

Title: Contrasting use of fruit trees by sympatric primate groups differing in habituation status/

Running title: Habituation status and food competition of sympatric species

Authors:

Ahebot Hazitai¹, Yuxuan Fan¹, Xi Chen¹, Yu Yang¹, Hanchi Zhang¹, Colin A. Chapman^{2,3,4,5}, Pengfei Fan^{1*}

Affiliations:

¹ School of Life Sciences, Sun Yat-Sen University, Guangzhou 510275, Guangdong, China

² Biology Department, Vancouver Island University, Nanaimo, British Columbia, V9R 5S5, Canada

³ Wilson Center, 1300 Pennsylvania Avenue NW, Washington, DC 20004, USA

⁴ School of Life Sciences, University of KwaZulu-Natal, Scottsville, Pietermaritzburg 3209, South Africa

⁵ Shanxi Key Laboratory for Animal Conservation, Northwest University, Xi'an 710127, China.

Corresponding author:

Pengfei Fan,

School of Life Sciences, Sun Yat-Sen University, No. 135, Xingang Xi Road, Guangzhou, Guangdong 510275, China,

Email: fanpf@mail.sysu.edu.cn;

Phone: +86-020-84112950

¹ This research was supported by the Fundamental and Interdisciplinary Disciplines Breakthrough Plan of the Ministry of Education of China (JYB2025XDXM902) and National Natural Science Foundation of China (Grant Nos. 32525017, 32171485, and 32170520).



Zoological
Research

ABSTRACT

While humans have been considered as super predators in diverse ecosystems, many animals are habituated to humans in research or tourist sites, releasing them from the fear of humans. However, the impacts of habituation on interspecific competition remain poorly understood. We studied competition for fruits of *Choerospondias axillaris* between sympatric langurs (*Trachypithecus crepusculus*) and gibbons (*Nomascus concolor*) with different habituation statuses using satellite positioning collars, full-day follows, and canopy camera traps. In areas where both species were habituated, 99.4% of *C. axillaris* fruits were consumed by langurs because langurs always started feeding on the fruit much earlier in the season and had larger feeding parties and longer feeding bouts. In contrast, in areas where langurs were not habituated to humans, only 20.7% of *C. axillaris* fruits were consumed by langurs because the unhabituated langur group reduced access to fruit trees mainly located in the lowland area outside the reserve. These findings identify a context-specific case in which human-associated risk altered access to an important shared seasonal resource among sympatric primates, with implications for understanding how human presence can modify species interactions.

KEYWORDS

Camera traps; Gibbons; GPS tracking; Habituation; Interspecific competition; Landscape of fear; Langurs.

INTRODUCTION

Human activity now dominates Earth's ecosystems, creating an era that scientists define as the Anthropocene (Dirzo et al., 2014; Dirzo & Raven, 2003). In this era, humans function as "super predators", removing wildlife at rates far exceeding natural predation (Darimont et al., 2009). Much like natural predators, humans create landscapes of fear: spatial mosaics of perceived



Zoological
Research

risk in which animals adjust where and when they move, feed or rest in response to variation in risk (Gaynor et al., 2019; Moleón & Sánchez-Zapata, 2023). Species, including non-human primates, respond to this fear reactively (immediate flight, hiding) or proactively (lasting changes in range or diel rhythm) (Bersacola et al., 2021; Bshary, 2001; Fujioka, 2020; Nowak et al., 2014; Ordiz et al., 2019; Spitz et al., 2019). However, these anti-predator strategies carry hidden costs, as reduced access to resources can cascade through communities (Lodberg-Holm et al., 2019; Suraci et al., 2019). Two patterns are well documented for human induced fear: (i) trophic cascades, where suppression of apex predators releases mesopredators or herbivores, altering vegetation (Estes et al., 2011; Ripple et al., 2001; Suraci et al., 2019; Yovovich et al., 2021); and (ii) guild-level niche shifts, where co-occurring species partition time or space differently in response to human presence (Lesmeister et al., 2015; Schuette et al., 2013; Villalva et al., 2025; Wang et al., 2015). These dynamics parallel those driven by natural predators.

However, humans differ fundamentally from natural predators in many ways, as humans often habituate animals for research or tourism purposes (Williamson & Feistner, 2003; Woodford et al., 2002). Habituation is the gradual decline in response to repeated neutral stimulation (Williamson & Feistner, 2003). While habituation enables detailed behavioral observations and individual identification, it also raises ethical concerns: the loss of fear may alter foraging or ranging behavior, affect responses to natural predators, change interspecific interactions, and increase the risk of disease transmission by increasing proximity to humans (Hobaiter et al., 2017; Nowak et al., 2014; Shutt et al., 2014; Williamson & Feistner, 2003; Woodford et al., 2002). Despite widespread reliance on habituation in field studies of primates, its broader behavioral and ecological consequences remain poorly understood, particularly whether habituation-related changes in behavior and space use affect interactions among sympatric



species (Crofoot, 2021; Hanson & Riley, 2018; Hernández Tienda et al., 2022; Williamson & Feistner, 2003).

We investigated the consequences of habituation and reduced fear of humans through an observational natural contrast in two arboreal primate species living in sympatry: the western black-crested gibbon (*Nomascus concolor*, Critically Endangered; IUCN, 2026) and the Indochinese grey langur (*Trachypithecus crepusculus*, Endangered; IUCN, 2026) in the montane forests of Wuliangshan Nature Reserve (hereafter, the reserve), southwest China. The western black-crested gibbon is the flagship species of Mt. Wuliangshan, as this area supports one of the two global strongholds of the species, with an estimated 104 groups in Mt. Wuliangshan as of 2021 (Fan et al., 2022). Mt. Wuliangshan also supports the largest Indochinese langur population in China ($\approx 2\,000$ individuals) (Ma et al., 2015). Although gibbons are the main conservation target in Mt. Wuliangshan, the gibbon population at Dazhaizi on the western slope of Mt. Wuliangshan declined from five groups to three from 2003 to 2023 (Fan et al., 2006; unpublished long-term monitoring data). In contrast, the langur population at Dazhaizi increased from approximately 80 individuals in one group in 2010 (Fan et al., 2015) to more than 180 individuals in three groups in 2023, according to unpublished long-term monitoring data. Gibbons are predominantly frugivorous and generally prefer ripe fruits (Chen et al., 2025; Ma et al., 2017). Langurs are foregut-fermenting colobines that, although often characterized as folivorous, seasonally consume substantial proportions of unripe fruits and seeds (Chen et al., 2020; Fan et al., 2015) but rarely consume ripe fruit to avoid high-sugar “intoxication” (Davies & Oates, 1994). Previous research at Dazhaizi found that 14 of 26 primary gibbon food items, together comprising 56.7% of the annual diet, were also consumed by langurs and suggested that food competition between the two species may constrain recovery of the gibbon population (Chen et al., 2020). In addition, langur females reach sexual maturity at 4–5 years old and give birth every 2 years, while gibbon females reach



Zoological
Research

sexual maturity at 8–10 years old and give birth every 3–5 years at Dazhaizi (Hu et al., 2018; Huang et al., 2022; Ma et al., 2015). Consequently, the increase in the langur population may further suppress gibbon recovery in the area over the long term.

In this study, we took advantage of existing differences in habituation status of two langur-gibbon group pairs to examine whether habituation status was associated with contrasting lowland use and fruit competition. Specifically, the southern langur-gibbon group pair comprised habituated Langur-GA and Gibbon-G2 groups, whereas the northern group pair comprised an unhabituated Langur-GB group and a habituated Gibbon-G4 group. Langur-GB continued to show alarm or avoidance responses to people, whereas the other three focal groups tolerated the presence of observers in a distance of 5-20 m. These groups live in a montane forest ranging from 1600-2700 m where the reserve principally protects forest above approximately 1,900 m (Fan & Jiang, 2010; Ma et al., 2026). Although lower-elevation community forest outside the reserve provides more food resources for both gibbons and langurs, this area experiences more frequent human activities, including grazing, firewood collection and harvesting of non-timber forest products (Fan & Jiang, 2010a; Ma et al., 2026). Trees of the fruit species *Choerospondias axillaris* are mainly distributed in lowland forests outside the reserve. Across three consecutive years, *C. axillaris* consistently ranked among the top seven primary food species in the langur diet (Fan et al., 2015), and its fruits were consumed for approximately six months each year, from August to January (Chen et al., 2020). For gibbons, *C. axillaris* was also an important seasonal fruit resource from October to December, accounting for 1.72% of annual feeding records (Chen et al., 2020). Among the shared primary food items of the two primates, *C. axillaris* showed the highest combined dietary relevance based on a simple index integrating the dietary contribution of both species (Table S1).



Zoological
Research

We evaluated habitat use and *C. axillaris* fruit competition patterns of these groups using satellite positioning collars, full-day follows, vegetation surveys and arboreal camera traps. We predicted that unhabituated Langur-GB would use the human-disturbed lowland forest outside the reserve less frequently than habituated Langur-GA. If reduced lowland use limits langur access to the focal fruit trees, we further predicted that Langur-GB would consume less fruit of *C. axillaris* compared to Langur-GA. Consequently, Gibbon-G4, which was sympatric with Langur-GB, would account for a larger share of estimated fruit consumption at the monitored trees than Gibbon-G2, which shared a home range with Langur-GA.

