

Environmental drivers of ranging behavior in the Javan gibbon (*Hylobates moloch*)

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Abstract. Simokar A, Sumarga E, Oktaviani R, Prasetio Y. 2025. Environmental drivers of ranging behavior in the Javan gibbon (*Hylobates moloch*). *Biodiversitas* 26: 3903-3915. Environmental factors and food availability shape the foraging strategies and ranging behavior of primates. The Javan gibbon (*Hylobates moloch*), endemic to Java Island, Indonesia, inhabits the remaining forest patches such as Gunung Halimun Salak National Park (GHSNP). This study investigated the effects of environmental variables and food availability on Javan gibbon ranging in GHSNP, using behavioral and ecological data collected from January to December 2022. We observed three habituated gibbon groups through scan sampling and collected monthly plant phenology and daily temperature and rainfall data. The data were analyzed to: (i) calculate the activity budget; (ii) map and quantify ranging patterns, using QGIS; (iii) determine the Food Abundance Index (FAI); (iv) calculate mean monthly temperature and rainfall; (v) analyze the effects of environmental conditions and food availability on ranging behaviour/pattern using linear mixed models in RStudio. Results showed that Javan gibbon activities were dominated by resting, followed by feeding, locomotion, and social interaction. The mean home range size and daily path length were 38.68 ± 7.17 ha and 3.25 ± 0.30 km, respectively. Important food sources included *Ficus* spp., *Cordia bantamensis*, *Sandoricum koetjape*, and *Knema cinerea* with the highest FAI values for fruits, young leaves, and flowers occurred in September, July, and March, respectively. The average minimum temperature, maximum temperature, and monthly rainfall were $17.77 \pm 0.34^\circ\text{C}$, $26.59 \pm 0.76^\circ\text{C}$, and 418.23 ± 179.68 mm, respectively. Ranging patterns were significantly affected by rainfall, temperature, and food availability (p -value < 0.05), with observed differences among groups due to food resources distribution, foraging strategies, and environmental responses.

Keywords: Conservation area, habitat management, *Hylobates moloch*, wildlife behavior, wildlife ecology

INTRODUCTION

Primate behavior is highly influenced by environmental conditions, which shape their foraging strategies, ranging patterns, and social interactions (Almeida-Warren et al. 2022). Most primates inhabit tropical and subtropical regions (Mandl et al. 2018; Joly et al. 2023), characterized by high rainfall and latitudinal seasonal variations. Abiotic factors, such as temperature and rainfall, influence plant phenology, which in turn drives fluctuations in food availability. These patterns influence the development of foraging strategies in primates (Mandl et al. 2018; Green et al. 2020). Some primates may minimize the energy expenditure during foraging, while others expend more energy to obtain higher quality and preferred food (Green et al. 2020).

Environmental variation also affects primate movements. For instance, red-tailed monkeys (*Cercopithecus ascanius*) adjust their ranging pattern in response to food abundance and weather (McLester et al. 2019). Similarly, the yellow-cheeked gibbons (*Nomascus gabriellae*) adjust their range according to weather conditions and food sources (Bach et al. 2020). In the case of Western black-crested gibbons (*Nomascus concolor*), their activity patterns are influenced by food availability,

temperature, and rainfall (Ni et al. 2015). Additionally, this species has also been observed to exhibit adaptability to varying land cover types and to visit specific fruiting plant species during particular months (Ni et al. 2018). Understanding the effects of these factors on primate behavior is crucial for conservation efforts, especially for endangered species such as the Javan gibbon (*Hylobates moloch*), which is increasingly threatened by habitat loss and climate change.

The Javan gibbon is an endangered, arboreal, and diurnal primate endemic to western and central areas of Java Island, Indonesia (Nijman et al. 2019). It was estimated that 4,000-4,500 individuals of the remaining Javan gibbon (Nijman 2004; Kim et al. 2011; Iskandar et al. 2018). They live in a monogamous social system and form groups composed of an adult male and female pair with 1 to 4 offspring. As territorial animals, Javan gibbons avoid contact with other social groups by engaging in vocal calling to defend their home range. This behavior is performed by the adult female and often imitated by the offspring (Yi et al. 2022). As frugivorous primates, their primary food sources are fruits, although they also consume young leaves, flowers, and small invertebrates (Kim et al. 2011; Oktaviani et al. 2018; Zulfa et al. 2021). Therefore, they also serve as a seed disperser, thus

contributing to forest regeneration and sustainability (Martiyani et al. 2022).

However, extensive deforestation and forest fragmentation, mainly caused by the high population density of Java have isolated the Javan gibbon populations in the remaining forest patches (Nijman et al. 2019). One of the most significant remaining habitats is Gunung Halimun Salak National Park (GHSNP) (Martiyani et al. 2022; Yi et al. 2022; Oktaviani et al. 2023), which covers 87,699 hectares with the most biodiverse tracts of forest on the island (Nijman 2015). However, anthropogenic activities, including infrastructure development, settlement, encroachment, and illegal mining, have caused forest degradation in GHSNP (Martiyani et al. 2022; Sardjo et al. 2022). Therefore, we need comprehensive studies of animal behavior, including their home range, to manage effective wildlife conservation efforts. Most studies have linked Javan gibbon movements to food availability (Kim et al. 2011, et al. 2012; Jang et al. 2021). However, recent comprehensive investigations into the relationship between home range, food abundance, and environmental factors are lacking. Filling this gap is essential, particularly in the context of climate change and increasing anthropogenic pressures on forest habitats.

This study aims to examine the effects of environmental conditions (rainfall and temperature) and food availability on Javan gibbon ranging through linear modeling, with a case study in GHSNP. We expected the home range of Javan gibbons to decrease with an increase in their primary food sources and with increased temperature and rainfall. Additionally, we analyze their spatial dynamics, including the overlap of home ranges and their stability. By examining the relationship between environmental variables, food availability, and Javan gibbon behavior, this study can provide valuable insights into how future changes may affect their habitat use and movement patterns. Understanding these dynamics is crucial for

formulating effective climate change adaptation strategies, especially in tropical forest ecosystems, where gibbons play critical ecological roles.

MATERIALS AND METHODS

Study area

We collected data in Gunung Halimun Salak National Park, West Java, Indonesia, from January to December 2022. We conducted this research in the forest area around Citalahab Sentral Village ($6^{\circ}44'21.40''S$ and $106^{\circ}31'48.99''E$), which is part of the administrative unit of Cikaniki Resort, Section II Bogor area. The research location map is shown in Figure 1.

The research area is a lower montane forest at 950-1,100 m asl, consisting of primary and secondary forest with connected multilayered canopy. The soil types at the research site consist of an association of reddish-brown latosol and brown latosol. The tree and liana vegetation commonly found in the research area are Fagaceae, Moraceae, Meliaceae, Lauraceae, and Myrtaceae. The research area is a harbor for many endemic and endangered wildlife, such as the Javan hawk-eagle (*Nisaetus bartelsi*) and Javan leopard (*Panthera pardus*). Although the habitat of the Javan gibbon remains relatively well-preserved, it is directly adjacent to human-modified landscapes, such as agricultural fields, settlements, and tea plantations. According to Kim et al. (2011), the area experienced minor disturbances, such as occasional bird hunting; however, the area has had low levels of anthropogenic disturbance and stable boundaries for several decades (Lappan et al. 2023). Throughout the long-term monitoring period, we did not observe interactions between Javan gibbons and domestic animals. Nonetheless, gibbons were occasionally seen foraging in peripheral or edge area at canopy heights ranging from 10 to 15 meters.

