* group (hence of *T. delacouri*) was mainly black like *T. laotum hatinhensis* (Hatinh lutung) and located in the limestone hilly regions of northern Annam (Vietnam). At the end of the upper Pleistocene, the range expanded northeastward and the species began diverging at the beginning of the Recent epoch (about 9,000 years ago). The trend of color change was the progressive whitening of the black body adapted to bare limestone substrates, presumably to cryptically break up the formerly black body outline.

DISTRIBUTION

Trachypithecus delacouri occurs in only Ninh Binh, Ha Nam, Hoa Binh, Thanh Hoa, and Ha Tay provinces of Vietnam (Fig. 3; Nadler 2004). It can readily be seen in Van Long Nature Reserve, Ninh Binh Province (Fig. 4). It is possible that *T. delacouri* may occur in Laos (Deuve 1972 [not seen, cited in Duckworth et al. 2010]), since "... the extensive karsts in NE Lao closest to those in [Vietnam] where [*T. delacouri*] lives have never been surveyed ..."



Fig. 4.—Limestone habitat of *Trachypithecus delacouri* in Van Long Nature Reserve, Vietnam. Individuals are often seen on the cliffs at right. Photograph by Lee Harding.

(J. W. Duckworth, Wildlife Conservation Society, Lao Program, in litt.).

FOSSIL RECORD

Trachypithecus fossils have been found at Chaingzauk, Myanmar (Ogino et al., in press). Harding (2010) gives a general account of fossil evidence and forces driving evolution of Colobini and the divergence of *Semnopithecus*, *Presbytis*, and *Trachypithecus* in Southeast Asia. The 1st unequivocal colobine fossils, differentiated postcranially from the cercopithecoid-like *Victoriapithecus* and adapted for a more arboreal habit, were found in Kenya dated to 9.8–9.9 million years ago (Nakatsukasa et al. 2010). Unidentified Pleistocene *Trachypithecus* fossils nearly identical to extant *Trachypithecus francoisi* and *T. phayrei* (Phayre's leaf-monkey) have been found in Yunnan, southern China (Jablonski 2002). Mid- to late Pleistocene *Trachypithecus* fossils (identified as “*Trachypithecus* or *Presbytis*”, but the latter is unlikely, given its known past and current distribution) have been found at Tam Hang in northeastern Laos (Bacon et al., 2008:279; Bacon et al., in press). Late Pleistocene *Trachypithecus* fossils were reported from Lang Trang in Vietnam (Long et al. 1996 [not seen, cited in Tougard and Montuire 2006]) and from Thum Wiman Nakin in Thailand, the latter dated to 169 ± 11 thousand years ago (Tougaard 2001; Tougaard and Montuire 2006).

FORM AND FUNCTION

Form.—Harding (2010) describes form and function of *Trachypithecus* relative to other Colobini. The dental formula of *Trachypithecus delacouri* is $i\ 2/2, c\ 1/1, p\ 2/2, m\ 3/3$, total 32 (Ankel-Simons 2000). Molars of *T. delacouri* (and *T. hatinhensis*) are larger than 2 approximately

sympatric species of *Pygathrix* (duoc langurs). The median ratio of molar area to vault length was 56.3, compared to 47.1 for the *Pygathrix*. The 2 *Trachypithecus* species also had larger mandibles and deeper mandibular corpora and symphyses than the 2 *Pygathrix* species, suggesting an ability to masticate tougher leaves (Wright et al. 2008a).

As with other colobines, *Trachypithecus* is distinguished from its cercopithecine relatives by an enlarged and sacculated, ruminant-like stomach and large salivary glands that neutralize stomach acid, adaptations to a folivorous diet (Strasser and Delson 1987). *Trachypithecus* stomachs have 3 large chambers. Unlike the 4-chamber arrangement of *Pygathrix*, *Procolobus*, *Rhinopithecus*, and *Nasalis*, it lacks a well-developed presacculus (Caton 1998); however, it has an enlarged colic chamber, similar to that in cercopithecines and apes, that may act as a secondary fermentation chamber (Caton 1999). There is no sternal gland, as reported for some primates (cf. Wislocki and Schultz 1925) and no other specialized scent glands have been reported (Napier and Napier 1985).

