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ORIGINAL ARTICLE

Sex differences in habitat use, positional behavior, and gaits of Golden Snub-Nosed Monkeys (*Rhinopithecus roxellana*) in the Qinling Mountains, Shaanxi, China

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Abstract

Studies of positional behavior, gait, and habitat use are important for understanding how animals adapt to the challenges of their environment. In turn, this information is useful for advancing research on primate morphology, life history, and ecology. Data on eco-mechanical variables can be used to develop concrete conservation and management plans for understudied and threatened primate groups. The present study explores the positional behavior, gaits, and habitat use of male and female adult golden snub-nosed monkeys (*Rhinopithecus roxellana*), an endemic, endangered, and highly dimorphic species of central China. Using focal animal sampling and opportunistic videorecording in the Guanyinshan National Nature Reserve on the southern slopes of the Qinling Mountains, it was determined that gait parameters were largely the same between sexes. By contrast, habitat use and, to a lesser extent, positional behavior varied significantly between males and females. In general, males were more terrestrial than females. When they moved arboreally, males also used a greater proportion of horizontal and large substrates compared to females. Furthermore, males used more standing postures, forelimb suspensory positional behaviors, and quadrupedal walking. These data suggest that, when faced with the mechanical challenges of large body size, primates such as *R. roxellana* are more likely to respond by altering habitat use rather than positional behaviors or intrinsic kinematics and timing.

Keywords Arboreal · China · Locomotion · Odd-nosed colobines · Postures

Introduction

Studies of positional behavior (Prost 1965), gait, and habitat can help reveal how animals use behavior to mitigate various challenges of their environment. These eco-mechanical variables present natural history information that is important for advances in morphology, fossil reconstruction, life history, and ecology (Saunders et al. 2017). Apart from traditional evolutionary analyses, the link between specific locomotor and postural repertoires and effective habitat exploitation should also be considered in conservation terms (Mekonnen et al. 2018; Ma and Fan 2020). Understanding the use of positional behaviors in relation to specific habitat features provides insight into how an animal responds to differing environmental conditions in order to survive and reproduce (Clemente et al. 2019). Information about behavioral adjustments to the environment leads to better understanding of the animal's niche, which is crucial for conservation planning, habitat management, and captive breeding/rehabilitation programs (Aronsen 2005; Mekonnen et al. 2018; Clemente et al. 2019; Ma and Fan 2020). Positional behavior, gait, and habitat use are particularly important when considering the Asian odd-nosed colobines, for whom such information is limited due to restricted geographic

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range, dwindling population sizes, and insufficient representation in zoo and museum collections.

The odd-nosed colobines diverged from other Asian colobines around 7–8 mya (Roos et al. 2011; Liedigk et al. 2012) and consist of four genera: snub-nosed monkeys (*Rhinopithecus*, 5 species), douc langurs (*Pygathrix*, 3 species), proboscis monkeys (*Nasalis larvatus*) and pig-tailed langurs (*Simias concolor*). They probably stem from the widespread Eurasian late Miocene and early Pliocene colobine genus *Mesopithecus* (Jablonski 2002; Pan et al. 2004; Liedigk et al. 2012; Jablonski et al. 2020). Habitat fragmentation throughout Asia may have led to the differentiation of *Mesopithecus* into the diversely adapted *Rhinopithecus* species and the other odd-nosed colobines (Liedigk et al. 2012; Jablonski et al. 2020). The generalized morphology and arboreal-terrestrial adaptations of this stock provided the evolutionary flexibility for the remarkable differentiation of the group (Jablonski 2002; Youlatos et al. 2012; Jablonski et al. 2020).

Currently, there are five recognized species of *Rhinopithecus* distributed in many isolated and highly threatened populations (Su and Jablonski 2009; Kirkpatrick and Greuter 2010; Liedigk et al. 2012; Yu et al. 2016; Zhou et al. 2016). *Rhinopithecus* is morphologically and behaviorally adapted to arboreal-terrestrial activities across extended home ranges in high-altitude low-temperature mixed deciduous-coniferous forests (Kirkpatrick and Greuter 2010).

Golden snub-nosed monkeys (*Rhinopithecus roxellana*) are large primates that show a high degree of sexual dimorphism (SD) in body mass (males: 15–19 kg, females: 6.5–12 kg, SD ratio = 1.59–1.74) (Jablonski and Pan 1995; Greuter and van Schaik 2009) and in some postcranial features, including distal humeral, distal femoral, tibial, and calcaneal width, as well as iliac and talar length (Jablonski and Pan 1995). From a mechanical perspective, the high SD of *R. roxellana* represents an ideal test of how body size can affect interactions with the environment. Interspecific differences in body size influence aspects of habitat utilization such as vertical space and substrate choice (Fleagle and Mittermeier 1980; Youlatos 1999; Kamilar and Pokempner 2008). Body size may also impact the frequency of particular positional behaviors (Cant 1992; Fleagle and Mittermeier 1980; Granatosky 2018) and the intrinsic kinematics and timing associated with those behaviors (e.g., Isler and Thorpe 2003; Stevens 2008; Granatosky et al. 2019). When intraspecific body mass differences are observed, as in *R. roxellana*, differences in habitat use (Gebo 1992; Doran 1993; Remis 1999; Fan et al. 2013; Greuter et al. 2013; Le 2014) and frequency of particular positional behaviors (Cant 1987; Gebo 1992; Doran 1993; Fan et al. 2013; Le 2014) or neuromuscular control are expected.

