1 Taxonomy, Ecology and Conservation of Cao Vit Gibbon (*Nomascus nasutus*) since Its Rediscovery

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1.1 Introduction

Gibbons (family Hylobatidae) are small arboreal apes that inhabit tropical and subtropical forests of Southeast Asia, Northwest India and Bangladesh. They are well known for their coordinated vocal duets, small group sizes and acrobatic locomotion, all three characteristics being distinct from great apes (Fan and Bartlett, 2017). All gibbon species prefer fruits when they are available, and rely heavily on ripe juicy fruit (Bartlett, 2011). Because of their critical ecological requirements and low reproductive rate, gibbons are very sensitive to habitat degradation and destruction and to illegal hunting. The Hainan gibbon (Nomascus hainanus), endemic to Hainan Island of China, is the most endangered primate species in the world. Its population declined to nine known individuals in two groups in the 1980s (Liu et al., 1989), but has since increased to more than 30 individuals in five groups after intensive conservation management (Chan et al., 2020). Except for N. hainanus, populations of all other gibbon species are declining (IUCN, 2021). In addition, all gibbon species are suffering habitat loss; on average, each species has lost 11 (range 3-28) per cent of its potential habitat between 2000 and 2014 (Fan and Bartlett, 2017). Consequently, except for the eastern hoolock gibbon (*Hoolock leuconedys*), which is described as vulnerable, all the other 19 species recognised by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species are listed as endangered (15 species) or critically endangered (four species) (IUCN, 2020). However, gibbons receive little conservation and research attention relative to the great apes (Fan and Bartlett, 2017).

Against the background of a global conservation crisis, the rediscovery of the Cao vit gibbon (*Nomascus nasutus*) in 2002 (La *et al.*, 2002) was one of the most exciting events for gibbon conservationists in the twenty-first century. However, its importance was largely hindered by disputation of its species status. Since its rediscovery, a great deal of research and conservation actions have been taken to conserve this species and its habitat. This chapter provides a comprehensive review of its taxonomy, ecology and conservation.

1.2 Taxonomy and Morphology of Cao Vit Gibbon (*N. nasutus*)

At present, there are seven species of crested gibbons (genus *Nomascus*) (Thinh *et al.*, 2010a; Mootnick and Fan, 2011; Mittermeier *et al.*, 2013), including three species of

black gibbons (black crested gibbon, *Nomascus concolor*; *N. hainanus*; and *N. nasutus*) and four species of buff-cheeked gibbons (northern white-cheeked gibbon, *N. leucogenys*; southern white-cheeked gibbon, *N. siki*; northern buff-cheeked gibbon, *N. annamensis*; and yellow-cheeked gibbon, *N. gabriellae*). As the adult males are almost completely black and their morphological differences are subtle (Figure 1.1a–c), the taxonomy of black gibbons has long been under dispute.

Kunckel d'Herculais (1884) first described a specimen of black gibbon from northeastern Vietnam as Hylobates nasutus (there was only one genus -Hylobates – in the Hylobatidae family at that time; see Fan, 2012). Another new species, H. hainanus, was described from a captive male black gibbon from Hainan Island by Thomas (1892). However, de Pousargues (1904) and Pocock (1927) both thought H. nasutus and H. hainanus were synonyms of H. concolor, a species first described by Harlan (1826). Delacour (1951) recognised two subspecies in H. concolor: H. c. concolor in the mainland and H. c. nasutus on Hainan Island. Later, H. c. hainanus was used for the island subspecies (Simonetta, 1957; Groves, 1972). In 1983, Dao Van Tien reported that both of these subspecies were distributed in the mainland of Vietnam and he was the first to suggest the Red River as the geographical boundary between them (Dao, 1983). Geissmann (1989) described a female crested gibbon at the Tierpark in Berlin, which originated from the east bank of the Red River in northeastern Vietnam. This female resembled H. c. concolor in some characteristics but was different in others, and he therefore suggested that this female might represent a new subspecies. Groves and Wang (1990) and Geissmann (1995) considered H. c. nasutus from the east bank of the Red River in the mainland as a distinct subspecies of H. c. hainanus on the island. In 2004, Brandon-Jones et al. (2004) elevated N. nasutus as a species, including N. n. nasutus and N. n. hainanus, different from N. concolor (Nomascus was elevated to a genus by Roos and Geissmann in 2001), and first assigned an English name for N. c. nasutus as the eastern black crested gibbon. However, the taxonomy of black gibbons from the east bank of the Red River remained unsolved because gibbons were thought to be extinct from this area in both China (Tan, 1985) and Vietnam (Geissman et al., 2003).

In 2002, Fauna and Flora International (FFI) Vietnam discovered a small gibbon population in a karst forest patch in Trung Khanh district of Cao Bang Province, Vietnam, close to the China–Vietnam international border (La *et al.*, 2002). This population was located on the east bank of the Red River, and it was initially reported as a population of '*Nomascus* sp. cf. *nasutus*' (La *et al.*, 2002). In 2006, another three groups were discovered in the neighbouring forest patch on the China side (Chan *et al.*, 2008). Since the rediscovery of this population, more data have been collected regarding its morphology (Mootnick and Fan, 2011), vocalisations (Thinh *et al.*, 2010b, 2011; Feng *et al.*, 2013) and genetics (Monda *et al.*, 2007; Thinh *et al.*, 2010a, 2011).

Although males of all three species are black, they can be easily distinguished by the shape of the crest, colour of the chest and visibility of the ear (Figure 1.1a–c). *Nomascus concolor* and *N. hainanus* have a sharp crest while *N. nasutus* has a short crest, creating a round face. In addition, males of *N. nasutus* have a brown chest.