Trachypithecus delacouri, like other lutungs, normally has a 2-lobed, hemo-monochorial type of placenta in which only 1 trophoblastic layer separates the villous structures from the maternal intervillous blood (Benirschke 2008). The placenta structure is similar to that of rhesus monkey (*Macaca mulatta*), common chimpanzee (*Pan troglodytes*), and human (*Homo sapiens*). In 2 specimens of *T. delacouri*, placental masses were 145 and 82 g and umbilical cord lengths were 26 and 21 cm (Benirschke 2008).

Trachypithecus species (unfortunately, *T. delacouri* was not included in the analysis) have relatively short legs relative to arms, compared to species of *Presbytis*; and compared to several *Pygathrix* species, *Trachypithecus* species have shorter forearms relative to upper arms and shorter arms relative to legs (Washburn 1944). *T. delacouri* has a mean intermembral index (humerus + radius in percent of femur + tibia) of 76.5 (Workman 2010b), which is about the same as that of *Presbytis* and other lutungs of the *francoisi* group, but lower than more arboreal *Trachypithecus* species (Huang and Li 2005; Washburn 1944). Even another *francoisi*-group species, *T. hatinhensis*, has a greater intermembral index: mean 82.2, range 77.1–87.0, $n = 5$ adult females (unpublished data of T. Nadler, cited by Schempp et al. [2008]).

Function.—Caton (1999) defined the *Trachypithecus* digestive strategy as gastro-colic fermentation, unlike that of some other forestomach fermenters in which the hindgut fermentation is of secondary importance. Foregut fermentation of seed coats releases rich nutrients from the cotyledons and was probably an ancestral preadaptation to the more highly specialized folivory of langurs and lutungs (Benefit 2000). For *T. delacouri* to consume a diet of mostly leaves (Workman 2010a), its digestive system must be able to break down the structural polysaccharides by microbial fermentation (cf. Caton 1999).

Larger molars and larger, deeper mandibles, combined with differences in stomach morphology noted above, enable

2 *Pygathrix* species to chew more slowly than *T. delacouri* to extract similar food value (Wright et al. 2008a, 2008b). By chewing much more rapidly for about the same amount of time, *T. delacouri* relies more on dental mastication and oral comminution of foods before exposure to stomach microbes in its tripartite stomach. This enables *T. delacouri* to handle tougher foods and to grind them finer before swallowing.

Byron and Covert (2004) found that >90% of positional and locomotor movements of captive *T. delacouri* are quadrupedal walking, running, and bounding on tops of arboreal supports, whereas <10% use forelimb suspension. In the wild, *T. delacouri* spends nearly 80% of its time on rocks with sitting dominating stationary postures (95%); it walks or runs across cliff faces and associated forest patches quadrupedally more than twice as often (67%) as climbing (33%), and leaping only 6% of the time (Workman 2010b).

Trachypithecus delacouri in captivity uses forelimb suspensory movements relatively less than the 2 more strictly arboreal *Pygathrix* species studied (Stevens et al. 2008; Workman and Covert 2005). The young use more suspensory locomotion than do adults (Workman and Covert 2005). In the wild, suspensory locomotion is infrequent (0.8% of bouts observed) and includes bimanual and unimanual swings, bimanual and unimanual drops, and bimanual pullups (Workman 2010b). Accordingly, the term “semibrachiator,” often applied to colobines including *Trachypithecus* (Harding 2010), does not describe locomotion of *T. delacouri*.

Trachypithecus delacouri exhibits more variability in tail posture than the other langur species at the Endangered Primate Rescue Center, Vietnam, often arching its tail higher in a downward arc similar to that of *Pygathrix*, but in contrast to that of *T. laotum hatinhensis*, which arches its tail in an upward arc and a sharper angle (Stevens et al. 2008). *T. delacouri* also moves at significantly greater velocities in all locomotor events than *T. l. hatinhensis* and 2 species of *Pygathrix*, which is associated with tail position. When stationary, *T. delacouri* sits more often than does *T. l. hatinhensis*, which prefers prone positions; and *T. delacouri* leaps and bounds more often than *T. l. hatinhensis*, whereas both species use less suspensory locomotion than *Pygathrix* (Stevens et al. 2008). *T. delacouri* also incorporates sweeping motions of its tail to assist with balance when negotiating steep limestone karst formations. Hence, the shorter, thicker tail is likely an adaptation to karst habitat.

