

## *Nomascus leucogenys* (Primates: Hylobatidae)

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**Abstract:** *Nomascus leucogenys* (Ogilby, 1840) is a crested gibbon of northern Vietnam, northern Laos, and southern China. Males are black with white cheeks and females are a rich buff color with a dark brown sagittal crest. It is among the largest of hylobatids (except siamang) and has unusually long arms for a hylobatid. Its diet includes fruits, leaves, small animals, and flowers. It is territorial and lives with stable pair-bonds in nuclear families consisting of a male and female and their offspring. It is “Critically Endangered,” possibly extirpated from China with only isolated populations remaining in Laos and Vietnam.

**Key words:** gibbons, Laos, *Nomascus concolor*, *Nomascus gabriellae*, *Nomascus nasutus*, *Nomascus siki*, primates, Vietnam

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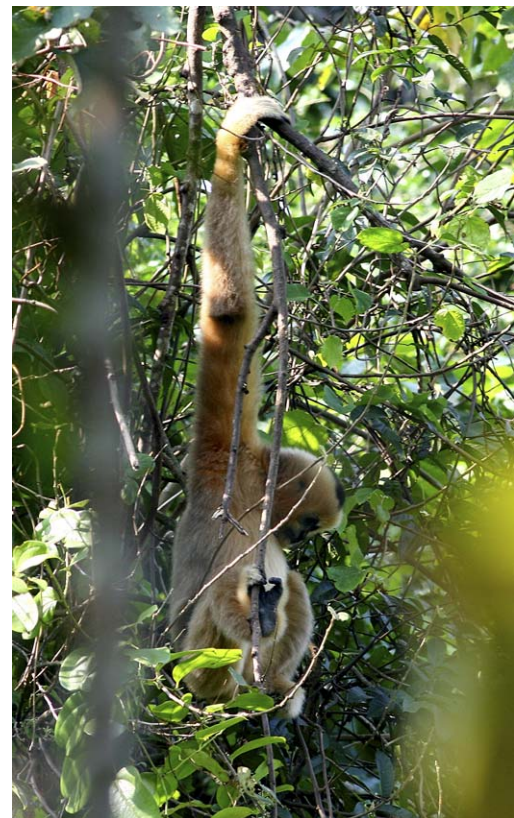
### *Nomascus* Miller, 1933

*Simia*: Harlan, 1827:231. Part, not *Simia* Schreber, 1775.  
*Hylobates*: Ogilby, 1840:20. Part, not *Hylobates* Illiger, 1811.  
*Nomascus* Miller, 1933:159. Type species *Hylobates leucogenys* Ogilby, 1840, by original designation; described as a subgenus of *Hylobates* Illiger, 1811.

CONTEXT AND CONTENT. Order Primates, suborder Haplorhini, infraorder Simiiformes, superfamily Hominoidea, family Hylobatidae. Hylobatidae includes 4 genera: *Hylobates* with 6 or more species (*agilis*, *klossii*, *lar*, *moloch*, *muelleri*, and *pileatus*—Whittaker et al. 2007); the perhaps monophyletic genera *Symphalangus* and *Hoolock*; and *Nomascus*. *Nomascus* is distributed parapatrically in China, Myanmar, Vietnam, Laos, and Cambodia. Within *Nomascus* 6 species are currently recognized (Chan et al. 2008; Geissmann 2007a; Monda et al. 2007): *N. concolor*, *N. gabriellae*, *N. hainanus*, *N. leucogenys*, *N. nasutus*, and *N. siki*. A recent analysis of the complete mitochondrial cytochrome-*b* gene from 79 *Nomascus* individuals from known locations, and morphological distinctions, have identified a putative 7th species, *Nomascus annamensis* (Thinh et al. 2010a, 2010b).

The key is adapted from Osgood (1932), Groves (1972, 1984, 2001), and Thinh et al. (2010a); measurements are from Groves (1972, 2001).

1. Males all black; skull narrower than the white-cheeked species, cranial width < 62 mm; females buff or grayish with brown or black crowns ..... 2



**Fig. 1.**—Adult female *Nomascus leucogenys* showing the long arms and opposable, grasping 1st toe. This individual disappeared from the semiwild enclosure of the Endangered Primate Rescue Center in 2008, likely shot by a poacher (Nadler 2008). Photograph by L. Harding at the Endangered Primate Rescue Center, Vietnam.

- Males with white, buff, or ochraceous cheeks; females buff with black crowns and lack dark chests; skull width  $\geq 62.0$  mm ..... 4
2. Males all black; adult females lacking a dark chest patch ..... 3
- Females yellow to fawn-gray with a blackish chest or “breast plate” and a broad, black face ring that is connected on the forehead to the occipital cap, which is creamy to brownish gray and usually 120 mm in length but may be as short as 80 mm; males jet black, dorsal hair silky, 43–52 mm in length; baculum length short, 9.0–9.2 mm; skull length 110.9 mm  $\pm 1.37$  SD, cranial width 61.7  $\pm 2.34$  mm, based on *N. c. concolor*—subspecies *N. c. lu* varies from the type ..... *N. concolor*
3. Male entirely black; female brown-gold with a broad (67 mm), long (300 mm) black crown cap that extends down to cover the shoulders, underside gold, lacking dark chest patch; skull length 110 mm, bizygomatic breadth 78 mm .... *N. nasutus*
- Dorsal hair 35–75 mm and “brittle-appearing,” crown hair “very little elongated;” adult female silvery gray without complete face ring either black or white but with some white hairs on sides of face and chin, with no black on the chest; the crown hair is “strikingly indistinct” and 108 mm long; skull larger (length 102–105 mm) but narrow-skulled compared to *N. concolor* ..... *N. hainanus*
4. Males have white cheeks; females lack the black chest zone and the black lining of face and black crown are not connected; skull broader than all-black species ..... 6
- Males have buff, reddish, or ochraceous cheek patches ..... 5
5. Male cheek hair buff, reddish, or ochraceous and less in extent under the chin than *N. siki*; body hair 37–54 mm in length, black in male and juvenile with silvery hairs intermixed as in *N. leucogenys*, but with a brownish chest contrasting with the black body; female red-gold with little or no pale circumfacial ring and black crown cap shorter (65–89 mm) and narrower than *N. siki* or *N. leucogenys* and pointed in back; body smaller than *N. leucogenys* and *N. siki*, skull length 105.9 mm  $\pm 1.23$  SD, cranial width 62.5  $\pm 1.47$  mm ..... *N. gabriellae*
- Cheek patches in males are deeper orange-gold, in the darker scale of coloration compared to *N. gabriellae*; female coloration like *N. gabriellae* but the black portion of the crown hair tends to be reduced or absent ..... *N. annamensis*
6. Hair coarser than *N. concolor*, dorsal hair 40–70 mm in length mixed with silvery hairs in male, crown very high in male, short in female; white cheek hairs in male reach upper borders of ears and

usually meet under the chin but fail to reach the mouth corners and are marked off from the face by a straight border; female rich creamy orange and lacks black chest, circumfacial hair white, black or brown crown hair 68–121 mm in length; skull broader than all-black species (length 110.1 mm  $\pm 1.40$  SD, cranial width 64.6  $\pm 1.30$  mm) with smaller teeth ..... *N. leucogenys*

Body hair 33–42 mm in length, color as in *N. leucogenys*, white cheek hairs in male reach only half way to the ears but surround the lips and almost meet under the chin; female with black or brown crown indistinguishable externally from *N. leucogenys*; skull (single adult specimen) narrower than most *N. leucogenys* (length 110.0 mm, cranial width 62.0 mm) and a very large M3 (breadth 7.30 mm versus  $\leq 6.8$  mm for other *Nomascus* species); 3 of 4 subadult skulls lacked fontanelle bones (present in other *Nomascus* species) .... *N. siki*

### *Nomascus leucogenys* (Ogilby, 1840) Northern White-cheeked Gibbon

*Hylobates leucogenys* Ogilby, 1840:20. Type locality “Siam,” Thailand; restricted to “northern neighbourhood of Pak Lay on the Mekong,” French Laos by Kloss (1929:125) and amended to “Muang Khi, 18°27'N, 101°46'E” by Fooden (1987:109).

*Hylobates concolor leucogenys*: Pocock, 1927:738. Name combination.

*Hylobates (Nomascus) leucogenys*: Miller, 1933:159. Name combination.

*Hylobates (Nomascus) concolor leucogenys*: Groves, 1972:60. Name combination.

*Nomascus leucogenys*: Geissmann et al., 2000:13. First use of current name combination.

CONTEXT AND CONTENT. As for genus *N. leucogenys* currently has no recognized subspecies because *N. l. siki* is now considered a full species (Thin et al. 2010b, 2011).

NOMENCLATURE NOTES. Harlan (1827:231) 1st described a gibbon, *Simia concolor*, from “Borneo,” but this black, long-haired gibbon could not have been a Bornean species (cf. Jungers 1984; Kloss 1929; Pocock 1927). After seeking but failing to find Harlan’s (1827) specimen, and considering other information related to its provenance, Groves (1972) designated a *Nomascus* specimen collected by J. Delacour and W. Lowe at Chapa, northern Vietnam (Osgood 1932), as the neotype for *S. concolor*.

Meanwhile, Müller’s Bornean gibbon was renamed *Hylobates harlani* by Lesson (1827) and finally *H. mülleri* Martin (1841), changed to *H. muelleri* in accord with the *International Code of Zoological Nomenclature* (International

Commission on Zoological Nomenclature 1999), 4th edition, Article 27, which stipulates that diacritic marks shall not be used in a scientific name. Nevertheless, for a century and a half after Harlan (1827), *H. concolor* continued to be associated with the Borneo gibbons as either a junior or senior synonym for *H. muelleri* (Anderson 1878; Dahlbom 1856; Elliot 1913; Lyon 1911; Martin 1841; Rennie 1838; Schlegel 1837, 1876; Schultz 1973).

Ogilby (1840) had described *H. [N.] leucogenys* and mentioned the possibility that it might be the same as *Hylobates niger* from Tonkin, an evident error for *concolor*. Künckel d'Herculais (1884) described and figured *H. nasutus*, (eastern black crested gibbon), attributing *nasutus* to Milne-Edwards (1867–1874) on the basis of a menagerie animal from Tonkin, probably in the neighborhood of Halong Bay; this name is now applied to the eastern black crested gibbon. Thomas (1892) described *H. hainanus* (Hainan gibbon), after which Matschie (1898), evidently realizing that Harlan (1827) had erred and guessing that his specimen may actually have been from Hainan Island, another large island in the South China Sea north of Borneo, transferred *concolor* to these 2 all-black crested gibbons. Pocock (1927) recognized that gibbons east of the Mekong River in Laos, Vietnam, and China were similar to each other and different from the other hylobatids. He therefore brought them together under the species name *concolor*, with subspecies *concolor* Harlan, *leucogenys* Ogilby, and *gabriellae* Thomas (yellow- or buff-cheeked gibbon). Pocock (1927) followed Matschie (1898) in referring to these as the “concolor group.” Miller (1933) formalized this grouping in a new subgenus *Nomascus* for the crested gibbons, with *H. [N.] leucogenys* Ogilby, 1840, as the type species of the subgenus. However, Schultz (1933) and others did not realize the significance of the transfer of the name *concolor* and continued to use *concolor* for Bornean hylobatids. Delacour (1951) described another pale-cheeked subspecies, *H. [N.] siki* (southern white-cheeked gibbon), and another all-black subspecies, *H. [N.] c. lu*. Groves (1972) and others (e.g., Marshall and Sugardjito 1986) maintained the crested gibbons in the subgenus *Nomascus*. Because of the persistent confusion over “concolor”—Schultz (1973), for example, gave metrics for “*H. concolor*” that were actually *H. muelleri* (see discussions in Jungers [1984] and Groves [1972])—older accounts of *Nomascus* biology and behavior must be read with care to determine which genus is being described.