MATERIALS AND METHODS

Study area

This research was conducted at the Dazhaizi Gibbon Research Station (N 24°21', E100°42'), on the western slope of Mt. Wuliangshan, central Yunnan, China. The region experiences marked seasonality, with mean annual temperatures of 16.1–18.3°C. The annual rainfall exceeds 1 500 mm and over 84% of precipitation falls between May and October (Guan et al., 2013; Huang et al., 2022). The mountainous terrain features steep slopes, frequent cliffs (up to 100 m) supporting a series of distinct vegetation belts by elevation: monsoon evergreen broadleaf forest (1 300–1 800 m), semi-humid evergreen broadleaf forest (1 900–2 100 m), mid-montane humid evergreen broadleaf forest (2 200–2 750 m), mossy dwarf forest (2 800–3 000 m), and rhododendron shrubland (>3 000 m) (Tian et al., 2007). The reserve was established in 1986 and upgraded to national status in 2000. It principally protects forest above approximately 1,900 m and threatened wildlife, including western black-crested gibbons.



Zoological
Research

Lower elevations remain community forest and are exposed to activities such as firewood collection, gathering of forest products and livestock grazing (Fan et al., 2015).

Study species and group composition

Long-term monitoring of gibbons at Dazhaizi began in 2003, when 5 gibbon groups could be found around the field station (Fan et al., 2006). The population decreased to three groups due to habitat destruction and degradation caused by intense human disturbances including logging and grazing before 2006. Habituation of both species involved repeated exposure to researchers and rangers during long-term monitoring and refers here specifically to tolerance of these observers in a distance of 5–20 m without sustained alarm calling, fleeing, or disruption of normal activities. Thereafter, researchers and rangers could conduct continuous dawn-to-dusk follows. Habituation began for Gibbon-G3, Gibbon-G2, and Gibbon-G4 in 2003, 2009, and 2011, and these groups met the criteria in 2005, 2010, and 2012, respectively. We selected Gibbon-G2 and Gibbon-G4 because their home ranges included the lowland community forests where the focal trees were monitored; Gibbon-G3 was excluded because its higher-elevation range did not overlap this area. During the study period, group sizes were 9–11 individuals in Gibbon-G2 and 8–9 individuals in Gibbon-G4, reflecting changes associated with births and dispersal (Table S2).

Monitoring of Langur-GA began in 2009. Langur-GA was monitored regularly for behavioral studies by researchers and rangers and was considered habituated in 2010. Langur-GB had been followed only occasionally for group censuses since 2013, and often displayed alert responses (hiding, alarm calling, or running away) when encountering rangers or researchers; the group was therefore considered unhabituated to humans. During the study, Langur-GA contained about 104 individuals, while the unhabituated Langur-GB was estimated to comprise approximately 80 individuals. Reliable sex–age composition was unavailable for either group



because their large group sizes and incomplete individual identification prevented accurate classification of all individuals.

Field data collection

Tracking of langurs: We deployed 6 satellite positioning collars (model HQAN40S, Huanqiu Xinshi) on langurs, including 4 individuals from the habituated Langur-GA and two from the unhabituated Langur-GB. Collars were programmed to record hourly positions between 0600 and 1900 h to conserve battery life. Data were collected from July 2022 to March 2024, when most collars ran out of battery power. Capturing and collaring were performed under anaesthesia via blowpipes; Supplementary Table S3 lists collar IDs, monitoring durations, and total fixes per individual.

Ethics: All procedures involving the anaesthesia and collaring of langurs were conducted under permit No. [2022] 251, issued by the Department of Wildlife and Plant Conservation, National Forestry and Grassland Administration (NFGA), China. All operations complied with national regulations for the handling of Class I protected species in China. No injuries or mortalities occurred during capture, anaesthesia, or collaring, and all collared individuals were alive at the time of writing.

Direct observation of gibbons: Due to the Critically Endangered status of western black-crested gibbons, collars were not used. Instead, we followed two habituated groups, Gibbon-G2 and Gibbon-G4, five full days per month from October 2022 to September 2023. Groups were located using morning calls or known sleeping and feeding trees. A handheld GPS unit (GARMIN GPSMAP 639Csx) recorded group locations at 5 min intervals. This yielded 62 full-day follows for Gibbon-G2 and 61 for Gibbon-G4 (Table S4). Behavioral observations followed established protocols (Fan et al., 2009).



Spatial analyses: Home ranges were estimated separately for each langur and gibbon group using 95% kernel density estimation (HR95) implemented in the R package adehabitatHR (Calenge, 2006). For langurs, the elevation of each fix was extracted from a 30-m Shuttle Radar Topography Mission digital elevation model (DEM; EPSG 32647; WGS-84/UTM Zone 47 N). For gibbons, the elevation of each location was obtained from handheld GPS readings collected during direct observations. Then we computed group-specific median elevation and interquartile range (IQR) based on these data. Although sampling methods and frequencies differed between species, both datasets were sufficient to characterize group-level home ranges and broad spatial patterns.

To evaluate use of areas inside and outside the reserve, we overlaid group locations on the reserve polygon. We then classified each location as inside or outside the reserve. To assess whether observed use deviated from availability, we estimated the proportion of each group's HR95 located inside and outside the reserve. Expected proportions were calculated as:

$$\text{Expected outside / inside proportion} = \frac{\text{HR95 outside / inside reserve}}{\text{HR95}}$$

Observed versus expected use was compared using chi-square goodness-of-fit tests.

Plot-based vegetation surveys and analyses: Additionally, to assess forest structure and the potential distribution and abundance of food resources, we conducted systematic plot-based vegetation surveys from December 2024 to March 2025. We divided the elevational range from 1,600 to 2,600 m into 200-m bands and established 135 plots (20 × 20 m each) along altitudinal contours within the HR95 of Langur-GA and Langur-GB, covering the core elevational range at 200 m intervals. In each plot, we recorded all trees with a diameter at breast height (DBH) ≥ 5 cm and all lianas with a DBH ≥ 1 cm. For each woody stem, circumference at breast height (CBH, cm), height (m), and crown diameter (m) were measured. CBH was converted to DBH



Zoological
Research

as $DBH = CBH/\pi$. Plant identification was attempted for every recorded woody stem by experienced botanists and field assistants, and was further checked by the first author referring to iPlant, a Plant Species Information System maintained by the Institute of Botany, Chinese Academy of Sciences.

We classified vegetation plots by elevation into Low (<2000 m, outside the reserve) and High (≥ 2000 m, inside the reserve) classes. Low plots mainly corresponded to monsoon evergreen broadleaf forest and the lower part of semi-humid evergreen broadleaf forest, whereas High plots mainly corresponded to semi-humid evergreen broadleaf forest and mid-montane humid evergreen broadleaf forest. We calculated species richness (S) and Shannon diversity (H') for each plot using the *vegan* package in R (Oksanen et al., 2026). Mean DBH was calculated for each plot across all recorded woody stems and used as an index of forest structure. Differences in S, H', and mean DBH between langur areas and elevation classes were tested using Wilcoxon rank-sum tests, with P-values adjusted for multiple comparisons using the Holm method (Holm, 1979).

To quantify potential distribution and abundance of langur food resources, we incorporated 35 primary food species previously identified from a three-year feeding study of the same population (Fan et al., 2015; Table S5). Each species was assigned an importance index defined as its mean annual proportion of total langur feeding time across the three-year study. DBH was used as a structural weighting term reflecting the relative size of recorded food-plant stems. Potential food-plant abundance (PFA) was calculated for each stem as:

$$PFA_{tree} = ImportanceIndex_{species} \times DBH_{stem}$$



Plot-level PFA was obtained by summing these values across all stems of the 35 food species within each plot and was compared between groups and elevation classes using Wilcoxon rank-sum tests with P-values adjusted by the Holm method (Holm, 1979).

Camera trap survey and feeding-bout annotation

We selected *Choerospondias axillaris* as the focal fruit species to investigate fruit competition between langurs and gibbons because it is an important fruit resource for both primate species and occurs mainly in lowland community forests outside the reserve (Chen et al., 2020). We carefully surveyed the whole study area and located 21 mature *C. axillaris* trees. In total, 20 of these trees were located in lowland forests outside the reserve. We carried out camera trapping surveys between July 2022 and January 2023, covering the full fruiting period of *C. axillaris* at all focal trees in the study year. For each tree, we mounted 4–7 infrared cameras (total N = 104; Dongfang Hongying, Yianweishi, Lieke Cam, BOLLY, YeYing, ForestCam) to monitor the whole tree crown 7–25 m above ground. Larger or more structurally complex crowns received more cameras. To reduce potential detection differences among camera brands, brands were evenly distributed across focal trees whenever possible, and all cameras were positioned using the same placement criteria, with sensors directed towards major fruit-bearing branches and likely feeding positions (Table S6). Cameras were operated in 24-hour motion-trigger mode, recording one photo and a 15–20 s video, with a 30 s interval between triggers. Trained rangers checked the cameras monthly, replacing batteries and memory cards, checking function and adjusting positions.

Photos and videos obtained from camera traps were manually annotated for species identity and feeding behavior by the first author using digiKam 5.90.0. Time stamps and species IDs were extracted with Exiftool and R package *CamtrapR* (Niedballa et al., 2016). Only valid records containing identifiable animals were retained for subsequent analyses. To define



independent visit events, we applied a temporal threshold of ≥ 30 min between successive detections of the same taxon at the same tree, following common practice in camera trap studies (Kelly & Holub, 2008; O'Brien et al., 2003; Sollmann, 2018). An independent visit did not necessarily include feeding. A feeding bout was then identified when one or more individuals were clearly observed biting, chewing, or swallowing *C. axillaris* fruits (Figure S1). Consecutive feeding records of the same primate species at the same focal tree were merged into a single feeding bout when they occurred within 30 min; records separated by at least 30 min were treated as independent feeding bouts. Simultaneous records from different cameras at the same tree were assigned to the same feeding bout. For each feeding bout, we recorded the start and end times from camera time stamps. Because a feeding bout could involve multiple individuals and be recorded by several cameras, camera-derived feeding party size was defined as the maximum number of distinct individuals visible simultaneously during the bout. We reviewed all available clips and preferentially used the view with the widest crown coverage. Counts from different cameras were not summed; where camera views overlapped, duplicate individuals were excluded whenever they could be recognized from their position, movement, or appearance.