There has been much debate whether the “limestone langurs,” the *T. francoisi* group that includes *T. delacouri*, are somehow limestone-dependent (cf. Nadler et al. 2003). Workman (2010b:108) noted that the morphology of *T. delacouri*, for example, its intermembral index, “... does not suggest terrestriality or an evolutionary adaptation for limestone karst;” this, together with other evidence, such as its diet being composed of plants that are not limestone-dependent, led her to conclude that “... it seems probable

that limestone langurs occupy limestone karst habitat primarily because they have been forced exclusively into it as a refuge from deforestation and conversion of forested valleys between karsts into rice agriculture.”

ONTOGENY AND REPRODUCTION

Ontogeny.—Young are precocial, born with eyes open, well furred, and with strong forearms capable of clinging to the mother. The orange skin of neonates of *Trachypithecus delacouri* changes color within days of birth to black as in adults, whereas the orange fur changes slowly. At about 4 months the body pelage changes to black and parts of the head and flanks become a washed dark gray, essentially completing the transition to the adult black and white by about 3 years (Nadler et al. 2003). Infants are weaned at 19–21 months in wild populations of *T. francoisi* (Zhao et al. 2008) and probably at a similar age in *T. delacouri*. Maternal rejection facilitated infant independence in the early stages of infant development in *T. francoisi*, and mothers stopped investing in their infants when they resumed estrus (Zhao et al. 2008). However, the weaning age of this wild population was longer than that of captives, possibly as a result of the nutritional differences (a consequence of habitat fragmentation) between wild and captive populations (Zhao et al. 2008).

Males of *T. delacouri* reach reproductive maturity at about 5 years of age and females at 4 years (Nadler et al. 2003). Workman (2010b) defined age classes based on visible size and pelage differences as follows: orange infants 0–4 months, juveniles 4–36 months, subadult females 36–48 months, subadult males 36–60 months, adult females (full somatic growth 7.5 kg) 48+ months, and adult males (full somatic growth 8.5 kg) 60+ months. Life span is unknown, but 2 males acquired by the Endangered Primate Rescue Center in 1993 and estimated to be 3 years old at that time were still alive at the end of 2009 and a female acquired as an adult in 1994 died in November, 2009; hence, life span is at least 20 years for males and 19 for females (age data from Nadler [2010b]).

Reproduction.—Reproductive parameters of *Trachypithecus delacouri* are similar to those of other *Trachypithecus* species and few differences among the *francoisi*-group species have been reported (Jin et al. 2009). For all *francoisi*-group species, the gestation period is 170–200 days, the estrous cycle is 24 ± 4 days, and the interbirth interval is about 17–25 months, for example, 19.1 ± 2.2 months for *T. francoisi* and 24.8 ± 1.5 months for *T. hatinhensis* (Nadler et al. 2003 and references therein). In the closely related *T. poliocephalus leucocephalus*, the average age at 1st birth for female langurs was 5–6 years ($n = 5$), the interbirth interval was 23.2 ± 5.2 months (median = 24.5 months, $n = 27$), and infants were weaned at 19–21 months of age (Jin et al. 2009). In *T. francoisi*, an interbirth interval of 8.0–9.5 months can occur if an infant does not survive (Gibson and Chu 1992).

Litter size is usually 1, but twins are born occasionally (Hayssen et al. 1993).

ECOLOGY

Population characteristics.—*Trachypithecus delacouri* occurs in 17 or fewer isolated wild populations (see “Conservation” below) that may total no more than 200 individuals (Workman 2010b). Natural population density cannot be estimated reliably in such fragmented, remnant populations, but at Van Long Nature Reserve it was 26.4 individuals/km² in 2008 (Workman 2010b). For the closely related *T. poliocephalus leucocephalus*, densities of 17–20 individuals/km² have been reported, but only 0.08–6.94 individuals/km² in heavily fragmented habitat (Huang et al. 1998; Li et al. 2003). These meager densities contrast with those of other *Trachypithecus* species, for example, island populations of *T. obscurus* (dusky leaf-monkey) of 72 individuals/km², and *T. cristatus* (silvered lutung) of 150 individuals/km² (cf. Harcourt 2002).