*Hylobates [Nomascus] leucogenys* was separated from *H. [N.] concolor* by Đào (1983) and Ma and Wang (1986). Roos (2004) confirmed *N. gabriellae*, *N. nasutus*, *N. leucogenys*, and *N. concolor* as distinct species with *nasutus* basal and the most different, whereas *N. siki* is a paraphyletic group with southern representatives forming a sister clade to *N. gabriellae*, and some northern individuals clustering together

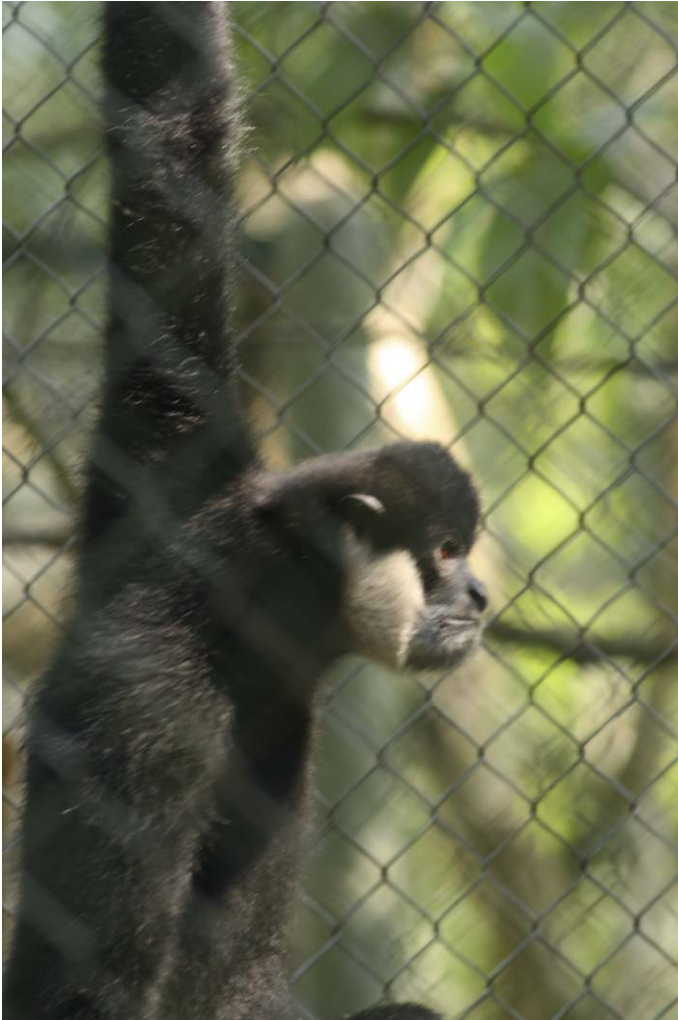
with *N. leucogenys*. Unfortunately, he did not at that time have a sample of *N. hainanus*. Several authors (e.g., Carbone et al. 2009; Geissmann et al. 2000; Konrad and Geissmann 2006; Roberto et al. 2007) have referred to *N. l. leucogenys* to differentiate it from *N. l. siki*, which was subsequently elevated to full species. Vocalizations throughout the range of *N. siki* and *N. gabriellae* separate into 3 clades, suggesting the possibility of an undescribed subspecies (Ruppell 2010); molecular analysis confirms the 3rd as a new species that Thinh et al. (2010a) described as *Nomascus annamensis*, northern buff-cheeked gibbon. *N. concolor lu* (Delacour 1951) also was thought to be possibly conspecific with *N. concolor* (Geissmann 2007b), but has now been confirmed as a genetically, physiologically, and vocally distinct subspecies of *N. concolor* (Thinh et al. 2010b, 2011). Thinh et al. (2010b) found no support for *N. c. jingdongensis* and *N. c. furovogaster* and considered them synonyms of *N. c. concolor*. The validity of *N. nasutus* also has been considered uncertain (Groves 2005), but recent genetic and acoustical analyses confirm its distinctiveness at the species level (Thinh et al. 2011).

## DIAGNOSIS

Compared to *Nomascus concolor* (western black crested gibbon), which has fine, almost silky, jet black hair, the hair of *N. leucogenys* (and *N. gabriellae* [red-cheeked gibbon]) is longer and coarser with silvery hairs inconspicuously intermixed (Groves and Wang 1990). White cheek hair extends from below the level of the mouth corners to above the level of the tops of the ears (Figs. 1 and 2). Females lack the black or dark gray zone in the chest and belly fur that identifies female *N. concolor*. The crown patch is “dark brown, often with a maroon tinge, and more trapezoidal (ending bluntly on the nape, not a point)” (Groves and Wang 1990:148). The hair in the center of the crown that rises in a prominent tuft in the male is almost entirely absent in the female; this contrasts with *N. concolor* in which the female has a tuft similar to that of the male and has longer hair over the ears that is lacking in female *N. leucogenys*. Female fur color, including that of the crown, varies considerable among individuals.

## GENERAL CHARACTERS

As with other hylobatids north of the Isthmus of Kra (Chivers 2001), *Nomascus leucogenys* is sexually dichromatic. Adult males and juveniles of both sexes are completely black except for the cheek fur (Fig. 2). Females are reddish tan (more richly colored than *N. concolor*; Fig. 1) with a black or brown crest from the crown to the nape. Males have a semipendulous scrotum, but no prominent



**Fig. 2.**—Adult male *Nomascus leucogenys*. This individual was confiscated from a poacher in 1999. Photograph by L. Harding at the Endangered Primate Rescue Center, Vietnam.

genital tuft as in other genera. The natal coat is light yellow or golden yellow, like the adult female, with no facial or other markings and changes to black in a few months.

All *Nomascus* species have a straight sagittal profile of the skull from in front of nasal bones to the level of the upper margins of the orbits (Fig. 3), and a flattened orbital rim, that differentiate them from other hylobatids (Pocock 1927). Groves and Wang (1990) give the following mean skull measurements (length by width) of *N. leucogenys* for 8 males and 9 females, respectively: 114.9 by 75.2 mm, 109.3 by 68.7 mm. Geissmann (1989) gives the following mean ( $\pm$  *SD*) measurements (ranges in parentheses, mixed sexes): maximum length of skull,  $111.1 \pm 5.7$  mm (98–122 mm,  $n = 14$ ); basal length,  $78.2 \pm 3.8$  mm (73–84 mm,  $n = 11$ ); length of palate  $43.9 \pm 3.1$  mm (33–48 mm,  $n = 14$ ); breadth of palate,  $35.3 \pm 1.2$  mm (34–38 mm,  $n = 12$ ); bizygomatic breadth,  $72.1 \pm 5.9$  mm (60–78.5 mm,  $n = 9$ ). Mean ( $\pm$  *SD*) Sneath size variables (Sneath 1967) for cranial measurements

in “*H. concolor*” (subspecies not stated) are smaller than those of *Symphalangus*, about the same as those of *Hoolock*, and larger than in all the measured *Hylobates* species:  $37.33 \pm 0.21$  ( $n = 16$ ) for females and  $37.73 \pm 0.55$  ( $n = 18$ ) for males (Creel and Preuschoft 1984).

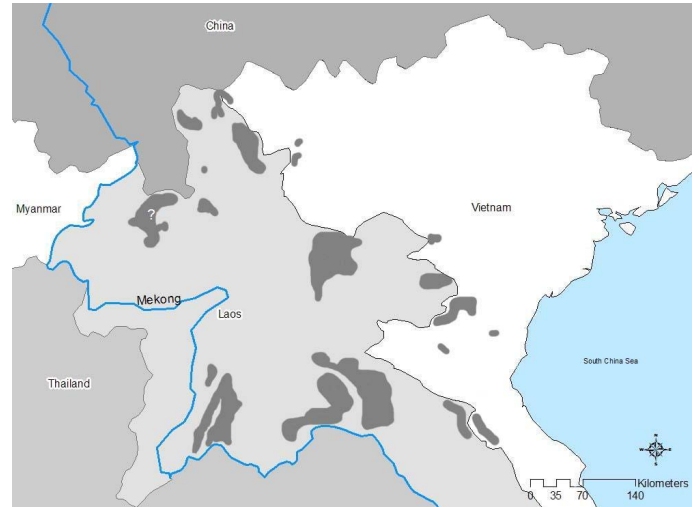
*Nomascus leucogenys* usually has a longer baculum (mean of 4 adults = 10.4 mm, range 9.1–12.1 mm) than *N. concolor* (mean of 3 adults = 9.1 mm, range 9.0–9.2 mm), *N. siki* (single adult 7.5 mm), and *N. gabriellae* (single adult 8.3 mm—Groves and Wang 1990). The shape of the baculum also is unique relative to the other genera, having a bony projection at the distal end (Groves 1972). The clitoris is long and slender (Groves 1972).

Wild males and females have body masses of about 7.5 kg. For example, mean of 6 wild-shot males was  $7.27 \pm 0.44$  *SD* and mean of 2 wild-shot females was  $7.65 \pm 0.21$  kg (Geissmann 1993). However, in captivity mass may be larger (e.g., a 9.5-kg female—Zihlman et al. 2011). In *N. siki* and *N. concolor* males had slightly larger body masses than females, suggesting that the apparently smaller body masses in males of *N. leucogenys* were due to variation in a small sample size. *N. leucogenys* exhibits more sexual dimorphism in size than do *N. concolor* and *N. gabriellae*, having, for example, twice the difference in skull length (7 mm) between males and females (see Groves and Wang [1990] for measurements).

Forelimbs of *Nomascus* are “elongate even for a lesser ape” (Jungers 1984:167; Fig. 1). In *N. leucogenys*, the intermembral index (arm length  $\times$  100/leg length) ranged from 121 to 140 in a sample of 14 individuals (Groves and Wang 1990). Brachial index is  $115.5 \pm 2.3$  *SD*, crural index is  $87.5 \pm 1.7$ , and humerofemoral index is  $122.2 \pm 4.6$  (Jungers 1984). M3 appears noticeably smaller than M1, whereas in *N. concolor* they are the same size; relative to *N. concolor*, the canines are more slender, with the longitudinal groove less marked (Groves and Wang 1990). A gular sac is present in males only.

## DISTRIBUTION

*Nomascus leucogenys* formerly occurred in southwestern Yunnan, China (where it was on the edge of extirpation in 2008—Fan and Huo 2009) and still occurs in northern Vietnam and northern Laos (Fig. 4). Historically, the Red River (called the Yuan Jiang in China and the Sông Hồng in Vietnam) was the boundary between *N. leucogenys* to the south and *N. concolor* to the north (Groves and Wang 1990); within Vietnam, the Song Da (Black River), a southern tributary that parallels the Red River for most of its length, is the boundary. Recent studies on vocalizations and genetics indicate that distribution of the species extends as far south in Laos as the Ka Ding River at about 17°36'N–18°23'N; and in Vietnam, to the Rao Nay River at similar latitudes (Thin et al. 2010b)



**Fig. 4.**—Distribution of *Nomascus leucogenys* is restricted to northern Laos with small populations in remote mountains of Vietnam (adapted from International Union for Conservation of Nature and Natural Resources 2009).

