

# Positional behavior and canopy use of black snub-nosed monkeys *Rhinopithecus strykeri* in the Gaoligong Mountains, Yunnan, China

Yin Yang<sup>a,b,c,#</sup>, Dionisios Youlatos<sup>d,\*,#</sup>, Alison M Behie<sup>b</sup>, Roula Al Belbeisi<sup>d</sup>, Zhipang Huang<sup>a,c</sup>,  
Yinping Tian<sup>e</sup>, Bin Wang<sup>e</sup>, Linchun Zhou<sup>e</sup>, Wen Xiao<sup>a,c,\*</sup>

<sup>a</sup>Institute of Eastern Himalaya Biodiversity Research, Dali University, Dali, Yunnan 671003, China

<sup>b</sup>School of Archaeology and Anthropology, Australian National University, Canberra, ACT 0200, Australia

<sup>c</sup>International Centre of Biodiversity and Primate Conservation, Dali University, Dali, Yunnan 671003, China

<sup>d</sup>Department of Zoology, School of Biology, Aristotle University of Thessaloniki, Thessaloniki, GR-54124, Greece

<sup>e</sup>Lushui Bureau of Gaoligongshan National Nature Reserve, Liuku, Yunnan 673229, China

\*Address correspondence to Dionisios Youlatos and Wen Xiao, E-mail: [dyoul@bio.auth.gr](mailto:dyoul@bio.auth.gr) and [xiaow@eastern-himalaya.cn](mailto:xiaow@eastern-himalaya.cn)

#Yin Yang, Dionisios Youlatos contributed equally to this work.

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## Abstract

Studies on positional behavior and canopy use are essential for understanding how arboreal animals adapt their morphological characteristics and behaviors to the challenges of their environment. This study explores canopy and substrate use along with positional behavior in adult black snub-nosed monkeys *Rhinopithecus strykeri*, an endemic, critically endangered primate species in Gaoligong Mountains, southwest China. Using continuous focal animal sampling, we collected data over a 52-month period and found that *R. strykeri* is highly arboreal primarily using the high layers of the forest canopy (15–30 m), along with the terminal zone of tree crowns (52.9%), medium substrates (41.5%), and oblique substrates (56.8%). We also found sex differences in canopy and substrate use. Females use the terminal zones (56.7% versus 40.4%), small/medium (77.7% versus 60.1%), and oblique (59.9% versus 46.5%) substrates significantly more than males. On the other hand, males spend more time on large/very large (39.9% versus 22.3%) and horizontal (49.7% versus 35.2%) substrates. Whereas both sexes mainly sit (84.7%), and stand quadrupedally (9.1%), males stand quadrupedally (11.5% versus 8.3%), and bipedally (2.9% versus 0.8%) more often than females. Clamber, quadrupedalism, and leap/drop are the main locomotor modes for both sexes. *Rhinopithecus strykeri* populations never enter canopies of degenerated secondary forest and mainly use terminal branches in the middle and upper layers of canopies in intact mid-montane moist evergreen broadleaf forest and hemlock coniferous broadleaf mixed forests across their habitat.

**Key words:** arboreal, locomotion, Myanmar snub-nosed monkey, postures.

Studies of positional behavior (=locomotion and postures; Prost 1965) and canopy use are important for understanding aspects of evolutionary and adaptive morphology, life history traits, and ecology of species (Saunders et al. 2017). Understanding the ways positional behaviors relate to specific habitat features provides insights into how animals may effectively respond to different environmental conditions (Clemente et al. 2019). In this way, information about how animals perform in their environment is essential for understanding their niche, which is crucial for conservation planning and habitat management (Aronsen 2005; Mekonnen et al. 2018; Clemente et al. 2019; Ma and Fan 2020). Studies linking positional behavior and canopy use to conservation are also important when considering the Asian odd-nosed colobines, as 60% are Critically Endangered, mainly due to human population expansion, forest transformation and destruction, oil and gas exploitation, and hunting, in

combination with their restricted geographic range and small isolated population sizes (Roos et al. 2014).

The snub-nosed monkeys (*Rhinopithecus* spp.) diverged from other Asian colobines around 7–8 mya and currently consist of the Tonkin snub-nosed monkey *Rhinopithecus avunculus*, the grey snub-nosed monkey *Rhinopithecus brelichi*, the golden snub-nosed monkey *Rhinopithecus roxellana*, the black-and-white snub-nosed monkey *Rhinopithecus bieti*, and the black snub-nosed monkey *Rhinopithecus strykeri*, distributed in a few isolated and highly threatened populations in central and south China and southeast Asia (Li et al. 2018; Kuang et al. 2020). They are large and sexually dimorphic and mainly live in a multilevel or modular society (Kirkpatrick and Greuter 2010). The different species occupy a variety of habitats, exhibit different degrees of arboreal–terrestrial activities, and use a diversity of positional behaviors. *Rhinopithecus avunculus* is possibly the most arboreal