To validate the camera trap data, we compared feeding bouts of gibbons recorded by both cameras and direct observation during overlapping sampling periods. For the 16 paired feeding bouts, we compared feeding party size and bout duration using paired Wilcoxon signed-rank tests.

Analyses of feeding patterns and estimated consumption: We compared feeding-bout characteristics and estimated consumption of *C. axillaris* between gibbons and langurs at the monitored trees. Bouts shorter than 1 min were excluded because the limited number of



Zoological
Research

photographs or video frames available for such records did not allow reliable assessment of feeding behavior.

Species-specific intake rates were estimated from 58 direct-observation video clips of habituated gibbon and langur groups in which fruit handling by one individual was clearly visible. These clips were used only to estimate intake rates. For each clip, intake was measured for one individual that remained clearly visible during the measured interval. Timing began when that individual first ingested a fruit and ended when the clip ended or when the individual was no longer clearly visible. Intake rate was calculated as the number of fruits consumed per minute. The resulting mean intake rates were 4.63 fruits/min for gibbons and 4.48 fruits/min for langurs (Table S7).

For each feeding bout, we then calculated a composite Fruit Consumption Index as:

Fruit Consumption Index = Bout Duration (min) × Feeding Party Size (number of feeding individuals) × Species-specific Intake Rate (fruits/min) [Unit: number of fruits per bout]

Subsequently, we estimated the proportion of fruit consumed by langurs relative to sympatric gibbons as:

$$\text{Proportion}_{\text{langur}} = \frac{\sum \text{Fruit consumption}_{\text{langur}}}{\sum \text{Fruit consumption}_{\text{langur}} + \sum \text{Fruit consumption}_{\text{gibbon}}}$$

We summarized the number, duration, and party size of feeding bouts for each primate species and group to describe overall feeding patterns. To test the effects of primate species and habituation status, we analyzed feeding bout duration and feeding party size separately. Bout duration was right-skewed; we therefore log-transformed duration and fitted a linear model after inspecting the residual distribution. Feeding party size was analyzed as count data. Because it showed overdispersion relative to a Poisson model, we fitted a negative binomial



generalized linear model. These analyses used the R packages stats and MASS (Venables & Ripley, 2002).

Langurs began feeding on *Choerospondias axillaris* during the unripe-fruit stage, before the main period of gibbon use during the ripe-fruit stage. We tested whether earlier langur feeding intensity was associated with subsequent gibbon feeding bout duration and party size. Gibbon feeding data were aggregated by tree and week from October to January, when 96.1% of gibbon feeding bouts were recorded. The single monitored tree located inside the reserve was excluded from this analysis, leaving 20 trees across 18 calendar weeks and producing 360 tree-week analytical units for modelling. A tree-week analytical unit represented one focal tree during one calendar week, regardless of whether gibbon feeding occurred. For each tree-week, we calculated weekly total gibbon feeding bout duration and weekly summed feeding party size; tree-weeks without a gibbon feeding bout were assigned zero values. The predictor was cumulative langur feeding intensity, calculated as the total number of langur feeding bouts recorded at the same tree from the beginning of the camera-trap survey to the end of each focal week.

We fitted two generalized linear mixed models (GLMMs) to account for distributional characteristics of the response variables and repeated measures within trees. The weekly sum of gibbon feeding party sizes was modelled using a zero-inflated negative binomial GLMM (*nbinom2* family, log link) to account for overdispersion and excess zeros. The conditional component included the cumulative number of langur feeding bouts per tree per week as the fixed effect and tree identity as the random intercept. The zero-inflation component was specified as an intercept-only model, representing the probability of structural zeros independent of predictors. Weekly total gibbon feeding bout duration was modelled with a Tweedie GLMM (log link), appropriate for continuous data with a point mass at zero and a



Zoological
Research

right-skewed distribution of positive durations; tree identity was again included as the random intercept. All models were fitted using the *glmmTMB* package (Brooks et al., 2017) in R. All analyses were conducted in R version 4.5.2 (R Core Team, 2025).

RESULTS

Home range and altitudinal range use

We collected 22,982 valid fixes of 4 individuals in Langur-GA, and 4,587 fixes of two individuals in Langur-GB (Table S3). The HR95 ranges of the four Langur-GA individuals overlapped extensively (mean $\pm$ SD = $95.9 \pm 2.2\%$, range = 92.5–97.3%, Table S8). Therefore, we used the home range of one individual to represent the home range of the whole group. For Langur-GA, we used the individual with the largest number of valid GPS fixes (individual 51; $n = 8,160$) to represent the group home range. Because the two individuals in Langur-GB were tracked in different time periods, we combined their fixes to estimate their home range. The spatial datasets for Gibbon-G2 and Gibbon-G4 comprised 7,640 and 7,156 group locations, respectively.

Within the southern group pair, Langur-GA occupied an HR95 of 5.04 km², while Gibbon-G2 occupied an HR95 of 2.64 km²; their home ranges overlapped by 2.16 km², equivalent to 82.1% of the Gibbon-G2 range (Figure 1A). Within the northern group pair, Langur-GB occupied an HR95 of 4.89 km², while Gibbon-G4 occupied an HR95 of 3.27 km²; their home ranges overlapped by 1.65 km², equivalent to 50.3% of the Gibbon-G4 range.

Median elevations of group locations differed markedly among groups (Figure 1B). Langur-GA occurred at the lowest median elevation (median = 1,948 m, IQR = 1,848–2,071 m), while Langur-GB occurred at the highest elevations (median = 2,453 m, IQR = 2,270–2,581 m).



Gibbon-G2 used intermediate terrain (median = 2,044 m, IQR = 1,914–2,213 m), while Gibbon-G4 ranged higher (median = 2,205 m, IQR = 2,084–2,345 m).

For Langur-GA, 95.4% of GPS fixes were located outside the reserve, and only 4.6% were within it. The HR95 of Langur-GA was largely outside the reserve, with only ~10% of its area inside the reserve. Observed use differed significantly from availability ($\chi^2 = 264.7$, $df = 1$, $P < 0.001$), indicating that Langur-GA preferentially used lowland areas outside the reserve. For Langur-GB, 4.4% of GPS fixes were located outside the reserve, while 95.6% were within it. Its HR95 was predominantly inside the reserve (87.6% of the area). Observed use differed significantly from availability ($\chi^2 = 272.7$, $df = 1$, $P < 0.001$), indicating that Langur-GB largely avoided lowland areas outside the reserve (Figure 1A).

Both gibbon groups used areas outside the reserve. For Gibbon-G2, 29.6% of group locations were within the reserve, while 70.4% were outside ($\chi^2 = 4.2$, $df = 1$, $P < 0.05$). For Gibbon-G4, 79.3% of group locations were inside the reserve, and 20.7% were outside ($\chi^2 = 695.2$, $df = 1$, $P < 0.001$). These patterns indicate that the habituated gibbon groups, like habituated Langur-GA, used lowland forest outside the reserve more than expected from availability.

Vegetation structure and food availability across elevation zones

A total of 7,287 woody stems were recorded across 135 vegetation plots. Of these records, 7,164 (98.31%) were identified to species, 42 (0.58%) to genus, 5 (0.07%) to family, and 76 (1.04%) remained taxonomically undetermined. These records represented 221 taxonomic units. Sampling included 49 low-elevation (<2,000 m, outside the reserve) and 17 high-elevation ($\geq 2,000$ m, inside the reserve) plots within the Langur-GA home range, and 20 low- and 49 high-elevation plots within the Langur-GB home range.



Zoological
Research

Woody-plant diversity and species richness showed no significant differences between groups and across elevations. Langur-GA plots showed slightly higher mean Shannon diversity ($H' = 2.31 \pm 0.47$, $n = 66$) and richness ($S = 16.0 \pm 5.7$) than Langur-GB plots ($H' = 2.25 \pm 0.57$; $S = 15.6 \pm 6.2$, $n = 69$). Within groups, high-elevation plots showed similar diversity and richness to lowland plots (Langur-GA high: $H' = 2.29$, $S = 16.6$ vs. low: $H' = 2.32$, $S = 15.8$; Langur-GB high: $H' = 2.27$, $S = 16.1$ vs. low: $H' = 2.19$, $S = 14.5$). Overall, both groups inhabited forests of similar compositional complexity across elevations.

Mean woody-stem diameter at breast height (DBH) was lower in Langur-GA plots than in Langur-GB plots (56.6 ± 57.6 vs. 62.2 ± 57.9 cm, $P < 0.001$; Figure 2A). Within both home ranges, high-elevation plots supported larger woody stems than low-elevation plots, but this difference was not significant for Langur-GA (Langur-GA: 63.1 ± 65.4 vs. 54.5 ± 54.8 cm, $P = 0.23$; Langur-GB: 67.2 ± 63.8 vs. 50.9 ± 39.5 cm, $P < 0.001$; Figure 2B). These patterns indicate that high-elevation forests within the reserve harboured larger woody stems than low-elevation plots outside the reserve.

