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Dynamic foraging strategy adaptation to heterogeneous environments contributes to social aggregation in snub-nosed monkeys

Lan Zhao[1,2,#], Sheng-Nan Ji[3,#], Xiao-Bing Du[1], Jia-Hui Liu[1], Bo-Lun Zhang[1], Pei-Hua Li[1], Yi-Jun Yang[1], Bao-Guo Li[1], Yan-Qing Guo[1], Xiao-Guang Qi[1,*]

[1] *College of Life Sciences*, *Northwest University*, *Xi'an*, *Shaanxi* 710069, *China*

[2] *Chengdu Institute of Biology*, *Chinese Academy of Sciences*, *Chengdu*, *Sichuan* 610041, *China*

[3] *State Key Laboratory of Environmental Criteria and Risk Assessment*, *Chinese Research Academy of Environmental Sciences*, *Beijing* 100012, *China*

ABSTRACT

The dynamics of animal social structures are heavily influenced by environmental patterns of competition and cooperation. In folivorous colobine primates, prevailing theories suggest that larger group sizes should be favored in rainforests with a year-round abundance of food, thereby reducing feeding competition. Yet, paradoxically, larger groups are frequently found in high-altitude or high-latitude montane ecosystems characterized by a seasonal scarcity of leaves. This contradiction is posited to arise from cooperative benefits in heterogeneous environments. To investigate this hypothesis, we carried out a six-year field study on two neighboring groups of golden snub-nosed monkey (*Rhinopithecus roxellana*), a species representing the northernmost distribution of colobine primates. Results showed that the groups adjusted their movement and habitat selection in response to fluctuating climates and spatiotemporal variability of resources, indicative of a dynamic foraging strategy. Notably, during the cold, resource-scarce conditions in winter, the large group occupied food-rich habitats but did not exhibit significantly longer daily travel distances than the smaller neighboring group. Subsequently, we compiled an eco-behavioral dataset of 52 colobine species to explore their evolutionary trajectories. Analysis of this dataset suggested that the increase in group size may have evolved via home range expansion in response to the cold and heterogeneous climates found at higher altitudes or latitudes. Hence, we developed a multi-benefits framework to interpret the formation of larger groups by integrating

environmental heterogeneity. In cold and diverse environments, even smaller groups require larger home ranges to meet their dynamic survival needs. The spatiotemporal distribution of high-quality resources within these expanded home ranges facilitates more frequent interactions between groups, thereby encouraging social aggregation into larger groups. This process enhances the benefits of collaborative actions and reproductive opportunities, while simultaneously optimizing travel costs through a dynamic foraging strategy.

Keywords: Social evolution; Folivore paradox; MLS; *Rhinopithecus roxellana*; Multi-benefits framework

INTRODUCTION

Given the diversity of mammalian social systems, many important questions regarding their origins and impacts remain unresolved (Clutton-Brock, 2021). Although variation in feeding competition associated with differences in food distribution plays an important role in restricting group size, our understanding of this variation remains incomplete (Clutton-Brock & Janson, 2012). Several socioecological models predict that within-group feeding competition is weak among folivorous primates because food resources are presumed to be superabundant and evenly distributed, theoretically allowing individuals the freedom to form larger groups in areas with a high and consistent food supply (Isbell, 1991; Isbell & Young, 2002; Janson & Goldsmith, 1995). In contradiction to these models, however, many folivores live in relatively small groups, a phenomenon referred to as the

folivore paradox (Steenbeek & Van Schaik, 2001; Sterck & Roth, 2022).

The ecological constraints model posits that folivorous primates, which typically forage for food located in discrete patches, face increasing challenges with increasing group size. Specifically, the depletion of resources within these patches and escalating travel costs associated with searching for new patches intensify with group expansion (Chapman & Chapman, 2000; Snaith & Chapman, 2005; Teichroeb & Sicotte, 2009). The increase in travel costs predicts the occurrence of within-group scramble competition, effectively constraining folivore groups to smaller sizes (Chapman & Teichroeb, 2012). This hypothesis provides an ecological rationale for why most colobine primates inhabiting leaf-rich tropical areas tend to form small groups, characterized by one-male multi-female families, often consisting of fewer than 20 individuals (Figure 1A).

However, certain species exhibit considerable deviations from the predictions of the ecological constraint model. Notably, snub-nosed monkeys (*Rhinopithecus* species), Rwenzori Angolan colobus monkeys (*Colobus angolensis ruwenzorii*), Himalayan langurs (*Semnopithecus schistaceus*), and Indochinese gray langurs (*Trachypithecus crepusculus*), which inhabit high-altitude or high-latitude montane forests with relatively scarce and patchy vegetation, typically form large, cohesive groups consisting of hundreds of individuals (Figure 1A) (Adams et al., 2021; Grueter et al., 2020; Qi et al., 2014, 2023). Among these species, the endangered golden snub-nosed monkey (*Rhinopithecus roxellana*), recognized as the most northerly distributed colobine primate (Yu et al., 2022), resides in a complex multi-level society (MLS) comprised of hundreds of individuals organized into extensive social matrices (Figure 1A). The foundational one-male multi-female families within their social system do not exist autonomously, but rather integrate into larger groups where multiple such families coalesce, forming a cohesive breeding band. Concurrently, non-breeding males congregate in all-male bachelor bands, which are composed of several all-male units (Grueter et al., 2017; Qi et al., 2014). Bachelor males within these units typically travel in pursuit of different breeding bands in order to secure potential mating opportunities, leading to an unstable unit composition (Fang et al., 2018a; Li et al., 2020; Qi et al., 2017). A cohesive breeding band forms associations with one or more dynamic all-male bands, together constituting a herd. These herds aggregate seasonally to form a troop, during which members are exchanged to facilitate gene flow and prevent inbreeding (Qi et al., 2014). Ancestral state reconstruction studies have revealed that this complex MLS evolved from the aggregation of independent one-male, multi-female groups, a social structure characteristic of ancestral Asian colobines and similar to that found in most tropical colobines (Grueter & Van Schaik, 2010; Qi et al., 2023). Among the four hierarchical levels of the MLS—unit, band, herd, and troop—the breeding band is regarded as a relatively stable core structure. Members of breeding bands engage in various collective activities, such as traveling, resting, and foraging, necessitating access to ample food resources (Qi et al., 2014, 2017). Nonetheless, colobine species residing in high-altitude regions encounter substantial energetic challenges due to cold temperatures and seasonal food scarcity (Grow et al., 2014; Hemingway & Bynum, 2005). Understanding how these species resolve such energetic constraints to form large,

cohesive bands is a critical question in socioecological research (Grueter et al., 2020).

Social complexity in animal groups is shaped by both the size of the social unit and the interactions among its members (Kappeler, 2019). The heterogeneity hypothesis posits that in montane ecosystems, where climate and resources vary both spatially and temporally, there is an increased likelihood of encounters between one-male multi-female groups in colobines (Grueter, 2022), particularly when food resources are low in quality and spatiotemporally and heterogeneously distributed. In such cases, a small home range may not be sufficient for group survival across all seasons, necessitating an expansion of the home range to encompass diverse habitat types year-round. The larger the home range, the higher the probability of encountering other groups or individuals with similar spatial and dietary requirements. Considering the trade-offs in group living (Garcia et al., 2021; Markham & Gesquiere, 2017), larger group aggregation may be favored over smaller independent groups if it offers greater benefits, such as foraging and reproduction, assuming travel costs are not a limiting factor. Therefore, we speculate that high-altitude Asian colobines may adapt to their heterogeneous environments by extending their home ranges, and therein gain higher foraging or other benefits from living in larger groups, leading to the formation of a breeding band.

The above hypothesis has not yet been tested and requires empirical evidence for validation. First, it is essential to establish the relationship between environmental heterogeneity and group size, specifically whether colobines residing in large bands encounter highly heterogeneous resources. Second, it is necessary to clarify whether bands modify their ranging behaviors to access heterogeneous resources. Third, it is also important to determine whether larger groups gain enhanced benefits, such as access to food and reproductive opportunities, without a significant increase in travel costs. Additionally, when exploring evolutionary trajectories, two further hypotheses should be examined based on comparative eco-behavioral analysis across colobine species, notably, whether there is an expansion of home range in heterogeneous environments and whether an increase in home range size is correlated with larger group sizes.

To test the socioecological hypothesis, extensive, long-term monitoring of intraspecific variation within a model species is necessary, alongside comparative studies that integrate ecological and phylogenetic data (Clutton-Brock & Janson, 2012; Kappeler et al., 2019). The golden snub-nosed monkey, which inhabits temperate montane forests with seasonally variable food availability and is characterized by an MLS (Tan et al., 2016), serves as an excellent model species for such research. While golden snub-nosed monkey bands typically select habitats according to food availability (Fan et al., 2019; Huang et al., 2021; Li et al., 1999, 2000; Tan et al., 2007), it remains unclear whether they adjust their ranging behaviors to exploit heterogeneous resources, as predicted by the heterogeneity hypothesis. Tracking these primates poses a significant challenge. Direct observations and long-term monitoring of wild populations in montane forests are exceptionally demanding tasks, with the reliability of radio telemetry often hindered by fluctuating weather conditions and difficult terrain (Beyer & Haufler, 1994). The adoption of global positioning system (GPS) collars has helped address these tracking challenges (Tomkiewicz et al., 2010), allowing for the

collection of accurate activity data (Fang et al., 2018b; Qi et al., 2014). In 2012, we initiated a continuous monitoring program using GPS collars to determine the home range and core areas of the golden snub-nosed monkey, which enabled vegetation sampling across diverse habitats to evaluate habitat quality. Given the close association between travel behaviors and habitat quality, the precise movement data obtained from GPS tracking also provided the opportunity to track the dynamic patterns of habitat utilization (Van Moorter et al., 2016).