A disjunct population of *N. c. lu* (Laotian black crested gibbon) occurs in Bokeo Province, northwestern Laos, isolated within the range of *N. leucogenys* (Duckworth et al. 1999; Hamada et al. 2007). As well, a 2005 survey using sonograms for identification (Johnson et al. 2005) showed that the gibbons northeast of there in Luang Namtha Province, formerly considered *N. leucogenys* range, contained only *N. concolor* (subspecies not determined).

### FOSSIL RECORD

Several studies indicated that the *Laccopithecus* fossils from the late Miocene Lufeng deposits of Yunnan may represent an ancestral gibbon (Jablonski 1993; Tyler 1993; Wu and Pan 1984, 1985). Hylobatid fossils, including *Lufengpithecus*, dated to 8 million years ago, have been found in China from the middle Miocene to the late Pleistocene (Gu 1989; Ma 1997). *Hylobates* (then including *Nomascus* and *Hoolock*) possibly developed from *Dionyso-pithecus shuangouensis* found in southeastern China, or more likely from *Laccopithecus robustus*, whereas *Dianopithecus progressus* discovered in Yunnan was the likely ancestor of

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**Fig. 3.**—Dorsal, ventral, lateral, and frontal views of skull of an adult male *Nomascus leucogenys*, NMH (Natural History Museum, London, United Kingdom) specimen 1926.10.4.1 collected by Jean Delacour and Willoughby Lowe at Xieng Khouang, Laos. Photograph by Phil Hurst, Natural History Museum, used with permission.

*Hylobates* [*Nomascus*] *concolor* via an unknown lineage of late Miocene to Pliocene age (Ma 1997).

The most northerly *Nomascus* is a mid-Pleistocene mandibular fragment assigned to *N. concolor* (although this species was not distinguished from *N. leucogenys* at the time) that was found in the Yangtze River floodplain (Gu 1989). Other Pleistocene “*N. concolor*” fossils have been found in Guanxi and Yunnan (Gu 1989; Ma 1997; Zhao et al. 1981). Pleistocene fossils of gibbons found at Lang Trang and Lang Song, Vietnam, have been dated to 80,000 years ago (Jablonski and Chaplin 2009; Long et al. 1996). A partial cranium identified as *Hylobates* (but now probably referable to *Nomascus*) was found in a karst cave, Tham Khuyen, in the province of Thanh Hoa, northern Vietnam (Ciochon and Olsen 1986).

### FORM AND FUNCTION

**Form.**—Dental formula is i 2/2, c1/1, p 2/2, m 3/3, total 32 (Elliot 1913). The vertebral formula is 7 C, 14 T, 5 L, 4–5 ( $\bar{X}$  = 4.6) S, total 30–31 (Groves 1972; Pilbeam 2004; Prouty et al. 1983a; Shultz and Straus 1945). The slender, elongated forelimb long bones and other skeletal and muscular adaptations of hylobatids for brachiation, their function, and associated behaviors have been well described (e.g., Andrews and Groves 1976; Bertram et al. 1999; Chang et al. 2000; Hollihn 1984; Jungers and Stern 1981; Napier 1963; Preuschoft and Demes 1984; Usherwood and Bertram 2003).

*Nomascus* species have relatively longer skeletal trunk length and forelimb length and shorter hind-limb length than the average among the hylobatids; and they have higher intermembral and humerofemoral indexes than all hylobatids except *Symphalangus* (Jungers 1984; Napier 1963). *N. leucogenys* and other hylobatids have massive hip and knee extensors, relative to other primates, to support their leaping ability (Channon et al. 2009).

Dandelot (1960) reported that *N. leucogenys* produced colored droplets when perspiring. *N. leucogenys* has no sternal glands per se, as do some other hylobatids, but macroscopically visible modifications of the skin on the medial anterior part of the chest suggest a concentration of cutaneous glands (Geissmann 1993 and references therein). Microscopic examination of analogous areas of other hylobatid genera revealed high concentrations of apocrine glands and lower concentrations of eccrine glands. Geissmann (1993:303) lists results of chemical analysis of skin secretions in the sternal and axillary areas for steroids (dehydroepiandrosterone, androstenedione, and testosterone) in 2 adult male and 2 female *N. leucogenys*. Among all taxa sampled (which included *Pongo pygmaeus* [Bornean orangutan] and *Pan troglodytes* [common chimpanzee]), the concentrations of all steroids in both sternal and axial samples regardless of sex were highest in *Symphalangus syndactylus* (simang) and lowest in *N. leucogenys*, suggesting that olfactory communication is less important in the latter.

In addition to the sternum and axial areas, *N. leucogenys* has high densities of colored pores in the clavicle, ankle, and hip areas; dried, reddish brown secretions can be seen at the base of the hair roots and discoloration of the fur of females in these areas suggests that they may exude glandular secretions (Geissmann 1993).

*Nomascus* songs (see “Communication”), as with other hylobatids, include hoots or booms produced by inhalation and exhalation of the throat sacs; and frequency-modulated, multiharmonic calls of the vocal cords (Geissmann 1993). The vocal apparatus includes both true vocal cords and vestibular ligaments, or false vocal cords (Haimoff 1984a). Partial separation of the epiglottis from the palate (although not as complete as in *Homo sapiens* [humans]), backward direction of the larynx that directs exhaled air to mouth instead of the nose, and specialized larynx musculature are the physiological foundation of the songs (Lindahl 1970; Tembrock 1974).

**Function.**—The defining feature of hylobatid locomotion is brachiation (arm-swinging) combined with ricochetting locomotion. The former, used at slower rates of forward progression, is a continuous-contact gait characterized by a dual-limbed support phase during a stride cycle; in the latter, individuals propel themselves from 1 point and spring vigorously from a 2nd point to land at a 3rd point (Bertram et al. 1999; Chang et al. 2000; Jungers and Stern 1984; Usherwood and Bertram 2003). *Nomascus leucogenys* has at least 4 distinct types of leaps, defined by the number of feet used during takeoff and the orientation of the trunk: orthograde single-footed, orthograde 2-footed, orthograde squat, and pronograde single-footed (Channon et al. 2010). Of these, 3 are broadly similar in the center of mass trajectory, whereas the last exhibits less vertical displacement and has the highest ratio of kinetic energy to mechanical energy. The highest mechanical work and power are generated during orthograde squat leaps. Takeoff angle decreases with takeoff velocity and the hind limbs show a proximal-to-distal extension sequence during takeoff. Shoulder joints are always flexed during takeoff (Channon et al. 2010).

Zihlman (2011) found that *N. leucogenys* has the heaviest body and limb proportions among the Hylobatidae (other genera of *Nomascus* were not included in the analysis), suggesting greater power in shoulder, hip, and knee motions. These capabilities allow *N. leucogenys* to “progress, like gymnasts, by means of their long and powerful arms, and throw themselves from one branch to another for distances of thirty feet and more” (Delacour 1933:72).

In *N. leucogenys*, mean forelimb angles at initial contact and release of arm-swinging behaviors were remarkably similar to those of 2 *Pygathrix* species, despite the fact that *N. leucogenys* typically uses more continuous brachiation (Wright et al. 2008). However, *N. leucogenys* exhibits a lower range of forelimb angles than *Pygathrix*. In addition, trunk

orientation tends to be more vertical at initial contact for *N. leucogenys* than for *Pygathrix*, perhaps because the latter more frequently uses quadrupedal sequences directly before or after forelimb suspension.

Among captive *N. leucogenys* and *N. gabriellae*, adults more than subadults showed a hand preference during brachiation maneuvers, about equally divided between right- and left-handedness; and hand preference increased with the difficulty or danger of the maneuvers (Barker 2008). Foot function during hylobatid bipedal locomotion has been described (Ishida et al. 1984; Vereecke et al. 2005; Vereecke and Aerts 2008).

## ONTOGENY AND REPRODUCTION

**Ontogeny.**—Neonates have a mean body mass of 480 g (*SD* 79.2 g, range 395–567, *n* = 5) for pooled sexes and there is no difference between males and females (Geissmann and Orgeldinger 1995). Females are born buff-colored, turn black after about a year (although with light cheek patches as in the male), and begin changing to adult coloration at 4–5 years of age, which takes about 6 months (Osgood 1932; Schilling 1984a).

Ontogeny in development of both sexual dichromatism and songs in *Nomascus leucogenys* includes long phases during which young animals resemble adult animals of the opposite sex (Geissmann 1993). Juvenile males and females have the black adult coloration and sing the female song. When they reach sexual maturity, female coat color changes to orange and males begin singing the male songs. In effect, juveniles adopt a “unisex” pattern both in fur coloration and song repertoire, only revealing their sex-specific differences when they mature. Geissmann (1993) suggests that the masking effect evolved as a mechanism for inbreeding avoidance, by reducing sexual attractiveness of young family members to each other and to their parents.

In captive *N. leucogenys*, solo play and play solicitations peaked by 5 years of age, but continued until at least age 7; spatial separation from parents and aggression from the father to male offspring accompanied the transition to subadulthood (Burns et al. 2011).

Hylobatidae in general are long-lived; for example, a Müller’s Bornean gibbon lived 60 years, mostly in captivity (Geissmann et al. 2009). *N. leucogenys* lives at least 28 years in the wild (Rowe 1996) and a southern white-cheeked gibbon lived 44.1 years in captivity (Weigl 2005).

**Reproduction.**—In *Nomascus leucogenys*, the ovarian cycle averages 21.9 days  $\pm$  2.9 *SD* (range 12–27 days—Lukas et al. 2002). Gestation is 200–212 days (summarized by Geissmann 1991).

In *N. gabriellae* (which has mean cycle lengths virtually identical to those of *N. leucogenys*) the interval between any peak in estrone concentration and the corresponding estradiol peak had a range of 0–1 days, and cycle lengths

determined with estrone differed from those determined with estradiol by 0–2 days (Geissmann and Anzenberger 2009). Neither hormone tended to peak earlier than the other. Although menarche usually occurs just before or around the beginning of the color transition from the black juvenile to the adult yellow fur coloration, an older female did not begin to exhibit regular cycles until years after changing to adult fur coloration (Geissmann and Anzenberger 2009).

In *Nomascus hainanus* and probably other *Nomascus* species, the female solicits copulation when she is ready (Zhou et al. 2008b); however, copulation is relatively infrequent and rarely observed in the wild. Although captive males of *N. leucogenys* may breed at the age of 4 years (Geissmann 1991), both sexes normally reach sexual maturity at age 7 or 8 years (Keeling and McClure 1972). The age at birth of 1st offspring was 7–9 years for both males and females in captivity (summarized by Geissmann 1991).

## ECOLOGY

**Population characteristics.**—Being strictly arboreal, all gibbon species require mature forest, and therein lie their greatest threats: deforestation and fragmentation. Delacour (1933:71) heard *Nomascus leucogenys* (or other *Nomascus* species) at all of his camps throughout northern Vietnam and Laos “except in deforested areas and [heavily settled] northeast Tonkin.” All modern reports of *N. leucogenys* are in relatively inaccessible primary lowland or montane forest. Currently, population data are insufficient to estimate the global population or the population in either country in which it still occurs (Bleisch et al. 2008; Geissmann 2007a). Population parameters such as recruitment, mortality, and survivorship are not known.