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*Rhinopithecus* species, with terrestrial activity very rarely recorded, despite long-term studies (Dong 2012; Le 2014). Although *R. brelichii* is primarily arboreal, it also uses terrestrial habitats, only when there is no canopy path available (Ren et al. 2000; Niu 2010) or when animals forage on hidden or embedded foods on the ground (Xiang et al. 2013). The degree of terrestriality appears more extensive in provisioned populations. Unprovisioned snub-nosed monkey populations demonstrate lower rates of terrestrial activities, ranging from 1.5% to 5.5% for *R. roxellana* in Shennongjia National Nature Reserve (NNR; Li 2007), and 15–19.5% for *R. bieti* in Yunling Mountains (Kirkpatrick and Long 1994; Xiang et al. 2009; Greuter et al. 2013). In contrast, provisioned *R. roxellana* populations demonstrate the highest rates of terrestrial activities, up to 36.6–52.2% in Zhouzhi NNR (Zhu et al. 2015) and 62.1–67.2% in Guanyinshan NNR (Youlatos et al. 2021). Moreover, when comparing arboreality between sexes, for those species for which data are available, lighter females have been found to be significantly more arboreal than the larger males (*R. roxellana*: Li 2007; Zhu et al. 2015; Youlatos et al. 2021; *R. bieti*: Xiang et al. 2009; Greuter et al. 2013). In addition, larger males also tend to use the central parts of tree crowns and larger substrates (*R. avunculus*: Le 2014; *R. roxellana*: Youlatos et al. 2021; *R. bieti*: Greuter et al. 2013) and, on most occasions, horizontal substrates (*R. roxellana*: Youlatos et al. 2021; *R. bieti*: Greuter et al. 2013) more than females.

In terms of postural behavior, sit and stand dominate among snub-nosed monkey species, followed by suspensory postures (*R. avunculus*: Le 2014; *R. roxellana*: Zhu et al. 2015; Youlatos et al. 2021; *R. bieti*: Greuter et al. 2013), with males sitting less and standing more than females (*R. avunculus*: Le 2014; *R. roxellana*: Youlatos et al. 2021). Regarding locomotor behavior, quadrupedalism dominates in all species, followed by considerable proportions of leap, climb, and less frequent suspensory locomotion (*R. brelichii*: Niu Kefeng, unpublished data; *R. avunculus*: Le 2014; *R. roxellana*: Zhu et al. 2015; Youlatos et al. 2021). The most saltatorial species were the highly arboreal *R. brelichii* (39%, Niu Kefeng, unpublished data) and *R. avunculus* (22–26%, Le 2014). On the other hand, the most suspensory species were the semi-terrestrial *R. roxellana* in the relatively dense forests of Guanyinshan NNR (bridge and arm-swing: 15.3–17%; Youlatos et al. 2021) and the primarily arboreal *R. brelichii* (14%; Niu Kefeng, unpublished data). Finally, in contrast to postural behavior, no significant sex differences in the locomotor profile of the species have been detected (*R. avunculus*: Le 2014; *R. roxellana*: Zhu et al. 2015; Youlatos et al. 2021).

*Rhinopithecus strykeri*, also known as the Myanmar snub-nosed monkey, was discovered in 2010 in the Gaoligong Mountains of northeastern Kachin state, Myanmar (Geissmann et al. 2011). Subsequently, 2 other populations of the species were discovered in the core areas of the Gaoligong Mountains National Nature Reserve (GLGMNNR) in Northwestern Yunnan Province, China (Long et al. 2012; Yang et al. 2018; Figure 1). Their range is thus limited to only 3,575 km<sup>2</sup> from E 98°20' to 98°50', N 25°40' to 26°50' in the northern Myanmar-China border (Ma et al. 2014; Meyer et al. 2017; Ren et al. 2017). As with other snub-nosed monkeys (Jablonski and Pan 1995), *R. strykeri* is a sexually dimorphic species, with females measuring between 52 and 54 cm [Head-Body Length (HBL)], 63–66 cm [Tail Length (TL)], and weighing 9–11.6 kg, and males measuring ~55.5 cm (HBL),