Over six years, we collected meteorological, home range, diet, and habitat data of two golden snub-nosed monkey bands. Based on these data, we explored three predictions of the heterogeneity hypothesis. (1) We analyzed spatial and temporal variations in the home range of a single band to clarify habitat utilization, then compared habitat parameters, including food richness and food diversity across different levels of habitat use, providing direct evidence of resource heterogeneity. (2) We tracked spatiotemporal movement, diet, and habitat characteristics of a single band to determine how it adjusts its ranging behaviors to access heterogeneous food resources. (3) We compared the social organization, home range, daily travel distance (DTD), and habitat quality between two neighboring bands to determine whether the larger band achieves superior feeding and reproductive opportunities and manages travel costs more efficiently compared to the smaller band. Subsequently, we compiled an eco-behavioral dataset covering bioclimate, elevation, body mass, group size, and home range across colobines to evaluate the last two aspects of our hypothesis. (4) We conducted a comparative phylogenetic analysis to examine the correlations between ecological variables and group size to determine whether heterogeneous climates affect group size. (5) We employed causal models with phylogenetic path analysis to explore the evolutionary relationship between home range and group size and ascertain whether (and how) an expanded home range leads to a larger group size. Based on the results, we assessed the validity of the heterogeneity hypothesis in the social evolution of colobines, which, if valid, can be incorporated into existing theoretical frameworks for a better understanding of the social evolution of these primates and potentially of mammals.

MATERIALS AND METHODS

Study sites and subjects
This field study focused on wild groups of the Qinling golden snub-nosed monkey (*R. roxellana qinlingensis*) inhabiting the Yuhuangmiao area within Zhouzhi National Nature Reserve on the northern slopes of the Qinling Mountains, Shaanxi Province, China (Figure 1B). The area experiences fluctuating temperatures typical of its temperate climate, leading to seasonal withering and prolonged periods of leaflessness in winter. The mountainous terrain includes three forest types distributed along an elevational gradient: (1) deciduous broadleaf forest (1 400–2 200 m above sea level (a.s.l.)), (2) mixed coniferous and broadleaf forest (2 200–2 600 m a.s.l.), and (3) coniferous forest (above 2 600 m a.s.l.) (Li et al., 2000).

The study area is home to the wild West Ridge troop (WRT), which includes the Gongnigou herd (GNG) and Dujiafen herd (DJF) (Figure 1C, D). In December and June each year, we recorded the number of adults (males >7 years

old, females >5 years old), subadults (males 3–5 years old, females 4–7 years old), juveniles (males 1–4 years old, females 1–3 years old), and infants (<1 year old) in both herds. From 2013 to 2017, the GNG-herd consisted of 160–190 individuals, including a breeding band with 11–15 one-male units (OMUs) and an all-male band of 24–40 individuals, while the DJF-herd consisted of 60–80 individuals, including a breeding band with 6–7 OMUs and an all-male band of 11–12 individuals. The focus of this study was on the cohesive breeding bands due to the frequent migration of members of the all-male bands (Huang, 2015). The GNG breeding band (GNG-BB) has been habituated to receiving food provisions in spring and autumn since 2001 (Qi et al., 2009). Thus, the GPS data obtained in summer (June to August) and winter (December to February) without provisioning are reflective of its natural living conditions. The DJF breeding band (DJF-BB) is a free-ranging group. Additional details are provided in the Supplementary Materials (Supplementary Method S1).

Ethics approval
All animal procedures performed in this research were conducted following the ethical guidelines on the care and use of animals for scientific purposes, as outlined by the Animal Care Committee of the Wildlife Protection Society of China (SL-2012-42) and the Specialist Committee of the National Forestry Administration of China (SFA: LHXZ-2012-2788) and following the regulatory requirements of Zhouzhi National Nature Reserve, China.

Meteorological data collection
A meteorological station was established in the study area (E108°14′, N33°49′) in 2003 (Qi et al., 2008), which monitored air temperature, relative humidity, solar radiation, and evaporation hourly. Daily average, maximum, and minimum air temperatures, relative humidity, and solar radiation were determined using the meteorological data. Climate data were collected from October 2013 to April 2017 (1 278 days).

Estimation of GPS location and ranging behaviors
From December 2012 to January 2018, seven GPS collars were attached to adult members of GNG-BB and eight to those of DJF-BB, enabling the tracking of both groups (Supplementary Table S1). The GPS collars were programmed to record locations every 2 h from 0500h to 1900h each day (Supplementary Method S2). To eliminate significant positional errors, we applied data screening criteria, including three-dimensional fixes and a dilution of precision (*DOP*) no greater than 10, as a higher *DOP* indicates poor satellite geometry and less accurate measurements (Bjørneraas et al., 2010). A total of 38 374 GPS location records (33 059 valid data points after filtering) were used to analyze the ranging behaviors of GNG-BB and DJF-BB. To mitigate the impact of food provisioning on GNG-BB, we excluded its data from spring and autumn. In addition, we removed duplicate locations recorded for individuals at the same time to prevent pseudoreplication. In total, 6 158 location data points (longitude, latitude, elevation) were used for calculating the ranging behavior (home range, core area, and DTD) of GNG-BB in summer and winter and 8 192 location data points were used to calculate the ranging behavior of DJF-BB across all seasons. The kernel density estimation method in ArcGIS v.10.6 (ESRI., USA) was used to calculate the home range and core area each year
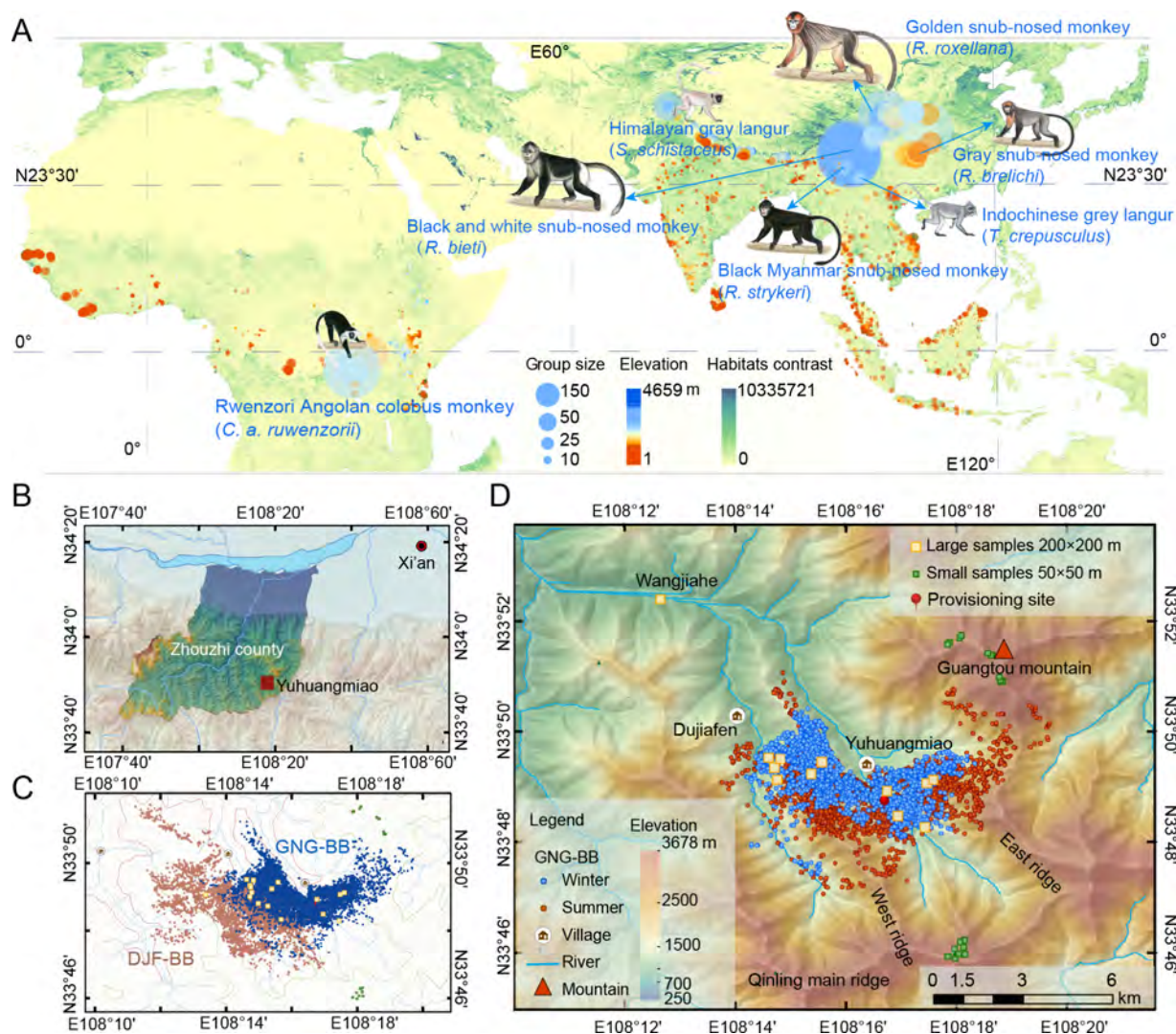
Figure 1 Distribution of colobines and geographical location of study area

A: Distribution of colobines. Map displays exponentially weighted difference in Enhanced Vegetation Index (EVI) between adjacent pixels, indicating spatial heterogeneity of habitats, i.e., habitat contrast. Distribution coordinates are scaled by average group size or population size and colored by elevation. B: Geographical location of study sites. C: Mountainous terrain around study area. D: GPS coordinates and sample sites in this study. Illustrations of monkeys: copyright 2013, Stephen D. Nash/IUCN SSC Primate Specialist Group. All illustrations are used with permission.

(Supplementary Method S3). Habitats were then classified into four categories: core area (50%), moderately utilized area (non-core area within the home range, 50%–95%), seldom utilized area (area outside the home range but within the range scope of activity, 95%–100%), and non-utilized area (area outside the range scope of activity) (Supplementary Figure S1; Supplementary Tables S2–S3). The Tracking Analyst module in ArcGIS v.10.6 was employed to track monkey movements and compute distances between adjacent anchor points based on time series coordinates (Supplementary Method S3).

A multi-year home range calculation was conducted to compare home range sizes between the two bands using data from periods when location information was simultaneously available for both bands.