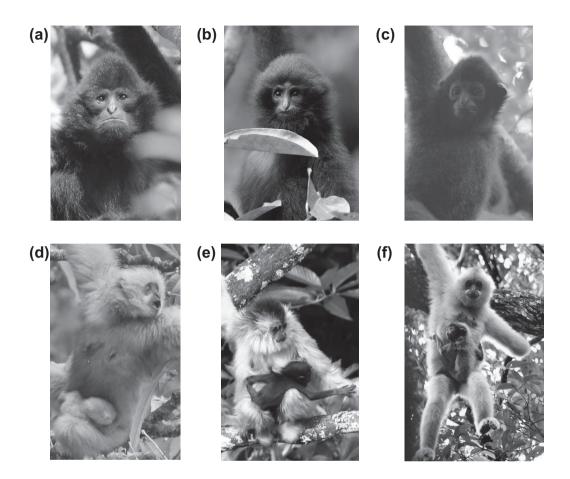


Figure 1.1 Diagnostic morphological characteristics of three black crested gibbon species (black crested gibbon, *N. concolor*; Cao vit gibbon, *N. nasutus*; Hainan gibbon, *N. hainanus*). *Nomascus concolor*: male has a sharp crest (a); female has black chin and a black abdomen with ageing; newborn infant is buff yellow (d). *Nomascus nasutus*: male has a short crest and a brown chest (b); female has a white face ring and big black crown; newborn infant is black (e). *Nomascus hainanus*: male has a moderate crest and ears are visible (c); female has a round face and yellow chin; newborn infant is yellow with black forehead (f). Sources: (a) Zhao Chao; (b) Huang Songhe; (c) Zhao Chao; (d) Tang Yun; (e) Huang Songhe; (f) Bosco P.L. Chan.

Probably due to the short hair in *N. hainanus*, the ears are visible from the front (Mootnick and Fan, 2011; Figure 1.1). There are also obvious morphological differences in adult females between *N. nasutus*, *N. concolor* and *N. hainanus* (Mootnick and Fan, 2011). Adult females of *N. nasutus* have an obvious white face ring and the black crown extends past the nape and across the shoulders. Adult females of *N. concolor* have a small crown, black chin and black abdomen with age. Adult females of *N. hainanus* have yellow chins and round faces (Mootnick and Fan, 2011; Figure 1.1d–f). Noticeably, the newborn infant of *N. nasutus* is black. The newborn infant of

N. hainanus is grey to buff yellow with some black hairs on the forehead, while the newborn infant of all other *Nomascus* species are buff yellow (Mootnick and Fan, 2011; Figure 1.1d–f).

Both male and female sequences produced in the coordinated duet are also distinguishable (Thinh *et al.*, 2010b, 2011; Feng *et al.*, 2013). Interestingly, not only are male and female acoustic spectrograms different, but also the ways in which males and females coordinate their singing. In *N. nasutus*, males continue to produce 'aa' notes (a short note produced by males) when females start singing the great call sequence, and males respond to the female great call with a coda that consists of more modulated notes. In *N. concolor*, males stop singing soon after females have sung the great call and respond with a coda that is similar to the normal male sequence after a female has finished the great call. In *N. hainanus*, males stop when the females begin singing the great call, but the male will respond before the end of the great call sequence (Figure 1.2). Whether this difference in structure is genetically determined or learned by young gibbons (i.e. culture) remains unknown and needs more investigation.

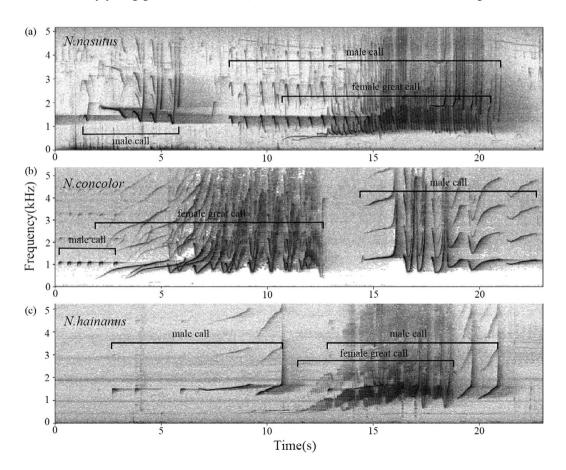


Figure 1.2 Duet sequence produced by three black crested gibbons: (a) Cao vit gibbon, *N. nasutus*; (b) black crested gibbon, *N. concolor*; (c) Hainan gibbon, *N. hainanus*.

Furthermore, genetic studies also support the theory that these three taxa are distinct species (Monda *et al.*, 2007; Thinh *et al.*, 2010a, 2011). Thinh *et al.* (2010a) showed that the divergence between *N. hainanus* and *N. nasutus* is actually the deepest within *Nomascus*, and this sister-species pair is a sister clade to all other *Nomascus* gibbons. They represent the most divergent and evolutionarily distinct species within the genus. If so, the black infant of *N. nasutus* should be an ancestral trait of *Nomascus*. How and why newborn infants have evolved a white-grey to buff yellow natal coat in other *Nomascus* species needs further investigation. 'Cao vit gibbon', a name used by local people in some areas of northeastern Vietnam, was used to represent this population in Vietnam and since 2004 has been accepted by primatologists (La and Trinh, 2004).

1.3 Distribution and Population

Nomascus nasutus was originally thought to be widespread east of the Red River in both southern China and northern Vietnam, which is dominated by a karst limestone formation (Zhou et al., 2003; Do Tuyet, 2010). However, because of uncontrolled logging and agricultural encroachment (Do Tuyet, 2010), much of the forest in this area has been severely degraded. As a result, the N. nasutus population had declined rapidly and was considered extinct in China in the 1950s (Tan, 1985) and in Vietnam in 1960s (Geissmann et al., 2003). Numerous field and interview surveys were conducted during the 1990s in the previous range of the species in Vietnam, but no population was confirmed (reviewed in La and Trinh, 2004) until a small remnant population was rediscovered by an FFI survey team in Trung Khanh district of Cao Bang Province, Vietnam, in 2002 (La et al., 2002, Figure 1.3). After that, several surveys were conducted at the site and a population of up to 10 groups was confirmed (Geissmann et al., 2003; Trinh, 2004; La, 2005; Vu et al., 2005). In 2006, a small population with three groups was observed in the same forest patch on the China side (Chan et al., 2008). To obtain accurate information of population size in both countries, two transboundary surveys were conducted in 2007 and 2016. The surveys indicated that there were 17–18 groups including 102–110 individuals in 2007, and this population increased to 20–22 groups with 107–136 individuals in 2016 (Ma et al., 2019; Figure 1.3), making it the second rarest ape species in the world, after N. hainanus (Zhou et al., 2005). It is now listed as critically endangered on the IUCN's Red List of Threatened Species (IUCN, 2020), and considered one of the 'world's 25 most endangered primates' (Long and Nadler, 2009).