Currently available data on *R. roxellana* are insufficient to address this issue. In Shennongjia National Nature Reserve (SNNR; Hubei Province), Li (2007) reported that the species is mainly arboreal (97.1%), exploiting the middle (74.4%) and upper (17.4%) layers of the forest canopy. Li (2007) also found that the larger-bodied male monkeys spent more time on the ground (means 5.4% vs. 1.4% for females) and the low forest stratum (means 7.4% vs. 3.3%), where they used larger branches while foraging. In the Zhouzhi National Nature Reserve (ZNNR) on the northern slopes of the Qinling Mountains (Shaanxi Province), Zhu et al. (2015) showed that the species is semiterrestrial, primarily using the ground (44.8%) and the middle canopy (32.1%). The same study showed that quadrupedal walking (41.8%), leaping (26.6%), climbing (19.8%), and sitting (87.3%) were the most frequent positional modes, and the use of small (49.3%) and medium-sized (30.5%) substrates dominated. However, no behavioral or habitat use differences were observed between the two sexes (Zhu et al., 2015). A similar profile emerged for the smaller and equally dimorphic *R. avunculus* (BM = 7–16 kg, SD ratio = 1.88; Le 2014) in Khau Ca Forest in northeastern Vietnam. This species is mostly arboreal, using mainly horizontal branches. Its dominant positional modes were quadrupedalism (53.3%), leaping/dropping (26.1%), climbing (13.2%), and sitting (81.1%) and standing (13.4%) (Le 2014). Le (2014) did not find significant differences between sexes, except that males stood more than females (13.4% vs. 7.5%), used more branches (73.5% vs. 70.3%), more horizontal substrates (45.2% vs. 43.2%), and more flexible substrates than females (54.1% vs. 48.5%), but sat less (81.1% vs. 86.3%), and made less use of twigs than females (7.8% vs. 5.8%). Data on the closely related and equally dimorphic *R. bieti* (SD ratio = 1.68; Greuter and van Schaik 2009) in Baimaxueshan Nature Reserve (BNR; Yunnan Province) indicate that more males used the ground (37% vs. 34% for females) and used the central parts of trees (61.4% vs. 37.0% for females), larger branches (35.1% vs. 28.1% for females), and slightly more horizontal substrates (55.5% vs. 49.3% for females; Greuter et al. 2013). Although there are no data on spatiotemporal gait characteristics for *R. roxellana,* available data on *R. bieti* demonstrate generally similar gait characteristics between the sexes, except for the proportion of flexed versus extended elbow postures during climbing (Isler and Greuter 2006).

This study aimed to provide new data on habitat use, postural and locomotor behaviors, and gaits of male and female *R. roxellana* at a site on the southern slopes of the Qinling Mountains (Guanyinshan National Nature Reserve; GNNR) in central China. The forest of GNNR is denser than the northern slopes of the same mountains (i.e., ZNNR; Zhu et al. 2015). Considering these habitat differences, we expected higher use of clambering and suspensory locomotion (bridging, arm-swinging, etc.), less leaping, fewer sitting postures, and more suspensory behaviors for both sexes. Considering the mechanical challenges imposed by a larger body size (Grand 1972, 1984; Cant 1992), we expected larger males to use the ground more often and to use a greater proportion of large, horizontally oriented substrates compared to females when in trees. With respect to positional modes, we predicted more quadrupedalism, seated postures, and suspensory locomotion and postures, and less leaping in males than the lighter females. Finally, in terms of neuromuscular control, both males and females should alter gait strategies during quadrupedal locomotion to improve stability (i.e., reduced swing times and increased diagonality, duty factors, and number of limbs in contact with the substrate) and reduce substrate oscillations (i.e., longer stride times and reduced stride frequency) when moving on arboreal substrates (Cartmill 1985; Schmitt 1999, 2003; Stevens 2008; Granatosky and Fitzsimons 2017; Granatosky et al. 2019). We expected these effects to be greater for males than females. As snub-nosed monkeys and their environments in China are facing severe threats, conservation and management plans should incorporate information on habitat use by both sexes to help ensure the survival of their populations (Pan pers. comm.; Pan et al. 2016; Li et al. 2018).

Methods

All data collection and analyses complied with the laws of the Chinese Government and the Province of Shaanxi and adhered to the IUCN Policy Statement on Research Involving Species at Risk of Extinction (https://portals.iucn.org/library/efiles/documents/PP-003-En.pdf). All research protocols were approved by the School of Biology of the Aristotle University of Thessaloniki, the College of Life Sciences of the Northwest University of Xi’an, and the Institute of Zoology of the Shaanxi Academy of Sciences.

Study site and subjects

The study took place in the Dapingyu area of the GNNR (Fig. 1), on the southern slopes of the Qinling Mountains, Shaanxi Province, China (107° 52′–108° 02′ E, 33° 20′–33° 44′ N). The area is predominantly mountainous at an elevation of 1150–2574 m above sea level (asl). The vegetation varies with altitude and is dominated by deciduous broadleaf forest at elevations below 1500 m asl, coniferous and deciduous broadleaf mixed forest from 1500 to 2200 m asl, and coniferous forest above 2300 m asl. The area has a semi-humid montane climate with average annual rainfall of approximately 924 mm. Mean annual temperature is 11.5 °C, with a minimum of −14.3 °C in January and a maximum of 36.4 °C in July (Wang et al. 2016).

The Dapingyu study area is characterized by mountainous terrain of deep valleys and steep slopes. It has a dense and continuous mixed canopy of broadleaf and pine trees with a well-developed understory, composed of broadleaf saplings and bamboo. Within the study area, there is a single population of wild golden snub-nosed monkeys, comprising over 100 individuals. As the monkeys have an extensive home range in this uneven terrain and are extremely difficult to follow, to facilitate research, subjects are provisioned by the GNNR wardens with corn and apples once per day [see also Zhu et al. (2015) in ZNNR]. During this time, which lasts around 10–15 min, monkeys usually descend to the ground to collect the food items. This wild golden snub-nosed

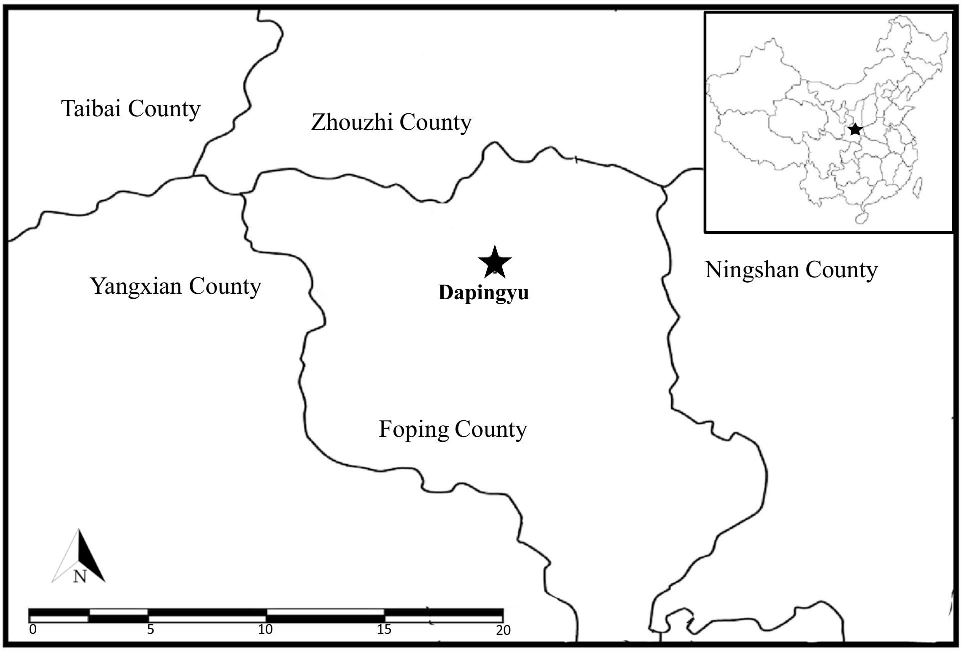

Fig. 1 Location of Dapingyu study area in the Guanyinshan National Nature Reserve (GNNR), Foping County, Shaanxi Province, China

monkey (*Rhinopithecus roxellana*) population has been the subject of ongoing field research by the College of Life Sciences of the Northwest University of Xi'an; they are therefore fully habituated to human presence.