Plot-level potential food-plant abundance (PFA; cumulative DBH of important food species per plot) did not differ significantly between Langur-GA and Langur-GB (669.0 ± 798.4 vs. 870.3 ± 894.2 , $P = 0.130$; Figure 2C). Within the Langur-GA home range, PFA was similar between low- and high-elevation plots (696.5 ± 811.0 vs. 589.9 ± 779.5 , $P = 0.53$). Within the Langur-GB home range, low-elevation plots had nearly threefold higher PFA than high-elevation plots ($1,591.8 \pm 807.9$ vs. 575.9 ± 754.3 , $P < 0.001$; Figure 2D). Despite this higher estimated PFA, Langur-GB used lowland forest outside the reserve less than expected from availability.

Camera trap data



The camera trap survey yielded 7,419 valid records containing animal visits. Across 21 *C. axillaris* trees, we identified 811 independent visits. The most frequent visitors were flying squirrels (Pteromyinae; 326 visits), followed by western black-crested gibbons (166 visits) and Indochinese grey langurs (163 visits); other species were recorded less frequently (Figure 3A). Although flying squirrels were frequently detected at *C. axillaris* trees, no direct feeding observations were obtained from these records. Of these, only langurs, gibbons and squirrels (Sciurini) were recorded feeding on the fruit of *C. axillaris* trees. Squirrels always visited the tree alone and were recorded feeding on the fruit in only 6 of their 50 visits. Therefore, we did not consider squirrels as significant competitors with gibbons and langurs. Gibbons and langurs together accounted for 329 feeding bouts and were retained for subsequent analyses (Figure 3A).

Of the 20 feeding bouts recorded during periods covered by both methods, 16 (80%) were detected by both camera traps and direct observation, two only by direct observation, and two only by camera traps (Table S9). Direct observation yielded a larger mean feeding party size (mean $\pm$ SD = 4.67 ± 2.45 , $n = 16$) than camera traps (3.28 ± 1.78 , $n = 16$; paired Wilcoxon $V = 11.5$, $P = 0.0167$; Figure 3C). Among the 16 feeding bouts detected by both methods, feeding bout durations were similar (direct observation: median = 15.00 min, range = 3.00–40.00 min; camera traps: median = 13.18 min, range = 0.02–41.00 min; paired Wilcoxon $V = 63.0$, $P = 0.82$; Figure 3B). Camera traps provided comparable estimates of feeding bout duration for paired bouts but recorded smaller feeding party sizes than direct observation, indicating that camera-derived party sizes should be interpreted as conservative estimates because incomplete crown visibility may have caused underestimation.

Group-level use of the shared fruit resource



Zoological
Research

417 A road from the closest village to the field station separated the home ranges of the two gibbon
418 groups. Only 0.14% of Langur-GA locations occurred north of the road, supporting this spatial
419 classification (Figure 1A). Therefore, we considered that fruits from the 11 *C. axillaris* trees
420 south of the road were consumed by Langur-GA and Gibbon-G2, whereas fruits from the 10
421 *C. axillaris* trees north of the road were consumed by Langur-GB and Gibbon-G4.

422 Of the 329 feeding bouts recorded for gibbons and langurs, 260 lasted ≥ 1 min and were retained
423 for subsequent analyses. South of the road, camera traps recorded 125 feeding bouts by Langur-
424 GA and 9 by Gibbon-G2. Most Langur-GA feeding bouts (74.7%) occurred when fruit was
425 unripe (July–September) (Figure 4B). Langur-GA accounted for 99.4% of estimated fruit
426 consumption at the monitored trees south of the road. North of the road, 6 bouts were recorded
427 for Langur-GB and 120 for Gibbon-G4. Gibbon feeding bouts were concentrated between
428 October and January (96.1%) when fruits were fully ripe. Langur-GB accounted for 20.7% of
429 estimated fruit consumption at the monitored trees north of the road (Table S10).

430 Feeding bout duration and party size consistently differed between gibbons and langurs, with
431 gibbons forming smaller feeding parties ($z = 6.82$, $P < 0.001$) and exhibiting shorter feeding
432 bout durations ($t = 5.98$, $P < 0.001$). Gibbon-G2 showed shorter feeding bouts (17.2 ± 29.2
433 min, $n = 9$) and smaller feeding parties (1.11 ± 0.33 individuals, $n = 9$) than Langur-GA (48.3
434 ± 63.6 min; 4.75 ± 3.57 individuals, $n = 125$) (Figure 5A–B). Similarly, Gibbon-G4 also had
435 shorter feeding bouts (15.2 ± 11.8 min, $n = 120$) and smaller parties (2.68 ± 1.65 individuals,
436 $n = 120$) than Langur-GB (32.3 ± 42.1 min; 5.83 ± 3.76 individuals, $n = 6$) (Figure 5C–D).
437 Habituation status showed no significant effect on either feeding bout duration or party size
438 (LM: 95% CI = -1.232 – 0.515 ; GLM-NB: 95% CI = -0.192 – 0.818).

439 During October–January, greater cumulative langur feeding intensity was associated with a
440 lower weekly sum of gibbon feeding party sizes (Estimate = -0.201 , SE = 0.060 , $z = -3.33$, P



Zoological
Research

< 0.001) and lower weekly total gibbon feeding bout duration (Estimate = -0.239, SE = 0.082, $z = -2.91$, $P = 0.0036$). Together, these results indicate that greater langur feeding intensity was consistently associated with smaller gibbon feeding parties and shorter feeding bouts.

DISCUSSION

By integrating high-resolution tracking, long-term behavioral observations, vegetation plot surveys and arboreal camera trap surveys, langur habituation status was associated with differences in interspecific competition for *C. axillaris* fruit between langurs and habituated gibbons. The habituated langur group, Langur-GA, used the monitored trees mainly during the unripe-fruit stage and accounted for most estimated consumption in the southern group pair. In contrast, the unhabituated langur group, Langur-GB, used lowland forest outside the reserve less frequently and consumed a small proportion of fruits, meanwhile the sympatric Gibbon-G4 consumed the majority of the fruits, mainly during the ripe-fruit stage.

Human exposure and contrasting lowland use

Langur-GB used the lowland forest outside the reserve less frequently than Langur-GA and the two gibbon groups. This pattern is consistent with previous studies showing that animals may reduce their use of areas associated with predictable human activity (Moleón & Sánchez-Zapata, 2023; Palmer et al., 2022; Ma et al., 2026). Lowland forests outside the reserve contained more food resources despite being close to villages and exposed to human activities. Notably, 20 of the 21 monitored *C. axillaris* trees were located outside the reserve. The habituated langur group, Langur-GA, regularly used low elevations and dominated use of the monitored *C. axillaris* trees.



Zoological
Research

Vegetation surveys revealed that the highlands within the Langur-GB home range supported larger woody stems than lowland plots because these areas are located within the reserve. However, low-elevation plots within this home range exhibited substantially higher abundance of food trees than high-elevation plots, including multiple primary food species such as *Litsea elongata*, *Castanopsis hystrix* and *Helicia silvicola*, which are important dietary resources for these langurs (Fan et al., 2015). A nine-year study at the same location also demonstrated that the habituated langur group, Langur-GA, initially shifted to higher altitudes, avoiding human presence despite lower food availability. As the degree of habituation to researchers increased, Langur-GA later moved to lower, resource-rich areas outside the reserve with more high-quality food (Ma et al., 2026). The observed pattern is consistent with anticipatory avoidance of humans, with high-elevation forest inside the reserve potentially serving as a refuge. Comparable human-avoidance strategies have also been documented in black bears (*Ursus americanus*) and wolves (*Canis lupus*) under anthropogenic disturbance (Kautz et al., 2021; Palmer et al., 2022).

Contrasting use of *C. axillaris* by langurs and gibbons

Choerospondias axillaris represents an important fruit for both primate species and occurs in lowland areas often outside the reserve. Langurs started consuming the fruit of *C. axillaris* before the fruit ripened sufficiently for gibbons to eat (Figure 4B). This likely reflects their differing fruit preferences: langurs can eat unripe fruits, whereas gibbons prefer ripe ones (Chen et al., 2025; Davies & Oates, 1994; Ma et al., 2017). In addition, langurs formed larger feeding parties and had longer feeding bouts than gibbons, potentially increasing their consumption of *C. axillaris* fruit during the unripe phase before gibbons consumed the fully ripened fruit. Consequently, temporal niche separation reduced direct encounters and competition between langurs and gibbons, but early langur consumption may have reduced the fruits available to gibbons, potentially producing asymmetric exploitative competition. Similar



Zoological
Research

asymmetric competition may also occur over other shared fruit resources (Chen et al., 2020). In contrast, where unhabituated Langur-GB used lowland areas less frequently, Gibbon-G4 dominated use of the monitored *C. axillaris* trees.

Conservation implications of habituation

Beyond its roles in research and ecotourism, habituation can alter how wildlife responds to people, with beneficial or harmful consequences (Higham & Shelton, 2011). Manipulating the “landscape of fear” through habituation may be a valid attempt to protect the target species. Selective habituation of threatened species may in some situations reduce avoidance of humans, potentially leading to changes in food competition with unhabituated species, reduced predation risk from unhabituated predators, and increased access to human-disturbed habitats (Shannon et al., 2014; Wheat & Wilmers, 2016). For example, habituated mountain gorillas tolerate the regular presence of researchers and tourists, allowing use of areas with frequent human activity under carefully managed conditions (Williamson & Feistner, 2003). Habituation also enables coexistence of endangered Przewalski’s horses (*Equus ferus przewalskii*) and nearly threatened Asiatic wild ass (*Equus hemionus*) in the desert by allowing Przewalski’s horses to safely exploit important habitats near human activity (Cao et al., 2025). Similarly, habituated bears (*Ursus arctos*) in the Chilkoot watershed, with largely diurnal activity patterns, can significantly increase their capture rates of salmon (Crupi Jr, 2004; Wheat & Wilmers, 2016). In Grand Teton National Park, ungulates use human presence as a refuge from predation risk, adjusting their behavior accordingly (Shannon et al., 2014). Similar patterns have been documented in urban birds and marine mammals at fishing ports (Benmazouz et al., 2021; Hückstädt & Antezana, 2003). In human-disturbed, especially those predator-free landscapes, deliberately habituation of threatened species to humans rather than



clinging to idealized "wilderness" may be essential to reclaim human-altered terrain for biodiversity.