1.4 Habitat and Climate

The last refuge of *N. nasutus* is a karst forest patch that is bordered by two branches of the Quay Son River $(22^{\circ} 49' 59'' \text{ N}, 106^{\circ} 22' 35'' \text{ E}, 486–926 \text{ m}$ above sea level; Fan *et al.*, 2013a). However, there are historical gibbon records (e.g. in Difangzhi) from

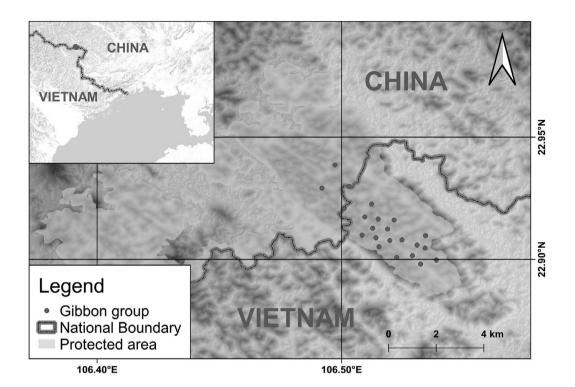


Figure 1.3 Distribution of the only known Cao vit gibbon (*Nomascus nasutus*) population along the China–Vietnam international border.

widely across Guangxi Province, showing a wider distribution of gibbons that may well have been this species, and presumably reported from landscapes that were not just karst. This refuge is characterised by a typical karst limestone landscape consisting of densely packed outcrops, sharp-peaked mountains with very steep slopes and ridges, doline depressions and interconnected collapsed valleys. The site is surrounded by broad alluvial valley bottoms consisting mainly of cultivated land, settlements and secondary vegetation on isolated karst features (Fan *et al.*, 2013a). At first glance, the karst forest habitat of *N. nasutus* is a highly unusual gibbon habitat; besides *N. nasutus*, only two gibbon populations are known to live in karst forest, namely the white-cheeked gibbons *N. siki* and *N. leucogenys* in Phong Nha-Ke Bang National Park in Vietnam (Ruppell, 2007).

The forest was not protected before the rediscovery of the species and was degraded by intensive human activities (as indicated by charcoal-making signs in nearly every valley). Local people used the forest for timber and fuelwood collection, charcoal production, agricultural cultivation, livestock grazing and food gathering before the reserves were established (La and Trinh, 2004; Fan *et al.*, 2011). The mean canopy height in the site was 10.5 m, with 71 per cent of trees between 5 and 10 m high (Fan *et al.*, 2013a), making it the gibbon habitat with the lowest canopy height reported. However, tree density was high and the number of

trees with diameter at breast height of 10 cm or more in one 20×20 m plot was on average 21 (range 9–36, n = 44). Plant diversity was also high, with 113 tree species and 46 woody liana and epiphyte species in 113 genera in 60 families recorded in 44 plots (Fan *et al.*, 2011).

Climate in the area shows great seasonal and annual variation. The monthly mean temperature varied from 9.8 °C in February 2008 to 26.6 °C in September 2008 (Fan *et al.*, 2010). The lowest temperature was below 8 °C and mean monthly temperature was below 20 °C between November and March, during which rainfall was very limited. The rainy season normally starts from May to October with the coming of monsoon, but annual variation exists. Annual precipitation was 1804 mm in 2008 and 1363 mm with less rainfall between August and October in 2009 (Fan *et al.*, 2010).

Fruit production shows seasonal variation, with more fruit availability between May and September (Fan *et al.*, 2012), generally in accordance with the rainy season. The abundance of buds peaks in April. Figs do not show the obvious pattern of seasonal abundance observed in fruits and buds, but few figs were available between March and April 2009. The mature leaves eaten by the gibbons were available throughout the year (Fan *et al.*, 2012).

1.5 Habitat Use and Locomotion Pattern

Nomascus nasutus occupies home ranges of approximately 130 ha (Fan *et al.*, 2010), which is comparable with the home range size of gibbons living in northern seasonal habitats (*N. hainanus*, 300–500 ha, Liu *et al.*, 1989; *N. concolor*, 151 ha, Fan and Jiang, 2008a; *H. leuconedys*, 93 ha, Zhang *et al.*, 2014), but substantially larger than that of gibbons living in tropical forests (on average 40 ha, reviewed in Bartlett, 2011). Important food trees were patchily distributed in their habitat (Fan *et al.*, 2015). In order to secure food requirements across different seasons, *N. nasutus* occupies a large home range to cover the distribution of different food species. Low densities of important food species caused by human activities may also explain why *N. nasutus* occupies such large home range in *N. nasutus* is likely natural for the species rather than an artefact of a remnant population existing in a possibly suboptimal habitat refuge (Bryant *et al.*, 2015).

Although canopy height is noticeably lower compared with the habitat of other gibbons, the combination of locomotion modes performed by *N. nasutus* is dominated by brachiation (59.6 per cent) for foraging and travelling in the canopy, like other gibbons (Fleagle, 1976; Gittins, 1983; Cannon and Leighton, 1994; Fan *et al.*, 2013a). *Nomascus nasutus* climbs (including bridging) more often (20.5 per cent) and walks less often (1 per cent) compared with other gibbon species, except the largest gibbon, the siamang *Symphalangus syndactylus* (reviewed in Fan *et al.*, 2013a). Differences in body weight and support size may explain the differences in locomotion patterns observed. The larger the size of the gibbons, the less likely they are able to brachiate and jump because large animals are more liable to break supports and risk falling. The

structure of the lower karst forest may also cause this difference. As previously mentioned, tree density is still high in this site. Gibbons always climb in trees with dense branches (personal observation of several gibbon species); in contrast, tall trees with large branches which provide support for walking are rare in their habitat. Brachiation is energy conserving because of the alternating transformation of potential energy into kinetic energy and vice versa (Fleagle, 1974; Preuschoft and Demes, 1984; Bertram *et al.*, 1999), and has less energetic cost than climbing (Jungers and Stern, 1984). Therefore, *N. nasutus* may spend more energy when travelling compared with other gibbons.