For this study we focused on adult members of the group: 12 males and 14 females. Golden snub-nosed monkeys demonstrate significant sexual dimorphism. Adult males are easily differentiated by their large size and robust build, very long guard hairs on the back and cape, fleshy nodules on both sides of the upper lip, and visible long canines. Adult females are much smaller and more gracile, with shorter guard hairs on the back and cape, no lip nodules or long canines, and show visible signs of nursing (Fig. 2). The exact identity of all individuals could not be definitively ascertained.

Behavioral data collection and analysis

Behavioral observations were conducted on 20 days during May and June 2018, starting at 8:00 and ending at 17:00. The behavior of focal individuals was observed using binoculars (Monarch 10×42, Nikon Corporation, Tokyo, Japan). During data collection, each focal individual was followed for 5 min, and then focus was shifted to the next available adult individual. If the focal individual was lost from view during that period, we shifted to the next available subject. In this way, our sampling protocol assured that almost all available adults in sight were observed every 2.5 h. Using this rotation, each focal individual was usually followed at least three or four times per observation day. Moreover, we ceased data collection during provisioning when the monkeys descended to collect provisioned food and interacted with the wardens. Data collection restarted at least 30 min after provisioning ended.

We used focal individual bout sampling for collecting data on locomotion, postures, and habitat use (Martin and Bateson 1993). A bout ended when one of the recorded variables changed. The variables of interest were (i) forest layer, (ii) tree type, (iii) substrate type, (iv) substrate size, (v)

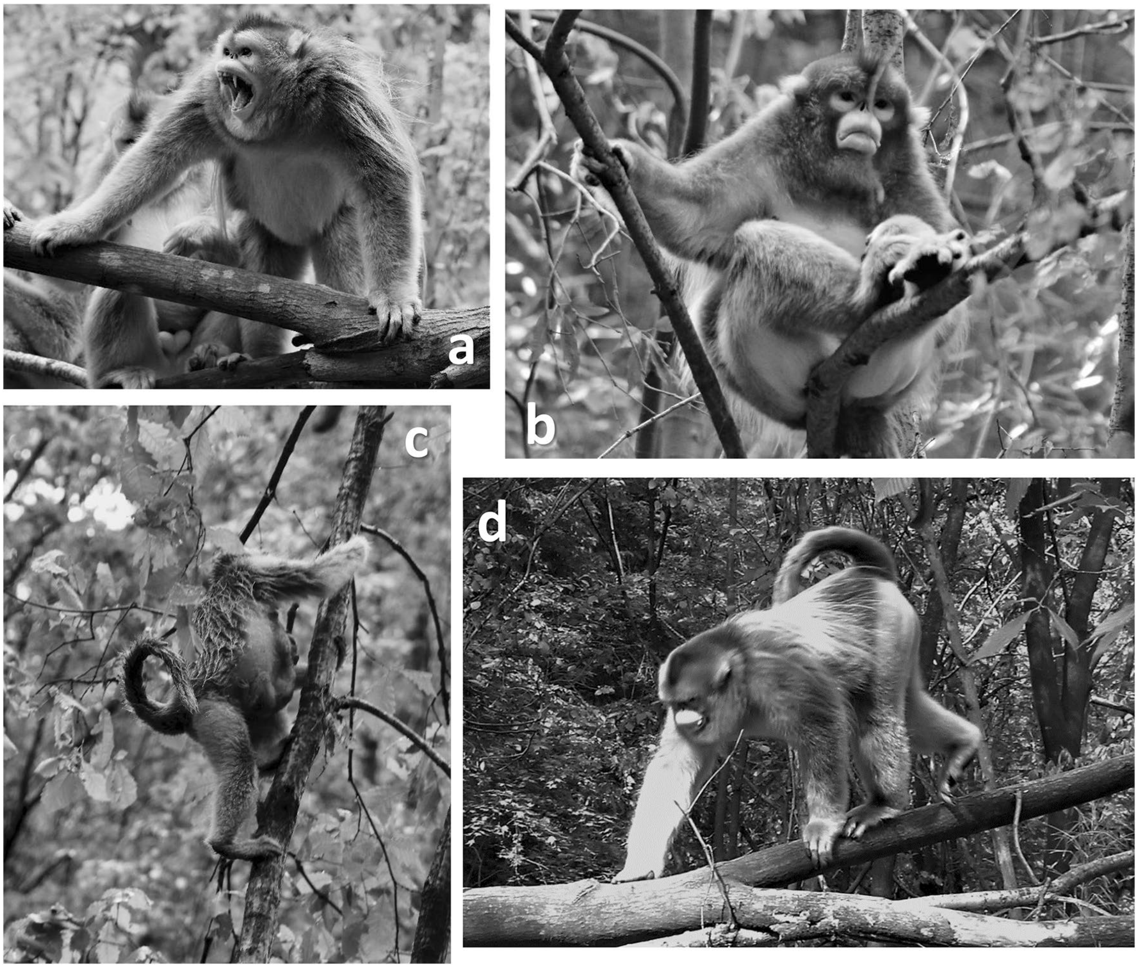

Fig. 2 Main positional modes of *Rhinopithecus roxellana* in GNNR: **a** standing, **b** sitting, **c** vertical climbing, and **d** quadrupedalism

substrate inclination, (vi) substrate number, (vii) behavioral context, and (viii) locomotor/postural mode. Table 1 shows the different categories recorded for each variable. The bout method ensures the recording of successive events, whether rare or common, and reveals subjects' choices with respect to habitat challenges. However, one major problem is the autocorrelation of successive sampling events, as subsequent samples from the same individuals usually lack independence (Dawkins 2007). Therefore, to ensure independence, we used a bout trimming procedure. Initially, because focal

Table 1 Definition and description of all the categories of the recorded variables for *Rhinopithecus roxellana* in GNNR, China (locomotor and postural definitions are based on Hunt et al. 1996; Youlatos 2008; Youlatos and Guillot 2015)