Vegetation sampling

Quadrats for vegetation sampling were established from July 2014 to October 2016. Seventeen large quadrats (200 m×200 m) below 2 200 m a.s.l. and 19 small quadrats (50 m×50 m) above 2 200 m a.s.l. were sampled (Figure 1D; Supplementary Table S2), covering the altitudinal gradient. For better

comparability and higher precision when measuring vegetation characteristics under complex terrains, we subdivided each of the original large samples into 16 small quadrats (50 m×50 m). Based on average seasonal habitat utilization over five years, we classified samples into four types of areas (core, moderate, seldom-utilized, and non-utilized) in two separate seasons (Supplementary Tables S2–S3). For example, the S-H-1 quadrat was classified as a highly utilized (core) area during the summer season, while the S-M-3 quadrat was classified as a moderately utilized area in summer but a core area in winter and was thus resampled as W-H-2 (Supplementary Figure S1). As a result, a total of 358 small quadrats were analyzed in the two seasons for GNG-BB. In addition, to minimize conflicts with humans, the study group avoided certain areas (Huang et al., 2021). Consequently, we selected plots within regions frequented by the monkeys that experienced minimal human disturbance to determine the dynamic patterns between habitat characteristics and movements.

A plant dataset encompassing 85 387 live trees within the study area and a diet dataset comprising 1 117.5 h of

observational records of the study group were used to determine habitat characteristics and dietary changes (Huang et al., 2021; Huang, 2015). The main food species were defined as edible foods that ranked within the top 75% of all food plants consumed by individuals in the BB (Huang, 2015). We calculated six basic parameters: the number of species and quantity of plants (PS, PQ), food (FS, FQ), and main food (MFS, MFQ). Additionally, nine vegetation parameters were calculated to evaluate plant and food resources, including the diversity, richness, and evenness of plants (PR, PD, PE), food (FR, FD, FE), and main food (MFR, MFD, MFE) within each quadrat. In addition, average diameter at breast height (a-DBH), total tree basal area (t-TBA), average tree height (a-TH), as well as average and total canopy density (a-CD, t-CD) were determined to characterize the trees in the quadrat. Detailed calculations are presented in the Supplementary Materials (Supplementary Method S4).

Construction of eco-behavioral dataset

An ecological dataset including 19 bioclimatic variables and elevation data for 70 colobine species (including subspecies) was established based on occurrence data from the Global Biodiversity Information Facility (GBIF) and bioclimatic data from WorldClim (Supplementary Method S5 and Dataset S1). A dataset detailing social and ranging behaviors was also complied for 72 colobine species (including subspecies) (Supplementary Method S5 and Dataset S2, S3). A colobine phylogenetic tree was then constructed by integrating existing phylogenetic data (Supplementary Method S5). Finally, data for 50 species and two subspecies were obtained for comparative phylogenetic analysis (Supplementary Dataset S4).

Data analysis

The differences in ranging parameters of GNG-BB between summer and winter were assessed using independent samples *t*- tests (parametric data), Mann-Whitney *U*-test (nonparametric data), and paired *t*-test (paired data). Similarly, seasonal differences in DJF-BB were determined using analysis of variance (ANOVA) and *post hoc* least significant difference tests. The Kaiser-Meyer-Olkin (KMO) and Bartlett's tests were used to measure partial correlations between variables. Due to the significant correlations among multiple parameters, principal component analysis (PCA) was conducted to extract the primary characteristics of the nine meteorological and 20 vegetation variables. The new principal components (PCs) served as proxies for the original variables. We examined the correlations between DTD and meteorological variables (original variables and PCs) using Pearson or Spearman correlation analysis to determine whether ranging behaviors were influenced by climatic changes. Correlations with original variables helped validate the PCA results, while the PCs themselves reflected the principal characteristics of the original variables. Furthermore, spatial and seasonal vegetation differences in the core area were determined using the Kruskal-Wallis test and *post-hoc* Dunn's all-pairs test with false discovery rate (FDR) correction. To understand the spatiotemporal dynamics of habitat utilization, we constructed a time-series framework for foraging behaviors and habitat selection for GNG-BB, integrating real-time movements, meteorological data, dietary records, and habitat parameters. K-means clustering was used to classify DTD into three categories: long, medium, and short. According to Huang (2015), the distances between two

OMUs within GNG-BB ranged from 14 to 385 m. To ascertain whether the band stayed in the same habitat patch or migrated to another, we calculated the multiplier of the clustering center of each category to the maximum distance (385 m). A multiplier less than 2 indicated that the band either remained at the same location or moved to a neighboring area within the same habitat patch, while a multiplier greater than 4 or 5 indicated that the band migrated a long distance to another habitat patch in that category.

Next, we compared the social organization, home range, DTD, and habitat quality differences between GNG-BB and DJF-BB using the methods mentioned above. The results were used to evaluate the reproductive benefits of mate access, travel costs, and foraging benefits between the two groups. Analyses were performed using R v.4.1.0 (R Core Team, 2022), SPSS v.26 (SPSS, USA), and Origin Pro 2018 (Origin Lab, USA). Specific analyses and detailed processes are illustrated in the Supplementary Materials (Supplementary Method S6).

For the interspecific eco-behavioral data, we performed correlations and extracted PCs. To accurately identify the effect of environmental variables in shaping home range and group size during evolutionary history, we used phylogenetic generalized least-squares (PGLS) analysis to model the phylogenetic regression relationship among the candidate variables. PGLS can control for the non-independence of data that arise from shared ancestry during analysis by incorporating a phylogenetic tree (Symonds & Blomberg, 2014). After identifying the most significant variables impacting home range and group size in the PGLS analysis, we performed phylogenetic path analysis (PPA) to estimate statistical support for the hypothesized causal links among variables using the R package "phylopath" (Van Der Bijl, 2018). As several variables in the PGLS analysis approached the significance threshold, their impact on the PPA results was uncertain. Consequently, we established three different variable sets (eight, nine, and six variables, respectively) by incorporating or omitting the variables with uncertain significance.

For each set of variables, we designed 16 candidate models to examine both direct or indirect associations among variables and to determine the direction of causality. Using the eight-variable dataset as an example, two models were categorized as direct models to assess the direct effect of elevation on group size, while the remaining models were categorized as indirect models, positing that elevation influences group size indirectly by altering bioclimate variables. To examine the direction of causality, we used odd ordinal models where home range size affects group size, and even ordinal models where group size affects home range size. This allowed us to investigate whether an increase in home range size across species led to an increase in group size. Similarly, the relationships between other variables were also tested by establishing control models for comparison. We assessed the goodness of fit of the candidate models to elucidate potential causal links, identifying the most likely pathways in the best-supported model. The three best-supported models for the three sets of variables were combined to confirm the fifth prediction of the heterogeneity hypothesis, i.e., whether an increase in home range would promote group size.

For all statistical analyses, significant differences were identified at the 95% confidence level (*P*<0.05).

RESULTS

Range pattern and habitat quality

From 2013 to 2016, the GNG-BB size was approximately 131±13, with an average of 18 more individuals in summer (141±6) compared to winter (123±11) (paired t-test: t=3.83, df=3, P=0.031). After accounting for age structure, significant seasonal differences were observed in juveniles (paired t-test: t=3.37, df=3, P=0.043) and infants (paired t-test: t=3.40, df=3, P=0.043), but not in adults (paired t-test: t=1.44, df=3, P=0.25) or subadults (paired t-test: t=0, df=3, P=1). The average home range size in summer (13.84±1.59 km^2) was more extensive than that in winter (7.03±2.87 km^2) (paired t-test: t=5.00, df=3, P=0.015), including shaded areas with low sunlight radiation that were seldom used in winter. The core areas, comprising only a small portion of the home range (summer: 4.73%, winter: 9.60%), did not show significant size differences between summer and winter (paired t-test: t=-0.06, df=3, P=0.873). However, the core area varied based on geographical location, with minimal seasonal overlap (8.5%±6.2%) (Figure 2A; Supplementary Figure S1 and Table S4). Several sites, especially where quadrat S-H-1 was located, were consistently selected by GNG-BB as core areas almost every summer but were seldom utilized in winter (Supplementary Figure S1).

From 2013 to 2016, the DTD for GNG-BB also varied between seasons and was significantly longer in summer (1 529.45±128.31 m) than in winter (939.18±48.18 m) (paired t-test: t=7.68, df=3, P=0.005; Figure 2B; Supplementary Table S5). To clarify the factors affecting DTD, we found no statistically significant correlation between band size and DTD (Pearson correlation: r=0.61, n=8, P= 0.105). For meteorological variables, PCA was conducted, informed by Bartlett's test (x^2=3 114.02, n=36, P<0.001) and the KMO test (KMO value=0.72), which indicated that the first two PCs accounted for 87.94% (PC1 49.00%, PC2 38.94%) of the variance (Supplementary Figure S2A). Daily evaporation (20.53%) and solar radiation (18.42%) contributed the most to PC1 (Supplementary Figure S2B); thus, PC1 was considered the main environmental parameter determining how much thermal energy the golden snub-nosed monkey can obtain from the environment. Correlation analysis showed that the lower the thermal energy available, the shorter the DTD of the breeding bands (Pearson correlation: r=0.44, n=332, P<0.01, Figure 2C). PC2 was primarily related to three humidity parameters (Supplementary Figure S2B) and was thus indicative of overall ambient humidity. PC2 was positively correlated with elevation and DTD (Figure 2C). Different patterns were observed when the data for each season were analyzed separately. DTD was significantly shorter on colder and drier days in winter, but it did not respond to PC1 and PC2 in summer (Figure 2D).

Habitats were reclassified into four levels based on the ranging patterns of the breeding bands. For each quadrat within these habitats, 20 variables were separately calculated in summer and winter. The correlation matrix revealed significant correlations among numerous habitat variables, such as food diversity, food richness, and food evenness (Supplementary Figure S3A, B). PCA was performed based on Bartlett's test (summer: x^2=3050.98, df=190, P<0.01; winter: x^2=3221.37, df=190, P <0.01) and the KMO test (summer: KMO value=0.76; winter: 0.8).