Hamada (2007) found *N. leucogenys* rather widely, although thinly, distributed in Houaphan, Luangprabang, and Phonsali provinces, northern Laos; however, this survey did not include Xayaboury and Xiengkhouan provinces, where populations also may occur. Bleisch et al. (2008) reported that population numbers of *N. leucogenys* are highest in northern Laos (relative to Vietnam), but this was by inference from the relatively high density of *N. c. lu* of 8.0–8.4 individuals/km<sup>2</sup> or 2.2 gibbon groups/km<sup>2</sup> in the Nam Kan Valley, Laos (Geissmann 2007b), the relatively low level of forest fragmentation, and the wide distribution, rather than by any quantitative surveys. Increased hunting since 1990 to support the wildlife trade threatens all *Nomascus* species (Bach and Rawson 2011; Bleisch et al. 2008). Taboos among some ethnic groups in Laos against killing gibbons, because they seem closely related to humans, because they represent spirits that would seek revenge on hunters, or because they sing pleasantly in the morning and do not raid crops, have resulted in lower rates of population decline relative to Vietnam (Duckworth et al. 1999; Geissmann 2007b; Hamada et al. 2007; Johnson et al. 2005).

In Vietnam, following chemical defoliation during the Vietnam War, rapid development of human agriculture and settlement along the valleys, and logging and hunting in the highlands (see “Conservation”), populations of *N. leucogenys* have become small and isolated. Even within protected areas, illegal hunting and other forms of human encroachment threaten all *Nomascus* species (Bach and Rawson 2011; Eames and Robson 1993; Geissmann et al. 2000; Mittermeier et al. 2009), and *N. leucogenys* is largely confined to the borders with Laos and Yunnan, China (Fig. 4). In a survey of 27 sites at which this species formerly occurred, it was only confirmed surviving at 4, and may survive in a further 3 with a total population of perhaps 50 individuals (Geissmann et al. 2000). Even some protected areas that have suitable remaining habitat and formerly held *N. leucogenys*, such as Cuc Phuong National Park, no longer hold any surviving populations (Geissmann et al. 2000). The largest extant population is in the 795-km<sup>2</sup> forested portion of Pu Mat National Park, Vietnam, where 130 groups of *N. leucogenys* were estimated from call counts at listening posts (Bach and Rawson 2011). They heard gibbons at 13 of the 24 listening posts, but found none near villages or in modified forest. They estimated densities at 0.051 groups/km<sup>2</sup> in forested areas under 700 m elevation and 0.271 groups/km<sup>2</sup> in forested areas above 700 m, found a positive correlation ( $P = 0.003$ ) between the number of groups heard and elevation, and estimated the population at 455 (based on 3.5 per group—Bach and Rawson 2011). Elsewhere in Vietnam, densities of relict populations of *N. leucogenys* may be assumed to be no higher than those of similarly isolated populations of *N. siki* (0.17 groups/km<sup>2</sup> and 2.1 individuals/km<sup>2</sup>—Dat et al. 2009), and *N. concolor* (1.6 groups/km<sup>2</sup> at Che Tao, northern Vietnam—Tallents et al. 2001).

**Space use.**—Groves (1972) noted that the mainland species of *Nomascus* occupy different climate regimes, that of *Nomascus leucogenys* having a mean monthly rainfall of 429 mm (maximum 624 mm), mean maximum daily temperature of 33.1–35.5°C, mean minimum daily temperature of 13.4–14.5°C, average humidity of 74%, and a 4- to 5-month dry season. This is drier than for *N. concolor* and *N. siki*, and warmer than for *N. concolor* and *N. gabriellae*, but similar to that of *N. c. lu* (Groves 1972).

Fan and Huo (2009) gave the habitats of historic populations of *N. leucogenys* in China as undisturbed primary forest from 590 to 1,189 m elevation. *N. leucogenys* ranges up to at least 1,650 m in Phou Louey National Biodiversity Conservation Area, Laos (Duckworth et al. 1999). Đào (1983) describes its habitat in northeastern Vietnam as 200–600 m elevation with a subtropical climate of short, mild winters with no frost and summers with a hot, dry wind from the west. Annual average temperatures were 23.6°C at Than Hoa and 21.2°C at Son La, and annual precipitation was 1,364 mm at Son La and 1,895 mm at Hoa Binh. The primary forest at these study sites is composed mainly of

*Castanopsis*, *Pasania*, *Phoebe cuneata*, and *Machilus*, with a secondary forest dominated by *Betula abnoides* and *Schimar wallichii* (Đào 1983).

In Pu Mat National Park, Vietnam, the habitat is a mixture of lowland and lower montane (up to 1,841 m elevation) evergreen forest with at least 2,461 plant species; other rare mammals there include *Pseudoryx nghetinhensis* (saola), *Panthera tigris* (tiger), and *Elaphas maximus* (Asian elephant—Bach and Rawson 2011). Lowland forests are dominated by Dipterocarpaceae, Fagaceae, and Lauraceae, whereas in montane forests Fagaceae, Lauraceae, and Myrtaceae dominate, with a minor component of dipterocarps (BirdLife International 2001).

Groups of *N. leucogenys* are territorial (Delacour 1933, 1961; Goussard 1984; Nisbett and Ciochon 1993). Delacour (1933:71–72) remarked that groups are “very sedentary and ... if there are no imperious reasons [to range further], they will roam over only about one hundred acres [~40 ha] at the most, as long as they have peace and food.” Their duet and other calls are assumed to play a strong role in territorial advertisement and defense (Geissmann 1993), although this has not been tested for *N. leucogenys*. Dooley and Judge (2007) showed, however, that duet calls were important in intergroup communication. Territorial disputes are probably similar to those described for *N. concolor* (Fan and Jiang 2010; Fan et al. 2007, 2009) and *N. hainanus* (Zhou et al. 2008a).

During the rainy season (May–October) when many fruits are available, *N. leucogenys* travels less, whereas in the dry season (November–April), it eats more leaves and travels for longer distances (Hu et al. 1989). The peak feeding time is at 0800–1000 h and individuals are active for about 9.5 h. Feeding, travel, and rest occupy 41.2%, 13.1%, and 45.7% of daily active time, respectively. Mean daily travel distance is 1,305 m (range 1,024–1,586 m—Hu et al. 1989).

*Nomascus gabriellae* called from just 3 tree species that were the tallest in a study area in Cambodia: *Dipterocarpus costatus*, *Terrietia javanica*, and *Shorea thorelli*; individuals spent 82.37% of their time in the high canopy, 17.14% in the medium canopy level, and 0.5% at a low canopy level (Channa 2007).

**Diet.**—The content of the stomach of 6 wild-shot *Nomascus* from Vietnam, including 3 *Nomascus leucogenys*, was 90–100% fruits, associated with some leaves and insects (Đào 1983). Food composition in southern Yunnan was 90.6% plants (including 39% fruits, 36% leaves, and 5% flowers) and 9.4% small animals (Hu et al. 1989). Relative to availability, fruits were the most preferred food, followed by leaves, buds, flowers, and animals. Carnivory in a hylobatid is surprising, but Fan and Jiang (2009) documented predation on *Petaurista philippensis* (giant flying squirrels), eggs or chicks of birds, and a lizard by the closely related western black crested gibbon.

**Diseases and parasites.**—In captivity, *Nomascus* species can suffer from chronic diarrhea and other ailments



common to these environments; also, a female captive *N. gabriellae* died of Crohn's disease (Geissmann and Anzenberger 2009). Antibodies to hepatitis A, a zoonotic disease that can occur in natural habitats, were prevalent in 9 (81.8%) of 11 captive *Nomascus leucogenys* in a zoo in Thailand (Sa-nguanmoo et al. 2010). Hepatitis B antigens are present in wild *Nomascus* species throughout northern and central Vietnam, northern Laos, and Cambodia (Sall et al. 2005). The nematode *Trichuris trichiura* has been isolated from feces of *N. gabriellae* (Cutillas et al. 2009). *Blastocystis* has been isolated from feces of captive *N. leucogenys* in a study that suggested its zoonotic potential in natural settings (Parkar et al. 2006).

Villagers in Yenidong, southern Yunnan, thought an epizootic disease was the main reason why *N. leucogenys* had disappeared, citing unexplained deaths of monkeys, wild boars, and mice in 1979 (Fan and Huo 2009).

**Interspecific interactions.**—Geissmann (1993) observed that captive hylobatids of various species, if kept in adjacent cages, tend to synchronize their great calls: females synchronize their own great calls with those of other, nearby species, and males in mixed species groups produce codas to great calls of females of other species. This suggests that both sexes recognize and respond to calls other than those of their own species. In the wild, however, *Nomascus* species are rarely or never sympatric with other hylobatids. Possible exceptions include that *Nomascus leucogenys* may have occurred in sympatry without interbreeding with *N. concolor* in Lai Chou Province, Vietnam (Đào 1983) and in Yunan, China (Ma and Wang 1986); and there may be a southern contact zone with interbreeding with *N. siki* (Ruppell 2010).

In 2007, I observed a female *N. leucogenys* in close proximity (about 2 m) to a *Trachypithecus delacouri* (Delacour's lutung) for about an hour in a semiwild enclosure near the Endangered Primate Rescue Center, Vietnam. Other than maintaining close proximity, they did not appear to interact, either affiliatively or agonistically; they both may have been trying to get near their respective conspecifics that were still in the Endangered Primate Rescue Center.

## HUSBANDRY

Moisson and Berthet (2007) provide information on dietary intake and nutrition for *Nomascus leucogenys* and *N. gabriellae*. Because males and females are vicious fighters, pairing of sexually mature individuals may be difficult. Males and even incompatible male–female pairs have been known to fight to the death in captivity (Keeling and McClure 1972). Delacour (1933:72), in addition to seeing many *N. leucogenys* (and other *Nomascus* species) in their natural habitat, also kept several in a garden enclosure for many years. He reported that although males are always gentle (presumably except when confronted with another

male), females after 4 years of age become vicious to each other and sometimes to juveniles and to humans; and they grow more “savage” with age. Keeling and McClure (1972) recommended housing only a male and female of approximately the same age together, preceded by an extensive period of separate caging within full sight of each other but limited contact.

Identification of morphologically similar females of all genera and *N. leucogenys* of either sex of unknown origin is often difficult, but necessary for proper management of captive groups and to prevent hybridization (which, however, is rare; see “Population genetics”). A taxon-specific DNA sequence variation in a 252-base pair region of the mitochondrial cytochrome-*b* gene, using plucked hair, can identify individuals of *N. leucogenys* and the other 2 species of *Nomascus* commonly found in Western zoos (Garza and Woodruff 1994). Carbone et al. (2009) present a simple polymerase chain reaction test on low-quality DNA to distinguish *N. leucogenys* from other gibbon taxa.

## BEHAVIOR

**Grouping behavior.**—Delacour (1933:71) stated that *Nomascus leucogenys* “live in small parties, probably families, of 5 to 10; there are usually 2 or 3 adult buff-colored females, and from 4 to 6 black individuals of different ages.” Goustard (1984) found smaller groups in northern Laos: group size (as determined mainly by vocalizations excluding infants) was 3.7 (range = 2–6,  $n = 11$ ). In a later study, groups of *N. leucogenys* were even smaller, averaging  $3.0 \pm 1.4$  ( $n = 12$ , range = 2–5—Lan 1989). In Yunnan, group size of *N. leucogenys* was 3.78 (range 3–5,  $n = 9$ —Hu et al. 1989).

In Thanh Hoa and Nghe An provinces (northern Vietnam), 3 groups of *N. leucogenys* had 3, 3, and 4 individuals (Nguyen Manh Ha et al. 2005 [not seen, cited in Bleisch et al. 2008]).