Forest layer	
Ground	Ground and related substrates (e.g. rocks, roots, logs)
Understory	Shrubs, bushes and sapling trees
Canopy	Main canopy composed of crowns of major trees
Tree type	
Broadleaf tree; pine tree; bamboo; liana	
Substrate type	
Ground dirt; rock; log; root; other; trunk; central tree branches; terminal tree branches	
Substrate size	
Small	Diameter ≤ 5 cm
Medium	5 cm < diameter ≤ 10 cm
Large	10 cm < diameter ≤ 20 cm
Very large	Diameter > 20 cm
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; Multiple	
Behavior	
Travel; feed/forage; rest; social (groom, play, mate, battle, etc.); other (eliminate, etc.)	
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 or fast bipedal progression along single horizontal and moderately inclined substrates and/or the ground
Vertical climbing	Upward (ascent) or downward (descent) progression along single very inclined substrates using a symmetrical quadrupedal gait
Clambering	Non-suspensory irregular quadrupedal progression keeping the body pronograde or orthograde in various directions across multiple variously angled substrates
Leaping/dropping	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
Bridging	Short gap-crossing mode, keeping the body pronograde and at least three limbs anchored
Suspensory locomotion	Below branch bimanual (arm swing) and quadrupedal locomotion (e.g. inverted quadrupedal walk, inverted clamber)
Swaying	Gap-crossing mode, using the body weight to bend a branch or tree for body transfer
Posture	
Sitting/squatting	Above-branch or ground bipedal seated posture with moderately or strongly flexed hind limbs
Quadrupedal standing	Above-branch or ground quadrupedal posture with either strongly flexed or semi-extended three or four limbs
Bipedal standing	Above-branch or ground standing on two moderately flexed limbs assisted by forelimbs
Clinging	Upward or downward flexed-limb posture most common on strongly inclined substrates
Lying	Above-branch or ground posture with the whole body, pronograde or supinograde, supporting the weight
Forelimb suspension	Below-branch hanging posture with the forelimbs only or fore- and hindlimbs supporting the body

individuals could not be identified with certainty, all observations were pooled into a common dataset. The complete dataset was then divided into locomotor and postural subsets. Subsequently, we considered only 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 two trimmed subsets were again merged to produce the final dataset, resulting in a total of 4548 bouts for adult females and 3036 bouts for adult males. Descriptive statistics were then used to compare patterns of habitat use and positional behavior between the sexes. We used randomization techniques in an attempt to eliminate sampling biases and ensure against accidental biases (e.g., Dagosto 1994; Zhu et al. 2015), followed by a two-sample randomization test, in which the test statistic is equivalent to Student's t statistic. We set the statistical significance level at $p < 0.05$ using 10,000 randomizations. Given the multiple variables tested in each set, the significance levels were adjusted using the Bonferroni inequality (Dagosto 1994).

Gait data collection and analysis

The monkeys' behavioral data were supplemented with opportunistic video recordings collected at 50 frames per second (fps) with a Sony digital video camera (FDR-AX33B; Sony Corporation, Japan). While 50 fps is considered well below the standard laboratory filming rate (e.g., 120–240 fps), the monkeys' average stride frequency of 0.78 Hz during quadrupedal walking in our sample is substantially lower than our recording rate, and so there was no trouble collecting the relevant gait parameters from the videos. The opportunistically collected video recordings were used for subsequent gait analyses of both arboreal and terrestrial quadrupedal locomotion. Only quadrupedal gaits were analyzed, as their prevalence allowed appropriate statistical power, and because of the amount of comparable data available in the literature.

Initially, we selected recordings in which the focal male and female monkeys were captured in parallel on camera. This was done at a distance that reduced parallax while the movements and touchdowns of all limbs were visible. We retained for analysis only strides in which the monkey was traveling in a straight path, not accelerating or decelerating (i.e., steady-state locomotion), and exhibiting a symmetric footfall sequence. Steady-state locomotion was determined by calculating the instantaneous velocity between subsequent video frames throughout an entire stride and then using regression analysis to determine whether velocity changed throughout the stride. Only strides with no detectable change in velocity were used for subsequent analyses. For all trials, symmetry was determined using the methods described by Cartmill et al. (2002), with a ±10 criterion such that the timing of opposite limb touchdown could vary between 40 and 60% of the stride cycle. A value of 50% indicates that the timing of opposing limbs is exactly one half of the cycle. For arboreal locomotion, only strides when moving on a horizontal substrate were analyzed. Although the above parameters may appear highly restrictive, our criteria ensured that gaits were analyzed in a controlled manner, meaning that any observed differences could be confidently attributed to variation in body size between the sexes.

From selected video recordings we collected standard spatiotemporal gait variables including diagonality, forelimb and hindlimb duty factor, percentage of each support limb combination, stride duration, and stride frequency (see Table 2 for information about variables). Statistically significant differences in the percentage of limb support between ground and arboreal locomotion were analyzed both within and between sexes using χ^2 tests. We used Mann–Whitney U tests to determine whether diagonality, forelimb and hindlimb duty factor, stride time, and stride frequency varied significantly between ground and arboreal locomotion both within and between sexes. Due to the limited number

Table 2 Spatiotemporal gait variables used to assess patterns of quadrupedal locomotion

Locomotor variable	Definition
Duty factor	The amount of time the limb (forelimb or hindlimb) is in contact with the support (s) divided by the duration of the stride (s)
Relative swing phase	The amount of time the limb (forelimb or hindlimb) is not in contact with the support (s) divided by the duration of the stride (s)
Diagonality	The percentage of the stride cycle interval the footfall of a forelimb follows behind the ipsilateral hindlimb. Diagonality can be divided into six classes: (a) pace ($0 < \text{pace} < 5$); (b) lateral sequence lateral couplets ($0 \le \text{LSLC} < 25$); (c) lateral sequence diagonal couplets ($25 \le \text{LSDC} < 45$); (d) trot ($45 < \text{trot} < 55$); (d) diagonal sequence diagonal couplets ($55 < \text{DSDC} \le 75$); and (e) diagonal sequence lateral couplets ($75 < \text{DSLC} < 100$)
Stride duration	Defined as the amount of time (in seconds) from one right hindfoot touchdown to the next right hindfoot touchdown
Stride frequency	The number of strides per second
Limb contact	The number of limbs contacting the substrate throughout a stride. An animal can only resist the effects of gravity and stabilize itself from falling when the limbs are contacting the substrate

Table 3 Percentages of arboreal and terrestrial substrate types used by male and female *Rhinopithecus roxellana* in GNNR, China