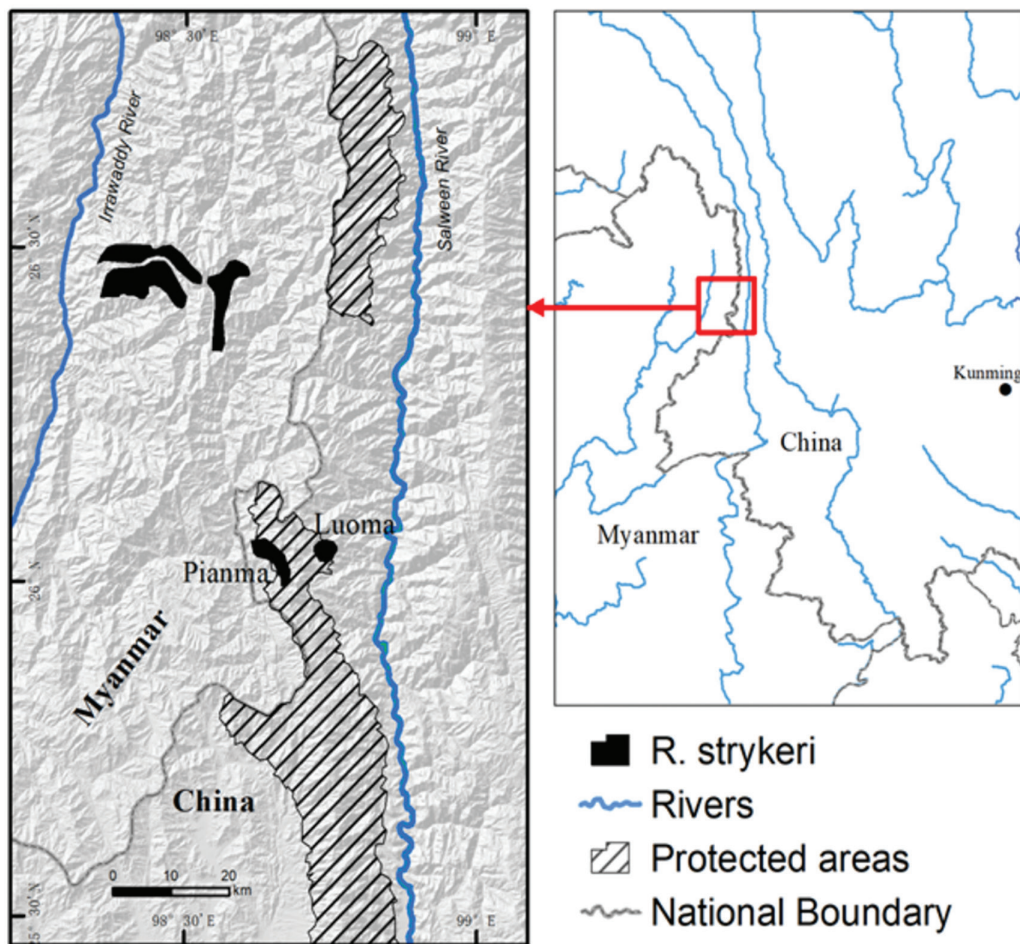
78 cm (TL), and 17 kg (Geissman et al. 2011; Yang 2019). *Rhinopithecus strykeri* is classified as Critically Endangered (<500 individuals) and faces several threats, including hunting for trophies and bushmeat, logging, nontimber forest product extraction, and road constructions (Meyer et al. 2017; Yang 2019). Until now, only a few studies on the species have provided some data on population distribution (Ma et al. 2014; Yang 2019), ranging behaviors (Li et al. 2014; Chen et al. 2015; Yang 2019), demography (Ma et al. 2014; Meyer et al. 2017; Yang 2019) and social organization (Li et al. 2014; Chen et al. 2015), feeding ecology (Yang et al. 2018, 2020), and habitat distribution (Ren et al. 2017).

To date, no data on the locomotor and postural behaviors or canopy use are available for the species, despite their importance for understanding how this species exploits and interacts with its environment. This study aims to provide such data on 2 wild populations: the Pianma and Luoma populations of *R. strykeri* on the western and eastern slopes of Gaoligong Mountains, Yunnan, China (Li et al. 2014; Yang et al. 2018). The following hypotheses are addressed: (1) as *R. strykeri* bears a long tail (Geissman et al. 2011), which is considered an arboreal adaptation (Bennet and Davies 1994), largely relies on arboreal food resources (buds, leaves, fruit, seeds, flowers, and lichens; Yang et al. 2018), and inhabits thick forests with dense canopies, we predict that this primate is very arboreal; (2) as most of their preferred foods are found in the peripheral branches of trees (Yin Yang, personal observation), we predict that *R. strykeri* will frequently use smaller and more oblique substrates, which are effectively negotiated by high rates of clambering and suspensory activities (Grand 1972, 1984); (3) given the high degree of sexual dimorphism in this species, we predict that the heavier males spend more time in the central parts of trees on larger and more horizontal substrates than the lighter females, similar to *R. roxellana* and *R. bieti* (cf. Greuter et al. 2013; Youlatos et al. 2021).

## Materials and Methods

### Study site and subjects

This field study was conducted in Pianma (26°08' N, 98°35' E) on the western slopes of Gaoligong Mountains, and in Luoma (26°00' N, 98°44' E) on the eastern slopes of Gaoligong Mountains in Yunnan, China (Long et al. 2012; Yang et al. 2018). These areas are dominated by steep peaks and deep valleys resulting in notable vertical differentiation in climate, vegetation, soil, and natural plant communities (Chaplin 2005). The vegetation changes from well-developed subtropical evergreen broadleaf forests at 1,600–2,800 m (semi-moist evergreen broadleaf forest below 2,000 m and mid-montane moist evergreen broadleaf forest from 1,900 to 2,800 m) to coniferous broadleaf mixed forests, dominated by Himalayan hemlock, *Tsuga dumosa*, between 2,700 and 3,200 m, to bamboo thicket and alpine scrub from 3,100 to 3,600 m (Yang 2019). Due to forest-crop rotation by the Lisu people, most of the old evergreen broadleaf forest below 2,300 m has been replaced by secondary deciduous broadleaf forest, dominated by *Alnus nepalensis* with some *Betula* spp., *Populus yunnanensis*, and *Pinus yunnanensis*. In the area, the mean annual precipitation increases from 903 mm and the mean annual temperature decreases from 13.3 °C on the eastern slope (Luzhang Township, 1,804 m a.s.l.) to 1,926 mm and 7 °C at the mountain top (Pianma Pass, 3,184 m a.s.l.), and then the mean annual precipitation decreases to 1,386 mm