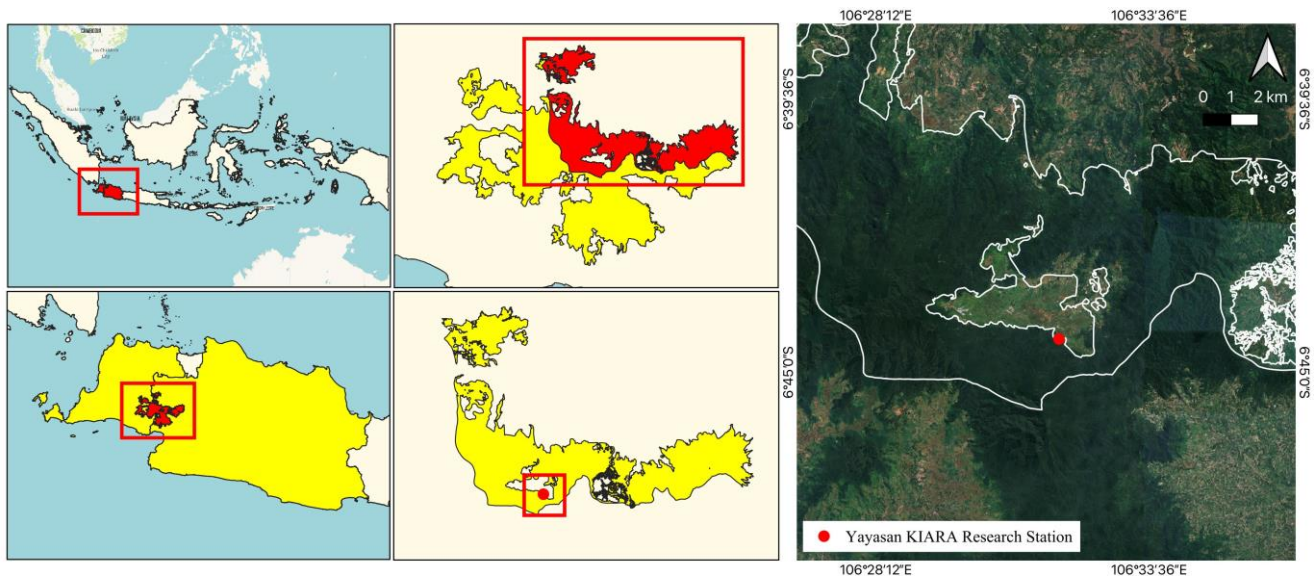


Figure 1. Research location map in Cikaniki Resort, Gunung Halimun Salak National Park, Bogor, West Java, Indonesia

Procedures

We conducted behavioral observations of three habituated Javan gibbon groups through scan sampling, and we observed the adult parent individuals from groups A, B, and S. During the observation periods, groups A, B, and S consisted of five, four, and five individuals, respectively. Group A consisted of one adult male, one adult female, one subadult, one juvenile, and one infant. Group B consisted of one adult male, one adult female, and two juveniles. Group S consisted of one adult male, one adult female, two juveniles, and one infant.

Javan gibbon monitoring

Each Javan gibbon group was followed for two to three consecutive days. Daily monitoring began with an initial search by the monitoring team between 06:30 and 07:00, followed by behavioral observations using scan sampling. On subsequent days, if the team successfully located the group's sleeping trees, observations commenced earlier at 05:30 to ensure full day follows from the sleeping site. The gibbon monitoring team consisted of seven trained local collaborators as part of the research team of Yayasan Konservasi Ekosistem Alam Nusantara (KIARA), Indonesia. There are two sub-teams, each comprising three to four observers, operating on a weekly rotating shift system. Accordingly, each team alternated between one week of active fieldwork and one week of rest. During each monitoring session, the author, together with one sub-team conducted a monitoring of a gibbon group. One to two observers were assigned to follow individual gibbons, including the adult male (parent), adult female (parent), and an offspring. Throughout the observation period, we maintained an appropriate distance from the gibbons. We collected individual gibbon behavior data (Table 1), food plants, the code of the trees used by the gibbons, and marking the locations every 10 minutes in a data book. At each 10-minute interval, we recorded the code of the tree or liana used by the gibbons during their activities. Trees and lianas utilized by the gibbons were pre-identified, assigned unique codes, and their coordinates were georeferenced using a GPS device prior to or during the observation period.

The total duration of behavioral observations was 1,089.6 hours over 137 days. The average observation for groups A and B was four days/month (range: 1-7 days/month). Group S was followed less frequently, with the average of observation was three days/month (range: 1-6 days/month), due to more challenging terrain. The total observation durations for groups A, B, and S were 414.8 hours, 385.1 hours, and 289.7 hours, respectively.

Environmental conditions and plant phenological data collection

We collected monthly plant phenology data in the middle of each month. The data were collected from 25 permanent plots measuring 10x50 meters. These plots were distributed across the home ranges of the gibbon groups, with 9 plots located in group A's range, 10 in group B's range, and 6 in group S's range. These permanent plots were originally established to monitor forest tree and liana

dynamics and included all plant species present within the plot boundaries, including individuals of the genus *Ficus*. Data collection involved measuring the trees with a DBH ≥ 10 cm and the lianas, also estimating the abundance of fruits, young leaves, and flowers for each observed individual tree and liana. Abundance estimation data were measured by counting every observed part and converting the results into scores of 0-4 (0: <1%, 1: 1-25%, 2: 26-50%, 3: 51-75%, and 4: 76-100%) (Green et al. 2020).

Environmental conditions data, including temperature and daily rainfall, were obtained from daily measurements at our field station. We measured temperature data using a digital thermometer and rainfall data using a rain gauge.

Data analysis

We analyzed the gibbon observation data to calculate their activity budget and food sources. The data were further analyzed using a chi-square test with a significance level of α : 0.05. Data analysis and visualization were performed using RStudio (R v.4.2.3).

Ranging area analysis was conducted by mapping and calculating the home range and Daily Path Length (DPL) of each gibbon group. We calculated the DPL based on the total distance between consecutive waypoints traversed by the gibbons (Green et al. 2020). DPL calculations were based on observations with total durations of 7 hours or more in one day. We estimated the home ranges based on the coordinates of the trees used by the gibbons during observations. Estimation methods included kernel density estimation and minimum convex polygon (minimum bounding geometry tool) (Joly et al. 2023). Home range analysis was performed using QGIS v.3.36 and RStudio (R v.4.2.3).

We collected daily temperature and rainfall data from January to December 2022. Temperature data were used to calculate the mean monthly minimum and maximum temperature, while rainfall data were used to calculate monthly total rainfall. Analysis and data visualization were performed using RStudio (R v.4.2.3).

Plant phenology data were analyzed to calculate gibbon food availability using Food Abundance Index (FAI). FAI values were calculated separately for each plant part, including fruits, young leaves, and flowers.