**Reproductive behavior.**—Although all modern surveys of *Nomascus leucogenys* report (or assume, during acoustic surveys) only 1 male and 1 female per group (Bach and Rawson 2011; Daoying 1989; Goustard 1984; Hu et al. 1989; Ruppell 2008, 2010), Delacour's (1933) observations of 2 or 3 buff-colored females in some groups suggests the possibility of a flexible mating system that may rarely include male–multifemale groups. In *N. concolor*, polygyny has been demonstrated by close observation of a group with 1 adult male and 2 adult females over 6 years, during which time both females gave birth (Fan and Jiang 2010). The authors suggest that this arose from unusual ecological and social circumstances: a large territory that provided adequate resources for the females and their offspring, and no other groups present (Fan and Jiang 2010).

Likewise, in the tiny, relict population of *N. hainanus*, groups with 2 adult females are the known, apparently a

necessary response to fruit shortage in fragmented forests (Zhou et al. 2008b). The finding of 2.8 adults per group of southern white-cheeked gibbons (Dat et al. 2009) also suggests a flexible mating system within *Nomascus*.

Regardless of the mating system, pair-bonds in *Nomascus* are stable, lasting for as many years as investigators have been able to observe known groups in the wild (Fan and Jiang 2010; Mootnick 1984; Zhou et al. 2008b), and often lifelong in captivity (Mootnick 1984; Schilling 1984a).

Dispersal patterns are not known for *N. leucogenys*. In *N. concolor*, both subadult males and females disperse from natal groups (Fan et al. 2006). At Mt. Wuliang, China, subadult males remained in the natal territory for many months, but kept their distance from the family. A “floating” female came in and out of a territory and was chased by the resident females (i.e., the 2 resident adult females rejected a 3rd—Fan et al. 2006).

**Communication.**—As noted above, the presence of glandular secretions in several areas of the integument suggests olfactory communication, although the low concentrations of steroids suggest less importance relative to other hylobatids. Although the sexually dichromatic pelage and the age-specific changes in pelage coloration are obvious candidates for signaling, this hypothesis has not been tested. Geissmann (1993) notes that although gibbons use facial expressions and gestures for communication, few detailed descriptions of such signals are available for hylobatids and none for *Nomascus leucogenys*.

The specificity of hylobatid calls, and especially their duets, to each species, and analysis of vocalizations in hybrids, supports the view that gibbon songs are largely genetically determined, rather than learned; and those of *Nomascus* species are the most complex and derived (Geissmann 1993). *N. leucogenys*, together with other *Nomascus* species, have “extreme divergence in the vocal repertoire” relative to other hylobatid genera and between males and females (Haimoff 1984a:345). Males produce a “boom” during inflation of the throat sac; short, single “aa” notes; and frequency-modulated “great calls” (= “loud calls”), which are part of the duet (Goustard 1984). Apart from their solo great calls and duets, females produce few other notes. Duets are almost always sung in pairs (Geissmann 1993). The female part includes twitter notes and a rapid note rhythm in her song’s climax. The great call duet duration is relatively short, <20 s, and its peak fundamental frequency is high, > 2.5 kHz. Geissmann (1993) described the duet: the female’s great call is an acceleration-type climax, usually totalling 15–30 (maximum 39) notes that begin with ascending frequency. The male then produces a multimodulated phrase as a coda at the conclusion of the female’s part. The 1st note of the multimodulated series has a long section of stable frequency at the beginning; rapid changes of frequency modulation occur on the 2nd and sometimes on the 3rd note. The duet may be joined by juveniles of both sexes, making it a chorus (Goustard 1984).

Mated males are not known to sing solo, but solitary males do (Geissmann 1993). At least in captivity, 2 adult males may sing duets (Goustard 1984). Surprisingly, in captivity at least, female *N. leucogenys* and *N. gabriellae* can produce male songs (Chen et al. 2008) and male *N. leucogenys* occasionally produce femalelike notes (Geissmann 2002).

Specific parts of the duets and choruses stimulate and synchronize stylized vocal responses by group members as well as gestures and postures that increase in intensity during the song. In successive songs, the vocal and gestural intensity further increases until finally the male “moves swiftly between branches, shaking them with his legs, and moving his arms rapidly” (Goustard 1984:414). Although stylized, the auditory and visual displays are not rigidly stereotyped, but vary depending on circumstances.

The adult females initiate loud-calling at dawn, and 80% of great calls are given by the female (Goustard 1984). The males call under various circumstances including within-group responses to abrupt auditory or visual cues, before play or during conflicts; and between groups when females are interacting, or in reply to great calls of a male or female out of visual contact (Goustard 1984).

In Dak Rong Nature Reserve, Vietnam, most singing bouts of *N. leucogenys* were between 0532 and 0707 h and were from 5 to 17 min long; they did not sing on days with rain and fog, but sang every sunny morning and sang longer on sunny days following several inclement days (Ha 2007). After singing, they feed, with feeding bouts peaking from 0800 to 1000 h (Hu et al. 1989).

An example of pair-bonding function is given by Dooley and Judge (2007). In a captive population consisting of a family of *N. leucogenys* (mated pair with offspring) and a pair without offspring, zoo managers exchanged the female without offspring for an unpaired, strange female. She at 1st sang a solo great call, then paired with the single male and they began singing duets, upon which the duetting rate of the family pair increased. Dooley and Judge (2007) also found that the pair that duetted most frequently also copulated most frequently, but allogroomed the least. Duet singing and both sexes’ solo calls therefore have pair-bonding, intra-group, and intergroup communication functions (Dooley and Judge 2007; Geissmann 2002; Goustard 1984; Haimoff 1984a, 1984b; Merker and Cox 2000; Schilling 1984b).

Male songs of *N. concolor* are sufficiently different among individuals and stable over time that they could be used to monitor individuals or family groups (Fan et al. 2011), and the same is probably true of *N. leucogenys*.

**Miscellaneous behavior.**—*Nomascus leucogenys* (and *N. gabriellae*) respond to their reflections in mirrors; responses ranged from social responses to progressive behavioral changes and contingency testing behaviors, indicating self-recognition (Ujhelyi et al. 2000).

Delacour (1933:71–72) noted that “they invariably sleep sitting on a branch, often a small one, at the top of a tree, several of them together and embracing one another very

tightly with their arms. [They] dislike water, except for drinking; this they generally do by dipping their hand and sucking it, but they can also drink by putting their lips into the water. This is especially true of young ones. If they fall into the water, they will swim to reach the nearest shore, but they never take to water willingly ...”

Daily activity budgets have not been reported for *N. leucogenys* but are probably similar to those of *N. concolor* and *N. gabriellae*. Fan et al. (2008) described activity for *N. concolor*. Feeding manifested a bimodal pattern of high activity levels in midmorning and midafternoon, whereas resting reached a peak at midday, with proportionally less time used for traveling. Annually, this group spent an average of 40.0% of the time resting, 35.1% feeding, 19.9% traveling, 2.6% singing, 1.2% playing, and 1.3% in other activities. The proportion of time allocated to activities showed significant monthly variations and was influenced by diet and temperature. Individuals increased traveling and playing time and decreased feeding time when they ate more fruit, and they decreased traveling, singing, and playing time and increased feeding time when they ate more leaves. When the temperature was low, they decreased time traveling and increased time resting.

Channa (2007) gave the activity budget for the red-cheeked gibbon. On average, it fed 38.26% of the time, traveled 18.92%, rested 34.69%, played 3.43%, scanned 2.5%, vocalized 1.64%, and groomed 0.57%.

## GENETICS

**Cytogenetics.**—All species of *Nomascus* have diploid chromosome numbers (2n) of 52, contrasting with other genera: *Hoolock* (38), *Hylobates* (44), and *Symphalangus* (50—Chatterjee 2006; Prouty et al. 1983b). The fundamental number (FN) is 94. The karyotype consists of 24 pairs of large metacentric and submetacentric chromosomes and 3 small acrocentric chromosomes, 2 of which have an achromatic filament in the region of the centromere opposite to the long arms, plus the sex chromosomes (Chiarelli 1972). The X chromosome is metacentric and of medium–large size. The Y chromosome is small and “appears to be acrocentric” (Chiarelli 1972:95). *Nomascus leucogenys* lacks the reciprocal translocation between chromosomes 1 and 22 as in *N. siki*, and the pericentric inversion on chromosome 7 as in *N. concolor*; and can be distinguished from *N. hainanus* by a pericentric inversion and from *N. gabriellae* by the presence of both of these 2 rearrangements (Carbone et al. 2009).

Hylobatids diverged rapidly 8.9 million years ago, with *Nomascus* splitting from the *Symphalangus*–*Hylobates* clade (*Hoolock* was not included in the analysis) <1 million years ago (Perelman et al. 2011). In contrast to other apes, which show limited chromosomal variation, chromosomes of Hylobatidae evolved rapidly, resulting in a diverse karyotypic pattern among different species and subspecies

(reviewed by Girirajan et al. 2009). The rates of rearrangements in gibbons are 10–20 times higher than the mammalian default rate. The majority of the chromosomal differences between extant hylobatid genera and humans result from rearrangements that occurred in the hylobatid ancestor (38 events), consistent with the hypothesis that *Hylobates* is the most recently evolved lesser ape genus (Misceo et al. 2008). Waves of synteny block rearrangements in the common hylobatid ancestor gave rise to the 4 genera with varying chromosomal numbers (Girirajan et al. 2009). Furthermore, 84 of the 107 synteny breaks in hylobatids, relative to homonids, were inherited from the common gibbon ancestor, whereas the remainder (23 of 107) occurred in the common hominoid ancestor. Interestingly, 14 of the 84 gibbon synteny breaks are specific to *N. leucogenys*, suggesting increased chromosomal rearrangement in that lineage (Girirajan et al. 2009).

**Molecular genetics.**—Because hylobatids do not swim or walk long distances on the ground and disperse only through the forest canopy, the Hylobatidae followed an “unorthodox course of evolution” resulting in a “bizarre distribution pattern” of taxa separated by rivers (Marshall and Sugardjito 1986:174). Using mitochondrial DNA analysis, Thinh et al. (2010b) found that the hylobatids separated from great apes and humans 16.3 million years ago and later underwent a rapid radiation into the 4 genera from 8.34 to 6.69 million years ago. The 3 northernmost species, *Nomascus hainanus*, *N. nasutus*, and *N. concolor* branched off 1st, suggesting that the genus originated in the north and successively migrated to the south. Matsudaira and Ishida (2010) also found, from whole-genome mitochondrial DNA, that *Nomascus* diverged from *Symphalangus* and *Hylobates* in the Pliocene, 8.0 million years ago. The most recent splits among *Nomascus* species occurred between *N. leucogenys* and *N. siki*, and between *Nomascus annamensis* (northern buff-cheeked gibbon) and *N. gabriellae* (Thinh et al. 2010b).

**Population genetics.**—Genetic population structure has not been identified within *Nomascus leucogenys*. Despite the fact that *Nomascus* species were the 3rd most abundant hylobatids in European (Schilling 1984a) and American (Mootnick 1984) zoos, intergeneric and interspecific hybridization have rarely been reported. A female *N. gabriellae* paired with a male *N. leucogenys* in captivity produced several hybrid offspring (Geissmann and Orgeldinger 1995). Geissmann (1993) gave a secondhand report of a wild *N. concolor* × *N. leucogenys* hybrid. Hirai et al. (2007) examined the chromosomes of a *N. leucogenys* × *Hylobates lar* (lar gibbon) hybrid.