The administrative borders were from the National Geomatic Center of China: <http://ngcc.sbsm.gov.cn>

**Figure 1.** Location of the Pianma and Luoma study areas in the GLGMNRR, Yunnan, China.

and the mean annual temperature increases to 13.6 °C on the western slope (Pianma Township, 1,786 m a.s.l.) (Yang 2019). The highest rainfall totals from February to September, with no obvious periods of drought or water shortage during the drier months (Li et al. 2000). The coniferous broadleaf mixed forest on the eastern slopes is more developed than on the western slopes in Gaoligong Mountains due to the cooler and drier natural environment on the eastern slopes (Li et al. 2000; Yin Yang, personal observation).

In the Gaoligong mountains, the forest zones used by *R. strykeri* range from 1,720 to 3,300 m (Geissmann et al. 2011; Meyer et al. 2017). The Luoma population lies ca. 14 km in a straight line, south-east of the Pianma population and 80 km south-east of the Myanmar site (Yang et al. 2018). The Pianma and Luoma populations are unhabituated, and their population sizes are estimated to be 130 individuals and >70 individuals, respectively (Yang 2019). For this study, we focused on the adult members of the 2 populations. Adults, in which ontogenetic processes have been completed, and the skeletal-muscular system and neuromotor control are fully developed, display matured behavioral responses to habitat challenges. Moreover, in sexually dimorphic species, body mass and proportion differences are more pronounced providing a test on the effect of body mass on positional behavior and canopy use. Adult *R. strykeri* males are the largest individuals in the band, with black/dark brown fur, more noticeably erect

and divided black fur on their heads, thicker tails, and pale pink faces and white testes, whereas adult females are also large but with less noticeably erect head fur, visible labia and vagina, or carrying an infant (Yang 2019).

### Behavioral data collection and analysis

In Pianma and Luoma, behavioral observations on the 2 unhabituated wild *R. strykeri* populations occurred during 3 study periods: a 12-month study period (November 2012 to November 2013: 70 working days), a 40-month study period (September 2015 to December 2016: 203 working days; June 2019 to May 2021: 313 working days). To locate the monkeys, we constructed and walked line transects along each sub-ridge in their potential home ranges. We then walked these transects between 7:00 and 20:00 for 7–21 days per month depending on the weather. When the monkeys were encountered, they were followed for as long as possible and were also filmed using a Canon Digital Camera (EOS 60D Body with Tamron 18–200 mm f/3.5–6.3 Lens). Observations ceased when the population entered a sleeping site, or the animals were lost from sight, and we could not locate them for the rest of the day. However, difficult terrain and dense rainfall and fog render the observation of unhabituated populations extremely difficult resulting in minimal information on their behavior and ecology. At the end of the

study period, we only obtained a total of 32 h (4 encounter days and  $8 \pm 0.6$  h/encounter days) and 141 h (24 encounter days and  $5.9 \pm 3.1$  h/encounter days) of direct field observations on the Pianma and Luoma populations, respectively. We obtained 175 records of canopy use (first sight observations of individuals or family units) with forest types on the Pianma population and 450 records on the Luoma population based on data collected upon first encounters of the focal animals. The number of contact hours was limited by the challenges encountered when following monkeys that moved across steep cliffs, thick forest, and in dense fog.

As done in similar studies (Wright 2007; Zhao et al. 2008; Workman and Schmitt 2012; Le 2014; Youlatos et al. 2021), we collected postural and locomotor data using continuous focal sampling on adult individuals. The monkeys were shy to the observers and, in many cases, tried to hide. Therefore, if an adult individual moved out of sight during the focal period, we shifted to another visible adult individual. We used the bout sampling for collecting data on the locomotion, postures, and canopy use (Martin and Bateson 1993). A bout ended when one of the recorded variables changed. During each bout, we recorded the: (1) tree crown part; (2) substrate size; (3) substrate inclination; (4) substrate number; and (5) locomotor/postural mode (see Table 1).