Table 1. Behavioral categories and descriptions of the Javan gibbon observed during the study period

Behavior	Description
Locomotion	Moving by jumping, climbing, using both hands (brachiation), or both feet (bipedal)
Resting	Sitting, lying, or hanging immobile
Social Interaction	Activities between individuals, include allogrooming, calling, reproducing, playing, and intra-aggressive behavior
Feeding	Using their hands or feet to reach parts of plants or insects and then consuming and swallowing them
Others	All other behaviors including drinking, mating, urination, and defecation

The FAI calculation formula, based on Basabose (2002) and Wittiger and Boesch (2013) is as follows:

$$FAI = \Sigma P_{km} \times B_k$$

$$P_{km} = \frac{0.25 \times N_{km(1)} + 0.5 \times N_{km(2)} + 0.75 \times N_{km(3)} + 1 \times N_{km(4)}}{N_{km}}$$

Where, P_{km} is the proportion of trees bearing fruit for species k in month m , B_k is the basal area per hectare for species k , $N_{km(x)}$ is the number of individuals for a species k in month m with score of x , and N_{km} is the number of individuals observed for species k in month m .

The analysis of the effects of environmental conditions (temperature and rainfall) and food availability on Javan gibbon ranging was conducted using Linear Mixed Models (LMM) with the lme4 and lmerTest packages in RStudio (R v.4.2.3) (Green et al. 2020; Joly et al. 2023). LMM were chosen due to the continuous and normally distributed nature of the data, as well as the necessity to analyze the effects of multiple predictor variables on the response variables. In this modeling, temperature, rainfall, FAI for fruits, FAI for young leaves, and FAI for flowers were the fixed effects variables, while individual ID was the random effects variable. DPL and home range were the response variables. The analysis was performed with monthly data. Subsequently, we identified the combinations of predictor variables with the highest explanatory power using the Akaike Information Criterion (AIC) (Kim et al. 2012) in RStudio (R v.4.2.3). We selected the model through backward elimination and forward selection. In backward elimination, the initial model included all candidate predictor variables with one variable removed at each step.

In contrast, forward selection started with no predictor variables with variables one at a time according to the AIC results. Meanwhile, the plant density and food sources of each group were calculated based on the number of individuals in the phenology observation plots.

Ethical note

This research was approved by a research permit from the study site, Gunung Halimun Salak National Park in Indonesia (SIMAKSI number 61/P/TNGHS/10/2022). We used non-invasive and behavioral observation data only. The authors declare that there are no conflicts of interest relevant to this work.

RESULTS AND DISCUSSION

Behavior of Javan gibbon

Five behaviors were identified during field observation of the Javan gibbon, including locomotion, resting, social interaction, feeding, and others. The Javan gibbon spent most of their time resting ($51.99 \pm 2.44\%$), followed by feeding ($30.22 \pm 2.11\%$), locomotion ($11.24 \pm 2.15\%$), and social interaction ($3.89 \pm 0.87\%$). The activity budget for each group is presented in Figure 2.A. According to the chi-square test, there were no significant differences in the

activity budgets among groups A, B, and S (χ^2 : 1.84; df: 8; p-value: 0.9855).

In addition to resting, Javan gibbons spent a considerable portion of their time feeding. The composition of their diet is presented in Figure 2.B, Tables S1 and S2. Their food sources primarily consist of various plant parts, including fruits, flowers, and young leaves. The diet of Javan gibbons consists mainly of two plant groups: fig plants (44.81%) and non-fig plants (53.34%). In this study, we identified fruits (70.02%) as the primary food source of Javan gibbons, with the proportion of ripe and unripe fruits were 64.47% and 5.55%, respectively. In addition to fruits, Javan gibbons also consumed young leaves (18.65%), flowers (9.48%), and small portions of animal matter, such as insects and caterpillars (1.84%).

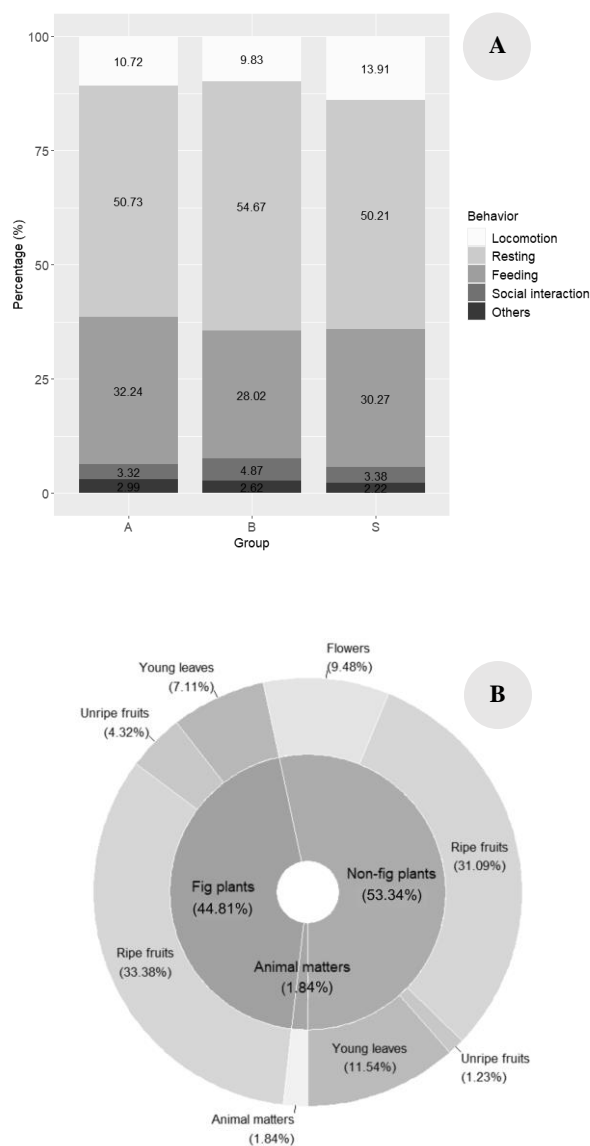


Figure 2. A. Proportion of time allocated to different behavioral activities by each Javan gibbon (*Hylobates moloch*) group, B. Food sources of Javan gibbon (*H. moloch*) during the research period from January to December 2022 were dominated by fruits, followed by young leaves, flowers, and animal matters

Home range

The home range of Javan gibbon groups A, B, and S, based on the minimum convex polygon method, are 33.32 ha; 46.82 ha; and 35.90 ha, respectively (Figure 3.A). The average home range size of the three observed gibbon groups was 38.68 ± 7.17 ha. The overlapping area between the home ranges of groups A-B and B-S are 6.60 ha and 7.35 ha, respectively. The average percentage of overlapping home range areas was 17.53%, with 16.96% for groups A-B and 18.09% for groups B-S. In this study, the core area usage by each Javan gibbon group is shown in Figure 3.B

During the observation period, all groups used the core area, most notably for feeding. Groups A and B also used the core area for social interactions. However, this condition was not observed in group S. The percentage of core area usage by each Javan gibbon group is shown in Figure 4.

Overall, the three Javan gibbon groups most frequently used the core area for foraging on food resources. The most consumed food plants by Javan gibbons in the core area are presented in Table 2.

Among the three groups, group B has the largest median home range size, followed by groups A and S.

Group S shows the widest range of variation with more extreme values. Additionally, outliers are observed in groups A and B. Statistical tests were conducted with a significance level of $\alpha: 0.05$. Based on the Shapiro-Wilk normality test, the p-values for the home range data of groups A, B, and S were 0.0518; 0.0025; and 0.2970, respectively. Since some data were not normally distributed, significance test was performed using the Kruskal-Wallis test. Based on the test, the p-value was 0.0155, indicated a significant difference. Subsequently, Dunn's test was conducted, resulting in p-values between groups A-B, A-S, and B-S were 0.0405; 1.0000; and 0.0362, respectively. Thus, there are significant differences in home range sizes between groups A-B and B-S.