## CONSERVATION

*Nomascus leucogenys* is “Critically Endangered” (Bleisch et al. 2008). It is 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). It occurs in the Phou Louey National Biodiversity Conservation Area, Nam Kading National Biodiversity Conservation Area, Nam Kam Provincial Protected Area, and possibly the Nakai-Nam Theun National Biodiversity Conservation Area in Laos (Duckworth et al. 1999; Hamada et al. 2007; Johnson et al. 2005). In Vietnam, all known populations are in protected areas or areas proposed for protection: the Pu Mat National Park, Vu Quang Nature Reserve, Ke Go Nature Reserve, Khe Nhet Proposed Nature Reserve, Pu Huong Nature Reserve, Pu Hoat Proposed Nature Reserve/Xuan Lien Nature Reserve, and Muong Nhe Nature Reserve (Bach and Rawson 2011; Thinh et al. 2010b).

Threats in Vietnam include hunting facilitated by new road development, logging, shifting hill cultivation by ethnic minorities, illegal gold mining, and collection of honey and bamboo shoots (Bach and Rawson 2011). If the species still occurs in China, the most likely locales are 3 nature reserves in southern Yunnan where primates are hunted by Chinese and Laotian hunters (Fan and Huo 2009). Poaching and forest fragmentation are threats in Laos (Hamada et al. 2007).

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### LITERATURE CITED

- ANDERSON, J. 1878. Anatomical and zoological researches, comprising an account of the zoological results of the two expeditions to western Yunnan in 1868 and 1875, and a monograph of the two cetacean genera, *Platanista* and *Orcella*. B. Quaritch, London, United Kingdom.
- ANDREWS, P., AND C. GROVES. 1976. Gibbons and brachiation: suspensory behavior, locomotion, and other behaviors of captive gibbons. Pp. 167–218 in *Gibbon and siamang*. Vol. 4. (D. M. Rumbaugh, ed.). Karger, Basel, Switzerland.
- BACH, L. T., AND B. M. RAWSON. 2011. Population assessment of the northern white-cheeked crested gibbon (*Nomascus leucogenys*) in Pu Mat National Park, Nghe An Province. Conservation International/Fauna & Flora International, Hanoi, Vietnam.
- BARKER, M. K. 2008. Gibbon hand preference studies at the Endangered Primate Rescue Center, Vietnam. *Vietnamese Journal of Primatology* 1:41–45.
- BERTRAM, J. E., A. RUINA, C. E. CANNON, Y. CHANG, AND M. J. COLEMAN. 1999. A point-mass model of gibbon locomotion. *Journal of Experimental Biology* 202:2609.
- BIRDLIFE INTERNATIONAL. 2001. Pu Mat Nature Reserve. www.birdlife.org, accessed 13 November 2011.
- BLEISCH, B., T. GEISSMANN, N. MANH HA, B. RAWSON, AND R. J. TIMMINS. 2008. *Nomascus leucogenys*. In [IUCN] International Union for Conservation of Nature and Natural Resources red list of threatened species. Version 2010.1. www.iucnredlist.org, accessed 13 March 2010.
- BURNS, B. L., H. M. DOOLEY, AND D. S. JUDGE. 2011. Social dynamics modify behavioural development in captive white-cheeked (*Nomascus leucogenys*) and silvery (*Hylobates moloch*) gibbons. *Primates* 52:271–277.
- CARBONE, L., ET AL. 2009. A chromosomal inversion unique to the northern white-cheeked gibbon. *PLoS ONE* 4:e4999.
- CHAN, B. P. L., X.-F. TAN, AND W.-J. TAN. 2008. Rediscovery of the critically endangered eastern black crested gibbon *Nomascus nasutus* (Hylobatidae) in China with preliminary notes on population size, ecology and conservation status. *Asian Primates Journal* 1:17–25.
- CHANG, Y. H., J. E. BERTRAM, AND D. V. LEE. 2000. External forces and torques generated by the brachiating white-handed gibbon (*Hylobates lar*). *American Journal of Physical Anthropology* 113:201–216.
- CHANNA, P. 2007. Habitat utilization of yellow-cheeked crested gibbon in Rattanakiri Province, Cambodia. M.Sc. thesis, Royal University of Phnom Penh, Phnom Penh, Cambodia.
- CHANNON, A. J., R. H. CROMPTON, M. M. GÜNTHER, K. D'AOÛT, AND E. E. VEREECKE. 2010. The biomechanics of leaping in gibbons. *American Journal of Physical Anthropology* 143:403–416.
- CHANNON, A. J., M. M. GÜNTHER, R. H. CROMPTON, AND E. E. VEREECKE. 2009. Mechanical constraints on the functional morphology of the gibbon hind limb. *Journal of Anatomy* 215:383–400.
- CHATTERJEE, H. J. 2006. Phylogeny and biogeography of gibbons: a dispersal–vicariance analysis. *International Journal of Primatology* 27:699–712.
- CHEN, H. C., S. KAMOLNORRANATH, AND G. KAPLAN. 2008. Female crested gibbons (genus *Nomascus*) sing male song. *Vietnamese Journal of Primatology* 2:47–53.
- CHIARELLI, B. 1972. The karyotypes of the gibbons. Pp. 90–102 in *Gibbon and siamang*. Vol. 1. (D. M. Rumbaugh, ed.). Karger, Basel, Switzerland.
- CHIVERS, D. J. 2001. The swinging singing apes: fighting for food and family in far-east forests. Pp. 1–27 in *Proceedings, the apes: challenges for the 21st century*. Chicago Zoological Society, Chicago, Illinois.
- CIOCHON, R. L., AND J. W. OLSEN. 1986. Paleoanthropological and archaeological research in the Socialist Republic of Vietnam. *Journal of Human Evolution* 15:623–633.
- CONVENTION ON INTERNATIONAL TRADE IN ENDANGERED SPECIES OF WILD FAUNA AND FLORA. 2010. Appendix I and appendix II. www.cites.org, accessed 19 January 2010.
- CREEL, N., AND H. PREUSCHOFF. 1984. Systematics of the lesser apes: a quantitative taxonomic analysis of craniometric and other variables. Pp. 562–613 in *The lesser apes: evolutionary and behavioural biology* (H. Preuschoft, D. J. Chivers, W. Y. Brockelman, and N. Creel, eds.). Edinburgh University Press, Edinburgh, United Kingdom.
- CUTILLAS, C., ET AL. 2009. *Trichuris suis* and *Trichuris trichiura* are different nematode species. *Acta Tropica* 111:299–307.
- DAHLBOM, A. G. 1856. *Studia zoologica, familiae regni animalis naturales tractantia*. Sverige, Lund, Sweden.
- DANDELLOT, P. 1960. Gracieux et merveilleux acrobates: les gibbons. *Science et Nature* 39:2–12.
- ĐÀO, V. T. 1983. On the north Indochinese gibbons (*Hylobates concolor*) (Primates: Hylobatidae) in North Vietnam. *Journal of Human Evolution* 12:367–372.
- DAT, L. T., D. TUOC, D. H. TRI, L. T. DINH, AND D. N. KIEN. 2009. Census of southern white-cheeked crested gibbons in U Bo and adjacent bufferzone forests, Phong Nha-Ke Bank National Park, Bo Trach District, Quang Binh Province. Vietnam Fauna and Flora International (FFI)—Vietnam Primate Programme, Phong Nha-Ke Bang National Park—Centre for Science Research and Wildlife Rescue, Hanoi, Vietnam.
- DELACOUR, J. 1933. On the Indochinese gibbon (*Hylobates concolor*). *Journal of Mammalogy* 14:71–72.