The bout method assures the recording of successive events, whether they are rare or common, and reveals the choice of animals with respect to habitat challenges. However, a major problem with this is the autocorrelation of successive sampling events, because subsequent samples from the same individuals usually lack independence (Dawkins 2007). To cope with this shortcoming and safely guaranteeing independence, we followed a bout trimming procedure. Initially, because the focal individuals could not be identified with certainty, all the observations from both populations were pooled together into a common dataset. The complete dataset was then divided into locomotor and postural subsets. Subsequently, we only considered every other bout in each subset ( $b$ ,  $b + 2n$ ), and deleted each intermediate bout ( $b + 1$ ,  $b + 1 + 2n$ ) in the subset. At the end, the 2 trimmed subsets were once more merged to produce the final dataset. Following this trimming procedure, we obtained a total of 2,644 bouts for adult females and 794 bouts for adult males (total of 3,438 bouts). Descriptive statistics were used to compare patterns of canopy use and positional behavior among the different sexes. We used randomization techniques to eliminate sources of sampling biases and ensure against accidental biases (e.g., Dagosto 1994; Zhu et al. 2015; Youlatos et al. 2021). Thereafter, we employed the 2-sample randomization test, and considering the total number of our observations, we set statistical significance at  $P < 0.05$  using 10,000 permutations. Given the multiple variables tested in each set, the significance levels were adjusted using the Bonferroni correction (Dagosto 1994).

## Results

### Canopy use

During the study period in Gaoligong Mountains, the 2 wild *R. strykeri* populations were not located regularly, due to the difficulties imposed by the terrain and the weather conditions. Despite this, we had a total contact time of 173 h with this critically endangered species. During these contacts, adults of the Pianma population were mostly found in the upper (45.7% of the canopy use records, 20–25 m) and middle (44.6%, 15–20

m) canopy of the mid-montane moist evergreen broadleaf forest, whereas only 5.1 and 4.6% in the lower canopy (<15 m) and emergent layer (25–30 m), respectively. Moreover, during our short period of observations, the Pianma population did not enter the broadleaf–coniferous mixed forests although forest rangers witnessed that the monkeys also used this vegetation in a few cases.

In Luoma, the adults showed a similar pattern, mainly using the upper (42.1%, 20–30 m) and middle (38.7%, 15–20 m) canopy of the forest, with only 11.6 and 7.6% in lower canopy (<15 m) and emergent layer (30–35 m). There were no significant differences in canopy use between the 2 populations ( $F = 6.54$ ,  $P = 0.089$ ). Whereas the Luoma population mainly used the broadleaf–coniferous mixed forests (85.2% of forest use records), neither population ever entered the canopy of the secondary degraded *A. nepalensis* forest, nor the bamboo thickets in the higher elevation ranges. The Luoma population also avoided entering a historically burned area in their core range. We observed that the Luoma population used the ground to cross a large bamboo patch and eat fruits of *Cotoneaster franchetii* in the alpine scrubs.

### Substrate use

As there were no significant differences in use of canopy layers between the 2 populations, data were combined for all subsequent analyses, and compared between males and females. We found that adult females and adult males differed significantly in the use of the canopy. Although both sexes mainly used the terminal zone of tree crowns (Table 2), adult females stayed in the terminal zone of the tree crown more often than males ( $F = 183.7$ ,  $P < 0.001$ ), whereas the latter used the central zone of tree crowns in higher frequency than the females ( $F = 181.9$ ,  $P < 0.001$ ). Whereas both sexes mostly used medium-sized substrates followed by small substrates (Table 2), females used medium and small substrates significantly more than males (Table 2; medium:  $F = 4.8$ ,  $P = 0.04$ ; small:  $F = 14.7$ ,  $P < 0.001$ ). On the other hand, males used significantly higher rates of large and very large substrates (Table 2; large:  $F = 27.5$ ,  $P < 0.001$ ; very large:  $F = 43.7$ ,  $P < 0.001$ ). In terms of substrate inclination, males used significantly more often horizontal substrates than females (Table 2;  $F = 52.3$ ,  $P < 0.001$ ), whereas females used oblique substrates at significantly higher rates than males (Table 2; 2-sample randomization test:  $F = 42.6$ ,  $P < 0.001$ ). Finally, males used significantly more single arboreal substrates (67.3%), whereas females mostly used multiple ones (53.6%;  $F = 46.7$ ,  $P < 0.001$ ).

### Postural and locomotor behavior

In Gaoligong Mountains, *R. strykeri* mainly used sit, quadrupedal stand, and, to a lesser extent, suspensory postures, with significant differences between the 2 sexes (Figure 2; Table 3;  $F = 28.8$ ,  $P < 0.001$ ). Male postural behavior was dominated by sit, with notable proportions of quadrupedal stand and, to a lesser extent, bipedal stand, and suspensory postures (Table 3). Females exhibited similar postural behavior, but with slightly significantly higher rates of sit (Table 3;  $F = 3.9$ ,  $P = 0.048$ ), and lower rates of quadrupedal stand ( $F = 4.7$ ,  $P = 0.044$ ), bipedal stand ( $F = 9.4$ ,  $P = 0.002$ ), and suspension ( $F = 5.9$ ,  $P = 0.035$ ). During suspensory postures, forelimb-hang dominated in both sexes but with significantly