The initial three PCs from the summer PCA were not readily

interpretable or visualizable in their original form. Thus, we rotated these PCs to obtain a new set of components with a more intuitive interpretation. These three rotated PCs (RCs) explained 73% of the variance in the original 20 variables (Figure 2E). RC1 was positively correlated with PS, PR, and PD (Figure 2E), indicating that a high RC1 score denoted a wide variety of plants. Given the herbivorous behavior of the golden snub-nosed monkey, plant parameters showed significant positive correlations with food-related parameters (Supplementary Figure S3A), implying that RC1 also represented the diversity and richness of food resources (i.e., FR, FS, and FD) (Figure 2E). Analysis using the RC plot and multiple comparisons showed that the RC1 scores of the utilized areas were significantly higher than those of the non-utilized areas; however, there was no significant difference between highly and moderately utilized areas (Figure 2F, G).

RC2 predominantly reflected the evenness, quantity, and diversity of the main foods (MFE, MFQ, and MFD) (Figure 2E). Main foods consisted of the 19 types of foods frequently consumed from the 86 available foods consumed in summer. Higher RC2 scores signified both a large quantity and high diversity of main foods in the plot, as well as their balanced proportions, serving as a comprehensive indicator of the quality and quantity of preferred foods. The RC2 scores decreased significantly in the order: core area, moderately utilized area, seldom utilized area, and non-utilized area (Figure 2F, G), suggesting that RC2 was a critical factor in differentiating levels of habitat utilization. RC3 showed positive correlations between tree characteristics and a-DBH, PQ, and a-CD (Figure 2E). Higher RC3 values suggested that trees in these quadrat areas were taller and thicker than those in the other areas. The value of RC3 in the core area was moderate but lower than that in the moderately utilized area and higher than that in the non-utilized area (Figure 2G).

In winter, PCA revealed three RCs accounting for 79% of the total variance (Figure 2H). RC1 was positively correlated with PD, PR, and PS, as well as FR, indicating that RC1 may be a representative variable for plant quality and food richness (Figure 2H). Both RC plot and multiple comparison analyses showed that RC1 scores were higher in utilized areas than in non-utilized areas but the differences between the three types of utilized areas were not significant (Figure 2I, J). Similarly, RC3 served as an indicator of tall and large trees within the quadrats, with findings suggesting that trees in the core area were of moderate size (Figure 2H–J). In contrast to summer, RC2 in winter was positively correlated with the quantity of food, main foods, and plants (FQ, MFQ, PQ), as well as total canopy density (Figure 2H), representing overall food abundance. The RC2 scores decreased significantly in the order: core area, moderately utilized area, and seldom utilized area (Figure 2J).

Spatiotemporal dynamics of habitat utilization

To understand the spatiotemporal dynamics of habitat utilization, we combined the dietary records of GNG-BB with their movement patterns and habitat characteristics. Using clustering analysis, DTD was divided into three categories: long, medium, and short, with respective clustering centers at 2.18 km, 1.37 km, and 0.74 km. The short-distance category indicated that the breeding band remained within the same habitat patch, with its cluster center to maximum diameter ratio being less than 2. Conversely, the long-distance category was indicative of migration over a long distance to gain access
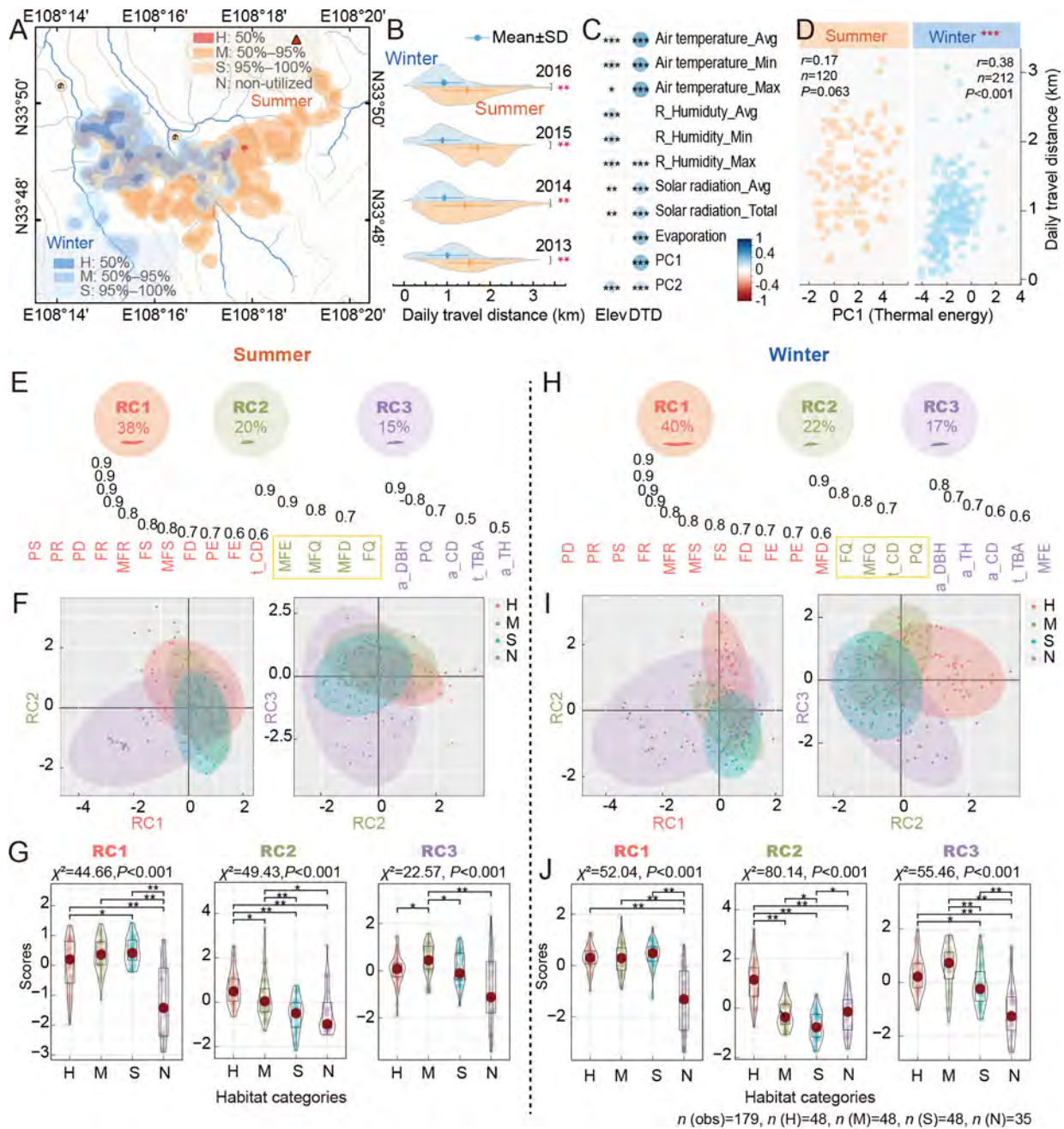
Figure 2 Seasonal ranging patterns and habitat characteristics of GNG-BB

A: Home range and core area in summer and winter for GNG-BB in 2014–2015. B: Differences in DTD between seasons in 2013–2016. C: Correlation matrix between elevation, daily movement parameters, and meteorological variables; Elev: daily average elevation, DTD: daily travel distance. D: Scatterplots showing correlation between DTD and PC scores. E–J: Habitat characteristics of GNG-BB in summer (E–G) and winter (H–J). E, H: Correlation between original variables and RCs in summer (E) and winter (H). Values above lines show correlation coefficient of variables to each RC. F, I: Scatterplot of three RCs in summer (F) and winter (I). G, J: Multiple comparisons of RC scores between different habitats in summer (G) and winter (J). Violin plots show distribution features of data. Kruskal-Wallis test detected differences between three categories and Dunn's test with FDR correction was used for *post-hoc* multiple comparisons. *: $P<0.05$; **: $P<0.01$; ***: $P<0.001$. H: highly utilized area; M: moderately utilized area; S: seldom utilized area; N: non-utilized area; PS: number of plant species; FS: number of food species; MFD: number of main food species; PQ/FQ/MFQ: quantity of all plants/food species/main food species; PD/FD/MFD: diversity of plants/food/main food species; PR/FR/MFR: richness of plants/food/main food species; PE/FE/MFE: evenness of plants/food/main food species; t-TBA: total tree basal area; a-DBH: average diameter at breast height; a-TH: average tree height; t-CD: total canopy density; a-CD: average canopy density.

to another patch, with its multiplier being greater than 5. The time series curve showed that DTD fluctuated dynamically throughout the year, with alternating peaks and valleys. A recurring pattern emerged where periods of long-distance migration were typically followed by phases of moderate and short-distance travel (Figure 3A).