Nomascus nasutus confines locomotion chiefly to the middle stratum of 5-10 m height (84.4 per cent) because the canopy connectivity of this stratum is greater than that of the upper canopy (>10 m in height), and moving close to the ground in the lower stratum may be dangerous due to the presence of terrestrial predators. Branches (2–10 cm) are most frequently used as supports (62.4 per cent), followed by twigs (<2 cm, 25.1 per cent), lianas (10 per cent) and boughs (>10 cm, 2.5 per cent) (Fan *et al.*, 2013a).

Nomascus nasutus also shows age–sex variation in their locomotion pattern (Fan *et al.*, 2013a). Climbing and bridging (with at least one limb attached for support) are thought to be safer than faster brachiation and leaping. Compared with males and juveniles, females climb and bridge more often regardless of whether they are carrying infants or not. In summary, the ability to negotiate low trees and small branches enables *N. nasutus* to efficiently forage in their degraded karst forest and defend their territories.

1.6 Diet Flexibility

During 2,432 observation hours, *N. nasutus* were observed to consume items from 81 plant species (approximately 50 per cent of total plant species recorded on the site) and several animal species (Fan *et al.*, 2011). They did not use plant species based on their abundance, and relied heavily on some uncommon species, such as *Ficus hookeriana, Spondias lakonensis* and *Choerospondias axillaris* (Fan *et al.*, 2011). However, these species have been targeted by local people and densities are therefore low in the forest (Fan *et al.*, 2011).

Fig species (genus *Ficus*) and liana species play a very important role in the diet of *N. nasutus*. The gibbons have been observed consuming eight different fig species. However, they consume three of them more often than others and these species make up a large proportion of their diet (*Ficus glaberrima*, 13 per cent; *Ficus hookeriana*, 6.6 per cent; *Ficus microcarpa*, 1.9 per cent; Fan *et al.*, 2011). *Nomascus nasutus* consume *F. glaberrima* and *F. hookeriana* whenever they are available. They are considered important monthly food items, defined as the minimum number of foods comprising 75 per cent of the monthly diet (Hill, 1997) during a 23-month study (Fan *et al.*, 2011). The gibbons occasionally consume other fig species, and as a result these gibbons do not show a positive relationship between total fig availability and

consumption (Fan *et al.*, 2012). However, nutritional analyses have shown that these two species do not contain more crude protein, water-soluble sugar or crude fat compared with other fig species (Ma *et al.*, 2017).

Twenty-seven liana species contributed 18.9 per cent of the diet of *N. nasutus* (Appendix A in Fan *et al.*, 2011). *Tetrastigma pubinerve* provides fruit between October and December and young leaves year round. In the study by Fan *et al.* (2011), it proved to be another important species for *N. nasutus* in 7 out of 23 months, and it contributed more than 5 per cent to the overall diet. *Trichosanthes kirilowii* produces young leaves year round and *N. nasutus* consumes the young leaves of this species between December and February (total contribution, 3.1 per cent; Fan *et al.*, 2011).

Nomascus nasutus is less frugivorous compared with other gibbons living in southern tropical forest (reviewed in Bartlett, 2011), but their diet of fruit is similar to that of N. concolor (Fan et al., 2009), H. leuconedys (Fan et al., 2013b) and S. symphalangus (reviewed in Bartlett, 2011). This is mainly caused by the unavailability of fruit between December and April (Fan et al., 2012). Like all other gibbons (Bartlett, 2011), N. nasutus prefer fruit when it is available (Fan et al., 2012). Here we provide proportional diet details to supplement the actual feeding times published in Fan et al. (2012). Nomascus nasutus spent more than 60 per cent of their feeding time on fruit between May and October when fruit was more abundant, except in July for one group (Figure 1.4). Leaves and buds contributed less than 2 per cent between June and September for both groups (Figure 1.4). They shifted to a diet consisting mainly of leaves and buds (>50 per cent) when fruit was not abundant between December and April (Figure 1.4). Leaves and bud consumption reached a peak in March (>95 per cent) while the proportion of fruit and figs was less than 2 per cent. Animal prey, especially invertebrates, contributed substantially between July and September during the rainy season. As a result, fruit including figs accounted for 52 per cent of the annual proportional diet; the remainder was made up of leaves and buds (35.2 per cent), animals (9.2 per cent) and others (averaged from two groups in figure 3 in Fan et al., 2012).

1.7 Activity Budget

Nomascus nasutus left their sleeping trees just after sunrise, and entered sleeping trees on average 88 minutes before sunset (Fei *et al.*, 2012). On average, they spent 10.4 hours outside sleeping trees during which they spent 37.3 per cent resting, 23.9 per cent feeding, 24.4 per cent travelling and 14.2 per cent engaging in social behaviour (averaged from monthly proportional activity time budget of two groups between January and December 2009). In comparison with other gibbons, *N. nasutus* did not increase active time (Table_1.1) or feeding time (reviewed in Fan *et al.*, 2008). Increased foraging time would translate into much more intensive use of the available resources, and thus gibbons appear to ensure continued access to highly favoured resources by exploiting their ranges less intensively (Bartlett, 2009).