Space use.—*Trachypithecus delacouri* is restricted to karst forest in limestone mountains. Mean daily temperature during 2007–2008 at the Van Long Nature Reserve, the location of the largest extant population, with a maximum elevation of 328 m above sea level, was 22.9°C (range 8.8–36.9°C) and total rainfall over 12 consecutive months was 127.56 cm (Workman 2010b). Plant species richness there is 145 species from 63 families, of which 30.4% were trees, 29.7% climbers, 25.4% herbs, 13.1% shrubs, and 1.4% grasses (Workman 2010b).

Groups will sleep in the caves of the limestone cliffs, using each cave for several nights before moving to another; they will also retreat into caves when threatened (Nadler 1996). They may use from 3 to 5 caves in their home range, typically arriving at the caves after dark and leaving before sunrise (Nadler 1996). However, unlike *T. francoisi* (Zhou and Huang 2010), *T. delacouri* does not seem to actively seek crevices or caves, but to use them if available close to their feeding sites; otherwise, they sleep on exposed rock surfaces at all elevations (Wang et al. 2011; Workman 2010b).

Nguyen and Le (2008a) studied 2 focal groups of 8–16 and 7 individuals in the same area before and after a dynamite blast as part of a limestone quarrying operation at the edge of the Van Long Nature Reserve. The explosion, some 400 m from the groups’ habitat, apparently caused the 1st group to abandon their home range, which was subsequently occupied by the 2nd group. The 1st group had occupied 36 ha with daily length of travel of 340–1,458 m. After the explosion and the disappearance of the 1st focal group, the 2nd focal group established a home range of 46 ha with daily travel from 420 to 1,530 m. These differences were statistically significant; because there was no correlation between the 2 groups’ day range length with weather condition parameters including temperature,

humidity, wind speed, and wind chill, and no correlation with food availability, the results suggested a strong impact of the explosion on the 2nd group’s home range and daily travel, following the displacement of the 1st group. In a later study (Workman 2010b), average daily path length was 476 m (range 230–978 m, $n = 16$ days).

Behavior of captive *T. delacouri* at the Endangered Primate Rescue Center demonstrates the importance of temperature in regulating space use (Nadler et al. 2007). The Endangered Primate Rescue Center provides isolated sleeping boxes in the enclosures of its *Trachypithecus* species. At temperatures below 15°C, *T. delacouri* used the boxes overnight and when temperatures were below 8–10°C, they also stayed inside the box during the day and exited only for feeding.

Diet.—Although *Trachypithecus delacouri* prefers some tree species associated with limestone, they feed on a much broader spectrum of tree species and readily use other vegetation types and plant communities in the same geographical region (Nadler and Long 2001). *T. delacouri* is highly folivorous, eating 78% foliage annually: 59.3% young leaves and leaf buds, 20.4% mature leaves, 9.2% unripe fruit, 5.1% flowers and flower buds, 0.6% seeds, 0.3% stems, 0.1% ripe fruit, and 5% unclassified items (Workman and Dung 2009). Young leaves dominate the diet with minor monthly, seasonal, and annual variations (Workman 2010a). In a 14-month study of *T. delacouri* in the Van Long Nature Reserve selected leaves had higher protein : fiber ratios than leaves that were present but not selected; leaves eaten and not eaten were no different in absolute amounts of protein, fiber, total phenolics, tannins, water, or ash (Workman 2010a; Workman and Dung 2009). However, feeding samples from the 4 most frequently consumed species contained lower amounts of tannins and total phenolics than the less frequently consumed foods, and higher protein : fiber ratios (Workman 2010a; Workman and Dung 2009). Although the protein content of eaten leaves averaged only 12% of dry matter, this does not appear to be limiting because the population increased during the study (Workman 2010a).

Despite distinct wet and dry seasons, over the study period, seasonal variation in plant part consumption was slight (Workman 2010a). *T. delacouri* ate 42 of 145 available species, and it concentrated on a subset of this number. The diet was composed mainly (60%) of 5 plant species; 16 species comprised more than 93%. More than one-half of the diet came from climbing vines. *T. delacouri* is among the most highly folivorous of studied colobines and, along with *T. p. leucocephalus*, the most folivorous of the Asian lutungs (Workman 2010a).