However, habituation may also pose risks to animals. One major concern is disease transmission, as close and repeated contact with people has contributed to fatal respiratory disease outbreaks and population declines in habituated chimpanzees (Köndgen et al., 2008). Habituation may also alter behavior and physiology, particularly where it is associated with tourism or provisioning. For example, tourist provisioning in Barbary macaques has been linked to poorer health, altered activity budgets and behavioral changes (Maréchal et al., 2016). In addition, reduced avoidance of humans can increase the likelihood of human–wildlife conflict, exposing animals to injury, persecution or management interventions, particularly in landscapes where wildlife frequently encounters people (Geffroy et al., 2015; Higham & Shelton, 2011; Williamson & Feistner, 2003). Where hunting or other forms of human-caused mortality persist, habituation may also increase vulnerability because animals become less vigilant and less likely to avoid people (Geffroy et al., 2015; Williamson & Feistner, 2003). Therefore, the ecological consequences of habituation are context dependent, requiring evaluation at the level of individual populations and sites (Doney et al., 2025).

Conclusions

Our findings indicate that differences in habituation status were associated with changes in habitat use and shared fruit consumption by sympatric primates. Habituated langurs accounted for most estimated *C. axillaris* fruit consumption during the unripe stage, which may have reduced fruit availability during the fully ripe stage preferred by gibbons. In contrast, unhabituated langurs reduced their access to *C. axillaris* fruits in lowland forest outside the reserve, and thereby habituated gibbons increased consumption of ripe fruit. This indicates that



even without direct hunting, fear of humans indirectly altered food access and interspecific competition.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHOR CONTRIBUTIONS

Pengfei Fan conceived the study and designed the methodology with Ahebota Hazitai. Ahebota Hazitai, Yuxuan Fan, Xi Chen and Yu Yang collected the data. Ahebota Hazitai analysed the data and prepared the figures, with support from Hanchi Zhang. Ahebota Hazitai wrote the first draft of the manuscript. Pengfei Fan and Colin A. Chapman revised the manuscript for important intellectual content. All authors read and approved the final version of the manuscript.

ACKNOWLEDGMENTS

We thank the Wuliangshan Nature Reserve for granting research permission and providing support. We are also grateful to Chengshun Qiu, Shiming Xiong, Youfu Xiong, Zhengkun Tao, Anwei Li, and An Liu from Dazhaizi Station for their assistance with fieldwork and data collection. We further thank Tao Chen and Zidi Wang for their help with data cleaning, methodological advice, and visualisation. Special thanks go to Yang Zhu, Jasar Jengsbek and Chengfeng Wu for their support in data organisation and species identification.

REFERENCES

Benmazouz I, Jokimäki J, Lengyel S, et al. 2021. Corvids in Urban Environments: A Systematic Global Literature Review. *Animals*, **11**(11): 3226. DOI: 10.3390/ani11113226.



556 Bersacola E, Hill CM, Hockings KJ. 2021. Chimpanzees balance resources and risk in an
 557 anthropogenic landscape of fear. *Scientific Reports*, **11**(1): 4569. DOI: 10.1038/s41598-021-
 558 83852-3.

559 Brooks ME, Kristensen K, Benthem KJ van, et al. 2017. glmmTMB Balances Speed and
 560 Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R*
 561 *Journal*, **9**(2): 378–400. DOI: 10.32614/RJ-2017-066.

562 Bshary R. 2001. Diana monkeys, *Cercopithecus diana*, adjust their anti-predator response
 563 behavior to human hunting strategies. *Behavioral Ecology and Sociobiology*, **50**(3): 251–256.
 564 DOI: 10.1007/s002650100354.

565 Calenge C. 2006. The package “adehabitat” for the R software: A tool for the analysis of
 566 space and habitat use by animals. *Ecological Modelling*, .

567 Cao QL, Zhang Y, Songer M, et al. 2025. Coexistence between Przewalski’s horse and
 568 Asiatic wild ass in the desert: The importance of people. *Journal of Applied Ecology*, **62**(5):
 569 1078–1090. DOI: 10.1111/1365-2664.70013.

570 Chen Y, Ma C, Yang L, et al. 2020. Asymmetric competition between sympatric endangered
 571 primates affects their population recovery. *Biological Conservation*, **248**: 108558. DOI:
 572 10.1016/j.biocon.2020.108558.

573 Chen Y, Zhong X, Fan P. 2025. Fruit Choice by Two Sympatric Primate Species:
 574 Determining Nutritional Composition Using Visual and Tactile Cues. *Integrative Zoology*, .
 575 DOI: 10.1111/1749-4877.12988.

576 Crofoot MC. 2021. “Next-Gen” Tracking in Primatology: Opportunities and Challenges. In:
 577 Dolins FL, Shaffer CA, Porter LM, et al. (eds.). *Spatial Analysis in Field Primatology*.
 578 Cambridge University Press, 42–63. DOI: 10.1017/9781107449824.004.



Zoological
Research

579 Crupi Jr AP. 2004. Foraging behavior and habitat use patterns of brown bears (*Ursus arctos*)
 580 in relation to human activity and salmon abundance on a coastal Alaskan salmon stream.
 581 Doctoral dissertation, Utah State University. Logan.

582 Darimont CT, Carlson SM, Kinnison MT, et al. 2009. Human predators outpace other agents
 583 of trait change in the wild. *Proceedings of the National Academy of Sciences*, **106**(3): 952–
 584 954. DOI: 10.1073/pnas.0809235106.

585 Davies G, Oates J. 1994. Colobine Monkeys: Their Ecology, Behavior and Evolution.
 586 Cambridge Univ. Press.

587 Dirzo R, Raven PH. 2003. Global State of Biodiversity and Loss. *Annual Review of*
 588 *Environment and Resources*, **28**(Volume 28, 2003): 137–167. DOI:
 589 10.1146/annurev.energy.28.050302.105532.

590 Dirzo R, Young HS, Galetti M, et al. 2014. Defaunation in the Anthropocene. *Science*,
 591 **345**(6195): 401–406. DOI: 10.1126/science.1251817.

592 Doney ED, Fry T, Donfrancesco V, et al. 2025. Reimagining habituation: The case for a
 593 reciprocal and contextual understanding. *People and Nature*, **7**(10): 2278–2290. DOI:
 594 10.1002/pan3.70140.

595 Estes JA, Terborgh J, Brashares JS, et al. 2011. Trophic Downgrading of Planet Earth.
 596 *Science*, **333**(6040): 301–306. DOI: 10.1126/science.1205106.

597 Fan P, Garber P, Ma C, et al. 2015. High dietary diversity supports large group size in Indo -
 598 Chinese gray langurs in Wuliangshan, Yunnan, China. *American Journal of Primatology*,
 599 **77**(5): 479–491. DOI: 10.1002/ajp.22361.

600 Fan P, Jiang X. 2010. Altitudinal ranging of black-crested gibbons at Mt. Wuliang, Yunnan:
 601 effects of food distribution, temperature and human disturbance. *Folia Primatologica*, **81**(1):
 602 1–9.



Zoological
Research

603 Fan P, Jiang X, Liu C, et al. 2006. Polygynous mating system and behavioral reason of black
 604 crested gibbon (*Nomascus concolor jingdongensis*) at Dazhaizi, Mt. Wuliang, Yunnan,
 605 China. *Zoological Research*, **27**(2): 216–220.

606 Fan P, Ni Q, Sun G, et al. 2009. Gibbons under seasonal stress: the diet of the black crested
 607 gibbon (*Nomascus concolor*) on Mt. Wuliang, Central Yunnan, China. *Primates*, **50**(1): 37–
 608 44. DOI: 10.1007/s10329-008-0114-1.

609 Fan P, Zhang L, Yang L, et al. 2022. Population recovery of the critically endangered western
 610 black crested gibbon (*Nomascus concolor*) in Mt. Wuliang, Yunnan, China. *Zoological*
 611 *Research*, **43**(2): 180–183. DOI: 10.24272/j.issn.2095-8137.2021.390.

612 Fujioka M. 2020. Alert and flight initiation distances of crows in relation to the culling
 613 method, shooting or trapping. *Ornithological Science*, **19**(2): 125–134.

614 Gaynor KM, Brown JS, Middleton AD, et al. 2019. Landscapes of Fear: Spatial Patterns of
 615 Risk Perception and Response. *Trends in Ecology & Evolution*, **34**(4): 355–368. DOI:
 616 10.1016/j.tree.2019.01.004.

617 Geffroy B, Samia DSM, Bessa E, et al. 2015. How Nature-Based Tourism Might Increase
 618 Prey Vulnerability to Predators. *Trends in Ecology & Evolution*, **30**(12): 755–765. DOI:
 619 10.1016/j.tree.2015.09.010.

620 Guan Z, Huang B, Ning W, et al. 2013. Proximity association in polygynous western black
 621 crested gibbons (*Nomascus concolor jingdongensis*): network structure and seasonality.
 622 *Zoological Research*, **34**(E1): E1–8. DOI: 10.3724/SP.J.1141.2013.E01E01.