The monthly changes in home range sizes for each group are presented in Figure 5. It shows that the home range areas of each group shifted slightly but remained in the same general location. Overall, the home ranges of the three groups do not show notable differences, except during months with limited observations that happened due to heavy rainfalls during the study period, and we could not follow the gibbons in full-day observations. These periods of reduced data collection occurred primarily in March, April, May, and October.

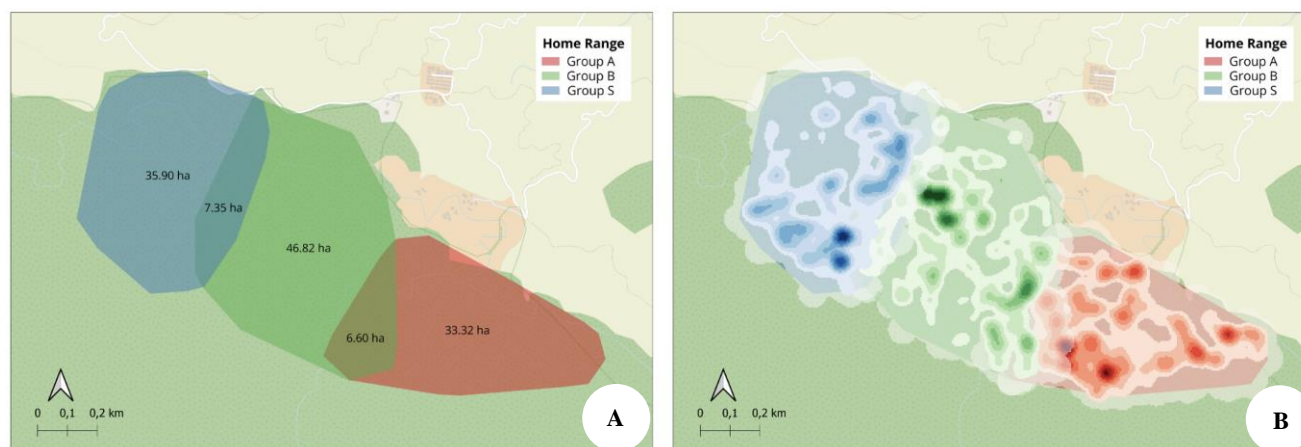


Figure 3. Home range map of each Javan gibbon (*Hylobates moloch*) group during the research period from January to December 2022. A. Minimum convex polygon, B. Kernel density estimation

Table 2. The most frequently consumed food plants in the core area by each Javan gibbon (*Hylobates moloch*) group during the research period from January to December 2022

Group	Local name	Scientific name	Month	Parts
A	Kecapi	<i>Sandoricum koetjape</i>	2-3, 6-7	Flowers; young leaves
	Ficus pohon	<i>Ficus annulata</i>	3, 12	Fruits
	Darangdan benyer	<i>Ficus cuspidata</i>	1, 3, 6	Young leaves
B	Kilaban	<i>Cordia bantamensis</i>	5-8, 11-12	Fruits
	Kidage	<i>Bruinsmia styracoides</i>	5-6, 9, 11	Fruits
	Ficus besar	<i>Ficus punctata</i>	1, 6, 7, 9	Fruits
S	Kilaban	<i>Cordia bantamensis</i>	6, 7	Fruits
	Ficus besar	<i>Ficus punctata</i>	1, 8, 10-12	Fruits
	Ficus kisigung	<i>Ficus villosa</i>	7-8	Fruits

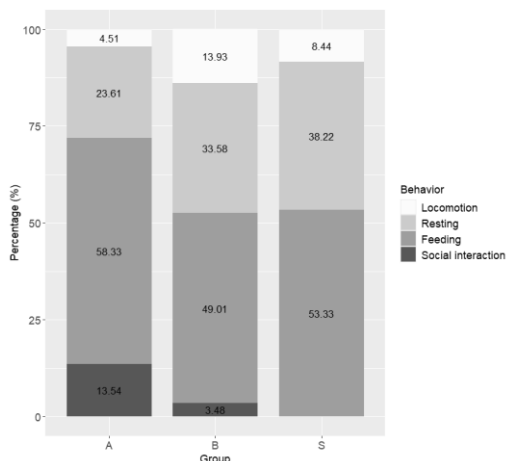


Figure 4. Core area utilization by each Javan gibbon (*Hylobates moloch*) group during the research period from January to December 2022

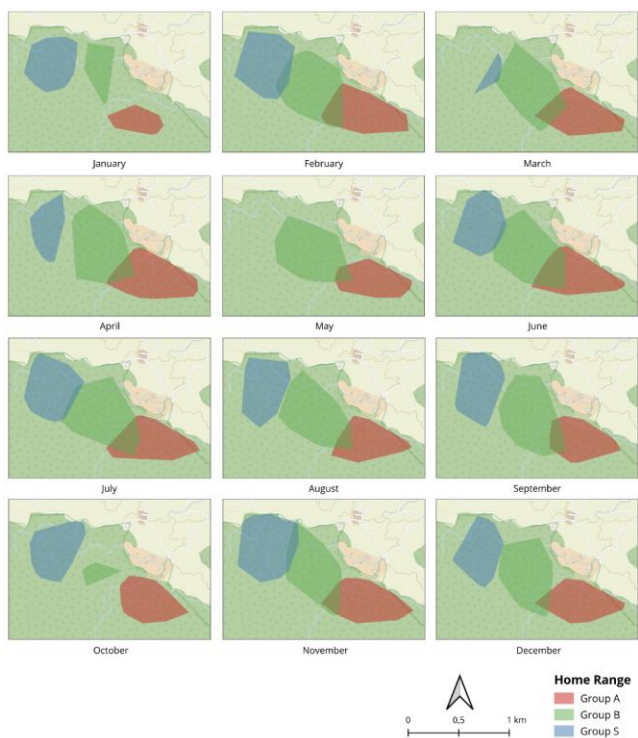


Figure 5. Spatial changes of the home range of groups A, B, and S during the research period in 2022

The average Daily Path Length (DPL) for groups A, B, and S were 2.83 ± 0.66 km; 3.46 ± 0.91 km; and 3.47 ± 0.81 km, respectively. Overall, the average DPL for the three groups was 3.25 ± 0.30 km. The highest DPL for groups A, B, and S occurred in August, November, and September, respectively (Figure S1). Each gibbon group exhibited uniform usage of their home ranges.

The boxplot of daily path length for each gibbon group can be seen in Figure 6.A. Statistical tests were conducted

with a significance level of $\alpha: 0.05$. Based on the Shapiro-Wilk normality test, the p-values for the DPL data of groups A, B, and S were 0.6357; 0.4888; and 0.6129, respectively. Since some data were normally distributed, a significance test was performed using the one-way ANOVA test. Based on the test, the p-value was 0.1320, indicating there was no significant difference. The monthly changes in DPL for each group are presented in Figure 6.B. The DPL of Javan gibbons increased during June to September.