Arboreal substrate type			Terrestrial substrate type		
	Females	Males		Females	Males
Trunk	17.9	26.8	Ground dirt	93.6	91.4
Central branches	63.4	60.9	Rock	3.9	6.2
Terminal branches	18.1	12.2	Log	2.3	2.2
Lianas	0.6	0.0	Root	0.1	0.1
			Other	0.0	0.1
N	1750	1014	*N*	2773	2010

Table 4 Percentages of arboreal substrate size and inclination categories used by male and female *Rhinopithecus roxellana* in GNNR, China

Arboreal substrate size			Arboreal substrate inclination		
	Females	Males		Females	Males
Small	44.8	37.2	Horizontal	41.4	46.7
Medium	49.0	49.9	Oblique	49.9	43.9
Large	4.4	7.8	Vertical	8.7	9.4
Very large	1.8	5.1			
N	1793	1045	*N*	1793	1045

Table 5 Percentages of postural modes used by male and female *Rhinopithecus roxellana* in GNNR, China

	Females	Males
Sitting/squatting	72.4	60.5
Quadrupedal standing	16.1	26.7
Bipedal standing	3.9	4.3
Clinging	1.3	0.5
Lying	0.6	0.6
Forelimb suspension	5.7	7.4
N	2894	1772

Table 6 Percentages of locomotor modes used by male and female *Rhinopithecus roxellana* in GNNR, China

	Females	Males
Quadrupedalism	59.2	63.0
Bipedalism	1.5	0.9
Vertical climbing	9.2	7.6
Clambering	1.7	0.9
Leaping/dropping	10.8	12.1
Bridging	10.7	10.8
Suspensory locomotion	6.3	4.5
Swaying	0.5	0.2
N	1654	1264

of arboreal cycles suitable for analysis, all arboreal cycles were grouped together, regardless of substrate size.

Results

Behavioral observations

Female and male monkeys displayed significant differences in habitat use. Although both used the ground extensively, males did so significantly more frequently (females: 62.1%, males: 67.2%, $p < 0.001$), whereas females used the canopy more often than males (females: 23.3%, males: 16.1%, $p < 0.001$). In the canopy, both females and males were found almost exclusively on broadleaf trees (94.4%, $N = 1745$ and 94.9%, $N = 1014$, respectively). Pine trees, bamboos, and lianas were seldom used.

There were significant differences in the substrate types used. Although both sexes were primarily found in the central branches, females used terminal branches more than males, whereas males made considerable use of tree trunks ($p < 0.001$; Table 3). Both sexes frequently used the forest floor. Additionally, males were found on rocks significantly more often than females ($p < 0.001$; Table 3).

In terms of arboreal substrates, almost half of all substrates used were medium-sized (Table 4). However, females used small substrates significantly more often than males ($p < 0.001$), whereas the latter used large and very large substrates at higher rates than the former ($p < 0.001$). A sex difference also emerged when comparing arboreal substrate inclination (Table 4), with females primarily using oblique substrates and males mainly using horizontal ones ($p < 0.001$). Lastly, single substrates dominated at comparable rates for both sexes (females: 79.1%; males: 77.7%, $p = 0.369$).

Concerning general behaviors, females spent more time resting (females: 46.1%; males: 38.9%; $p < 0.001$), while males spent more time traveling (females: 35.9%; males: 41.1%; $p < 0.001$). Rates of feeding (females: 14.1%; males: 14.2%) and social activities (females: 3.4%; males: 4.1%) were quite similar for both sexes. Female postural behavior was dominated by sitting, with substantial proportions of quadrupedal standing and, to a lesser extent, forelimb-assisted suspension (Fig. 2, Table 5). Males exhibited a similar postural profile, but with significantly lower rates of sitting ($p < 0.001$), and higher rates of quadrupedal standing ($p < 0.001$) and forelimb suspension ($p = 0.043$). During locomotion, the two sexes behaved similarly, with quadrupedalism being the dominant mode, followed by leaping/dropping, bridging, vertical climbing, and suspensory locomotion (Fig. 2, Table 6). However, compared to females, males showed higher rates of

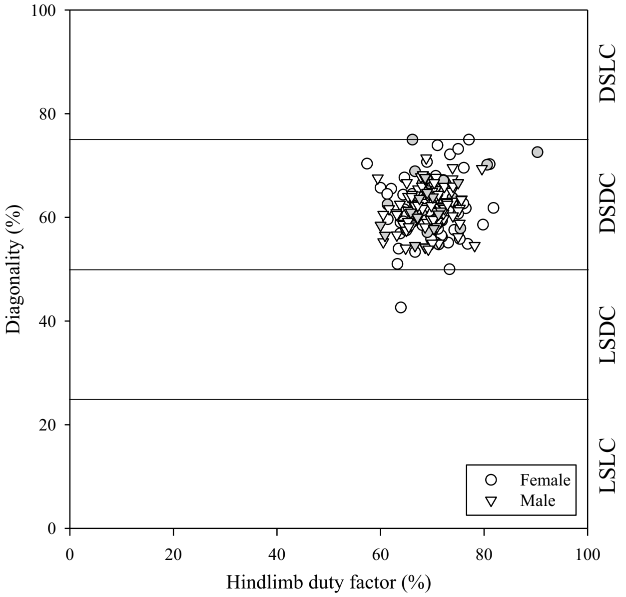

Fig. 3 Hildebrand plot displaying diagonality against hindlimb duty factor collected during terrestrial (white) and arboreal (gray) walking in male (triangles) and female (circles) *Rhinopithecus roxellana* in GNNR, China

quadrupedalism (p = 0.004) and suspensory locomotion (p = 0.005).

Gaits

All individuals, regardless of sex or substrate, used diagonal sequence diagonal couplet gaits, with the exception of one stride from a female on the ground (Fig. 3). Likewise, males and females showed no detectable differences in limb support combinations (Table 7), hindlimb duty factors, or relative swing phase (Table 8 and Fig. 4). Females used significantly fewer forelimb duty factors while moving on arboreal supports compared to the ground (p = 0.024). Males demonstrated significantly longer stride times (p = 0.025) and lower stride frequencies (p = 0.019) than females during arboreal locomotion (Fig. 5). No other significant differences in gait parameters were observed.