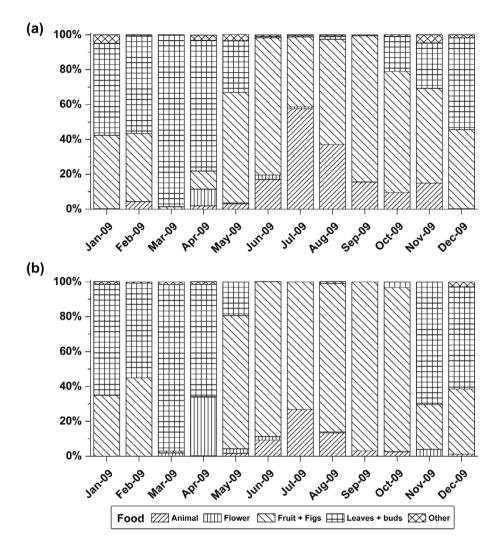


Figure 1.4 Proportional diet of two Cao vit gibbon (*N. nasutus*) groups between January and December 2009.

Nakayama *et al.* (1971) reported that the energy expenditure of outdoor-living captive Japanese macaques (*Macaca fuscata*) at 5.2 °C is 2.5 times greater than that at 29.5 °C. Although similar research has never been conducted in gibbon species, it seems there are thermoregulatory costs for *N. nasutus* at high altitudes in cold months: the gibbons increased resting time and decreased time engaging in social activities (Fan *et al.*, 2012); in addition, they always huddled together in the sunshine in the tops of trees (personal observation) and huddled together in sleeping trees in cold months (Fei *et al.*, 2012). These behavioural strategies were also adopted by *N. concolor*, *H. leuconedys* and skywalker hoolock gibbons (*Hoolock tianxing*) living in montane forests (Fan *et al.*, 2008; Fan *et al.*, 2013b; Fei *et al.*, 2019).

| Species | Study site | Time leaving sleeping trees after sunrise (minutes) | Time entering sleeping trees before sunset (minutes) | Active time period (hours) | Reference |
|--------------------------|-----------------------------------|---|---|----------------------------------|-----------------------|
| Nomacus concolor | Dazhaizi, Wuliangshan, China | 33 | 128 | 8.6 | Fan and Jiang (2008b) |
| Nomascus nasutus | Bangliang, Jingxi, China | 4 | 88 | 10.1 | Fei et al. (2012) |
| Hoolock hoolock | Lawachara and Chunati, Bangladesh | -2 | 153 | | Ahsan (2001) |
| Hoolock leuconedys | Nankang, Gaoligong, China | | | 9.1 | Fan et al. (2013b) |
| Symphalangus syndactylus | Ulu Sempam | A few minutes | 120 | 10.1 | Chivers (1974) |
| | Kuala Lompat | -12 | 126 | 11.1 | |
| Hylobates agilis | Sungai Dal | 7 | | | Gittins (1982) |
| Hylobates klossii | Siberut | 2 | 85 | | Whitten (1980) |
| Hylobates lar | Khao Yai, Thailand | -15 to +15 | 204 | 8.7 | Bartlett (2009) |

 Table 1.1 Time leaving and entering sleeping trees and active period of different gibbon species.

1.8 Social Structure and Reproduction

Most groups consisted of one adult male and two adult females, and the mean group size was 6.3 individuals in 2007 and 6.4 in 2016 (Ma *et al.*, 2019). According to intensive population monitoring of three groups in China, both females bred repeatedly (Fan *et al.*, 2015). The inter-birth interval was 31 months (range 23–38 months, n = 8), which is comparable to other gibbon populations (Fan *et al.*, 2015).

1.9 Conservation

Since the rediscovery of this population, conservation activities including the establishment of patrol teams, livestock removal (e.g. goats in Vietnam), fuelwood plantation, energy-saving stove construction, conservation education and ecological research have been implemented by FFI, our research team and local governments in both countries (Ma *et al.*, 2019). Transboundary cooperation between the governments of China and Vietnam was established to counter wildlife hunting, protect against forest fires and exchange experience on monitoring, programme management, public education and law enforcement (Ma *et al.*, 2019).

No hunting of gibbons has been reported since the discovery of the species. The Cao Vit Gibbon Conservation Area (CVGCA) was established in Vietnam in 2007. In China, the Bangliang Gibbon Nature Reserve was established in 2009 and was upgraded to a National Nature Reserve status in 2013. All suitable habitat currently used by *N. nasutus* has been legally protected by these reserves. Charcoal making, fuelwood collection and trap setting disappeared completely. Non-timber production has only occasionally occurred inside the reserves. No forest has been cleared for cultivation but some corn fields were maintained inside reserves. The current main threat to *N. nasutus* habitat is cattle grazing in China (Ma *et al.*, 2019). However, with the construction of a patrol road inside the nature reserve by border armies in 2012, it is easier for local people to graze their goats and cows inside the forest. The effect of grazing must be evaluated. Because of the strict conservation of this gibbon population and their habitat in the past decade, sympatric macaque (rhesus macaque, Macaca mulatta; Assam macaque, M. assamensis; and stump-tailed macaque, M. arctoides) populations have increased rapidly. Increased macaque populations may compete for food with gibbons in this small forest patch, which deserves more investigation and research (Chen et al., 2020).

Habitat evaluation and a population viability analysis suggested that this population is close to its carrying capacity (Fan *et al.*, 2013c). Remote sensing and geographic information system techniques estimated the high-quality forest in the area to be 2,176.8 ha (Fan *et al.*, 2013c). Given that the home range of one group is approximately 130 ha (Fan *et al.*, 2010) and that the area used exclusively by the group is 107 ha (Fei *et al.*, 2012), this forest can support approximately 20 groups. It can support approximately 26 groups if the low-quality habitat was rehabilitated to support gibbons. In 2016, 20–22 groups were recorded in this area (Ma *et al.*, 2019), suggesting it was very close to reaching the carrying capacity. Two potential habitats were located in a neighbouring forest. These potential habitats connected with the current gibbon habitat by a narrow forest corridor (900 m in length) above an underground river (Fan *et al.*, 2013c). Forest quality in potential habitats was not as good as gibbon habitat, but fine-scale habitat surveys have not yet been conducted. As this forest patch is the last habitat for *N. nasutus*, we suggested that it should be strictly protected and any grazing and agriculture should be prohibited (Fan *et al.*, 2013c).