623 Hanson KT, Riley EP. 2018. Beyond Neutrality: the Human–Primate Interface During the
 624 Habituation Process. *International Journal of Primatology*, **39**(5): 852–877. DOI:
 625 10.1007/s10764-017-0009-3.



Zoological
Research

626 Hernández Tienda C, Majolo B, Romero T, et al. 2022. The Habituation Process in Two
 627 Groups of Wild Moor Macaques (*Macaca maura*). *International Journal of Primatology*,
 628 **43**(2): 291–316. DOI: 10.1007/s10764-021-00275-7.

629 Higham JES, Shelton EJ. 2011. Tourism and wildlife habituation: reduced population fitness
 630 or cessation of impact? *Tourism Management*, **32**(6): 1290–1298.

631 Hobaiter C, Samuni L, Mullins C, et al. 2017. Variation in hunting behavior in neighbouring
 632 chimpanzee communities in the Budongo forest, Uganda. *PloS one*, **12**(6): e0178065.

633 Holm S. 1979. A Simple Sequentially Rejective Multiple Test Procedure. *Scandinavian*
 634 *Journal of Statistics*, **6**(2): 65–70.

635 Hu N, Guan Z, Huang B, et al. 2018. Dispersal and female philopatry in a long - term, stable,
 636 polygynous gibbon population: Evidence from 16 years field observation and genetics.
 637 *American Journal of Primatology*, **80**: e22922.

638 Huang X, Hu N, He K, et al. 2022. Disassociation of social and sexual partner relationships
 639 in a gibbon population with stable one - male two - female groups. *American Journal of*
 640 *Primatology*, **84**(7): e23394. DOI: 10.1002/ajp.23394.

641 Hückstädt L, Antezana T. 2003. Behavior of the southern sea lion (*Otaria flavescens*) and
 642 consumption of the catch during purse-seining for jack mackerel (*Trachurus symmetricus*) off
 643 central Chile. *ICES Journal of Marine Science*, **60**(5): 1003–1011.

644 IUCN. 2026. The IUCN Red List of Threatened Species. Version 2025-2.

645 Kautz TM, Fowler NL, Petroelje TR, et al. 2021. Large carnivore response to human road use
 646 suggests a landscape of coexistence. *Global Ecology and Conservation*, **30**: e01772. DOI:
 647 10.1016/j.gecco.2021.e01772.

648 Kelly MJ, Holub EL. 2008. Camera Trapping of Carnivores: Trap Success Among Camera
 649 Types and Across Species, and Habitat Selection by Species, on Salt Pond Mountain, Giles



Zoological
Research

County, Virginia. *Northeastern Naturalist*, **15**(2): 249–262. DOI: 10.1656/1092-6194(2008)15[249:CTOCTS]2.0.CO;2.

Köndgen S, Kühl H, N’Goran PK, et al. 2008. Pandemic Human Viruses Cause Decline of Endangered Great Apes. *Current Biology*, **18**(4): 260–264. DOI: 10.1016/j.cub.2008.01.012.

Lesmeister DB, Nielsen CK, Schaub EM, et al. 2015. Spatial and temporal structure of a mesocarnivore guild in midwestern north America: Midwestern Carnivore Guild Structure. *Wildlife Monographs*, **191**(1): 1–61. DOI: 10.1002/wmon.1015.

Lodberg-Holm HK, Gelink HW, Hertel AG, et al. 2019. A human-induced landscape of fear influences foraging behavior of brown bears. *Basic and Applied Ecology*, **35**: 18–27. DOI: 10.1016/j.baae.2018.12.001.

Ma C, Liao J, Fan P. 2017. Food selection in relation to nutritional chemistry of Cao Vit gibbons in Jingxi, China. *Primates*, **58**(1): 63–74. DOI: 10.1007/s10329-016-0577-4.

Ma C, Luo Z, Liu C, et al. 2015. Population and Conservation Status of Indochinese Gray Langurs (*Trachypithecus crepusculus*) in the Wuliang Mountains, Jingdong, Yunnan, China. *International Journal of Primatology*, **36**(4): 749–763. DOI: 10.1007/s10764-015-9852-2.

Ma C, Wang Y, Ma H, et al. 2026. Research-driven habituation linked to abandonment of high-altitude refuge in Indochinese gray langurs. *Biological Conservation*, **313**: 111642. DOI: 10.1016/j.biocon.2025.111642.

Maréchal L, Semple S, Majolo B, et al. 2016. Assessing the effects of tourist provisioning on the health of wild Barbary macaques in Morocco. *PLOS ONE*, **11**(5): e0155920. DOI: 10.1371/journal.pone.0155920.

Moleón M, Sánchez-Zapata JA. 2023. Extending the dynamic landscape of fear in a human-dominated world. *Trends in Ecology & Evolution*, **38**(3): 215–216. DOI: 10.1016/j.tree.2022.10.001.



Zoological
Research

674 Niedballa J, Sollmann R, Courtiol A, et al. 2016. camtrapR: an R package for efficient
 675 camera trap data management. *Methods in Ecology and Evolution*, **7**(12): 1457–1462. DOI:
 676 10.1111/2041-210X.12600.

677 Nowak K, Le Roux A, Richards SA, et al. 2014. Human observers impact habituated
 678 samango monkeys' perceived landscape of fear. *Behavioral Ecology*, **25**(5): 1199–1204.
 679 DOI: 10.1093/beheco/aru110.

680 O'Brien TG, Kinnaird MF, Wibisono HT. 2003. Crouching tigers, hidden prey: Sumatran
 681 tiger and prey populations in a tropical forest landscape. *Animal Conservation*, **6**(2): 131–
 682 139. DOI: 10.1017/S1367943003003172.

683 Oksanen J, Simpson GL, Blanchet FG, et al. 2026. vegan: Community Ecology Package.
 684 DOI: 10.32614/CRAN.package.vegan.

685 Ordiz A, Moen GK, Sæbø S, et al. 2019. Habituation, sensitization, or consistent behavioral
 686 responses? Brown bear responses after repeated approaches by humans on foot. *Biological*
 687 *Conservation*, **232**: 228–237. DOI: 10.1016/j.biocon.2019.01.016.

688 Palmer MS, Gaynor KM, Becker JA, et al. 2022. Dynamic landscapes of fear: understanding
 689 spatiotemporal risk. *Trends in Ecology & Evolution*, **37**(10): 911–925. DOI:
 690 10.1016/j.tree.2022.06.007.

691 R Core Team. 2025. R: A Language and Environment for Statistical Computing. Vienna,
 692 Austria: R Foundation for Statistical Computing.

693 Ripple WJ, Larsen EJ, Renkin RA, et al. 2001. Trophic cascades among wolves, elk and
 694 aspen on Yellowstone National Park's northern range. *Biological Conservation*, **102**(3): 227–
 695 234. DOI: 10.1016/S0006-3207(01)00107-0.

696 Schuette P, Wagner AP, Wagner ME, et al. 2013. Occupancy patterns and niche partitioning
 697 within a diverse carnivore community exposed to anthropogenic pressures. *Biological*
 698 *Conservation*, **158**: 301–312. DOI: 10.1016/j.biocon.2012.08.008.



Zoological
Research

699 Shannon G, Cordes LS, Hardy AR, et al. 2014. Behavioral responses associated with a
700 human-mediated predator shelter. *PloS One*, **9**(4): e94630. DOI:
701 10.1371/journal.pone.0094630.

702 Shutt K, Heistermann M, Kasim A, et al. 2014. Effects of habituation, research and
703 ecotourism on faecal glucocorticoid metabolites in wild western lowland gorillas:
704 Implications for conservation management. *Biological Conservation*, **172**: 72–79.

705 Sollmann R. 2018. A gentle introduction to camera - trap data analysis. *African Journal of*
706 *Ecology*, **56**(4): 740–749. DOI: 10.1111/aje.12557.

707 Spitz DB, Rowland MM, Clark DA, et al. 2019. Behavioral changes and nutritional
708 consequences to elk (*Cervus canadensis*) avoiding perceived risk from human hunters.
709 *Ecosphere*, **10**(9): e02864. DOI: 10.1002/ecs2.2864.

710 Suraci JP, Clinchy M, Zanette LY, et al. 2019. Fear of humans as apex predators has
711 landscape - scale impacts from mountain lions to mice. *Ecology Letters*, **22**(10): 1578–1586.
712 DOI: 10.1111/ele.13344.

713 Tian C, Jiang X, Peng H, et al. 2007. Tree species diversity and structure characters in the
714 habitats of black-crested gibbons (*Nomascus concolor*). *Acta Ecologica Sinica*, **27**(10): 4002–
715 4010. DOI: 10.1016/S1872-2032(07)60089-4.

716 Venables WN, Ripley BD. 2002. Modern Applied Statistics with S. Fourth ed. New York:
717 Springer.

718 Villalva P, Palomares F, Zanin M. 2025. Effect of uneven tolerance to human disturbance on
719 dominance interactions of top predators. *Conservation Biology*, **39**(2): e14364. DOI:
720 10.1111/cobi.14364.

721 Wang Y, Allen ML, Wilmers CC. 2015. Mesopredator spatial and temporal responses to
722 large predators and human development in the Santa Cruz Mountains of California.
723 *Biological Conservation*, **190**: 23–33. DOI: 10.1016/j.biocon.2015.05.007.



Zoological
Research

724 Wheat RE, Wilmers CC. 2016. Habituation reverses fear-based ecological effects in brown
 725 bears (*Ursus arctos*). *Ecosphere*, **7**(7): e01408. DOI: 10.1002/ecs2.1408.