Environmental conditions

From January to December 2022, the average rainfall at the study site was 418.23 ± 179.68 mm/month (range: 80.3-739.0 mm/month). Based on the graph in Figure 7.A, rainfall did not exhibit a clear seasonal pattern, with precipitation exceeding 250 mm every month, except in January 2022. However, it can be observed that the highest rainfall occurred in September 2022, while the lowest rainfall occurred in January 2022. The temperature at the study site tended to be stable throughout the year. The average minimum temperature was $17.77 \pm 0.34^\circ\text{C}$ and the average maximum temperature was $26.59 \pm 0.76^\circ\text{C}$.

Food availability

Phenological observations were conducted once per month on the 25 permanent plots (each measuring 10x50 meters), which were fixed in location to enable consistent and long term monitoring. These plots included 287 individual plants representing 86 species and 39 families. The plants observed in the plots included both non-food and food plants. Based on the routine monitoring results, Javan gibbons consumed 78 plant species belonging to 35 families. Based on the calculations of the Food Abundance Index (FAI) for plants in the permanent plots located within the home ranges of three gibbon groups from January to December 2022, the monthly FAI graph is presented in Figure 7.B. The highest FAI values for fruits, young leaves, and flowers occurred in September, July, and March, respectively.

Effects of environmental conditions and food availability on Javan gibbon ranging

Based on modeling using Linear Mixed Models (LMM) and AIC calculations through backward elimination and forward selection, the best model for analyzing the effects of environmental conditions and food availability on the home range of Javan gibbon is presented in Tables 3 and 4. In general, environmental conditions (Figure S2) and food availability significantly influence the home range of Javan gibbons. However, variations in their effects on each group were observed.

The estimated tree density in the home range of groups A, B, and S for all activities was 262.2; 222.0; and 223.3 individuals/ha, respectively. For foraging activities, the estimated tree density in the home range of groups A, B, and S was 91.1, 68.0, and 100.0 individuals/ha, respectively. These results indicate that the home range of the three gibbon groups exhibit different tree densities for ranging and foraging.

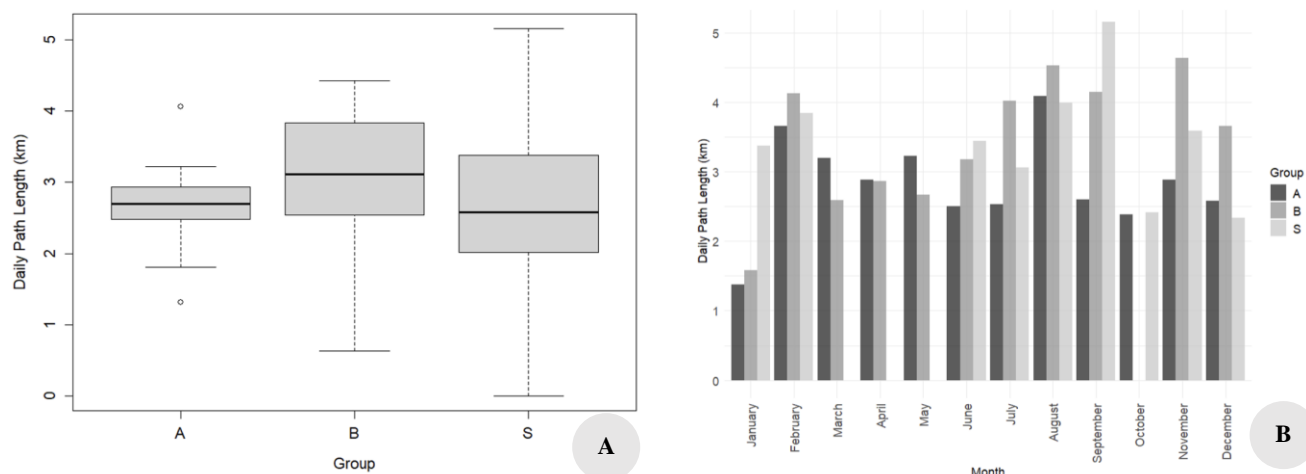


Figure 6. A. DPL of groups A, B, and S; B. DPL changes of each Javan gibbon (*Hylobates moloch*) group during the research period from January to December 2022

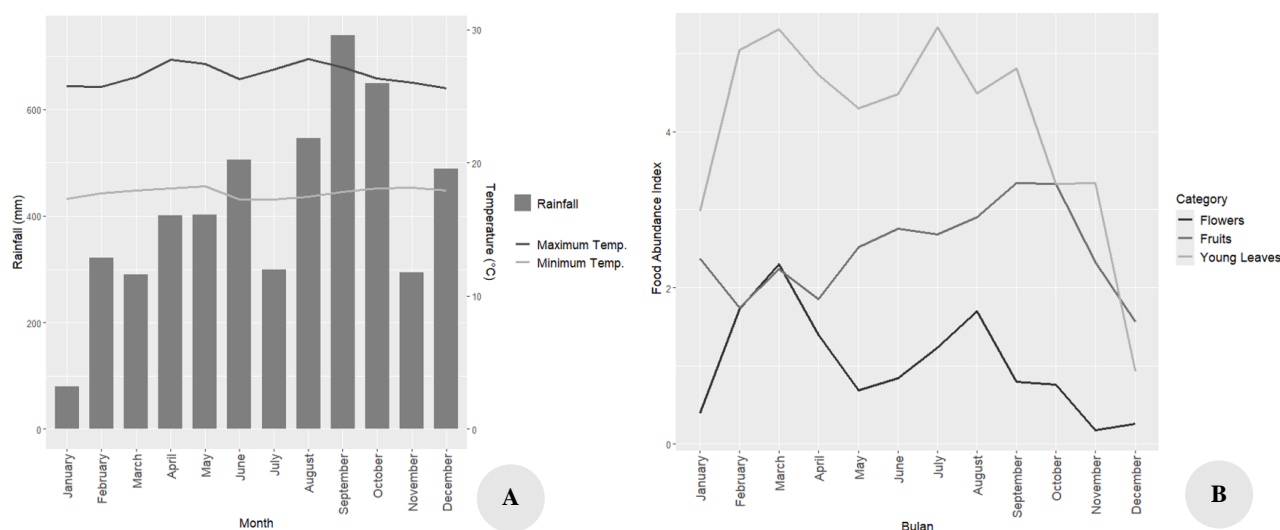


Figure 7. A. Average maximum and minimum daily temperature and monthly rainfall, B. Food abundance index of fruits, flowers, and young leaves during the research period from January to December 2022

Discussion

Our results show that the home range of gibbons in Citalahab is influenced by food availability and environmental conditions. Overall, the observed Javan gibbons exhibited a decrease in home range when fruits and flowers availability increased, but an increase as the availability of young leaves. This condition may be related to fruits and flowers as their main food sources (Oktaviani et al. 2018; Ning et al. 2019). Additionally, we found that the Javan gibbons exhibited a decrease in ranging when temperature increased, but an increase as the rainfall in a small ratio. The gibbons remain active during light rain but stop during heavy rain.

In this study, we found that fruits made up about three-quarters of the gibbon's diet, including the fruits from fig plants and non-fig plants. This dietary pattern is consistent with the characteristics of Javan gibbons as frugivorous

primates (Oktaviani et al. 2018). In addition, Javan gibbons also consumed young leaves, flowers, and a small amount of animal matter. These findings are consistent with the research conducted by Kim et al. (2011), Oktaviani et al. (2018), and Zulfa et al. (2021).