Habitat restoration to increase carrying capacity is urgently required for *N. nasutus* conservation (Fan *et al.*, 2013c). Because natural regeneration of karst forest takes a long time and large food trees have been extracted in peripheral areas whilst other species have remained, planting indigenous important food species in suitable degraded habitats to accelerate forest restoration was suggested (Fan *et al.*, 2011). Currently, the two potential habitats, mostly in Vietnam, are outside the CVGCA and have not been protected. There is only a narrow corridor connecting these potential habitats and the current gibbon habitat. We suggest that the Vietnam government expands the CVGCA in order to protect this corridor and the potential habitats (Fan *et al.*, 2013c).

1.10 Conclusions

Nomascus nasutus is a distinct species of *N. concolor* and *N. hainanus*. There is only one confirmed population of approximately 120 individuals surviving in a small karst forest along the China-Vietnam border, making it the second rarest ape species in the world. Although their habitat has been degraded by human activities, they seem well adapted to life in karst forest and have demonstrated a series of adaptive behavioural strategies, including (1) maintaining similar locomotor patterns as other gibbons while using smaller supports in lower forest; (2) consuming diverse food types and species, and digesting and obtaining energy from fallback foods (leaves) when preferred foods (fruit) are not available in winter; (3) occupying a large home range in response to the patchy distribution and low density of important food species and (4) increasing resting and huddling together in winter to conserve energy. However, the deaths of two juveniles in a cold winter (Fan et al., 2010) suggest that N. nasutus might face a serious energy stress in winter. Future research should focus on (1) long-term population monitoring to obtain life-history and reproductive parameters of this population, (2) techniques to restore the karst forest, (3) evaluating impacts of goat grazing on habitat restoration, (4) evaluating impacts of increasing human disturbance along the border patrol road on gibbon behaviour and (5) evaluating the impacts of intra- and inter-species food competition on the reproductive and social systems of N. nasutus. Habitat conservation and restoration is crucial for the long-term survival of this population and planting indigenous important food species in degraded sites should be considered a part of the long-term management of the site. As this population and its habitat cross the international border between China and Vietnam, conservation of this species would benefit from the close cooperation between conservation agencies in the two countries.

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References

- Ahsan, M.F. (2001). Socio-ecology of the hoolock gibbon (*Hylobates hoolock*) in two forests of Bangladesh. In *The Apes: Challenges for the 21st Century*, Brookfield Zoo, May 10–13, 2000, Conference Proceedings. Chicago Zoological Society, Brookfield, IL: 286–299.
- Bartlett, T.Q. (2009). *The Gibbons of Khao Yai: Seasonal Variation in Behaviour and Ecology*. Allyn and Bacon, Boston.
- Bartlett, T.Q. (2011). The Hylobatidae, small apes of Asia. In Campbell, C.J., Fuentes, A., Mackinnon, K.C., Bearder, S.K. and Stumpf, R.M. (eds.), *Primates in Perspective*, 2nd ed. Oxford University Press, New York: 300–312.
- Bertram, J.A., Ruina, A., Cannon, C.E., Chang, Y.H. and Coleman, M.J. (1999). A point-mass model of gibbon locomotion. *Journal of Experimental Biology*, 202: 2609–2617.
- Brandon-Jones, D., Eudey, A.A., Geissmann, T., et al. (2004). Asian primate classification. International Journal of Primatology, 25: 97–164.
- Bryant, J.C., Olson, V.A., Chatterjee, H.J. and Turvey, S.T. (2015). Identifying environmental versus phylogenetic correlates of behavioural ecology in gibbons: implications for conservation management of the world's rarest ape. *BMC Evolutionary Biology*, 15: 171.
- Cannon, C.H. and Leighton, M. (1994). Comparative locomotor ecology of gibbons and macaques: selection of canopy elements for crossing gaps. *American Journal of Physical Anthropology*, 93: 504–524.
- Chan, B.P.L., Tan, X.F. and Tan, W.J. (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.
- Chan, B.P.L., Lo, Y.F.P. and Mo, Y. (2020). New hope for the Hainan gibbon: formation of a new group outside its known range. *Oryx*, 54: 296.
- Chen, Y., Ma, C., Yang, L., et al. (2020). Asymmetric competition between sympatric endangered primates affects their population recovery. *Biological Conservation*, 248: 108558.
- Chivers, D.J. (1974). *The Siamang in Malaya: A Field Study of a Primate in a Tropical Forest*. Contributions to Primatology Vol. 4. Karger, Basel.
- Dao, V.T. (1983). On the north Indochinese gibbons (*Hylobates concolor*) (Primates: Hylobatidae) in North Vietnam. *Journal of Human Evolution*, 12: 367–372.

Delacour, J. (1951). La systématique des Gibbons Indochinois. Mammalia, 15: 118-123.