Discussion

The goals of the present study were to provide new data on the positional behavior, habitat use, and gait parameters from a previously unstudied population of *Rhinopithecus roxellana*. Additionally, considering the high degree of sexual dimorphism of the species, we were interested in understanding whether male/female eco-mechanical differences would be most evident in habitat use, the frequency of positional behaviors, or neuromuscular control. It should be noted that a study of this nature is faced with some limitations that may impact upon the results. First, the short sampling period (i.e., May and June 2018) makes it possible that some aspects of positional behavior and habitat use were not recorded. However, the number of sampled individuals (12 adult males and 14 adult females), the intensive sampling schedule (bout method from dawn to dusk resulting in a total 4548 bouts for adult females and 3036 bouts for adult males after trimming), and sufficient filming (193 strides analyzed) provided an adequate comparative sample for the species. Furthermore, the statistical randomization techniques we

Table 7 Percentage of each support limb combination used during horizontal walking by male and female *Rhinopithecus roxellana* in GNNR, China

Sex	Substrate	*N*	Aerial	Monopod	Diagonal bipod	Lateral bipod	Tripod	Four limb support
Male	Terrestrial	89	0.00 ± 0.00	0.09 ± 0.86	42.15 ± 10.33	0.48 ± 1.61	42.58 ± 11.75	14.70 ± 9.28
	Arboreal	15	0.00 ± 0.00	0.00 ± 0.00	46.57 ± 14.82	0.46 ± 1.00	38.86 ± 15.73	14.11 ± 5.80
Female	Terrestrial	73	0.00 ± 0.00	0.26 ± 2.04	41.02 ± 10.19	1.26 ± 3.51	40.08 ± 11.66	17.38 ± 11.48
	Arboreal	16	0.19 ± 0.75	2.60 ± 7.20	39.65 ± 16.53	1.61 ± 3.92	37.47 ± 12.98	18.49 ± 16.11

Table 8 Summary statistics for spatiotemporal gait variables during horizontal walking used by male and female *Rhinopithecus roxellana* in GNNR, China

Sex	Substrate	*N*	Diagonality (%)	Forelimb duty factor (%)	Hindlimb duty factor (%)	Relative forelimb swing phase (%)	Relative hindlimb swing phase (%)	Stride time (s)	Stride frequency (strides/s)
Female	Arboreal	16	64.28 ± 5.85	62.29 ± 13.39	71.02 ± 6.88	34.96 ± 8.65	28.98 ± 6.88	1.30 ± 0.27	0.80 ± 0.18
	Terrestrial	73	61.97 ± 5.79	67.42 ± 9.60	69.54 ± 4.91	33.97 ± 8.21	30.46 ± 4.91	1.27 ± 0.30	0.83 ± 0.22
Male	Arboreal	15	61.67 ± 4.14	64.03 ± 9.91	67.75 ± 3.88	34.21 ± 7.97	32.25 ± 3.88	1.54 ± 0.26	0.67 ± 0.10
	Terrestrial	89	62.01 ± 3.85	66.66 ± 7.81	69.32 ± 3.99	32.70 ± 7.68	30.68 ± 3.99	1.34 ± 0.37	0.81 ± 0.24

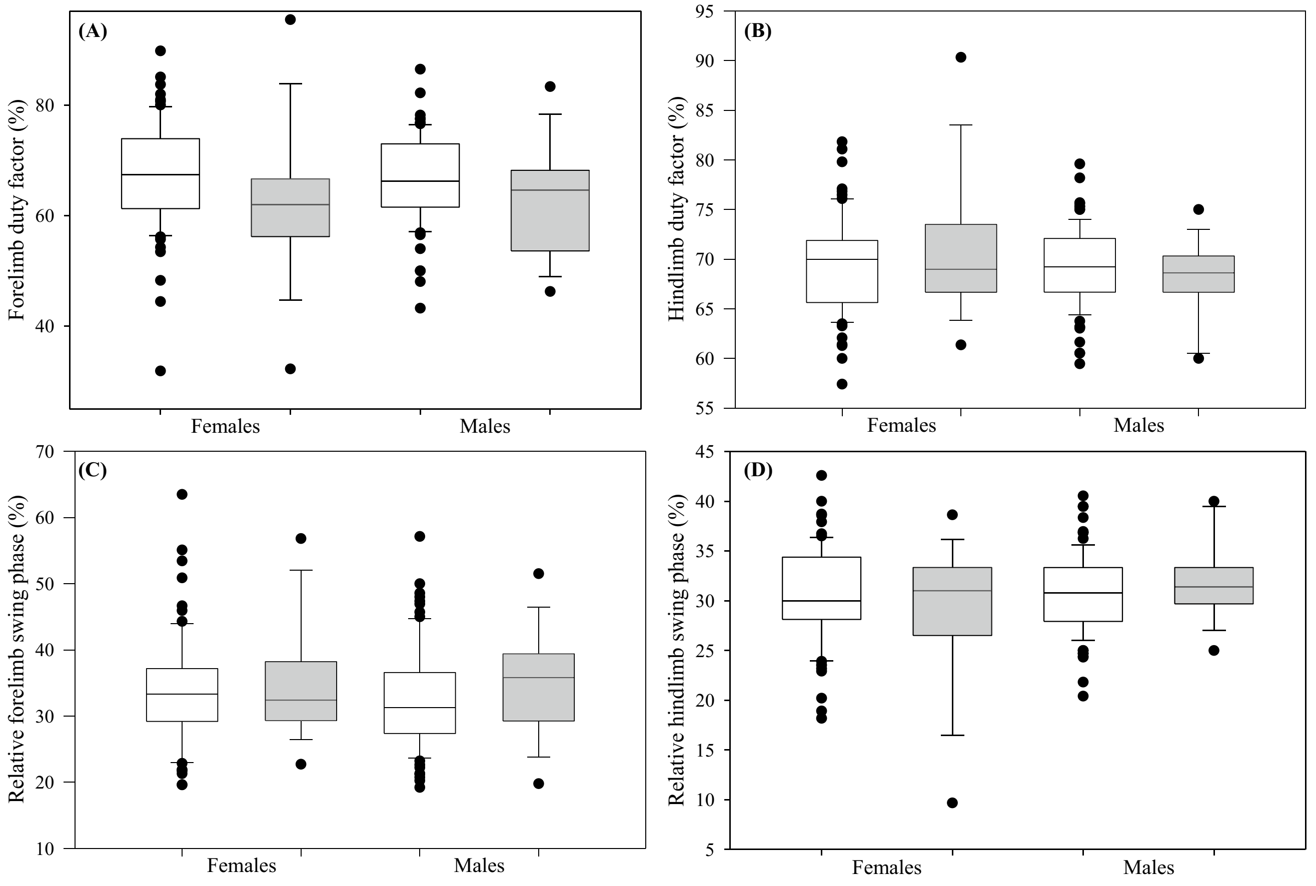

Fig. 4 Boxplots of **a** forelimb and **b** hindlimb duty factor and **c** relative forelimb and **d** hindlimb swing phase collected during terrestrial (white) and arboreal (gray) walking in male and female *Rhinopithecus roxellana* in GNNR, China. Data plotted as median, 10th, 25th, 75th, and 90th percentiles. Open circles represent outliers in the data