**Table 1.** Definition and description of all the categories of the recorded variables for *R. strykeri* in Gaoligong Mountains, Yunnan, China (Forest layer modified after Yang 2019; locomotor and postural modes modified after Hunt et al. 1996; Youlatos et al. 2021; all other variables modified after Youlatos et al. 2021)

Forest layer <sup>a</sup>	
Ground	Ground and related substrates (e.g., rocks, roots, logs)
Lower canopy (<15 m)	Lower, young, and sapling trees
Middle canopy (15–20 m)	Main levels of the canopy
Upper canopy	
Evergreen broadleaf forest (20–25 m)	Upper levels of the canopy
Broadleaf–coniferous mixed forests (20–30 m)	—
Emergent	
Evergreen broadleaf forest (25–30 m)	Trees emerging over the main canopy
Broadleaf–coniferous mixed forests (30–35 m)	—
Tree crown part	
Central zone	Primary bifurcations and central part of tree crown
Middle zone	Intermediate network of branches of tree crown
Terminal zone	Network of branches at the crown periphery
Substrate size	
Small	Diameter ≤5 cm
Medium	5 cm < diameter ≤15 cm
Large	15 cm < diameter ≤25 cm
Very large	25 cm < diameter
Substrate orientation	
Horizontal	Angle between 0° and 22.5°
Oblique	Angle between 22.5° and 67.5 °
Vertical	Angle between 67.5° and 90°
Substrate number	
Single	Body supported by a single substrate
Multiple	Body supported by >1 substrate
Posture	
Sit	Above-branch or ground Bipedal seated or squatting posture with moderately or strongly flexed hind limbs
Quadrupedal stand	Above-branch or ground quadrupedal posture with either strongly flexed or semi-extended 3 or 4 limbs
Bipedal stand	Above-branch or ground posture on 2 moderately flexed limbs assisted by forelimbs
Cling	Upward or downward flexed-limb posture most common on strongly inclined substrates
Lie	Above branch or ground posture with the whole body, pronograde or supinograde, supporting the weight
Suspensory posture	Below-branch hanging posture with the forelimbs only or fore and hindlimbs supporting the body
Locomotion	
Quadrupedalism	Slow/moderate symmetrical and/or fast asymmetrical quadrupedal progression along single horizontal and moderately inclined substrates and/or the ground
Bipedalism	Slow/moderate symmetrical progression on the hindlimbs along single horizontal and moderately inclined substrates
Vertical climb	Upward (ascent) or downward (descent) progression along single very inclined substrates using a symmetrical quadrupedal gait
Clamber	Nonsuspensory irregular quadrupedal progression keeping the body pronograde or orthograde in various directions across multiple variously angled substrates
Leap/drop	Gap-crossing mode involving an airborne phase; leap, active hindlimb propulsion for covering a longer horizontal component; drop, a more passive fall covering a longer vertical component
Bridge	Short gap crossing mode, keeping the body pronograde and at least 3 limbs anchored at a time
Suspensory locomotion	Below-branch bimanual (arm swing) and less frequently inverted quadrupedal locomotion
Sway	Gap-crossing mode, using the body weight to bend a branch or tree for body transfer

<sup>a</sup>Generally, the mixed conifer–broadleaf forest (the mean height of mature hemlock trees ≥27 m) has a higher canopy than the evergreen broadleaf forest (the mean height of major dominate tree species ≤25 m) (Li et al. 2000). These 2 forests are the dominated vegetations in the black snub-nosed monkey's habitats, we therefore divide the canopy according to their respective height characteristics.

higher use in females (94.4% of female suspensory posture subsample) than in males (66.7% of male suspensory posture subsample,  $F = 3.9$ ,  $P = 0.049$ ).

The dominant locomotor modes of *R. strykeri* in Gaoligong Mountains were clamber, quadrupedalism, leap/drop, and suspensory locomotion (Figure 2, Table 4;  $F = 5.0$ ,  $P = 0.682$ ). Both sexes exhibited similar profiles with no significant differences. However, females used more clamber and quadrupedalism (Table 4; clamber:  $F = 1.3$ ,  $P = 0.247$ ;

quadrupedalism:  $F = 0.2$ ,  $P = 0.687$ ), whereas males used more leap/drop and suspensory (arm swing) locomotion (Table 4; leap/drop:  $F = 0.9$ ,  $P = 0.117$ ; suspensory:  $F = 0.8$ ,  $P = 0.379$ ).

## Discussion

Our study on the positional behavior and canopy use of the Critically Endangered *R. strykeri* demonstrates that the species is very arboreal and mainly uses the upper and middle canopy of the mid-montane moist evergreen broadleaf forest and broadleaf–coniferous mixed forests in the Gaoligong Mountains. Canopy use and postural behavior were marked by differences between the sexes. In contrast, locomotor behavior showed no sex differences. These findings provide valuable information regarding canopy requirements and use for a little-known species and increase our knowledge of how males and females of the species with high degrees of sexual dimorphism navigate the canopy.