Furthermore, we observed that the highest abundance of fruits occurred during the rainy season in September. Otherwise, the highest abundance of young leaves and flowers occurred during the dry season in July and March, respectively. The findings related to flowering and fruiting periods are consistent with studies conducted in other tropical gibbons, Hainan gibbon (*Nomascus hainanus*) (Du et al. 2020; Xue et al. 2023). The highest abundance of fruits and flowers in their habitats occurred in August–October and April, respectively. This condition was mainly influenced by monthly temperature and precipitation (Du et al. 2020).

Table 3. The most suitable model based on linear mixed models (LMM) and AIC values for DPL of each Javan gibbon (*Hylobates moloch*) group

Group	Variables	Estimates	Std. error	p-value
A (AIC: 140.1481 R ² : 0.1321)	Intercept	7.8881	55.2195	0.8880
	Temperature	0.1903	2.5734	0.9420
	FAI fruits	-3.1071	2.1612	0.1670
	FAI young leaves	1.1956	1.4326	0.4140
B (AIC: 125.8290 R ² : 0.5948)	FAI flowers	-0.0198	2.6141	0.9940
	Intercept	153.8370	44.1067	0.0030
	Rainfall	0.0246	0.0060	0.0009
	Temperature	-7.2544	2.0633	0.0029
S (AIC: 89.2075; R ² : 0.6730)	FAI fruits	-1.2432	2.3021	0.5966
	FAI young leaves	3.0201	1.2655	0.0297
	FAI flowers	-0.5766	2.0710	0.7843
	Intercept	88.9150	68.0840	0.2142
	Temperature	-3.5930	3.2510	0.2891
	FAI fruits	-5.3870	2.1210	0.0247
	FAI young leaves	4.4760	1.0250	0.0008
	FAI flowers	-3.8020	2.3600	0.1312

Table 4. The most suitable model based on Linear Mixed Models (LMM) and AIC values for home range of each Javan gibbon (*Hylobates moloch*) group

Group	Variables	Estimates	Std. error	p-value
A (AIC: 134.9912; R ² : 0.6706)	Intercept	34.1953	41.4250	0.4200
	Rainfall	0.0300	0.0057	4.97e-05
	Temperature	-0.5090	1.9368	0.7960
	FAI fruits	-10.0939	1.8624	3.78e-05
B (AIC: 133.9621; R ² : 0.5078)	FAI young leaves	2.6776	1.0777	0.0230
	FAI flowers	-0.9071	1.8472	0.6290
	Intercept	96.4842	56.8702	0.1091
	Rainfall	0.0336	0.0078	0.0005
S (AIC: 132.0045; R ² : 0.4461)	Temperature	-3.4606	2.6603	0.2118
	FAI fruits	-7.9365	2.9683	0.0166
	FAI young leaves	3.9873	1.6317	0.0265
	FAI flowers	-3.1375	2.6703	0.2572
	Intercept	81.4790	73.2300	0.2813
	Temperature	-2.8340	3.4240	0.4193
	FAI fruits	-1.6890	2.5400	0.5149
	FAI young leaves	4.1670	1.6730	0.0233
	FAI flowers	-11.4320	3.2240	0.0025

This pattern can be explained by the influence of environmental conditions, including temperature and rainfall, on plant phenological phases. Flowering occurs during periods of relatively low rainfall or dry season to avoid pollen damage and to take advantage of various pollinators, including wind. Additionally, flowering during the dry season also benefits from higher temperature and solar radiation (Dagnachew et al. 2023; Xue et al. 2023). In tropical regions, the peak fruiting season usually occurs in rainy season. However, this condition also influenced by the location and vegetation communities in that area (Xue et al. 2023).

Temperature and rainfall are important factors that influence plant growth, development, and productivity

(Asfaw et al. 2019). Temperature affects processes such as chlorophyll synthesis, leaf formation and growth, germination, flowering, and seedling growth. However, excessively high temperatures can disrupt metabolic processes, desiccation, and thermal stress in plants. Rainfall influences soil moisture, cell growth, cell wall formation, photosynthesis, stomatal activity, respiration, and sugar accumulation (Sravani 2020).

Based on our observations, the plant species that most frequently consumed by Javan gibbon were dominated by figs (*Ficus* spp.) and non-fig, including *Cordia bantamensis*, *Sandoricum koetjape*, *Knema cinerea*, *Bruinsmia styracoides*, and *Dissochaeta reticulata*. These results are consistent with previous study on the same groups (Jang et al. 2021). Figs tend to have asynchronous fruiting pattern, therefore they are generally available throughout the year at the community level. This condition was also observed in fig communities in KwaZulu-Natal, South Africa (Raji and Downs 2022). In the case of the White-bearded gibbon (*Hylobates albibarbis*), figs were observed to be more consistently available and consumed. Notably, figs were predominantly eaten during periods of low fruit availability, and therefore have been considered as a fallback food for this species (Clink et al. 2017). In contrast, our study found that figs were observed to be regularly consumed by the Javan gibbon. This observation is consistent with the findings of Kim et al. (2012), which may be attributed to the limited availability of high-quality food resources or to the differences in fig species characteristics.

We also found that the average home range size of the gibbons in Citalahab is significantly larger than findings from other studies, which reported home ranges of Javan gibbons varying between 5-8 ha in Cisokan (Yaghsyah et al. 2022) and 15-17 ha in Turalak and Leuweung Sancang (Kappeler 1984; Malone 2007). Aside from methodological differences, most of the studies mentioned earlier were conducted in the lowland area. For comparison, the Lar gibbon (*Hylobates lar*) in Thailand, which also inhabits lower montane regions, has been reported to have an annual home range of approximately 25 ha (Suwanvecho et al. 2017). The variation in home range size among gibbon populations may be attributed to resource distribution, habitat conditions, human disturbance, habitat transformation, and group density (Cheyne et al. 2016; Keller 2019; Light et al. 2021; Zhang et al. 2023).

When we compared to previous studies at the same location, the home range size of Javan gibbon groups A, B, and S remained relatively stable over the long term, despite some observed fluctuations (Kim et al. 2011; Dewi et al. 2016; Yi et al. 2020). This phenomenon has also been observed in other gibbon species, including the White-bearded gibbon (*H. albibarbis*) and the Lar gibbon (*H. lar*) (Bartlett et al. 2015; Cheyne et al. 2019). The stability of home range size is related to the utilization of gibbons' territory. Gibbons not only traverse their home range in search of food sources, but also to defend their territory from other gibbon groups (Bartlett et al. 2015).

We found that differences in home range size among gibbon groups may be influenced by habitat conditions,

resource availability, and group size (Brockelman et al. 2014; Bryant et al. 2015). For instance, groups of Lar gibbon (*H. lar*) have been reported to exhibit variability in home range size, site fidelity, and habitat preferences. Light et al. (2021) suggested that this variation reflects adaptations to local ecological conditions. In this study, we observed intergroup differences in tree density, both for ranging and foraging. Furthermore, fluctuations in group size and presence of infant during the observation period may have also played a role in shaping their ranging behavior. Habitat degradation resulting from anthropogenic activities or hunting may result in the loss of food sources for gibbons. Such conditions typically cause gibbons to expand their home range in order to increase access to food sources and areas for their activities (Dewi et al. 2016). Additionally, tree density, tree height, and canopy cover also affect the distribution of gibbons (Bryant et al. 2015). A previous study on the White-bearded gibbon (*H. albibarbis*) in Central Kalimantan, Indonesia, found that the presence of gibbon was strongly associated with the vegetation conditions, including the number of seedlings, saplings, and trees (Nurvianto et al. 2022).