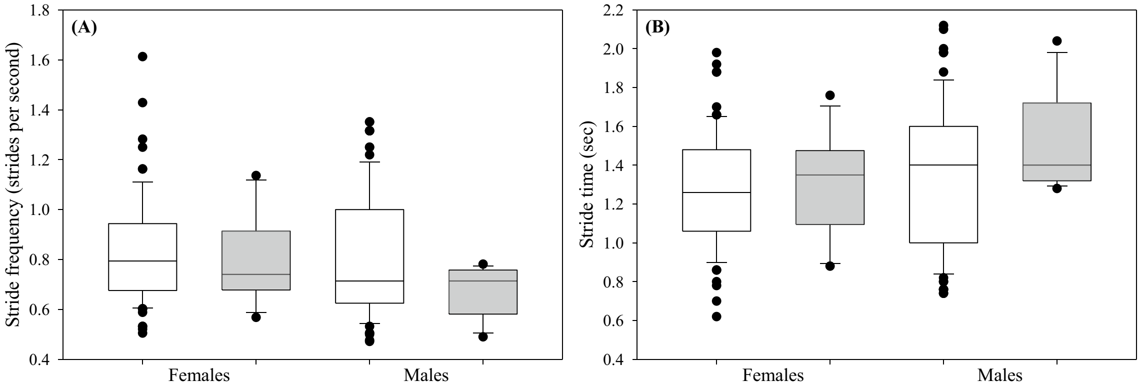

Fig. 5 Boxplots of **a** stride frequency and **b** stride time collected during terrestrial (white) and arboreal (gray) walking in male and female *Rhinopithecus roxellana* in GNNR, China. Data plotted as median, 10th, 25th, 75th, and 90th percentiles. Open circles represent outliers in the data

used further reduced any possible errors from the sampling procedure. We hope these data can be used in future, longer-term studies.

Second, for management reasons and to facilitate scientific research, the study population is provisioned by the GNNR wardens with corn and apples once per day. However, the research team never participated in provisioning. It is possible that provisioned animals show some changes from their normal behaviors, for example in terms of habitat use, positional behaviors, and gait. To limit possible similar biases, we ceased data collection during provisioning and restarted after at least 30 minutes from offset of provisioning. Finally, while we tried to ensure that only steady-state walking gaits were used for analysis (i.e., duty factor > 50%), there were natural variations in speed across trials and individuals. Furthermore, because there were no length landmarks available, it was not possible to analyze gait speed. Although speed variations result in differences in spatiotemporal gait variables (Granatosky and Fitzsimons 2017; Granatosky et al. 2019), it is unclear what, if any, effects this had on our data. For these reasons, our results should be interpreted with caution.

These limitations notwithstanding, our study demonstrated that *R. roxellana* in GNNR used both the ground and the canopy extensively. Ground rates in GNNR are much higher than those reported for the same species in ZNNR, on the northern slopes of the Qinling Mountains, (44.8%: Zhu et al. 2015), and in SNNR in Hubei Province (0.7–13.5%; Li 2007). These contrasts may be due to different factors. The use of bout sampling in this study—compared to 1- and 15-min instantaneous sampling by Zhu et al. (2015) and Li (2007), respectively—may overestimate sporadic descents to the ground versus continuous ground use (e.g., see Dagosto and Gebo 1998). Alternatively, these differences may be because our study was restricted to spring, whereas the two previous studies spanned a whole year. During spring, ground food sources (e.g., herbs) are more abundant, and monkeys tend to spend more time foraging on the ground for terrestrial food items (Guo et al. 2007; Li 2007). Finally, the differences may actually reflect habitat and behavioral variability. The generally higher ground use in the Qinling Mountains sites (Zhu et al. 2015; this study) is probably related to regular provisioning, less reliance by the monkeys on arboreal resources, and their habituation to human observers, the presence of which probably reduces predator pressure (Zhu et al. 2015). In contrast, the monkeys in Shennongjia live in a denser and continuous canopy and are not provisioned, feeding mainly on arboreal resources and descending only occasionally to the ground to collect specific herbs. The Shennongjia monkeys are only approached to within 20–30 m by humans, and experience predation by leopards and golden eagles (Li 2007). Similarly, non-provisioned bands of the larger *R. bieti* also show relatively lower proportions of terrestriality (19–20%; Greuter et al. 2013; Kirkpatrick and Long 1994). These factors may only partially explain the observed differences among populations, as other parameters such as population density, degree of intra- and interspecific competition, and nutritional quality and availability of variable food sources could also contribute. Our data, along with those of other studies (Kirkpatrick and Greuter 2010; Liedigk et al. 2012; Su and Jablonski 2009; Yu et al. 2016; Zhou et al. 2016), highlight the adaptive flexibility of the genus.

In support of our initial hypothesis, larger males were observed on the ground significantly more often than females. This was also the case for *R. roxellana* in SNNR (Li 2007) and *R. bieti* in the Baimaxueshan Nature Reserve in Yunnan Province (Greuter et al. 2013), but not for *R. roxellana* in ZNNR (Zhu et al. 2015). Increased terrestrial use by larger individuals may be related to reduced susceptibility to predator pressure (Ren et al. 2001), lower energetic costs of terrestrial versus arboreal locomotion (Pontzer and Wrangham 2004), and reduced ability to efficiently negotiate more compliant arboreal substrates (Fleagle and Mittermeier 1980; Cant 1992). In our case, all these factors may contribute to frequent ground use by the larger males. Furthermore, when the males in our study did use arboreal substrates, this was usually limited to larger and more horizontally oriented branches. Similar observations have been reported for male *R. bieti* (Greuter et al. 2013) and *R. avunculus* (Le 2014). Large and horizontal substrates are mechanically stronger and more stable, able to support the weight of heavier males, and enabling secure and effective use of more central parts of tree crowns (Grand 1984). In contrast, the lighter females were able to efficiently move around in the canopy by moving along small and obliquely oriented peripheral branches. This is also the case for female Yunnan (Greuter et al. 2013) and Tonkin snub-nosed monkeys (Le 2014). The relatively extensive use of small and oblique substrates by female snub-nosed monkeys may imply that females could be displaced to this unstable microhabitat by the more dominant males, who seek safer substrates for moving and resting (e.g., see Gebo 1992). Alternatively, the use of these substrates may afford the females advantages such as access to food resources less attainable by larger males or safety from heavier-bodied predators. Moreover, the tensile strength of oblique branches (Niklas 1992) may ensure efficient negotiation of these tree parts by the lighter females.