In captivity, *T. delacouri* obtains about 60% of its requirements for water through food, which is provided as freshly cut leaves, and about 40% through active drinking (Kullik 2010). At the Endangered Primate Rescue Center, the total water consumption was correlated with the air

temperature, and increased from 0.07 ml/g body weight at 24°C air temperature to 0.18 ml/g body weight at 32°C (Kullik 2010). In the wild, *T. delacouri* obtains water where it collects in holes and depressions in limestone, and from nearby permanent water bodies (Kullik 2010; Workman 2010b).

Diseases and parasites.—No instances of epizootics have been described for *Trachypithecus delacouri* (or any colobine); few instances of grossly diseased animals have been seen in the wild and disease is not known to have limited langur or lutung populations (Davies and Oates 2000; Yeager and Kool 2000). Pinworms such as *Coloboenterobius* are common in *Trachypithecus* species (Page and Charleston 2007).

Some *T. delacouri* seized from poachers and held at the Endangered Primate Rescue Center, especially young ones and those that had earlier received antibiotic treatment, developed dermatophytes, a skin disease (Streicher 2001). Digestive system problems were common, including gastritis, duodenitis, jejunitis, and several forms of ileus. Pneumonia also was common, although the causative agents were not reported. Nervous system disorders were apparent, but the need to preserve the heads for museum collections prevented autopsy. Some of these animals also had liver and other organ lesions, possibly resulting from a pesticide on lychee leaves that the poachers or rangers fed the lutungs. All animals were heavily infested with endoparasites including strongylids and *Trichuris*; filarids (Nematoda: Filarioidea) were found in 2 animals upon postmortem examination. Amoebae were never diagnosed. Ectoparasites (mainly biting lice) were rare (Streicher 2001). In fecal samples from 14 captive individuals, 4 semiwild individuals (in a 2-ha enclosure), and 2 groups of wild *T. delacouri*, Do (2009) found 6 nematode species (*Trichuris*, *Trichostrongylus*, *Oesophagostomum*, *Strongyloides stercoralis*, *Ancylostoma*, and *Physaloptera*); the most prevalent were *Trichuris* and *Oesophagostomum*. Only *Physaloptera* was found in the free-ranging animals, supporting the theory that small, isolated host populations harbor fewer parasite species (Do 2009).

Interspecific interactions.—*Trachypithecus delacouri* is rarely, if ever, sympatric with other colobines. In a general sense, its range overlaps with that of the gray lutung (*T. crepusculus*), which also occurs in limestone forest, although it is rare in Vietnam and has not been reported within habitats occupied by *T. delacouri* (Nadler et al. 2007). Brandon-Jones (1996) indicated that reports of sympatry with *T. laotum hatinhensis* were in error (it occurs well to the south). *T. delacouri* is generally sympatric with the northern white-cheeked gibbon (*Nomascus leucogenys*), which, however, does not occur in the same habitat; 2 species of loris: pygmy slow loris (*Nycticebus pygmaeus*) and Bengal slow loris (*N. bengalensis*); and 3 species of macaque: *Macaca mulatta*, Assam macaque (*M. assamensis*), and stump-tailed macaque (*M. arctoides*—Nadler et al. 2007).

Asian arboreal colobines appear to suffer low predation rates (Davies and Oates 2000). I observed Bonelli's eagles (*Hieraaetus fasciatus*) circling above lutung habitat in Van Long Nature Reserve and crested serpent-eagles (*Spilornis cheela*) and long-legged buzzards (*Buteo rufinus*) were seen nearby. Terrestrial predators that could take adult *T. delacouri* and that occur in Cuc Phuong National Park and nearby mountains include the dhole (*Cuon alpinus*), racoon dog (*Nyctereutes procyonoides*), tiger (*Panthera tigris*), leopard (*Panthera pardus*), clouded leopard (*Neofelis nebulosa*), Asian golden cat (*Catopuma temminckii*), leopard cat (*Prionailurus bengalensis*), fishing cat (*Prionailurus viverrinus*—<http://www.vqgcucphuong.com.vn/>, accessed 26 April 2009), and large snakes. A variety of smaller predators including genets, civets, palm civets, mongooses, domestic dogs, and the binturong (*Arctictis binturong*) that occur in the area (Francis 2008) could take infants (cf. Streck 2002). Although large snakes and small felids can be found at all heights up to the canopy, they are probably less agile than *T. delacouri*.