In this study, we found overlapping areas between groups. The results are similar to those of the White-bearded gibbon (*H. albibarbis*), with overlapping areas of 18.67% (Cheyne et al. 2019). However, the Cao vit gibbon (*Nomascus nasutus*), inhabiting the Vietnam-China border, exhibits a lower degree of home range overlap among groups (Wearn et al. 2024). The estimated population density of the Cao vit gibbons is 1 group/km², which is lower than the Javan gibbons in Citalahab, estimated at 3.8 groups/km². Thus, we assume higher population density may reduce the size of the home range, resulting in narrower areas for each gibbon group.

We observed that in overlapping areas, gibbon groups utilized the same areas simultaneously, mainly for feeding. Therefore, competition for food sources and agonistic behavior to defend territories may occur between neighboring groups within those areas (Cheyne et al. 2019). Besides defending food resources, agonistic behavior between gibbon groups also defends their mates and offspring. This is related to the gibbons' monogamous social structure, long interbirth interval, and slow infant development (Yi et al. 2020).

Our results indicate that the periodic use of plants by Javan gibbon also influences the core area of each group's home range. The core area is the most frequently used areas by gibbons for foraging and other activities. However, the core area may change temporally according to the distribution of resources used by the gibbons (Asensio et al. 2014). In addition, the level of consumption of each species also varies temporally based on the phenological cycles that affect the availability of resources for the gibbons (Asensio et al. 2014). Overall, the home range size of each gibbon group did not exhibit notable differences, except during months with limited observation duration. The same condition has also been observed in the Hainan gibbon (*N. hainanus*) which has a relatively stable home range. The home range stability may be influenced by the availability of food sources and territorial defense.

However, the gibbons did all activities in the same areas throughout the year, therefore there were no significant changes in home range size (Zhang et al. 2024).

The stability of home range location is a key aspect of gibbon behavioral ecology (Bartlett et al. 2015). Preferred food plants are evenly distributed in Citalahab, influencing gibbon foraging patterns. Therefore, all of the groups tend to travel their home range regularly to check on food plants. The same pattern is also observed in the Lar gibbon (*H. lar*) in Thailand (Bartlett et al. 2015). Furthermore, research on another gibbon species, the Skywalker hoolock gibbon (*Hoolock tianxing*), suggested that individuals may strategically plan their movement patterns according to the location of their fruit breakfast trees, thereby facilitating the efficient exploitation of dispersed food resources (Fei et al. 2023). Nevertheless, the gibbons in this study showed variations of foraging points and the smaller home range size is likely due to the limited observation period.

Overall, we found the DPL of Javan gibbons decreased when temperature, fruit, and flower availability increased. Conversely, the DPL increased with the availability of young leaves. The same condition was observed in the home ranges of all gibbon groups. Increased rainfall caused an increase in range size, though there were no significant ratio changes. When rainfall increased, we found gibbon generally reduced their movement. Additionally, gibbons tend to allocate most of their time to rest because traveling is energetically demanding and conserving energy during locomotion is considerably more challenging compared to resting periods (Bach et al. 2017).

We observed that when fruits and flowers availability increased, the DPL and home range size of Javan gibbon decreased. Fruits and flowers are primary food sources for Javan gibbons with high carbohydrate contents (Oktaviani et al. 2018). Additionally, the sugars in ripe fruits are easy to digest and quickly absorbed to provide energy for gibbons. Therefore, gibbons do not need to increase their foraging effort to look for another food sources (Ning et al. 2019). Conversely, when the young leaves availability increased, gibbons expanded their range to fulfil their nutritional needs. Young leaves have high protein content, but have lower nutritional value than flowers and fruits (Oktaviani et al. 2018; Ning et al. 2019). The changes in foraging strategies of gibbons are influenced by food sources quality. As a result, gibbons may adopt time minimizer or energy maximizer strategy based on the type and nutritional content of available food (Ning et al. 2019).

Moreover, we found that the lowest ranging tree density was observed in group B, with a slight difference from group S. This condition caused groups B and S travel farther to access resources. If the tree density was calculated based on their function as foraging tree, the lowest density was observed in group B, while groups A and S had similar densities. This condition is one of the factors that caused group B having the largest home range size to fulfil their dietary needs. Conversely, groups A and S had similar home range sizes that were smaller than the one of group B (Dewi et al. 2016).

Although our models identified some key factors, the relatively low R² values obtained from the models in

Tables 3 and 4 indicate that factors beyond those examined in this study may contribute to variation in home range size and DPL. Therefore, there are other factors influencing DPL and home range of Javan gibbon that require further research, including age structure, group size and composition, and interspecific interaction with other animals within the same area. The presence of infant in a gibbon group can significantly influence the foraging behavior of gibbons. In Lar gibbons (*H. lar*), DPL and home range size decreased, while resting time increased when there was a dependent infant. This condition may reduce the movement rate and cause the mother to avoid encounters or conflicts with other groups (Bartlett et al. 2015). In Javan gibbons, we observed competition and aggression from the parents within the same group increase as juvenile individuals mature. This condition is related to the dispersal of adults to travel and leave the group (Choi et al. 2023). In addition, interactions between Javan gibbon with the Javan langur (*Trachypithecus auratus*) and the Javan surili (*Presbytis comata*) in Citalahab also need further study to understand the effects of those interactions on Javan gibbon ranging behavior. Similar interactions between Western black-crested gibbons (*N. concolor*) and Indochinese gray langurs (*Trachypithecus crepusculus*) in Wuliang, China which caused overlapping home range and food resources (Chen et al. 2020).

Our study shows that the home range size of Javan gibbons generally decreases when the availability of fruits and flowers increases but tends to increase as the availability of young leaves rises. Additionally, their home range tends to decrease when temperature increases, but increases as rainfall increases in a small ratio to a certain level. The results underscore the importance of habitat management strategies that ensure sufficient spatial extent and food resource availability to support Javan gibbon ecological needs. Effective implementation of these strategies includes the protection of intact forest patches including key plant species consumed by gibbons, restoration of degraded habitats, reduction of landscape fragmentation, and the establishment of regular monitoring programs. Furthermore, the expansion of suitable habitats beyond the existing conservation areas has the potential to enhance population viability and connectivity. The findings of this study provide valuable insights into the spatial and dietary requirements that are essential for identifying appropriate release sites for rehabilitated individuals as part of reintroduction programs.