726 Williamson EA, Feistner ATC. 2003. Habituating primates: processes, techniques, variables
 727 and ethics. In: Curtis DJ, Setchell JM (eds.). *Field and Laboratory Methods in Primatology: A*
 728 *Practical Guide*. Cambridge: Cambridge University Press , 25–39. DOI:
 729 10.1017/CBO9781139165105.004.

730 Woodford MH, Butynski TM, Karesh WB. 2002. Habituating the great apes: the disease
 731 risks. *Oryx*, **36**(2): 153–160.

732 Yovovich V, Thomsen M, Wilmers CC. 2021. Pumas' fear of humans precipitates changes in
 733 plant architecture. *Ecosphere*, **12**(1): e03309. DOI: 10.1002/ecs2.3309.

734

Accepted



Zoological
Research

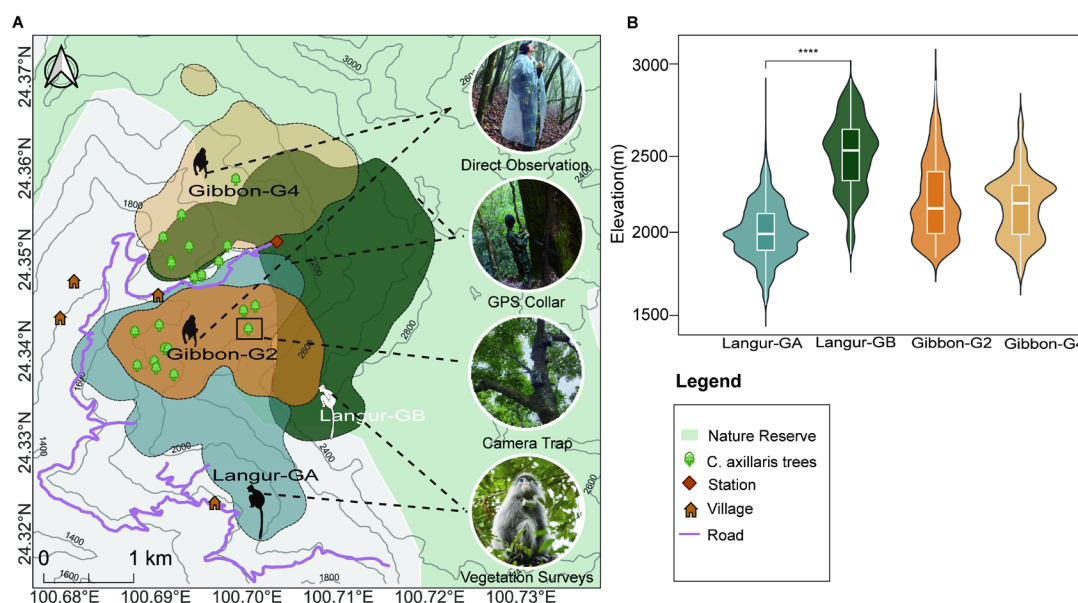


Figure 1

Spatial distribution and home range of langur and gibbon groups at Dazhaizi. (A) Home ranges (95% kernel density estimates) of four groups (Langur-GA, Langur-GB, Gibbon-G2 and Gibbon-G4) in relation to human settlements and survey trees. Insets illustrate the four principal data-collection methods: satellite positioning collars deployed on langurs, direct behavioral observations of gibbons, vegetation plot surveys, and arboreal camera traps installed at focal *Choerospondias axillaris* trees. The white silhouette indicates the unhabituated group, and the black silhouettes indicate the habituated groups. (B) Elevational distribution of the groups, with boxplots showing median, interquartile ranges, and variation in elevation use.

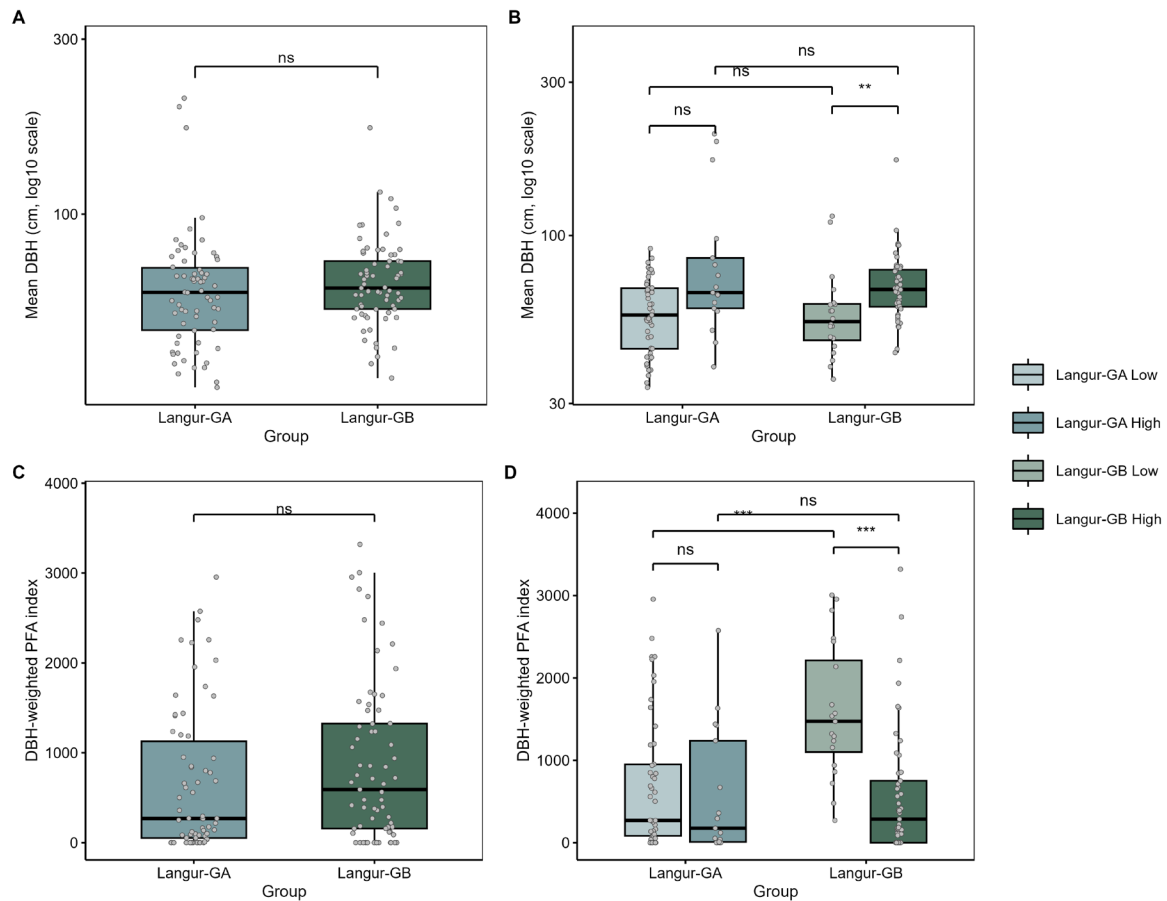


Figure 2

Comparison of woody-stem structure and potential food-plant abundance across the home range of langurs. (A) Plot level mean DBH in the Langur-GA and Langur-GB sampling areas. (B) Distributions of DBH stratified by elevation group (High vs. Low) within each home range. (C) Plot-level potential food-plant abundance (PFA) between GA and GB home ranges. (D) Distributions of plot-level PFA stratified by elevation group within each home range. In all boxplots, the horizontal line indicates the median, the box represents the interquartile range (IQR), and whiskers extend to $1.5 \times \text{IQR}$. Individual points represent outliers. Statistical significance is denoted as follows: ns, not significant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