The habit of *T. delacouri* sleeping in caves probably serves both antipredator and thermoregulatory functions; unfortunately, it facilitates trapping and capture by humans, long the main predator of this species (Adler 1991; Nadler et al. 2007).

BEHAVIOR

Trachypithecus delacouri has a variable social organization, including multimale–multifemale groups, 1-male groups, all-male bands, and solitary males (Nguyen and Le 2008b). Nadler et al. (2007) summarized historic reports of group sizes of 20–30 in Cuc Phuong National Park, as well as observations of singles. Groups of 2–20 were documented at other locations. Groups of 20–30 also had been reported in Pu Long Nature Reserve 20 years previously, but since about 2000 only groups of 5–7 have been seen there and the total number reduced (Nadler et al. 2007). Workman (2010b) reported mixed-gender group sizes of 4–16, plus a bachelor group of 2–4 males and 1 solo male at Van Long; of 7 mixed-gender groups, 5 had a single adult male and 2 had 2 adult males.

Observed intragroup interactions consist of female–female and male–male aggression, adult female–juvenile male aggression, infant-sharing between adult females, infant-sharing refusal, male–female copulations, and female–female and female–juvenile mounting (Nguyen and Le 2008b).

Males often sit on prominent rocks, apparently watching for danger and watching other groups if present, and they perform sentry duties along undefined group borders (Workman 2010b). During intergroup encounters, groups of *T. delacouri* defend territories (although these often overlap—Workman 2010b) with adult males playing the key role—females rarely—in intergroup conflicts (Nguyen and

Le 2008b). Males exhibit escalating levels of responses to encounters with other groups: loud calls that probably function to maintain group separation, male displays, and physical contact such as fighting and chasing (Nguyen and Le 2008b). Upon sighting a neighboring group, males exhibit a “bounding display,” jumping quadrupedally across rocks and emitting a “hoot” sound; rarely, a chase ensues within the overlap zone of adjacent territories (Workman 2010b:144).

Trachypithecus delacouri is diurnal and mainly terrestrial, although it spends some time in trees where it uses suspensory locomotion (Huang and Li 2005; Workman 2010a). Groups of *T. delacouri* display apparently thermoregulatory behavior by resting on bare rocks during winter and resting or playing in rocky, cavelike ledges in summer that were cooler than surrounding habitat (Workman 2010b).

Male infanticide has not been reported in *T. delacouri*. Although infanticide following male replacement was not directly observed in *T. poliocephalus leucocephalus* at the Fusui Reserve, 2 juveniles and an infant disappeared after serious fights during male takeovers (Li and Rogers 2004). They later observed male infanticide in *T. p. leucocephalus*, but it is rare, occurring only “once every several years” (Zhaoyuan Li, Faculty of Conservation Biology, Southwest China Forestry College, Kunming, in litt.).

Aside from the hoots mentioned above, descriptions of the calls of *T. delacouri* have not been published, but they make “loud calls” similar to those of other *Trachypithecus* species, particularly at dawn, and a variety of other calls. Stünkel (2003) found that the loud calls of 8 *Trachypithecus* species, including 2 in the *francoisi* group (*T. francoisi* and *T. laotum hatinhensis*), could be distinguished from each other. Individuals also communicate nonvocally with each other in social play, grooming, and light fighting.

Resting dominates the daily activity budget at 61% of the time, whereas feeding accounts for 29%, socializing 6% and traveling 4%, with relatively minor seasonal variations (Workman 2010b). Most socializing consists of grooming: females groom other females most often, and they groom males, subadults, and infants less often; males rarely or never groom females, but will groom each other when 2 are present (Workman 2010b).

GENETICS

Diploid chromosome number (2n) is 44. Harding (2010) summarizes karyological derivation within *Trachypithecus* and in relation to other Colobini.

From mitochondrial cytochrome-*b* gene sequences, Roos et al. (2007) concluded that *Trachypithecus delacouri* clearly separated from *T. francoisi* and *T. poliocephalus* (containing *T. p. poliocephalus* and *T. p. leucocephalus*) on one hand, and from *T. laotum* (containing *T. l. laotum* and *T. l. hatinhensis*) on the other; and that all of these *francoisi*-

group species, together with *T. crepusculus*, separated from the other *Trachypithecus* species.