In early summer 2014, GNG-BB often occupied the area encompassing the large S-H-1 quadrat, a site containing many diurnal and nocturnal locations (Figure 3B). This quadrat was predominantly populated with Liaodong oak trees (*Quercus liaotungensis* Koidz.*, 29.3% quantity proportion, same below), vines (*Celastrus gemmatus*, 14.9%), and all other main food
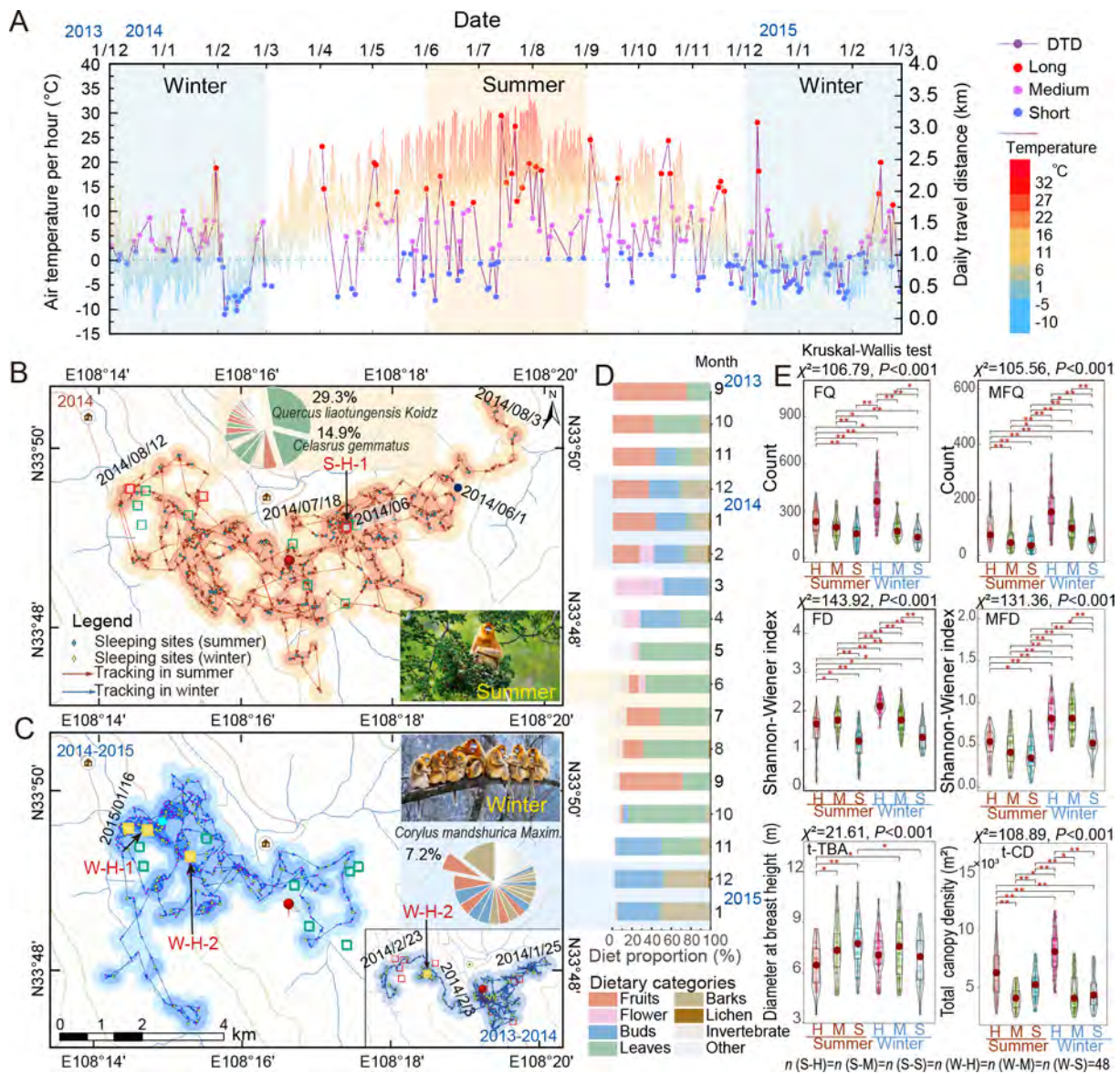
Figure 3 Seasonal differences in daily travel patterns and habitat utilization of GNG-BB

A: Dynamic changes in DTD and temperature from December 2013 to February 2015. Color of dots represents categories of distances. Red: long; purple: moderate; blue: short. B, C: Travel routes in summer (B) and winter (C). Arrows indicate direction of travel, and travel data are labeled above arrows. Pie chart highlights top 20 plant species in quadrats, with colors representing dietary categories. Diamond-shaped points are locations at night (1900h and 0500h), i.e., sleeping sites. D: Diet composition from September 2013 to January 2015. E: Differences in habitat characteristics between summer and winter. Abbreviations are as in Figure 2. Photographs of habitat are copyrighted by Kuan-Liang Ding and used with permission.

species typical of June (Figure 3B). Liaodong oak leaves are not only edible, but the tree branches are also suitable for roosting (Li, 2006). Despite the abundance of Liaodong oak in this area, monkeys preferred the tender leaves of *C. gemmatus*, which constituted the highest proportion of their diet in June (22.8%) (Figure 3B, D). Correspondingly, a large and dense number of feeding and sleeping locations were found in this small core area (<0.2 km^2) (Figure 3A). At the end of June, as the tender leaves of *C. gemmatus* matured, the group migrated to other areas, with a shift in their dominant food to *Actinidia kolomikta* (July 19.1%) and *Ilex polyneura* (August 26.8%).

With the onset of winter and declining temperatures, the monkeys gradually shortened their travel distances (Figure 3A), migrated to sunnier mountain slopes (Figure 3C), and shifted their diet to fruits (including seeds), bark, and buds

(Figure 3D). In the cold winter of 2013 (December 2013 to February 2014), when oak and birch fruits were abundant, the band traveled long distances to use the habitat covering quadrat W-H-2, which was rich in oak and hazel trees, for over half a month (Figure 3A, C, D). However, in the winter of 2014, characterized by an unusual climate leading to a scarcity of these seeds and fruits, GNG-BB reduced the utilization of W-H-2, instead expanding its home range to cover other habitat types such as W-H-1 and W-H-3 (Figure 3C). Overall, during the coldest periods of both years, the band traveled the shortest daily distances within the core areas, where food availability and canopy density were highest (Figure 3A, C, E).

Comparison of eco-behaviors between breeding bands

From 2013 to 2016, GNG-BB comprised approximately 12±1 adult males and 51±6 adult females with reproductive ability

(Figure 4A). The all-male band following GNG-BB, seeking access to adult females, expanded from 24 in June 2013 to 40 in June 2016, with the number of adult males increasing from 8 to 14. In contrast, DJF-BB contained 57±1 individuals, including 6–7 adult males and 14–16 adult females. The all-male band following DJF-BB consisted of 11–12 males, with the number of adults decreasing from 10 in 2013 to 8 in 2016. Consequently, the overall size of GNG-BB, along with its count of adult males and females, was approximately two to three times larger than that of DJF-BB during the same period (paired t-test: t=8.56, df=3, P=0.003; Figure 4A).

Similar to GNG-BB, DJF-BB also exhibited seasonal variations in home range size and DTD (Figure 4C; Supplementary Figure S4A and Tables S6, S7). Throughout the year, DTD displayed dynamic fluctuations with alternating peaks and valleys (Supplementary Figure S4B). These variations were significantly positively correlated with environmental thermal energy in spring and winter but were less influenced by it in summer and autumn (Supplementary

Figure S4C, D). However, notable differences were found between the two breeding bands. The multi-year home range of GNG-BB was smaller than that of DJF-BB in both summer (GNG: 16.83 km^2; DJF: 21.93 km^2) and winter (GNG: 11.27 km^2; DJF: 14.82 km^2), a pattern that persisted when combining the home ranges across both seasons (Figure 4B; Supplementary Figure S4A and Table S8). In addition, the multi-year DTD of GNG-BB (median: 1 495.15 m) was significantly greater than that of DJF-BB (median: 1 150.18 m) in summer (Mann-Whitney U-test, U=1 524, Z=−4.53, P<0.001), which also persisted when comparing the two bands separately in 2015 and 2016 (Figure 4C). However, there was no significant difference in DTD between the two bands in winter (Mann-Whitney U-test, U=4 786, Z=−1.50, P=0.135; Figure 4C; Supplementary Table S8).

When assessing the quality of habitats used by the bands, multiple variables, including food quantity and quality, were markedly higher in the core area of GNG-BB than in the core area of DJF-BB in both summer and winter (Figure 4D, E;
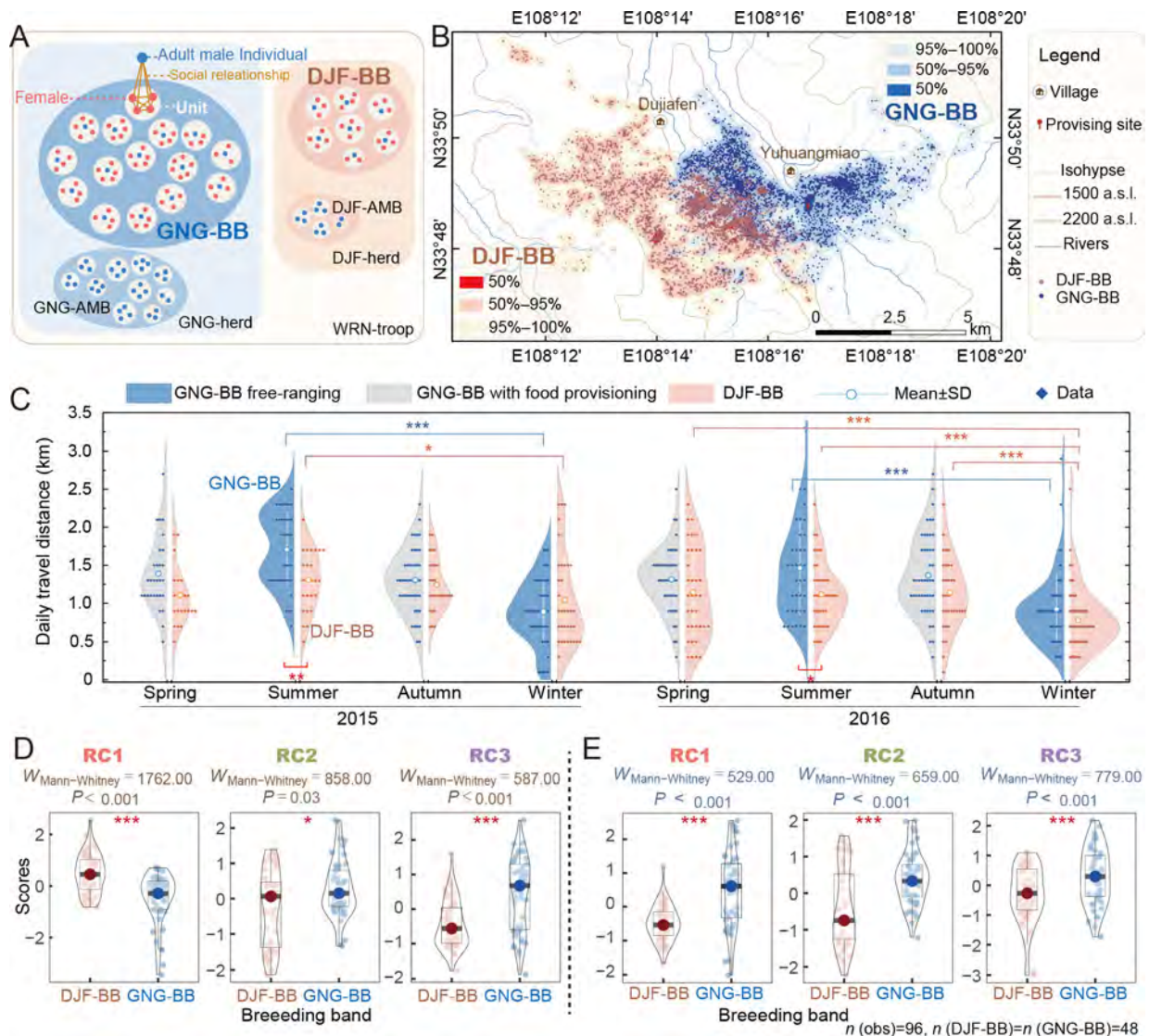