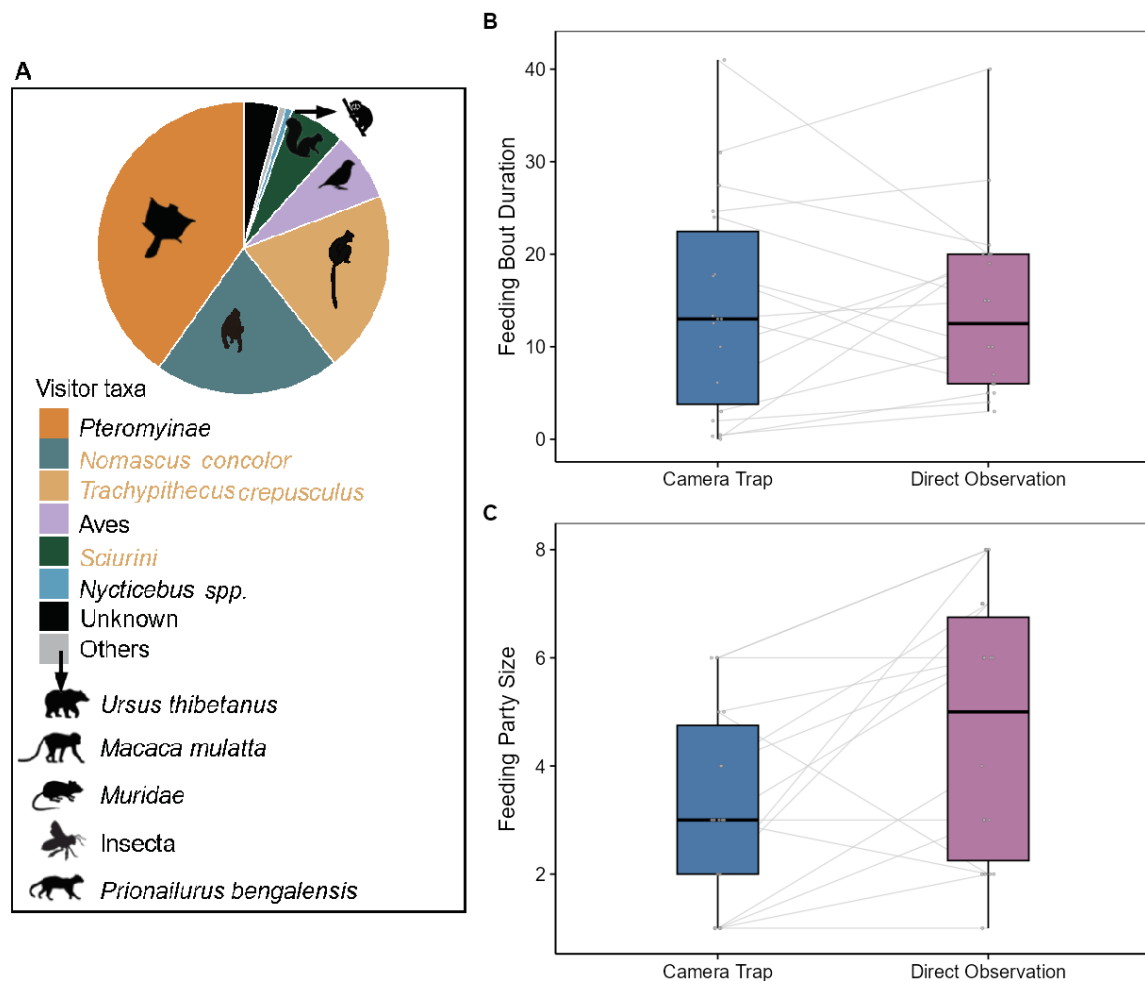


Figure 3

Visitor taxa detected by camera traps and comparison with direct observations. (A) Relative proportions of taxa detected by camera traps during the study. Silhouettes represent the most frequently recorded taxa. Taxon labels shown in yellow indicate taxa observed feeding on *C. axillaris* fruits. **(B)** Comparison of feeding bout durations and **(C)** Feeding party size detected by camera traps versus direct observations. Points represent individual feeding bouts, and grey lines connect measurements from the same paired feeding bout obtained using the two methods (n = 16 paired feeding bouts).

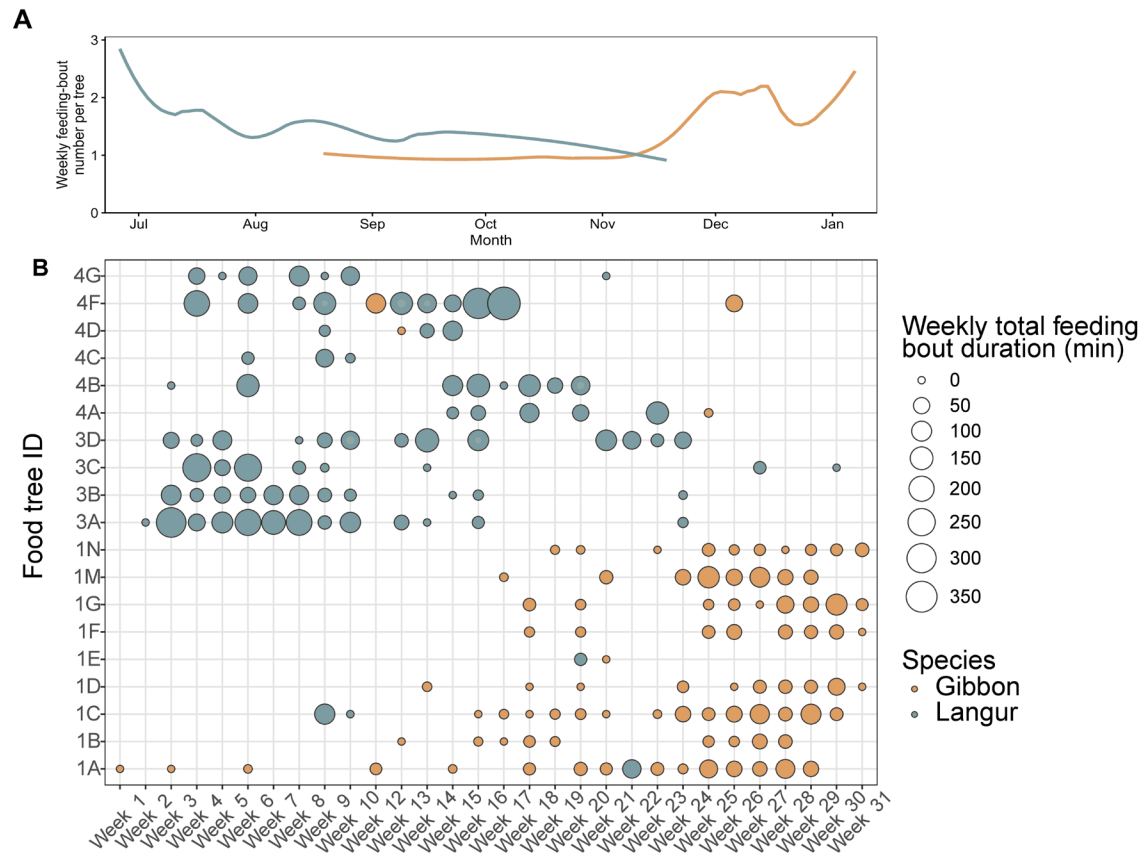


Figure 4

Temporal and tree-level patterns of feeding bouts by langurs and gibbons at focal *Choerospondias axillaris* trees. (A) Distribution of feeding bout number for both species. (B) Time of visit and feeding bout durations for langurs and gibbons on each tree of *C. axillaris*.

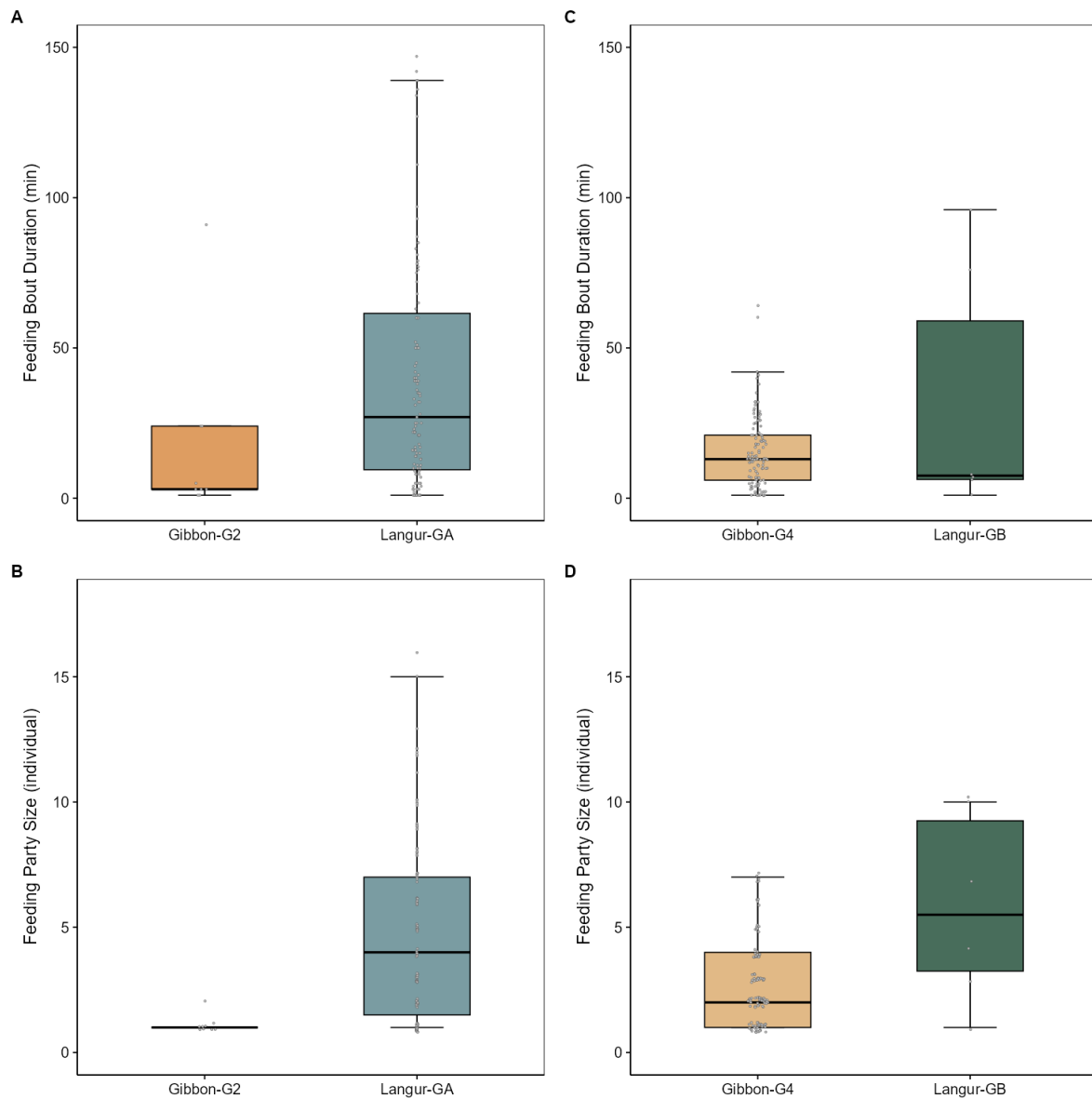


Figure 5

Comparison of feeding behaviors between sympatric langur and gibbon groups. (A, C)

Boxplots showing differences in feeding bout durations across groups. **(B, D)** Boxplots

showing differences in feeding party sizes across groups.