Our results show that like most other *Rhinopithecus* species, *R. strykeri* are mainly arboreal and confine their activities to the upper and middle layers of the canopy in the intact mid-montane moist evergreen broadleaf forest and hemlock coniferous broadleaf mixed forests. This finding supports our initial prediction and is similar to what has been reported for wild *R. avunculus* (Le 2014) and unprovisioned *R. roxellana* (Li 2007) in broadleaf forests. Moreover, in the Yunling Mountains, unprovisioned *R. bieti* mainly uses the middle and lower layers of the canopy in mixed deciduous broadleaf and conifer forests, but mainly forages in the middle and upper layers of deciduous broadleaf tree crowns, which are 5–10 m lower than the crowns of coniferous trees (Grueter et al. 2013; Huang Zhipang, personal communication). During our study, *R. strykeri* was observed to move terrestrially only twice, crossing bamboo thickets, and eating fruits

**Table 2.** Percentages of tree part, substrate size, and substrate inclination use by male and female *R. strykeri* in Gaoligong Mountains, Yunnan, China

	Males (%)	Females (%)	Total (%)
Tree crown part			
Central zone	35.3	13.9	18.8
Middle zone	24.3	29.4	28.2
Terminal zone	40.4	56.7	52.9
N	794	2,644	3,438
Substrate size			
Small	21.5	35.3	32.1
Medium	38.6	42.4	41.5
Large	25.4	15.8	18.0
Very large	14.5	6.5	8.4
N	794	2,644	3,438
Substrate inclination			
Horizontal	49.7	35.2	38.6
Oblique	46.5	59.9	56.8
Vertical	3.8	4.9	4.6
N	794	2,644	3,438



**Figure 2.** Main positional modes of *R. strykeri* in Gaoligong Mountains, Yunnan, China: (a) clamber, (b) quadrupedalism, (c) leap, (d) sit, (e) quadrupedal crouch, and (f) quadrupedal stand.

**Table 3.** Percentages of postural modes used by male and female *R. strykeri* in Gaoligong Mountains, Yunnan, China

	Males (%)	Females (%)	Total (%)
Sit	82.1	85.6	84.7
Quadrupedal stand	11.5	8.3	9.1
Bipedal stand	2.9	0.8	1.3
Cling	0.2	1.8	1.4
Lie	0.2	2.0	1.5
Suspensory postures	2.9	1.6	1.9
N	407	1,160	1,567

**Table 4.** Percentages of locomotor modes used by male and female *R. strykeri* in Gaoligong Mountains, Yunnan, China

	Males (%)	Females (%)	Total (%)
Quadrupedalism	30.0	31.1	30.9
Bipedalism	0.3	0.1	0.1
Clamber	32.1	35.2	34.5
Vertical climb	5.1	4.4	4.6
Leap/drop	15.8	13.2	13.7
Bridge	5.1	5.5	5.4
Suspensory locomotion	10.9	9.4	9.8
Sway	0.8	1.1	1.1
N	393	1,493	1,886

from a shrub. Previous studies have also reported terrestrial behavior in the species, but only through camera traps (Chen et al. 2015; Meyer et al. 2017). These findings suggest that terrestrial behaviors are only used in this species in specific occasions. This supports previous findings that terrestriality is related to specific behaviors, such as drinking ground water (Chen et al. 2015), foraging for terrestrial food sources (i.e., bamboo shoots and tubers; Meyer et al. 2017; Yang et al. 2018), or crossing in between forest patches (Ren et al. 2000; this study). Similar behaviors have been also recorded for the equally arboreal *R. brelichi* (Niu 2010; Xiang et al. 2013).

As expected, *R. strykeri* generally used the terminal zone of tree crowns, and medium, small, and oblique substrates. This finding is in accordance with the arboreal nature of the species (Meyer et al. 2017) and its reliance on arboreal food sources (Yang et al. 2018). Regardless of the different size categories used across studies, the use of medium-sized substrates also dominates in the other snub-nosed monkey species (Greuter et al. 2013; Le 2014; Zhu et al. 2015; Youlatos et al. 2021). What appears to discriminate *R. strykeri* from its congeners is the relatively high use of small substrates, which matches the proportions of *R. roxellana* in Guanyinshan NNR (Youlatos et al. 2021). Moreover, this profile is marked by significant sex differences. Male *R. strykeri* used the central zone of tree crowns and larger substrate size categories at significantly higher rates than females, which mainly used the terminal zone and spent significantly more time on medium and small substrates. Similar sex differences in tree part and substrate size use have also been observed in *R. bieti* (Greuter et al. 2013) and *R. roxellana* (Youlatos et al. 2021), and to a lesser extent, during feeding in *R. avunculus* (Le 2014). The

smaller body mass of female *R. strykeri* (9–11.6 kg versus 17 kg of males; Yang 2019) mechanically enables safe and efficient use of the relatively smaller substrates of tree crown peripheries (Grand 1984) and provides females with ecologically advantageous access to food resources less attainable by larger males (Youlatos et al. 2021).