Likewise, Osterholz et al. (2008), analyzing mitochondrial and Y chromosomal sequence data, confirmed the validity of *T. delacouri*, *T. laotum*, *T. poliocephalus*, and *T. francoisi* as full species within the *francoisi* group (unfortunately, *T. l. hatinhensis* and *T. p. leucocephalus* were not included in this analysis). Genetic distinctiveness among the 17 extant populations of *T. delacouri* has not been assessed.

Except for possible ancestral hybridization that may have given rise to a disparity between nuclear and mitochondrial DNA affinities among *Semnopithecus*, *Presbytis*, and *Trachypithecus* (Choudhury 2008; Karanth et al. 2008; Osterholz et al. 2008; Ting et al. 2008), no modern wild interspecific hybrids involving *T. delacouri* are known. However, Schempp et al. (2008) documented a hybrid between a red-shanked douc langur (*Pygathrix nemaeus*) and a *Trachypithecus laotum hatinhensis* and hybrids between other species of *Trachypithecus* are known (e.g., Choudhury 2008).

CONSERVATION

The International Union for Conservation of Nature and Natural Resources (2008) lists *Trachypithecus delacouri* as “Critically Endangered.” It is 1 of the world’s 25 most endangered primates (Mittermeier et al. 2009). Except for 3 *Trachypithecus* species on the *Convention on International Trade in Endangered Species of Wild Fauna and Flora Appendix I* (Convention on International Trade in Endangered Species of Wild Fauna and Flora 2010—Gee’s golden langur [*T. geei*], capped langur [*T. pileatus*], and Shortridge’s langur [*T. shortridgei*]), all others are included on *Appendix II*. The wild population of *T. delacouri* declined by 20% in the 5 years prior to 2004 and may have numbered no more than 200–250 at that time (Nadler 1996; Mittermeier et al. 2007). Since surveys began in 1994, *T. delacouri* was extirpated from 3 areas, leaving 19 isolated populations remaining at the end of 2006 (Mittermeier et al. 2007). During 2009, the size of the 4 monitored populations other than that at Van Long showed a “dramatic decline” (Nadler 2010b). By the end of 2009, 2 more of the populations (1 of which was in Ngoc Son Nature Reserve—Mittermeier et al. 2009) had been extirpated leaving 17, of which only the Van Long population may be viable in the long term (Nadler 2010b). At the end of 2009 the Endangered Primate Rescue Center had an additional 19 individuals—the only ones in captivity—of which 13 were born there (Nadler 2010b). The current average group size of 5 or 6 in smaller populations and 4–16 at Van Long, compared to normal group sizes of 20–30 (see “Population characteristics” above) is further evidence for population density declines and social system collapse in these isolated, fragmented, and still-hunted populations.

In 2007, 4 protected areas (Cuc Phuong National Park, Pu Luong Nature Reserve, Hoa Lu Cultural and Historical Site, and the Van Long Nature Reserve) harbored about 40% of the remaining *T. delacouri*; the other 60% occurred in isolated populations, “the loss of [which] is foreseeable without management, strict regulations and law enforcement” (Mittermeier et al. 2007:14). The largest remaining population of 68–70 animals in the Van Long Nature Reserve has approximately doubled since it was established in 2001 (Workman 2010b). Even with protection and the support of local villagers who recognize the benefits of ecotourism, this population is threatened by limestone quarrying with dynamite as described above; villagers’ collection of plants, wood, and stones; and habitat degradation by illegal grazing of domestic goats (Nadler et al. 2003; Nguyen and Le 2008a; Workman 2010b). Other remnant populations face these threats as well as habitat loss, illegal logging, and genetic degeneration due to inbreeding because of the fragmentation and isolation of small populations (Nadler et al. 2003).

Endangered primates are still hunted and trapped in Vietnam and the biodiversity protection law affords little protection for populations (Mittermeier et al. 2007; Nadler et al. 2007). A recent review of Vietnam’s wildlife trade policies (Ha et al. 2009) found that although the trade laws are adequate, conflicting laws and policies and poor enforcement lessen their effectiveness. Regular monitoring, improved integration of laws and policies, and better enforcement are needed.

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