- DELACOUR, J. 1951. La systématique des gibbons Indochinois. *Mammalia* 15:118–123.
- DELACOUR, J. 1961. Gibbons at liberty. *Der Zoologische Garten* 26: 96–100.
- DOOLEY, H., AND D. JUDGE. 2007. Vocal responses of captive gibbon groups to a mate change in a pair of white-cheeked gibbons (*Nomascus leucogenys*). *Folia Primatologica* 78:228–239.
- DUCKWORTH, J. W., R. E. SALTER, AND K. KHOUNBOLINE (EDS). 1999. Wildlife in Lao PDR: 1999 status report. International Union for Conservation of Nature and Natural Resources, The World Conservation Union, Wildlife Conservation Society, Centre for Protected Areas and Watershed Management, Vientiane, Laos.
- EAMES, J. C., AND C. R. ROBSON. 1993. Threatened primates in southern Vietnam. *Oryx* 27:146–154.
- ELLIOT, D. G. 1913. A review of the Primates. Vol. 3. American Museum of Natural History, New York.
- FAN, P. F., AND S. HUO. 2009. The northern white-cheeked gibbon (*Nomascus leucogenys*) is on the edge of extinction in China. *Gibbon Journal* 5:44–52.
- FAN, P. F., AND X.-L. JIANG. 2009. Predation on giant flying squirrels (*Petaurista philippensis*) by black crested gibbons (*Nomascus concolor jingdongensis*) at Mt. Wuliang, Yunnan, China. *Primates* 50:45–49.
- FAN, P. F., AND X.-L. JIANG. 2010. Maintenance of multifemale social organization in a group of *Nomascus concolor* at Wuliang Mountain, Yunnan, China. *International Journal of Primatology* 31:1–13.
- FAN, P. F., X. L. JIANG, C. M. LIU, AND W. S. LUO. 2006. Polygynous mating system and behavioural reason of black crested gibbon (*Nomascus concolor jingdongensis*) at Dazhaizi, Mt. Wuliang, Yunnan, China. *Zoological Research* 27:216–220.
- FAN, P. F., C. LIU, W. LUO, AND X. JIANG. 2007. Can a group elicit duets from its neighbours? A field study on the black-crested gibbon (*Nomascus concolor jingdongensis*) in central Yunnan, China. *Folia Primatologica* 78:186–195.
- FAN, P. F., Q. Y. NI, G. Z. SUN, B. HUANG, AND X. L. JIANG. 2008. Seasonal variations in the activity budget of *Nomascus concolor jingdongensis* at Mt. Wuliang, central Yunnan, China: effects of diet and temperature. *International Journal of Primatology* 29: 1047–1057.
- FAN, P. F., W. XIAO, J.-J. FENG, AND M. B. SCOTT. 2011. Population differences and acoustic stability in male songs of wild western black crested gibbons (*Nomascus concolor*) in Mt. Wuliang, Yunnan. *Folia Primatologica* 82:83–93.
- FAN, P. F., W. XIAO, S. HUO, AND X.-L. JIANG. 2009. Singing behavior and singing functions of black-crested gibbons (*Nomascus concolor jingdongensis*) at Mt. Wuliang, central Yunnan, China. *American Journal of Primatology* 71:539–547.
- FOODEN, J. 1987. Type locality of *Hylobates concolor leucogenys*. *American Journal of Primatology* 12:107–110.
- GARZA, J. C., AND D. S. WOODRUFF. 1994. Crested gibbon (*Hylobates* [*Nomascus*]) identification using noninvasively obtained DNA. *Zoo Biology* 13:383–387.
- GEISSMANN, T. 1989. A female black gibbon, *Hylobates concolor* subspecies, from northeastern Vietnam. *International Journal of Primatology* 10:455–476.
- GEISSMANN, T. 1991. Reassessment of age of sexual maturity in gibbons (*Hylobates* spp.). *American Journal of Primatology* 23:11–22.
- GEISSMANN, T. 1993. Evolution of communication in gibbons (Hylobatidae). Ph.D. dissertation, Zürich University, Zürich, Switzerland.
- GEISSMANN, T. 2002. Duet-splitting and the evolution of gibbon songs. *Biological Reviews* 77:57–76.
- GEISSMANN, T. 2007a. Status reassessment of the gibbons: results of the Asian Primate Red List Workshop 2006. *Gibbon Journal* 3:5–15.
- GEISSMANN, T. 2007b. First field data on the Laotian black crested gibbon (*Nomascus concolor lu*) of the Nam Kan area of Laos. *Gibbon Journal* 3:56–65.
- GEISSMANN, T., AND G. ANZENBERGER. 2009. Hormonal correlates of the ovarian cycle in the yellow-cheeked crested gibbon (*Nomascus gabriellae*), and a review of ovarian cycles in gibbons (Hylobatidae). *Gibbon Journal* 5:61–73.
- GEISSMANN, T., N. X. DANG, N. LORMEE, AND F. MOMBERG. 2000. Vietnam primate conservation status review 2002—part 1: gibbons. Fauna and Flora International Asia Pacific Programme, Indochina Programme, Hanoi, Vietnam.
- GEISSMANN, T., K. GESCHKE, AND B. J. BLANCHARD. 2009. Longevity in gibbons (Hylobatidae). *Gibbon Journal* 5:81–92.
- GEISSMANN, T., AND M. ORGELDINGER. 1995. Neonatal weight in gibbons (*Hylobates* spp.). *American Journal of Primatology* 37: 179–189.
- GIRIRAJAN, S., ET AL. 2009. Sequencing human–gibbon breakpoints of synteny reveals mosaic new insertions at rearrangement sites. *Genome Research* 19:178–190.
- GOUSTARD, M. 1984. Pattern and functions of loud calls in the concolor gibbon. Pp. 404–415 in *The lesser apes: evolutionary and behavioural biology* (H. Preuschoft, D. J. Chivers, W. Y. Brockelman, and N. Creel, eds.). Edinburgh University Press, Edinburgh, United Kingdom.
- GROVES, C. P. 1972. Systematics and phylogeny of gibbons. Pp. 1–89 in *Gibbon and siamang*. Vol. 1. (D. M. Rumbaugh, ed.). Karger, Basel, Switzerland.
- GROVES, C. P. 1984. A new look at the taxonomy of the gibbons. Pp. 542–561 in *The lesser apes: evolutionary and behavioural biology* (H. Preuschoft, D. J. Chivers, W. Y. Brockelman, and N. Creel, eds.). Edinburgh University Press, Edinburgh, United Kingdom.
- GROVES, C. P. 2001. Primate taxonomy. Smithsonian Institution Press, Washington, D.C.
- GROVES, C. P. 2005. Order Primates. Pp. 111–184 in *Mammal species of the world: a taxonomic and geographic reference* (D. E. Wilson and D. M. Reeder, eds.), 3rd ed. Johns Hopkins University Press, Baltimore, Maryland.
- GROVES, C. P., AND Y. WANG. 1990. The gibbons of the subgenus *Nomascus* (Primates, Mammalia). *Zoological Research* 11:147–154.
- GU, Y. 1989. Preliminary research on the fossil gibbons of the Chinese Pleistocene and recent. *Human Evolution* 4:509–514.
- HA, N. M. 2007. Survey for southern white-cheeked gibbons (*Nomascus leucogenys siki*) in Dak Rong Nature Reserve, Quang Tri Province, Vietnam. *Vietnamese Journal of Primatology* 1:61–66.
- HAIMOFF, E. H. 1984a. Acoustic and organizational features of gibbon songs. Pp. 333–353 in *The lesser apes: evolutionary and behavioural biology* (H. Preuschoft, D. J. Chivers, W. Y. Brockelman, and N. Creel, eds.). Edinburgh University Press, Edinburgh, United Kingdom.
- HAIMOFF, E. H. 1984b. The organization of song in the Hainan black gibbon (*Hylobates concolor hainanus*). *Primates* 25:225–235.
- HAMADA, Y., S. MALAIVIJITNOND, P. KINGSADA, AND P. BOUNNAM. 2007. The distribution and present status of primates in the northern region of Lao PDR. *Natural History Journal of Chulalongkorn University* 7:161–191.
- HARLAN, R. 1827. Description of a hermaphrodite orang outhang. *Proceedings of the Academy of Natural Sciences, Philadelphia* 5: 229–236.
- HIRAI, H., Y. HIRAI, H. DOMAE, AND Y. KIRIHARA. 2007. A most distant intergeneric hybrid offspring (Larcon) of lesser apes, *Nomascus leucogenys* and *Hylobates lar*. *Human Genetics* 122:477–483.
- HOLLIHN, U. 1984. Bimanual suspensory behavior: morphology, selective advantages and phylogeny. Pp. 85–95 in *The lesser apes: evolutionary and behavioural biology* (H. Preuschoft, D. J. Chivers, W. Y. Brockelman, and N. Creel, eds.). Edinburgh University Press, Edinburgh, United Kingdom.
- HU, Y., H. XU, AND D. YANG. 1989. The studies on ecology in *Hylobates leucogenys*. *Zoological Research* 10, supplement:61–67 (in Chinese with English summary).
- ILLIGER, C. D. 1811. *Prodromus systematis mammalium et avium additis terminis zoographicis utriusque classis*. C. Salfeld, Berlin, Germany.
- INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE. 1999. International code of zoological nomenclature. 4th ed. International Trust for Zoological Nomenclature, London, United Kingdom.
- INTERNATIONAL UNION FOR CONSERVATION OF NATURE AND NATURAL RESOURCES. 2009. International Union for Conservation of Nature and Natural Resources red list of threatened species. www.iucnredlist.org, accessed 18 January 2009.

- ISHIDA, H., T. KIMURA, M. OKADA, AND N. YAMAZAKI. 1984. Kinesiological aspects of bipedal walking in gibbons. Pp. 297–311 in *The lesser apes: evolutionary and behavioural biology* (H. Preuschoft, D. J. Chivers, W. Y. Brockelman, and N. Creel, eds.). Edinburgh University Press, Edinburgh, United Kingdom.
- JABLONSKI, N. G. 1993. Quaternary environments and the evolution of primates in East Asia, with notes on two new specimens of fossil Cercopithecidae from China. *Folia Primatologica* 60:118–132.
- JABLONSKI, N. G., AND G. CHAPLIN. 2009. The fossil record of gibbons. Pp. 111–130 in *The gibbons, new perspectives on small ape socioecology and population biology* (D. Whittaker and S. Lappan, eds.). Springer, New York.
- JOHNSON, A., S. SINGH, M. DUANGDALA, AND M. HEDEMARK. 2005. The western black crested gibbon *Nomascus concolor* in Laos: new records and conservation status. *Oryx* 39:311–317.
- JUNGERS, W. L. 1984. Scaling the hominoid locomotor skeleton with special reference to lesser apes. Pp. 146–169 in *The lesser apes: evolutionary and behavioural biology* (H. Preuschoft, D. J. Chivers, W. Y. Brockelman, and N. Creel, eds.). Edinburgh University Press, Edinburgh, United Kingdom.
- JUNGERS, W. L., AND J. T. STERN. 1981. Preliminary electromyographical analysis of brachiation in gibbon and spider monkey. *International Journal of Primatology* 2:19–33.
- JUNGERS, W. L., AND J. T. STERN, JR. 1984. Kinesiological aspects of brachiation in gibbons. Pp. 119–134 in *The lesser apes: evolutionary and behavioural biology* (H. Preuschoft, D. J. Chivers, W. Y. Brockelman, and N. Creel, eds.). Edinburgh University Press, Edinburgh, United Kingdom.
- KEELING, M. E., AND H. M. McCLURE. 1972. Clinical management, diseases and pathology of the gibbon and siamang Vol. 2. Pp. 207–249 in *Gibbon and siamang* (D. M. Rumbaugh, ed.). Karger, Basel, Switzerland.
- KLOSS, C. B. 1929. Some remarks on the gibbons, with a description of a new subspecies. *Proceedings of the Zoological Society of London* 1929:113–127.
- KONRAD, R., AND T. GEISSMANN. 2006. Vocal diversity and taxonomy of *Nomascus* in Cambodia. *International Journal of Primatology* 27: 713–745.
- KÜNCKEL D'HERCULAIS, J. 1884. Le gibbon du Tonkin. *Science et Nature* 2:86–90.
- LAN, D. 1989. Preliminary study on the group composition behavior and ecology of the black gibbons (*Hylobates concolor*) in southwest Yunnan. *Zoological Research* 10:119–126.
- LESSON, R.-P. 1827. *Manuel de mammalogie ou histoire naturelle des mammifères*. Collection de Manuels Formant une Encyclopédie des Sciences et des Arts, Librairie de Roret, Paris, France.
- LINDAHL, J. W. 1970. Some thoughts and speculations on the voice. *Proceedings of the Royal Society of Medicine* 63:591–594.
- LONG, V. T., J. DE VOS, AND R. S. CIOCHON. 1996. The fossil mammal fauna of the Lang Trang caves, Vietnam, compared with Southeast Asian fossil and recent mammal faunas: the geographical implications. *Bulletin of the Indo-Pacific Prehistory Association* 14:101–109.
- LUKAS, K. E., ET AL. 2002. Longitudinal study of delayed reproductive success in a pair of white-cheeked gibbons (*Hylobates leucogenys*). *Zoo Biology* 21:413–434.
- LYON, M. W., JR. 1911. Mammals collected by Dr. W. L. Abbott on Borneo and some of the small adjacent islands. *Proceedings of the United States National Museum* 40:53–146.
- MA, S. 1997. Probe on the Chinese origin of gibbons (*Hylobates*). *Acta Theriologica Sinica* 17:13–23.
- MA, S., AND Y. WANG. 1986. The taxonomy and distribution of the gibbons in southern China and its adjacent region—with description of three new subspecies. *Zoological Research* 7:393–410 (in Chinese with English summary).
- MARSHALL, J., AND J. SUGARDITO. 1986. *Gibbon systematics*. Pp. 137–185 in *Comparative primate biology* (D. R. Swindler and J. Erwin, eds.). Vol. I: systematics, evolution, and anatomy. Alan R. Liss, Inc., New York.
- MARTIN, W. C. L. 1841. *A general introduction to the natural history of mammiferous animals: with a particular view of the physical history of man and the more closely allied genera of quadrumanes, or monkeys*. Wright and Co., London, United Kingdom.
- MATSCHIE, P. 1893. Die unterscheidenden merkmale der *Hylobates*-Arten. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin* 1893:209–212.
- MATSUDAIRA, K., AND T. ISHIDA. 2010. Phylogenetic relationships and divergence dates of the whole mitochondrial genome sequences among three gibbon genera. *Molecular Phylogenetics and Evolution* 55:454–459.
- MERKER, B., AND C. COX. 2000. Development of the female great call in *Hylobates gabriellae*: a case study. *Folia Primatologica* 70:97–106.
- MILLER, G. S., JR. 1933. The classification of the gibbons. *Journal of Mammalogy* 14:158–159.
- MILNE-EDWARDS, A. 1868–1874. *Recherches pour servir à l'histoire naturelle des mammifères*. v. 1, E. Martinet, Paris.
- MISCEO, D., ET AL. 2008. Tracking the complex flow of chromosome rearrangements from the Hominoidea ancestor to extant *Hylobates* and *Nomascus* gibbons by high-resolution synteny mapping. *Genome Research* 18:1530–1537.
- MITTERMEIER, R. A., ET AL. 2009. Primates in peril: the world's 25 most endangered primates 2008–2010. *Primate Conservation* 24:1–57.
- MOISSON, P., AND M. BERTHET (EDS). 2007. *European studbook number 2*. Zoo Mulhouse. [www.gibbons.de/maine/index.html](http://www.gibbons.de/maine/index.html), accessed 13 November 2011.
- MONDA, K., R. E. SIMMONS, P. KRESSIRER, B. SU, AND D. S. WOODRUFF. 2007. Mitochondrial DNA hypervariable region-1 sequence variation and phylogeny of the concolor gibbons, *Nomascus*. *American Journal of Primatology* 69:1285–1306.
- MOOTNICK, A. R. 1984. Census of gibbons in North America. Pp. 61–73 in *The lesser apes: evolutionary and behavioural biology* (H. Preuschoft, D. J. Chivers, W. Y. Brockelman, and N. Creel, eds.). Edinburgh University Press, Edinburgh, United Kingdom.
- NADLER, T. 2008. Frankfurt Zoological Society: “Vietnam Primate Conservation Program” and Endangered Primate Rescue Center, Vietnam—report 2007. *Vietnamese Journal of Primatology* 1(2): 81–91.
- NAPIER, J. R. 1963. Brachiation and brachiators. *Symposia of the Zoological Society of London*, 10:183–194.
- NISBETT, R. A., AND R. L. CIOCHON. 1993. Primates in northern Viet Nam: a review of the ecology and conservation status of extant species, with notes on Pleistocene localities. *International Journal of Primatology* 14:765–795.
- NGUYEN, ET AL. 2005. Status of white cheek-crested gibbon (*Nomascus leucogenys*) in North Central of Vietnam. The Great Ape Conservation Fund, U.S. Fish and Wildlife Service and Centre for Natural Resource and Environmental Studies (CRES), Vietnam National University, and Allwetterzoo Münster, Germany and Hanoi, Vietnam (not seen, cited in Bleisch et al., 2008).
- Ogilby, W. 1840. On a new species of gibbon (*Hylobates leucogenys*). *Proceedings of the Zoological Society of London* 1840:20–12.
- OSGOOD, W. H. 1932. *Mammals of the Kelley-Roosevelts and Delacour Asiatic expeditions*. Field Museum of Natural History, Zoological Series 18:193–339.
- PARKAR, U., ET AL. 2006. Direct characterization of *Blastocystis* from faeces by PCR and evidence of zoonotic potential. *Parasitology* 134:359–367.
- PERELMAN, P., ET AL. 2011. A molecular phylogeny of living Primates. *PLoS Genetics* 7:e1001342.
- PILBEAM, D. 2004. The anthropoid postcranial axial skeleton: comments on development, variation, and evolution. *Journal of Experimental Zoology, B. Molecular and Developmental Evolution* 302:241–267.
- POCOCK, R. I. 1927. The gibbons of the genus *Hylobates*. *Proceedings of the Zoological Society of London* 97:719–741.
- PREUSCHOF, H., AND D. DEMES. 1984. Biomechanics of brachiation. Pp. 96–118 in *The lesser apes: evolutionary and behavioural biology* (H. Preuschoft, D. J. Chivers, W. Y. Brockelman, and N. Creel, eds.). Edinburgh University Press, Edinburgh, United Kingdom.
- PROUTY, L. A., P. D. BUCHANAN, W. S. POLLITZER, AND A. R. MOOTNICK. 1983a. *Bunopithecus*: a genus-level taxon for the hoolock gibbon (*Hylobates hoolock*). *American Journal of Primatology* 5:83–87.