In terms of substrate inclination, our initial prediction was also supported. We found that males used horizontal substrates significantly more often than females. This pattern supports what is found in other snub-nosed monkey species, where, in general, horizontal substrate use by males dominates, whereas females use significantly more oblique substrates (Greuter et al. 2013; Youlatos et al. 2021). In general, large and horizontal substrates are mechanically stronger and more stable (Niklas 1992), able to support the weight of the heavier males, and may enable secure and effective use of more central parts of tree crowns (Grand 1984). In contrast, the lighter females can efficiently move around in the canopy by using smaller and oblique peripheral tree branches.

During this study, the most common postures of *R. strykeri* was sit and stand. These findings are similar to those for *R. avunculus* in Vietnam (Le 2014), and *R. bieti* (Greuter et al. 2013) and *R. roxellana* in China (Zhu et al. 2015; Youlatos et al. 2021). Sit is the most common posture among primates, it ensures wide and secure contact with the substrate and provides above-branch stability required for both rest and food processing (Rose 1974; McGraw 1998). We also found significant sex differences in postures with male *R. strykeri* displaying significantly lower rates of sit and higher rates of quadrupedal and bipedal stand and suspensory postures than females. Similar sex differences are also observed in the postural behavior of *R. avunculus* in Vietnam (Le 2014) and *R. roxellana* in China (Youlatos et al. 2021). We expected heavier males to engage in higher rates of sitting than females, but as males usually are more vigilant than females in primates (cf. Gould et al. 1997; Stojan-Dolar and Heymann 2010), male *R. strykeri* also adopted more active standing postures. Males also engaged in higher rates of suspensory postures than females. Suspensory postures allow heavier primates to safely negotiate smaller arboreal substrates and efficiently reach otherwise inaccessible food sources (Grand 1972, 1984; Cartmill 1985; Granatosky and Schmitt 2019). *Rhinopithecus roxellana* in Guanyinshan NNR also displayed similar sex differences in suspensory postures (Youlatos et al. 2021), whereas, in *R. avunculus*, differences were insignificant, with a slightly higher use of suspension by females (Le 2014).

Following our predictions, the locomotion of *R. strykeri* was marked by relatively high rates of clamber and suspensory activities (suspensory locomotion and bridge), along with quadrupedalism and leap/drop. These findings contrast previous observations on the locomotion of other snub-nosed monkeys, which is dominated by quadrupedalism (*R. avunculus*: 53.3–56.2%, Le 2014; *R. roxellana*: 62.6%, Zhu et al. 2015; 59.2–63%, Youlatos et al. 2021; but see the highly arboreal *R. brelichi*: 34%; Niu Kefeng, unpublished data). This difference may be due to the fact that most of these studies included “clamber” within either “quadrupedalism” (Zhu et al. 2015) or “climb” (Le 2014), and not separately as we did. However, in Youlatos et al.’s (2021) study, “clamber” was used separately, but was rarely used by *R. roxellana* (0.9–1.7%). Clamber, along with arm-swing and bridge, enables monkeys to move effectively across multiple substrates of different sizes and inclinations whereas dealing with the

irregular, discontinuous, and unstable nature of tree crowns peripheries (Grand 1972, 1984; Cant 1992; Granatosky and Schmitt 2019). Habitual clamber and suspensory behavior require increased forelimb mobility, for a greater and more efficient reach (Selby et al. 2020). Preliminary personal observations on the post-cranium of *R. strykeri* show forelimb features similar to those of other clambering and suspensory primates, such as a craniocaudally wide scapula, relatively long forelimbs, a rounded humeral head, a well-developed rounded capitulum, a short olecranon, and a relatively long and curved radius (Su and Jablonksi 2009; Byron et al. 2017; Selby et al. 2020).

Finally, leap/drop rates of *R. strykeri* are lower than those of other snub-nosed monkeys (*R. brelichi* in Fanjingshan NNR: 39%; Niu Kefeng, unpublished data; *R. avunculus* in Vietnam: 22–26.1%; Le 2014; *R. roxellana* in Zhouzhi NNR: 18.4%; Zhu et al. 2015) but comparable to those of *R. roxellana* in Guanyinshan NNR, China (10.8–12.1%; Youlatos et al. 2021). It is very likely that the dense and more continuous forest canopies of Guanyinshan NNR (Youlatos et al. 2021) and the Luoma and Pianma sites leave fewer gaps that can be negotiated by leaps. On the other hand, the relatively discontinuous forest canopies in Fanjingshan NNR (Niu 2010), Vietnam (Le 2014), and Zhouzhi NNR (Zhu et al. 2015) most likely require higher rates of leaping to cross the larger number of wider gaps.

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## Authors' Contributions

D.Y., Y.Y., and W.X. designed the study. Y.Y., W.X., Z.H., C.Z., B.W., and Y.T. contributed to data collection. D.Y., Y.Y., and R.A.B. analyzed the data. D.Y. and Y.Y. drafted the manuscript. A.B., Y.Y., D.Y., and W.X. contributed to the manuscript revision and all authors approved the final version of the manuscript.

## Conflict of Interest Statement

The authors declare that they have no conflict of interest.

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