Figure 4 Differences in social organization, ranging behaviors, and habitat quality between bands
A: Differences in social organization between GNG-BB and DJF-BB. GNG-BB: GNG breeding band; GNG-AMB: GNG all-male band; DJF-BB: DJF breeding band; DJF-AMB: DJF all-male band. B: Multi-year (2014–2017) merged home range (summer and winter) of GNG-BB and DJF-BB. C: Differences in DTD in four seasons between GNG-BB and DJF-BB in 2015 and 2016. D, E: Comparison of RC scores between GNG-BB and DJF-BB in summer (D) and winter (E). Mann-Whitney U-test compared differences between GNG and DJF.

Supplementary Figure S5). In winter, almost all variables were greater for GNG-BB habitat (Supplementary Figure S5B), indicating that the larger group resided in higher quality habitats than the smaller group (DJF-BB).

Evolutionary pathways of colobines

Among the colobine species, those with larger groups inhabited larger home ranges, particularly in colder regions (Figure 5A). Notably, supergroups emerged in the cold high-altitude mountainous forests and occupied large home ranges, while smaller groups formed in the warmer environments and resided in smaller home ranges (Figure 5A). PGLS analysis revealed a significant positive relationship between home range and group size ($\lambda=0.57$, $n=52$, estimate=1.23, $t=5.96$, $P<0.001$). Further analysis detected significant correlations with multiple bioclimatic variables (log-transformed for non-normal data) (Supplementary Figure S6). Four PCs explaining 92.56% of the total variance in 19 bioclimatic variables. These PCs were characterized by isothermality, mean temperature of the warmest quarter, precipitation of the wettest quarter, and diurnal range of temperature (Supplementary Tables S9–S11). Total scores of the four PCs (PCT) were also calculated by weighting the variance percentages. Higher PCT scores indicated a stable, warm, and humid climate, i.e., a benign environment. Conversely, lower score indicated a cold, dry, and fluctuating climate, i.e., a harsh environment. The phylogenetic correlations among home range, group size, and all bioclimatic variables were further examined. Single-factor

PGLS revealed that home range was negatively correlated with mean temperature of the coldest quarter/month (bio11 and bio6). After log-transforming, group size had a positive effect on home range and elevation and was negatively correlated with PCT scores (Figure 5B; Supplementary Table S12). The effects of bio11, bio6, and temperature seasonality (bio4) on home range were statistically significant when group size and body mass were included as covariates (Supplementary Table S12).

Based on the PGLS results, we conducted phylogenetic path analysis to determine the inter-relationships among the factors affecting home range and group size (Supplementary Method S7). Of the 16 candidate models for the eight-variable set, the best-supported model suggested that cold winters and seasonal climatic fluctuations, often associated with high elevation or latitude in montane ecosystems, were predictive of group size via three pathways (Supplementary Table S13; Supplementary Figure S7). The first path predicted that an increase in seasonality would decrease the group size; the second path predicted that low PCT scores would influence large group size directly or increase body mass, leading to an expanded home range, ultimately favoring larger groups; and the third path suggested that cold winters predicted an increase in annual home range and enlargement of group size (Figure 5C).

The three best models from the three sets of variables supported the home range to group size direction (Figure 5C; Supplementary Figures S8, S9 and Table S14), whereas the
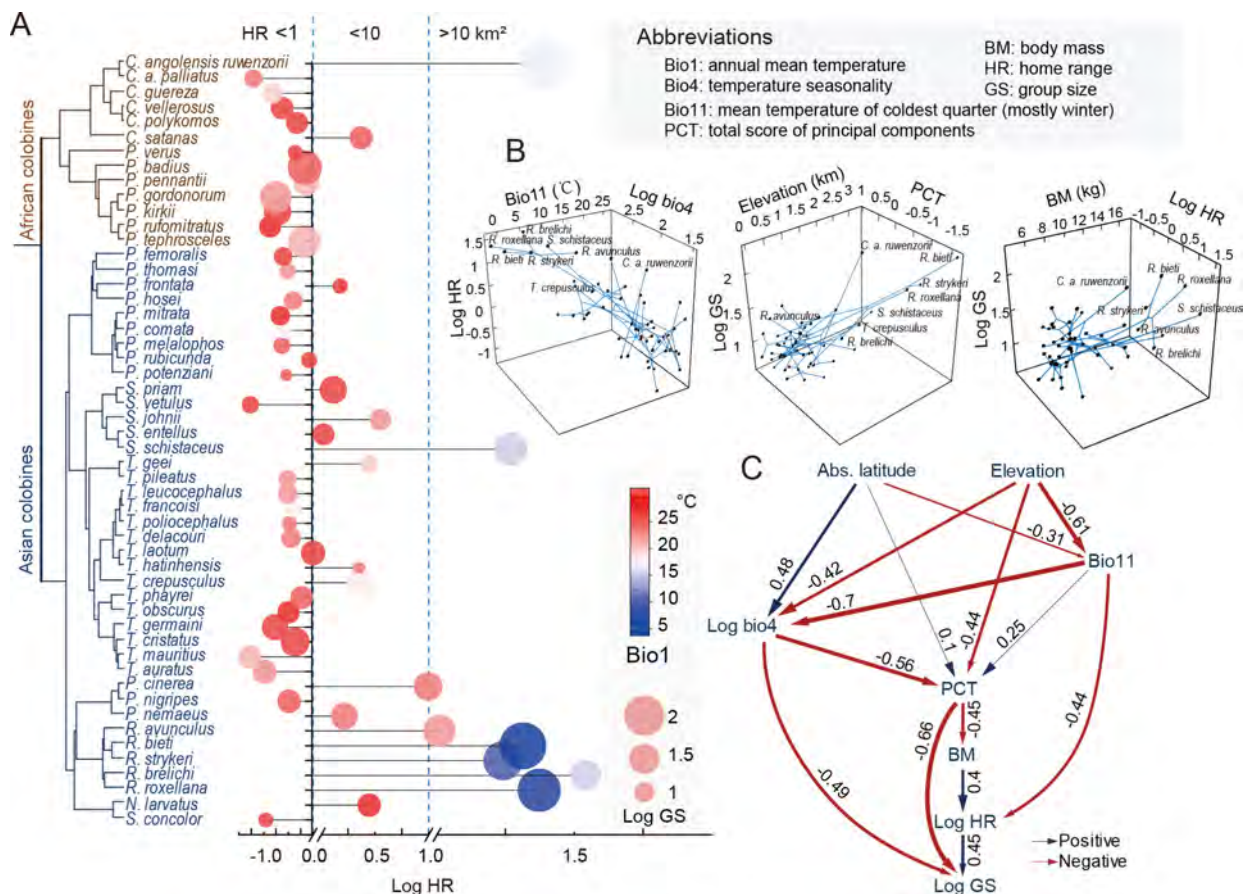

Figure 5 Ecology-associated evolution of home range and group size in colobine primates

A: Pattern of home range (HR) and group size (GS) along colobine phylogeny. B: Three-dimensional phylomorphospace plots of correlations of HR and GS with climatic and topographical factors, as well as with body size. C: Best-supported model with standardized path coefficients obtained from phylogenetic path analysis.

opposite direction was detected in the average model of the six variables (Supplementary Figure S9C). The evolutionary direction of home range to group size was more strongly supported because the standardized regression coefficient of home range to group size was greater than that of group size to home range (Supplementary Figure S9D).

DISCUSSION

Adaptative energetic strategy of golden snub-nosed monkeys to heterogeneous habitat

As elevation and latitude increases, the richness, diversity, and productivity of plant species generally decline due to reductions in temperature (energy) and humidity (water) (Kreft & Jetz, 2007). As such, montane ecosystems at high latitudes likely provide lower food densities and longer periods of resource scarcity for golden snub-nosed monkeys compared to their tropical leaf-eating colobine counterparts. To investigate this, we analyzed the ranging behaviors and food resources in the habitats of golden snub-nosed monkey breeding bands. Our goal was to determine whether this species faces highly heterogeneous resources as predicted by the heterogeneity hypothesis and to understand how they adapt to such environmental conditions.

Although the monkey breeding bands used a total home range of approximately 20 km², half of their locations were concentrated within the core area each season, each less than 1 km² in size (Figure 2). Moreover, these core areas were discretely distributed and exhibited seasonal variation within the home range, highlighting spatiotemporal habitat utilization. Quadrat sampling in summer identified higher diversity, evenness, and abundance of main food species in these core areas compared to other areas. In winter, these core areas showed the highest food resource abundance and canopy density (Figures 2, 3), providing protection from predators and cold winds (Davies et al., 2017; Li et al., 2002). These findings confirmed that habitat quality for golden snub-nosed monkeys varied spatially and temporarily in the mountainous forest, supporting the existence of heterogeneous resources.