- PROUTY, L. A., P. D. BUCHANAN, W. S. POLLITZER, AND A. R. MOOTNICK. 1983b. A presumptive new hylobatid subgenus with 38 chromosomes. *Cytogenetics and Cell Genetics* 35:141–142.
- RENNIE, J. 1838. *The menageries: the natural history of monkeys, opossums, and lemurs*. Vol. 1. Nattali & Bond, London, United Kingdom.
- ROBERTO, R., ET AL. 2007. Molecular refinement of gibbon genome rearrangements. *Genome Research* 17:249–257.
- ROOS, C. 2004. Molecular evolution and systematics of Vietnamese primates. Pp. 23–26 in *Conservation of primates in Vietnam* (T. Nadler, U. Streicher, and H. T. Long, eds.). Frankfurt Zoological Society, Hanoi, Vietnam.
- ROWE, N. 1996. *The pictorial guide to the living primates*. Pogonias Press, New York.
- RUPPELL, J. 2008. The gibbons of Pu Mat National Park in Vietnam. *Gibbon Journal* 4:39–46.
- RUPPELL, J. C. 2010. Vocal diversity and taxonomy of *Nomascus* in central Vietnam and southern Laos. *International Journal of Primatology* 31:73–94.
- SALL, A. A., ET AL. 2005. Frequent infection of *Hylobates pileatus* (pileated gibbon) with species-associated variants of hepatitis B virus in Cambodia. *Journal of General Virology* 86:333.
- SA-NGUANMOO, P., N. THAWORNISUK, P. RIANTHAVORN, A. SOMMANUSTWECHAI, P. RATANAKORN, AND Y. POOVORAWAN. 2010. High prevalence of antibodies against hepatitis A virus among captive nonhuman primates. *Primates* 51:167–170.
- SCHILLING, D. 1984a. Gibbons in European zoos, with notes on the identification of subspecies of concolor gibbon. Pp. 51–60 in *The lesser apes: evolutionary and behavioural biology* (H. Preuschoft, D. J. Chivers, W. Y. Brockelman, and N. Creel, eds.). Edinburgh University Press, Edinburgh, United Kingdom.
- SCHILLING, D. 1984b. Song bouts and duetting in the concolor gibbon. Pp. 390–403 in *The lesser apes: evolutionary and behavioural biology* (H. Preuschoft, D. J. Chivers, W. Y. Brockelman, and N. Creel, eds.). Edinburgh University Press, Edinburgh, United Kingdom.
- SCHLEGEL, H. 1837. *Essai sur la physionomie serpens, partie général*. Arnz & Company, Leiden, The Netherlands.
- SCHLEGEL, H. 1876. *Monographie 40: Simiae*. P. 356 in *Muséum d'Histoire Naturelle des Pays Bas. Revue méthodique et critique des collections d'éposées dans cet établissement*. Tome 7. Brill, Leiden, The Netherlands.
- SCHREBER, J. C. D. 1775. *Die säugethiere in Abbildungen nach der natur mit Beschreibung*. Vol. 1. T. D. Weigel, Leipzig, Germany.
- SCHULTZ, A. H. 1933. Observations on the growth, classification and evolutionary specialization of gibbons and siamangs. *Human Biology* 5:212–255, 385–423.
- SCHULTZ, A. H. 1973. The skeleton of the Hylobatidae and other observations on their morphology. Pp. 1–54 in *Gibbon and siamang*. Vol. 2. (D. M. Rumbaugh, ed.). Karger, Basel, Switzerland.
- SHULTZ, A. H., AND W. STRAUS, JR. 1945. The numbers of vertebrae in primates. *Proceedings, American Philosophical Society* 89: 601–626.
- SNEATH, P. H. A. 1967. Trend surface analysis of transformation grids. *Journal of the Zoological Society of London* 151:65–122.
- TALLENTS, L., T. GEISSMANN, T. D. HOANG, AND L. Q. TRUNG. 2001. Survey for crested gibbons (genus *Nomascus*) in Bach Ma National Park, Viet Nam, April 2001. *Fauna & Flora International, Indochina Programme*, Hanoi, Vietnam.
- TEMBROCK, G. 1974. Sound production of *Hylobates* and *Symphalangus*. Pp. 176–205 in *Gibbon and siamang*. Vol. 3. (D. M. Rumbaugh, ed.). Karger, Basel, Switzerland.
- THINH, V. N., C. HALLAM, C. ROOS, AND K. HAMMERSCHMIDT. 2011. Concordance between vocal and genetic diversity in crested gibbons. *BMC Evolutionary Biology* 11:36.
- THINH, V. N., A. R. MOOTNICK, V. N. THANH, T. NADLER, AND C. ROOS. 2010a. A new species of crested gibbon, from the central Annamite Mountain range. *Vietnamese Journal of Primatology* 4:1–12.
- THINH, V. N., ET AL. 2010b. Phylogeny and distribution of crested gibbons (genus *Nomascus*) based on mitochondrial cytochrome *b* gene sequence data. *American Journal of Primatology* 71:1–8.
- THOMAS, O. 1892. Note on the gibbon of the island of Hainan (*Hylobates hainanus*, sp. n.). *Annals and Magazine of Natural History Series* 6 9(50):145–146.
- TYLER, D. 1993. *The evolutionary history of the gibbon*. Centre of Asian Studies, the University of Hong Kong, Hong Kong, China.
- UJHELYI, M., B. MERKER, P. BUK, AND T. GEISSMANN. 2000. Observations on the behavior of gibbons (*Hylobates leucogenys*, *H. gabriellae*, and *H. lar*) in the presence of mirrors. *Journal of Comparative Psychology* 114:253–262.
- USHERWOOD, J. R., AND J. E. A. BERTRAM. 2003. Understanding brachiation: insight from a collisional perspective. *Journal of Experimental Biology* 206:1631–1642.
- VERECKE, E., K. D'AOUT, L. VAN ELSACKER, D. DE CLERCQ, AND P. AERTS. 2005. Functional analysis of the gibbon foot during terrestrial bipedal walking: plantar pressure distributions and three-dimensional ground reaction forces. *American Journal of Physical Anthropology* 128:659–669.
- VERECKE, E. E., AND P. AERTS. 2008. The mechanics of the gibbon foot and its potential for elastic energy storage during bipedalism. *Journal of Experimental Biology* 211:3661–3670.
- WEIGL, R. 2005. Longevity of mammals in captivity: the living collections of the world, a list of mammalian longevity in captivity. Schweizerbart, Stuttgart, Germany.
- WHITTAKER, D. J., J. C. MORALES, AND D. J. MELNICK. 2007. Resolution of the *Hylobates* phylogeny: congruence of mitochondrial D-loop sequences with molecular, behavioral, and morphological data sets. *Molecular Phylogenetics and Evolution* 45:620–628.
- WRIGHT, K. A., N. J. STEVENS, H. H. COVERT, AND T. NADLER. 2008. Comparisons of suspensory behaviors among *Pygathrix cinerea*, *P. nemaeus*, and *Nomascus leucogenys* in Cuc Phuong National Park, Vietnam. *International Journal of Primatology* 29: 1467–1480.
- WU, R. K., AND Y. R. PAN. 1984. A late Miocene gibbon-like primate from Lufeng, Yunnan Province. *Acta Anthropologica Sinica* 3: 193–200.
- WU, R. K., AND Y. R. PAN. 1985. Preliminary observations on the cranium of *Laccopithecus robustus* from Lufeng, Yunnan with reference to its phylogenetic relationship. *Acta Anthropologica Sinica* 4:7–12.
- ZHAO, Z., X. LI, AND L. WANG. 1981. Human fossils and associated fauna from Jiulang Shan Hill, Guanxi. *Vertebrate Palasiatica* 19:48–54.
- ZHOU, J., B. P. L. CHAN, AND F.-W. WEI. 2008a. Responses to intergroup encounters of the Hainan gibbon *Nomascus hainanus*. *Acta Metallurgica Sinica* 29:667–673.
- ZHOU, J., F.-W. WEI, M. LI, C. B. P. LOK, AND D. WANG. 2008b. Reproductive characters and mating behaviour of wild *Nomascus hainanus*. *International Journal of Primatology* 29:1037–1046.
- ZIHLMAN, A. L., A. R. MOOTNICK, AND C. E. UNDERWOOD. 2011. Anatomical contributions to hylobatid taxonomy and adaptation. *International Journal of Primatology* 32:865–877.

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