- de Pousargues, E. (1904). Mammifères de l'Indo-Chine. In Pavie, A. (ed.), Mission Parle Indo-Chine 1879–1895. Études Diverses, III. Recherches sur l'Histoire Naturelle de l'Indo-Chine Orientale. Ernest Leroux, Paris: 510–549.
- Do Tuyet. (2010). Characteristics of karst ecosystems of Vietnam and their vulnerability to human impact. *Acta Geologica Sinica*, 75: 325–329.
- Fan, P. (2012). Taxonomy and conservation status of gibbons in China. Acta Theriologica Sinica, 32: 248–258.
- Fan, P. and Bartlett, T.Q. (2017). Overlooked small apes need more attention! American Journal of Primatology, 79: e22658.
- Fan, P. and Jiang, X.L. (2008a). Effects of food and topography on ranging behavior of black crested gibbon (*Nomascus concolor jingdongensis*) in Wuliang Mountain, Yunnan, China. *American Journal of Primatology*, 70(9): 871–878.
- Fan, P. and Jiang, X.L. (2008b). Sleeping sites, sleeping trees and sleep-related behavior of black crested gibbons (*Nomascus concolor jingdongensis*) at Mt. Wuliang, Yunnan, China. *American Journal of Primatology*, 70(2): 153–160.
- Fan, P., Ni, Q.Y., Sun, G.Z., Huang, B. and Jiang, X.L. (2008). Seasonal variations in the activity budget of black crested gibbons (*Nomascus concolor jingdongensis*) at Mt. Wuliang, Central Yunnan, China: effects of diet and temperature. *International Journal of Primatology*, 29(4): 1047–1057.
- Fan, P., Ni, Q.Y., Sun, G.Z., Huang, B. and Jiang, X.L. (2009). Gibbons under seasonal stress: the diet of the black crested gibbons (*Nomascus concolor*) on Mt. Wuliang, Central Yunnan. *Primates*, 50(1): 37–44.
- Fan, P., Fei, H.L., Xiang, Z.F., et al. (2010). Social structure and group dynamics of the Cao vit gibbon (Nomascus nasutus) in Bangliang, Jingxi, China. Folia Primatologica, 81: 245–253.
- Fan, P., Fei, H.L., Scott, M.B., Zhang, W. and Ma, C.Y. (2011). Habitat and food choice of the critically endangered Cao vit gibbon (*Nomascus nasutus*) in China: implications for conservation. *Biological Conservation*, 144: 2247–2254.
- Fan, P., Fei, H.L. and Ma, C.Y. (2012). Behavioral responses of Cao vit gibbon (*Nomascus nasutus*) to variations in food abundance and temperature in Bangliang, Jingxi, China. *American Journal of Primatology*, 74: 632–641.
- Fan, P., Scott, M.B., Fei, H.L. and Ma, C.Y. (2013a). Locomotion behavior of Cao vit gibbon (*Nomascus nasutus*) living in karst forest in Bangliang Nature Reserve, Guangxi, China. *Integrative Zoology*, 8: 356–364.
- Fan, P., Ai, H.S., Fei, H.L., Zhang, D. and Yuan, S.D. (2013b). Seasonal variation of diet and time budget of eastern hoolock gibbons (*Hoolock leuconedys*) living in a northern montane forest. *Primates*, 54: 137–146.
- Fan, P., Ren, G.P., Wang, W., et al. (2013c). Habitat evaluation and population viability analysis of the last population of Cao vit gibbon (*Nomascus nasutus*): implications for conservation. *Biological Conservation*, 161: 39–47.
- Fan, P., Bartlett, T.Q., Fei, H.L., Ma, C.Y. and Zhang, W. (2015). Understanding stable bi-female grouping in gibbons: feeding competition and reproductive success. *Frontiers in Zoology*, 12: 5.
- Fei, H.L., Scott, M.B., Zhang, W., et al. (2012). Sleeping tree selection of Cao vit gibbon (Nomascus nasutus) living in degraded karst forest in Bangliang, Jingxi, China. American Journal of Primatology, 74: 998–1005.
- Fei, H.L., Thompson, C. and Fan, P. (2019). Effects of cold weather on the sleeping behavior of skywalker hoolock gibbons (*Hoolock tianxing*) in seasonal montane forest. *American Journal of Primatology*, 81(12): e23049.

- Feng, J.J., Ma, C.Y., Fei, H.L., Cui, L.W. and Fan, P. (2013). Call sonograms of eastern black crested gibbon (*Nomascus nasutus*). Acta Theriologica Sinica, 33: 203–214.
- Fleagle, J.G. (1974). Dynamics of a brachiating siamang Hylobates (symphalangus) syndactylus. Nature, 248: 259–260.
- Fleagle, J.G. (1976). Locomotion and posture of the Malayan siamang and implications for hominoid evolution. *Folia Primatologica*, 26: 245–269.
- Geissmann, T. (1989). A female black gibbon, *Hylobates concolor* subspecies, from northeastern Vietnam. *International Journal of Primatology*, 5: 455–476.
- Geissmann, T. (1995). Gibbon systematics and species identification. *International Zoo News*, 42: 467–501.
- Geissmann, T., La, T.Q., Trinh, D.H., *et al.* (2003). Rarest ape rediscovered in Vietnam. *Asian Primates*, 8: 8–10.
- Gittins, S.P. (1982). Feeding and ranging in the agile gibbon. Folia Primatologica, 38: 39-71.
- Gittins, S.P. (1983). Use of the forest canopy by the agile gibbon. *Folia Primatologica*, 40: 134–144.
- Groves, C.P. (1972). Systematics and phylogeny of gibbons. In Rumbaugh, D.M. (ed.), *Gibbon and Siamang*, Vol. 1. Karger, Basel: 1–89.
- Groves, C. and Wang, Y.X. (1990). The gibbons of the subgenus Nomascus (Primates, Mammalia). Zoological Research, 11: 147–154.
- Harlan, R. (1826). Description of a hermaphrodite orangutang, lately living in Philadelphia. Journal of the Academy of Natural Sciences of Philadelphia, 5: 229–236.
- Hill, D.A. (1997). Seasonal variation in the feeding behaviour and diet of Japanese macaques (*Macaca fuscata yakui*) in lowland forest of Yakushima. *American Journal of Primatology*, 43: 305–322.
- IUCN (International Union for the Conservation of Nature) (2021). *The IUCN Red List of Threatened Species*. Version 2020-1. Available at www.iucnredlist.org/
- Jungers, W.L. and Stern, J.T. (1984). Kinesiological aspects of brachiation in lar gibbons. In Preuschoft, H., Chivers, D.J., Brockelman, W.Y. and Creel, N. (eds.), *The Lesser Apes*. Edinburgh University Press, Edinburgh: 119–134.
- Kunckel d'Herculais, J. (1884). Le Gibbon du Tonkin. Sci. Nature, 2(33): 86-90.
- La, Q.T. (2005). Integrated report on capacity assessment of the community patrol group in training on using equipment for and recommendation of an annual work plan for monitoring the Eastern black crested gibbon (Nomascus nasutus nasutus) population. Fauna and Flora International, Indochina Programme, Hanoi, Vietnam.
- La, Q.T. and Trinh, D.H. (2004). Status review of the Cao vit black crested gibbon (*Nomascus nasutus nasutus*) in Vietnam. In Nadler, T., Streicher, U. and Ha, T.L. (eds.), *Conservation of Primates in Vietnam*. Haki Publishing, Vietnam: 90–94.
- La, Q.T., Trinh, D.H., Long, B. and Geissmann, T. (2002). Status review of black crested gibbons (*Nomascus concolor* and *Nomascus* sp. cf. *nasutus*) in Vietnam. In *Caring for Primates*. Abstracts of the XIXth Congress of the International Primatological Society, 4–9 August, 2002, Beijing, China: 131–132.
- Liu, Z.H., Zhang, R.Z., Jiang, H.S. and Southwick, C. (1989). Population structure of *Hylobates* concolor in Bawangling Nature Reserve, Hainan, China. *American Journal of Primatology*, 19: 247–254.
- Long, Y.C. and Nadler, T. (2009). Eastern black crested gibbon Nomascus nasutus (Kunkel d'Herculais, 1884) China, Vietnam. In Mittermeier, R.A., Wallis, J., Rylands, A.B., et al. (eds.), Primates in Peril: The World's 25 Most Endangered Primates 2008–2010. IUCN/