This study involved tracking the spatiotemporal movements, diets, and habitat characteristics of monkey breeding bands to elucidate their utilization of heterogeneous food resources. Typically, folivores are thought to require more rest for digestion and low-quality fiber fermentation but spend less time traveling because leaves tend to be uniformly distributed and widely abundant. This foraging strategy, feeding on low-quality food and traveling shorter distances to minimize energy expenditure, is referred to as an energy minimization strategy (Pyke et al., 1977) and has been reported in various colobine species such as white-headed langurs (*Trachypithecus leucocephalus*) (Zhang et al., 2021). In contrast, frugivores are predicted to spend more time traveling between food patches in pursuit of nutrient-dense fruits, which tend to occur in discrete clusters. This prediction has led to an energy maximization strategy, in which groups attempt to maximize the amount of energy obtained per unit of feeding time. Our results demonstrated that the golden snub-nosed monkey bands frequently traveled long distances to reach high-quality habitats in summer (Figure 3). This indicates that, although golden snub-nosed monkeys are largely folivorous, they employ the energy maximization strategy due to the spatiotemporal distribution of high-quality food resources in summer. In contrast, home ranges and DTD decreased in winter compared to summer, with DTD showing a positive correlation with thermal energy only in winter and spring, suggesting that the band adjusted its movement in response to climatic variations. During winter, when temperatures dropped and food became scarce, long-distance travel was more energetically costly than in summer. Spatiotemporal eco-behavioral tracking revealed that the band reduced its DTD to minimize energy expenditure, shifted their diet to lower-quality food, and remained in areas with abundant food and high canopy density (Figure 3), indicating a typical energy minimization strategy. Furthermore, during brief temperature rises during winter, the time-series temperature-movement curve demonstrated that the band traveled long distances to access high-energy diets, such as nutrient- and fat-rich oak and hazel seeds, reflecting an energy maximization strategy. Collectively, these results indicate a dynamic foraging strategy, whereby the band alternates between two strategies depending on climatic shifts and varying availability and distribution of different food items.

Previous studies have documented different foraging strategies among mountain-living colobines. Within the same genus as golden snub-nosed monkeys, most species exhibit shorter DTD in winter than in summer, except for the gray snub-nosed monkey (*R. brelichi*) (Supplementary Table S15). Black and white snub-nosed monkeys (*R. bieti*), which are distributed at the highest altitude (2 500–5 000 m a.s.l.), show reduced traveling time and DTD with decreasing temperatures, indicating an energy minimization strategy in winter (Grueter et al., 2013; Ren et al., 2009a, 2009b). However, these monkeys also display patterns of long-distance movement and concentrated use of small areas, indicative of an energy maximization strategy (Grueter et al., 2008). Recent comparative research on activity budgets suggests that while geographic or climatic gradients do not significantly impact colobine activities, *Rhinopithecus* species display a tendency towards energy maximization rather than energy minimization (Kraus & Strier, 2022). In African colobines, the Rwenzori Angolan colobus monkey, which inhabits high-altitude mountainous forests and lives in large multilevel societies (Adams et al., 2021), employs an energy maximization strategy likely shaped clustered resources (Arseneau-Robar et al., 2021; Miller et al., 2020). Thus, mountain-living colobines appear to utilize an energy maximization strategy in addition to the general energy minimization strategy of other colobines, suggesting that the dynamic foraging strategy may be a general pattern among these species. This behavior may offer further insights into how folivorous primates adapt to mountainous climates, whereby the fluctuating climate in montane ecosystems shapes the distribution of resources over time and space, prompting these species to adapt their foraging strategies dynamically, similar to the approach observed in golden snub-nosed monkeys.

By comparing the eco-behaviors of two neighboring bands, we further explored how heterogeneous resources affect the costs and benefits associated with group living. The larger breeding band contained twice as many adult males and three times as many adult females as the smaller band. The greater number of females in the larger band offered more potential reproduction opportunities for adult males, especially the bachelor males. This may have led to the increased size of the GNG all-male band, thereby providing females with additional mating partners outside their primary unit, potentially

improving their fitness through extra-unit mating (Qi et al., 2020). The ecological constraints model proposes that movement patterns and foraging efficiency are key determinants of the food resources available to the group; thus, ecological factors that affect them can also constrain group size (Chapman & Chapman, 2000; Chapman & Teichroeb, 2012). An essential component of the ecological constraints model is that an increase in group size must lead to an increase in within-group feeding competition (Chapman & Teichroeb, 2012), thereby predicting an increase in DTD and home range size as group size increases in order to meet the dietary needs of additional group members (Ganas & Robbins, 2005). Contrary to expectations from the ecological constraints model, our study revealed that the larger band did not occupy a home range significantly larger than that of the smaller band, but rather occupied a smaller home range characterized by higher richness, diversity, and evenness of food resources, especially in winter (Figure 4). As a result, during winter, the large band did not travel significantly longer distances to meet dietary needs compared to the small band, thereby mitigating travel costs. Similar patterns in home range sizes have been reported in other geographically distributed golden snub-nosed monkeys, with group sizes ranging from 60 to 236 but annual home ranges only ranging from 18.3 to 22.5 km^2 (Supplementary Table S16). The deviation of the golden snub-nosed monkey from the ecological constraints model could be attributed to the spatial and temporal heterogeneity of resources in high-latitude mountain ecosystems. The seasonal and uneven distribution of food resources allows larger groups to occupy higher-quality habitats. At the same time, their dynamic foraging strategies enable efficient resource utilization, thus avoiding a sharp increase in DTD. These results imply that, compared to the smaller group, the larger band secured greater reproductive benefits without experiencing a corresponding increase in travel costs to acquire feeding resources in the high-latitude montane ecosystem, supporting the third prediction of the heterogeneity hypothesis.

Social evolution of colobines is associated with environmental heterogeneity and cold temperature

Research has indicated that the complex MLS of snub-nosed monkeys evolved from the social aggregation of independent one-male, multi-female groups (Grueter & Van Schaik, 2010; Qi et al., 2023). In the current study, we compared eco-behaviors among species to explore the impact of environmental heterogeneity on social aggregation. PGLS analysis revealed a positive correlation between group size and home range size in colobines, along with significant correlations with climate variables (Figure 5). Specifically, species residing at higher altitudes with colder temperatures and stronger climatic fluctuations tended to have larger home ranges and group sizes. These findings support the fourth prediction of the heterogeneity hypothesis, suggesting an expansion of home range in heterogeneous environments. Furthermore, PPA confirmed that high-elevation and high-latitude mountain ecosystems resulted in strong temperature seasonality and cold winters, driving group expansion through three distinct pathways.

The first pathway, indicating that a stronger seasonal climate leads to smaller group sizes, aligns with the ecological constraints model. This pathway functions independently of cold temperatures and may explain the social organization of

colobines in warmer areas such as tropical rainforests, where plants are abundant and foliage remains available throughout the year, even in seasonal climates. In periods when food availability is reduced due to climate change, groups may mitigate within-group competition by reducing their size, avoiding the need to expand their home range or travel long distances for new food sources. This adaptation may explain the reduction in group size under this pathway, independent of changes in home range size.

The second pathway suggests that the combination of cold and seasonal climates leads to an increase in group size, distinct from the first pathway due to the significant role of cold. Studies have shown that glacial periods in the past six million years imposed intense survival pressures related to cold, influencing the evolution of genes linked to cold-adaptive energy metabolism and neurohormonal regulation in odd-nosed monkeys (Qi et al., 2023). Key among these adaptations are more efficient dopamine and oxytocin pathways, which have been implicated in extending maternal care, enhancing infant survival in colder environments. These genetic changes are thought to strengthen social bonds, increase male-male tolerance, and foster social affiliations, thereby encouraging social aggregation (Qi et al., 2023). This pathway aligns with the concept of cold-driven social aggregation.

The third pathway presents an indirect process wherein cold, dry, and fluctuating climates contribute to an increase in body size and home range, ultimately leading to the growth of group size (Figure 5C). Prior studies have typically considered home range as a consequence of group size, arguing that a greater number of individuals necessitates more resources, leading to a larger home range (Ganas & Robbins, 2005; Grove, 2012). However, this pathway supports the heterogeneity hypothesis, suggesting that expansive home ranges have historically led to the formation of large groups. In challenging environments, where resources are limited and unpredictable, and plants die off completely in winter, maintaining a sufficiently extensive home range to satisfy seasonal food requirements becomes essential for survival. This larger home range, in turn, facilitates more frequent encounters among groups, thereby creating conditions conducive to social aggregation.

Multi-benefits framework of social evolution in colobine primates

We demonstrated that group size in colobine primates is influenced through multiple pathways (Figure 5C; Supplementary Figures S7–S9). Our results indicated that the ecological constraints model, cold-related neurohormonal regulation model, and heterogeneity hypothesis each contribute to understanding the social evolution of colobine primates. Consequently, we integrated these concepts into a comprehensive framework to explain the evolution of social organization in colobine clades. A dual-benefit framework has previously been used to resolve the evolutionary transition from solitary living to cooperative breeding in groups (Shen et al., 2017), identifying two main categories of group benefits: i.e., resource defense (RD) benefits, derived from group-defense critical resources, and collective action (CA) benefits, derived from social cooperation such as foraging, breeding, and predator detection. For colobines, the evolutionary transition from small one-male units to large social bands is more complex. Notably, in addition to the above benefits, the

reproductive benefit (RP) of increased mating opportunities also plays a crucial role, as evidenced by comparisons of reproductive opportunities between the different bands. Furthermore, feeding competition (FC) and travel costs (TC) are critical factors constraining group size (GS). Thus, the net benefits of individuals in a group (G_f) can be simplified as:

$$G_f = RD + CA + RP - FC - TC + \varepsilon \qquad (1)$$

where the ε is the error term representing the effects that are either not included or are unknown. For a group to be stable, it is essential that the benefits outweigh or balance the costs (Figure 6A). Furthermore, for evolution towards a larger group, the net benefits for individuals in a larger group must be greater than those in a smaller group ($G_{fL} > G_{fS}$).