Our results indicate that the locomotor behavior of *R. roxellana* in GNNR was dominated by quadrupedalism, leaping/dropping, bridging, and suspensory locomotion. There were only slight differences between the sexes. Therefore, our initial hypothesis was not supported. In ZNNR, *R. roxellana* used quadrupedal walking/running at similar frequencies, but much higher rates of climbing and leaping, and less bridging and suspensory locomotion compared to our study subjects (Zhu et al. 2015). These differences may be due to the short duration of this study, compared to the year-long study of Zhu et al. (2015). Seasonal differences in locomotion and postures are known to be mainly related to differential within-tree and across-trees distributional patterns of food sources (Youlatos 1998). Available data on *R. avunculus* in Vietnam indicate a significant increase in rates of leaping, climbing, and suspensory locomotion during periods of food abundance (wet/warm seasons) (Le 2014). As spring sees the beginning of food abundance in the Qinling

Mountains (Guo et al. 2007), this could potentially explain the higher rates of suspensory behavior in GNNR. By contrast, the use of the bout method, which overestimates short-duration events (Dagosto and Gebo 1998), may account for the relatively higher rates of the brief bridging and arm-swinging events in GNNR. However, this cannot explain the higher percentages of leaping (also brief events) in ZNNR. It is possible that the leaping differences are related to forest use differences. In ZNNR, the forest is characterized by a relatively discontinuous canopy and a sparse understory (Zhu et al. 2015). This forest structure probably compels more leaping for crossing larger canopy gaps, as well as more climbing for entering and leaving trees, and moving vertically within the sparse understory. In contrast, the forest in GNNR has a relatively denser and more continuous canopy and well-developed understory that can be more easily negotiated by bridging across smaller gaps and suspensory locomotion along the more continuous, dense foliage.

Forest structural differences may also be responsible for the differences in postural behavior. Sitting dominated in both populations (Zhu et al. 2015; this study), but it was relatively less frequent in the GNNR monkeys, who also engaged in more standing and forelimb-assisted suspensory postures compared to ZNNR monkeys. As already mentioned, the more continuous canopy of GNNR includes a complex network of variously angled and sized substrates. Frequent use of seated postures has also been recorded for *R. avunculus* in Vietnam (Le 2014) and *R. bieti* in Yunnan (Greuter et al. 2013). However, the Tonkin monkeys were observed standing at rates only slightly lower (Le 2014) than the GNNR monkeys, whereas the Yunnan monkeys displayed similar percentages of suspensory behavior as the GNNR monkeys (Greuter et al. 2013).

Regarding sex differences in posture, our hypotheses were only partially supported. As expected, males used more suspensory postures, which permit negotiating fragile arboreal substrates in a safer manner (Grand 1972, 1984; Cartmill 1985; Cant 1992; Granatosky and Schmitt 2019). In contrast, males adopted seated postures less often than females. Sitting represents a more stable above-branch posture, as it ensures wide and firm contact with the substrate (Rose 1974; McGraw 1998; McGraw and Sciulli 2011). For that reason, we expected the heavier males to be seated more often than the lighter females, but our study females rested and fed more when on relatively wide arboreal substrates. By contrast, the more gregarious and active males' monitoring of movements by other males of the one-male units, and especially those of the all-male unit, may partly explain their increased rates of standing, which is a more active posture than sitting.

Gait parameters of *R. roxellana* are largely similar to other Asian colobines (Granatosky and Fitzsimons 2017; Isler and Greuter 2006), although stride times tend to be longer compared to the closely related *Pygathrix* and *Trachypithecus* (Granatosky and Fitzsimons 2017). For almost all locomotor parameters analyzed, males and females showed largely similar quadrupedal gaits regardless of substrate. The only notable difference was that males tended to have longer stride times than females when moving arboreally, arguably to increase stability on arboreal supports. This one difference notwithstanding, it does not appear that the mechanical challenges of a larger body size significantly alter gait mechanics in the highly dimorphic *R. roxellana*, similar to *R. bieti* (Isler and Greuter 2006) and some other highly dimorphic primate species (Isler and Thorpe 2003). The overall lack of differences in spatiotemporal gait characteristics associated with intraspecific body size variation can likely be explained by one of two scenarios. First, perhaps size differences between male and female *R. roxellana* are not large enough to require a significantly different biomechanical response. However, intraspecific spatiotemporal gait differences are commonly observed even with minimal differences in body size (Stevens 2008; Granatosky and Fitzsimons 2017; Granatosky et al. 2019). Rather, it seems more likely that intraspecific neuromuscular flexibility is quite low, and individuals within a species, regardless of body size differences, may be constrained in the ways in which they coordinate limb movements. This speculative hypothesis requires further comparative study, exploring levels of variation in spatiotemporal gait parameters between cycles, locomotor sequences, individuals, and species, in the style of Iriarte-Díaz et al. (2011).

Gait parameters were found to be similar between sexes. However, habitat use and, to a lesser extent, positional behavior did vary in accordance with our hypotheses regarding how substantially larger males interact with the environment compared to females. This suggests that given a large body size, primates, or at least *R. roxellana*, are more likely to respond by altering habitat use rather than positional behaviors or intrinsic kinematics and timing. These findings highlight the importance of ensuring habitat variability during conservation, management, and breeding efforts, as substrates designed with one sex in mind are probably insufficient. Logging and other reasons for habitat degradation may have severe impacts on how the different sexes navigate and disperse across space (Mekonnen et al. 2018; Ma and Fan 2020). The resulting changes in forest structure, such as decreased forest density, formation of larger, hard-to-cross gaps, and reductions in specific substrate types may affect travel route choice and associated locomotor and postural behaviors (Aronsen 2005; Mekonnen et al. 2018; Ma and Fan 2020). These changes may be even more severe for highly dimorphic species, such as *R. roxellana,* which already display sex differences in habitat use. Consequently, even mild microhabitat degradation may have serious effects on how various species behave in specific environmental conditions. This may ultimately severely affect the long-term survival of whole populations. However, these relationships remain largely speculative. The present study can serve as a background for future research on sex differences in habitat use, positional behavioral, and gait, and their possible influences long-term survivorship or fitness.

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Author contributions DY conducted field work. GH, SG, and BL assisted during fieldwork. DY, RAB, and MCG analyzed the data. DY and MCG wrote the manuscript. All other authors provided critical editorial advice.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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