SSC Primate Specialist Group (PSG), International Primatological Society (IPS), and Conservation International (CI), Arlington, VA: 60–61.

- Ma, C.Y., Liao, J.C. and Fan, P. (2017). Food selection in relation to nutritional chemistry of Cao vit gibbons in Jingxi, China. *Primates*, 58: 63–74.
- Ma, C.Y., Trinh-Dinh, H., Nguyen, V.T., *et al.* (2019). Transboundary conservation of the last remaining population of the Cao vit gibbon *Nomascus nasutus*. *Oryx*, 54(6): 776–783.
- Mittermeier, R.A., Rylands, A.B. and Wilson, D.E. (2013). Handbook of the Mammals of the World. Volume 3: Primates. Lynx Edicions, Barcelona.
- Monda, K., Simmons, R.E., Kressirer, P., Su, B. and Woodruff, D.S. (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. and Fan, P. (2011). A comparative study of crested gibbons (*Nomascus*). *American Journal of Primatology*, 73: 135–154.
- Nakayama, T., Hori, T., Nagasaka, T., Tokura, H. and Tadaki, E. (1971). Thermal and metabolic responses in the Japanese monkey at temperatures of 5–38°C. *Journal of Applied Physiology*, 31: 332–337.
- Pocock, R.I. (1927). The gibbons of the genus Hylobates. Proceeding of the Zoolological Society of London, 97: 719–741.
- Preuschoft, H. and Demes, B. (1984). Biomechanics of brachiation. In Preuschoft, H., Chivers, D.J., Brockelman, W.Y. and Creel, N. (eds.), *The Lesser Apes*. Edinburgh University Press, Edinburgh: 96–118.
- Roos, C. and Geissmann, T. (2001). Molecular phylogeny of the major Hylobatid divisions. *Molecular and Phylogenetic Evolution*, 19: 486–494.
- Ruppell, J. (2007). The gibbons of Phong Nha-Ke Bang National Park in Vietnam. Gibbon Journal, 3: 50–55.
- Simonetta, A. (1957). Catalogo e sinonimia annotata degli ominoidi fossili ed attuali (1758–1955). Atti della Società toscana di scienze naturali Set B, 64: 53–113.
- Tan, B. (1985). The status of primates in China. Primates Conservation, 5: 63-81.
- Thinh, V.N, Rawson, B., Hallam, C., et al. (2010a). Phylogeny and distribution of crested gibbons (genus Nomascus) based on mitochondrial cytochrome b gene sequence data. American Journal of Primatology, 72: 1047–1054.
- Thinh, V.N., Nadler, T., Roos, C. and Hammerschmidt, K. (2010b). Taxon-specific vocal characteristics of crested gibbons (*Nomascus* sp.). In Nadler, T., Rawson, B. and Thinh, V.N. (eds.), *Conservation of Primates in Indochina*. Frankfurt Zoological Society and Conservation International, Hanoi, Vietnam: 121–132.
- Thinh, V.N., Hallam, C., Roos, C. and Hammerschmidt, K. (2011). Concordance between vocal and genetic diversity in crested gibbons. *BMC Evolutionary Biology*, 11: 36.
- Thomas, O. (1892). Note on the gibbon of the island of Hainan (*Hylobates hainanus*, sp. n.). Annals and Magazine of Natural History, 9(6): 145–146.
- Trinh, D.H. (2004). A survey on the Cao vit gibbon (Nomascus nasutus) in Trung Khanh, Cao Bang Province: survey results and training for local people in survey techniques. Fauna and Flora International, Indochina Programme, Hanoi, Vietnam.
- Vu, N.T., Nguyen, X.D., Nguyen, M.H., Luu, T.B. and Nguyen, T.H. (2005). Survey and assessment of the Cao vit gibbon population, Phong Nam – Ngoc Khe Proposed Species/ Habitat Conservation Area, Trung Khanh District, Cao Bang Province. Fauna and Flora International Vietnam Programme, Hanoi.

- Whitten, P.L. (1980). *The Kloss gibbon in Siberut rainforest*. PhD thesis, University of Cambridge.
- Zhang, D., Fei, H.L., Yuan, S.D., et al. (2014). Ranging behavior of eastern hoolock gibbon (*Hoolock leuconedys*) in a northern montane forest in Gaoligongshan, Yunnan, China. Primates, 55: 239–247.
- Zhou, J., Wei, F.W., Li, M., et al. (2005). Hainan black crested gibbon is headed for extinction. International Journal of Primatology, 26: 453–465.
- Zhou, Y.Y., Li, S.S. and Huang, T.F. (2003). Features of karst forest ecosystem in China and its conservation in utilization: a case study on Maolan, Mulun, Nonggang typical karst forests in southwest China. *Journal of Guangxi Teachers College (Natural Science Edition)*, 20: 1–7.