In diverse environments, the benefits and costs associated with group living vary. In particularly, harsh, cold, and heterogeneous environments are characterized by limited resources per unit area and substantial spatiotemporal variations, making a small home range insufficient for meeting the survival needs of the ancestral OMUs in different seasons. Energy demands during cold winters necessitate access to a variety of high-quality complementary food resources, leading to the requirement of a larger home range during spring (Supplementary Figure S2). In addition, high-quality habitats are not only sparsely distributed but also exhibit variation both within and between seasons. Notably, an ideal summer habitat may be less so in winter, requiring a large home range covering high-quality habitats in different seasons. Within such an extensive home range, low-quality foods, which serve as fallback options, are widely available, and certain high-nutrient foods, like fruits, are abundant in specific seasons or brief periods. Consequently, habitat within this large home range would be underutilized by an ancestral OMU, with its size being smaller than the potential carrying capacity of the environment. In this context, additional individuals joining the group may gain collective action and reproductive benefits without significantly increasing within-group food competition, until reaching the maximum environmental capacity of the home range. In this study, we observed that larger bands of golden snub-nosed monkeys accessed higher-quality habitats

and more mating opportunities compared to smaller bands, illustrating the collective action and reproductive benefits of larger groups. Previous studies have also reported the reproductive benefits of OMU aggregation in MLS, whereby breeding males in MLS can more effectively ward off bachelor males through collective defense, creating a safety-in-numbers effect (Grueter & Van Schaik, 2010). This dynamic may result in bachelor males uniting into larger bands to obtain reproductive opportunities, with such an "arms race" between breeding and bachelor males potentially driving evolution towards larger band size for both groups (Grueter & Van Schaik, 2010; Qi et al., 2017). Furthermore, the increased number of breeding and bachelor males provides females with more mating choices, potentially enhancing female fitness through extra-unit mating or selection of alternative partners (Qi et al., 2020). Regarding travel costs, both our intraspecific data, as well as previously reported interspecific data, indicate that DTD does not increase proportionally with group size in cold and heterogeneous environments. For example, the largest band of *R. bieti*, encompassing around 400 individuals, has a reported average DTD of 1 514 m, only slightly more than the 1 068 m traveled by a significantly smaller seven-member group of Thomas's langurs (*Presbytis thomasi*) in a tropical primary rainforest (Grueter and Van Schaik, 2010). Hence, in cold and heterogeneous environments, the increased benefits of collective action and reproduction, coupled with constrained travel costs, likely contribute to the formation of larger groups. This, in turn, raises demand for resources, further facilitating home range enlargement and explaining the correlated evolution of social organization and home range (Supplementary Figure S9).

In tropical rainforests, however, the pattern may differ. In such warm, humid, and stable environments, abundant, evenly distributed, and regular food resources are available for colobines, and thus a small home range is sufficient to meet the year-round resource needs of an independent OMU. Typically, colobine species in tropical rainforests inhabit small home ranges of less than 1 km^2 (Figure 5A). We hypothesize that the evolutionary persistence of the one-male, multi-female social system may be attributed to the complete utilization of the habitat within these small home ranges by ancestral
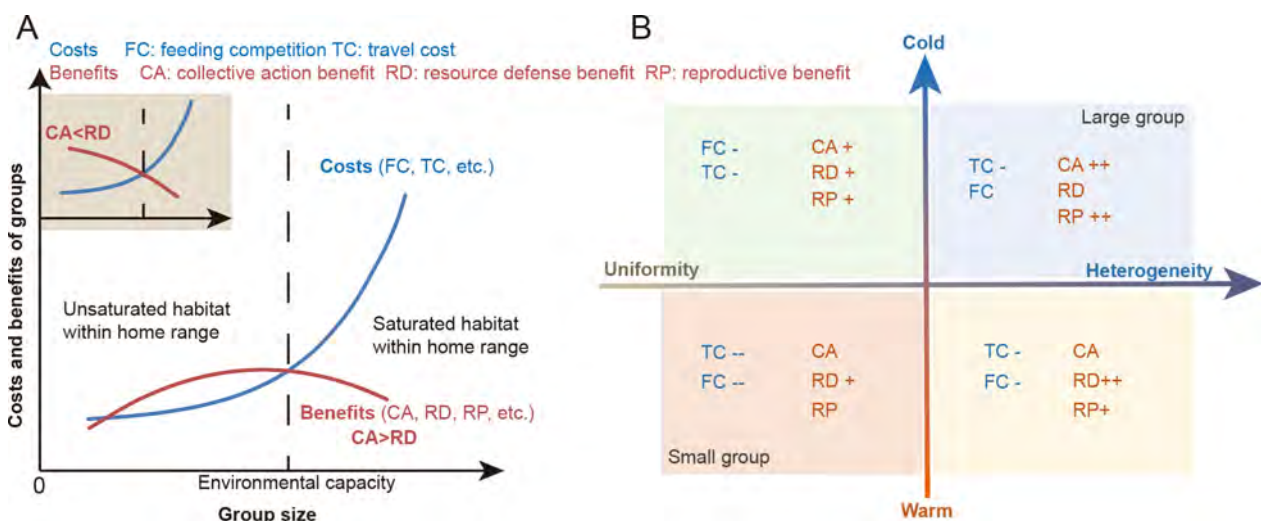

Figure 6 Multi-benefits framework for social evolution in colobines

A: Expected diagram of trade-offs between the costs and benefits of introducing environmental capacity. Expected relationship between group size and resource benefits (RD and CA) was obtained from Shen et al. (2017). B: Concept sketch of costs and benefits per additional capita to initial group in different environment types. Increasing effect is labeled "+" for benefits and "−" for costs; " ++" and "--"indicate stronger effects.

OMUs. In these saturated habitats, the addition of more individuals to an OMU may lead to increased costs rather than benefits, thus favoring autonomous living over integration into larger bands in tropical rainforests (Figure 6A). This hypothesis is supported by evidence from previous studies on population density and travel costs in these regions (Figure 6A). For example, the population density of pig-tailed langurs (*Simias concolor*) distributed in tropical rainforests reaches up to 220 animals/km^2, indicating extremely high habitat saturation (Watanabe, 1981) compared with the 7.2 animals/km^2 for golden snub-nosed monkeys (Tan et al., 2007). Furthermore, a striking contrast in travel costs is observed among different colobine species. For example, *R. bieti*, residing in cold and heterogeneous mountainous ecosystems, shows an increase of only 2 m in DTD for each additional group member, while tropical colobine *P. thomasi*, living in a more benign environment, requires an additional 60 m of travel per added individual (Grueter & Van Schaik, 2010), indicating considerably higher travel costs. This scenario, where high population density results in high feeding competition, may necessitate a strategy focused on resource defense within the group against outsiders (Figure 6B). According to the "insider-outsider conflict theory", when resource defense benefits are the primary driver of grouping, insiders gain higher fitness by cooperating with closely related individuals than by accommodating unrelated outsiders (Shen et al., 2017). This may contribute to the prevalence of colobine groups in tropical rainforests consisting of a male with mates and their offspring, often exhibiting territorial defense between groups.

In environments that are neither exceptionally harsh nor entirely benign, colobine species experience a nuanced balance of benefits and costs. This balance encompasses collective action benefits, resource defense benefits, and reproductive advantages. Such ecological conditions permit the inclusion of both distantly related and unrelated individuals, thereby fostering the development of diverse social group structures among these species (Figure 6B).

Apart from colobines, two other primate species known to form MLS have also adapted to harsh environments (Schreier & Swedell, 2012; Snyder- Mackler et al., 2012). Hamadryas baboons (*Papio hamadryas*) are distributed in sub-desert alpine grasslands (~3 300 m a.s.l.), while geladas (*Theropithecus gelada*) inhabit cold and windy highlands (1 800–4 400 m a.s.l.) (Rowe & Myers, 2017). The occurrence of large social groups in such challenging environments suggests the potential for larger-scale interspecies comparisons in future research to assess the applicability of the multi-benefits framework across different primate species.

CONCLUSIONS

Based on long-term fieldwork with the golden snub-nosed monkey and comparative analysis across colobine species, we proposed a multi-benefits framework integrating the ecological constraints model and heterogeneity hypothesis to explain the social evolution of colobines. The framework highlights that various benefits, including collective action, resource defense, reproduction, and the costs of food competition and travel associated with group living, differ across environments. In warm, tropical rainforests, the high abundance of plant resources available throughout the year enables colobines to satisfy their dietary needs within a relatively small home range. These resource-rich habitats

have prompted the adoption of a resource defense strategy, often involving close relatives, resulting in both small home ranges and small family groups. In contrast, during historical glacial periods, ancestral odd-nosed and snub-nosed monkeys, which dispersed to high latitude/altitude montane ecosystems, experienced survival stress due to the cold and dry environments and heterogeneous food resources (Qi et al., 2023). To adapt, these monkeys expanded their home range to accommodate year-round fluctuating resources and developed a dynamic foraging strategy integrating energy maximization to exploit resources and energy minimization to reduce energy expenditure in cold climates. This adaptation allowed large groups to occupy higher-quality habitats and access more mates without a proportional increase in travel costs for foraging, thus providing an ecological basis for social aggregation into larger groups in snub-nosed monkeys from the perspective of resource utilization. Additionally, during periods of intense survival stress from cold conditions, the ancestral odd-nosed and snub-nosed monkeys underwent selection for more efficient dopamine and oxytocin pathways. These pathways are known to facilitate social affiliation behaviors and provide a genetic and physiological basis for social aggregation (Qi et al., 2023). These cold-driven genetic changes and habitat-associated ecological adaptations jointly facilitated social aggregation from independent OMUs to larger breeding bands in high-altitude montane ecosystems. Our study combining fieldwork and comparative analysis distinguished the mixed effects of eco-dependent factors on group-level costs and benefits. Our findings shed light on how various factors have shaped social evolution via multiple pathways in a colobine clade of primates, offering insights into the complex and diverse social structures observed across a broad range of animal taxa.

AUTHORS' CONTRIBUTIONS

X.G.Q. conceived and designed the study. L.Z. and S.N.J. compiled the dataset. L.Z. analyzed the data. X.B.D, J.H.L, B.L.Z., and P.H.L. performed experiments. L.Z., S.N.J., J.H.L., Y.J.Y., B.G.L., Y.Q.G., and X.G.Q. wrote and revised the manuscript. All authors added materials, helped to revise the manuscript, and approved the final manuscript.

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