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Table S1. Summary of the diet of Javan gibbon (*Hylobates moloch*), showing food categories, food items, and observed consumption frequencies during the research period from January to December 2022

Category	Items	Frequency
Animal matters	Animal matters	66
Fig plants	Ripe fruits	1197
	Unripe fruits	155
	Young leaves	255
Non-fig plants	Ripe fruits	1115
	Unripe fruits	44
	Young leaves	414
	Flowers	340

Table S2. List of food plant species in the diet of of Javan gibbon (*Hylobates moloch*) during the research period from January to December 2022

Local name	Scientific name	Family
-	<i>Ficus cuspidata</i>	Moraceae
Asam kandis	<i>Garcinia xanthochymus</i>	Clusiaceae
Bambu	<i>Bambusa</i> sp.	Poaceae
Bingbin	<i>Pinanga coronata</i>	Arecaceae
Burunungul	<i>Sloanea sigun</i>	Elaeocarpaceae
Canar	<i>Smilax macrocarpa</i>	Smilacaceae
Cecer monteng	<i>Elaeagnus conferta</i>	Elaeagnaceae
Culak ketan	<i>Chrysophyllum roxburghii</i>	Sapotaceae
Dukuh hutan	<i>Lansium</i> sp.	Meliaceae
Epifit	-	-
Ficus	<i>Ficus</i> spp.	Moraceae
Ficus besar	<i>Ficus punctata</i>	Moraceae
Ficus K300 (Ficus pohon)	<i>Ficus annulata</i>	Moraceae
Ficus Kendeng bawah, HM 6	<i>Ficus vasculosa</i>	Moraceae
Ficus kisigung	<i>Ficus villosa</i>	Moraceae
Ficus kuning	<i>Ficus sumatrana</i>	Moraceae
Ficus oren HM 7, 22	<i>Ficus sinuata</i>	Moraceae
Ficus oren K200, HM 8, HM 15	<i>Ficus heteropleura</i>	Moraceae
Ficus sinuata	<i>Ficus sinuata</i>	Moraceae
Ganitri	<i>Elaeocarpus ganitrus</i>	Elaeocarpaceae
Gegedangan	<i>Ficus hirta</i>	Moraceae
Hamerang	<i>Ficus padana</i>	Moraceae
Hamirung	<i>Callicarpa pentandra</i>	Meliaceae
Harendang	<i>Dissochaeta reticulata</i>	Melastomataceae
Huru honje	<i>Litsea resinosa</i>	Lauraceae
Huru merang	<i>Litsea angulata</i>	Lauraceae
Huru tales	<i>Litsea mappacea</i>	Lauraceae

Ipis kulit	<i>Decaspermum fruticosum</i>	Myrtaceae
Kadongdong hutan	<i>Spondias pinnata</i>	Anacardiaceae
Kecapi	<i>Sandoricum koetjape</i>	Meliaceae
Kibalera	<i>Cayratia trifolia</i>	Vitaceae
Kibalera palsu	<i>Gnetum cuspidatum</i>	Gnetaceae
Kicentong	<i>Ficus deltoidea</i>	Moraceae
Kidage	<i>Bruinsmia styracoides</i>	Styracaceae
Kihaji	<i>Dysoxylum parasiticum</i>	Meliaceae
Kihiur	<i>Castanopsis javanica</i>	Fagaceae
Kihujan	<i>Engelhardia serrata</i>	Juglandaceae
Kijeruk	<i>Acronychia pedunculata</i>	Rutaceae
Kikadanca	-	Ericaceae
Kilaban	<i>Cordia bantamensis</i>	Boraginaceae
Kilimo	<i>Litsea cubeba</i>	Lauraceae
Kimokla	<i>Knema cinerea</i>	Myristicaceae
Kingkilaban	<i>Mussaenda frondosa</i>	Rubiaceae
Kipeut	-	Melastomataceae
Kisampang	<i>Melicope denhamii</i>	Rutaceae
Kisereh	<i>Cinnamomum parthenoxylon</i>	Lauraceae
Kiterong	<i>Schoutenia kunstleri</i>	Symplocaceae
Kokosan monyet	<i>Dysoxylum motan</i>	Meliaceae
Kondang	<i>Ficus variegata</i>	Moraceae
Kondang kecil	<i>Ficus glandulifera</i>	Moraceae
Kopi dengkung	<i>Nyssa javanica</i>	Nyssaceae
Kopo	<i>Syzygium littorale</i>	Myrtaceae
Kurai	<i>Trema orientalis</i>	Ulmaceae
Liana buah gantung	<i>Vaccinium korthalsii</i>	Ericaceae
Liana bunga ungu	<i>Polkilospermum suaveolens</i>	Urticaceae
Liana daun tebal	<i>Hoya macrophylla</i>	Apocynaceae
Liana enak	<i>Melodinus orientalis</i>	Apocynaceae
Liana ficus unknown	-	Moraceae
Liana gurita	-	Vitaceae
Liana mirip ficus	-	-
Liana telur gabus	<i>Artabotrys suaveolens</i>	Annonaceae
Liana unknown	-	Elaeagnaceae
Lolo	<i>Scindapsus marantaefolius</i>	Araceae
Maja	<i>Magnolia elegans</i>	Magnoliaceae
Manganeh	-	-
Mangga pari	<i>Mangifera laurina</i>	Anacardiaceae
Mara bangkong	<i>Macaranga tanarius</i>	Euphorbiaceae
Pakis keras	<i>Blechnum spicant</i>	Polypodiaceae
Pakis liana	<i>Rhaphidophora pinnata</i>	Araceae
Pasang	<i>Quercus sundaica</i>	Fagaceae
Polyalthia	<i>Polyalthia lateriflora</i>	Annonaceae
Pongrang	<i>Schefflera aromatica</i>	Araliaceae
Rotan	<i>Calamus manan</i>	Arecaceae
Sarai	<i>Caryota mitis</i>	Arecaceae
Senu	<i>Pipturus argenteus</i>	Urticaceae
Suwangkung	<i>Caryota rumphyana</i>	Araceae
Tereup	<i>Artocarpus elasticus</i>	Moraceae
Tulak tanggul	<i>Schefflera lucida</i>	Araliaceae

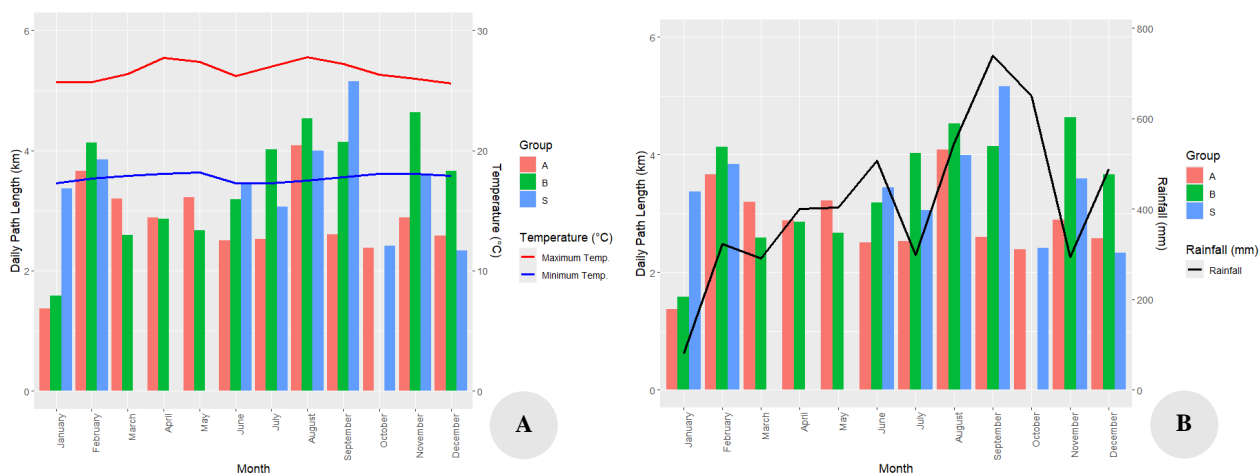


Figure S1. DPL changes of each Javan gibbon (*Hylobates moloch*) group. A. Average maximum and minimum daily temperature, B. Monthly rainfall during the research period from January to December 2022

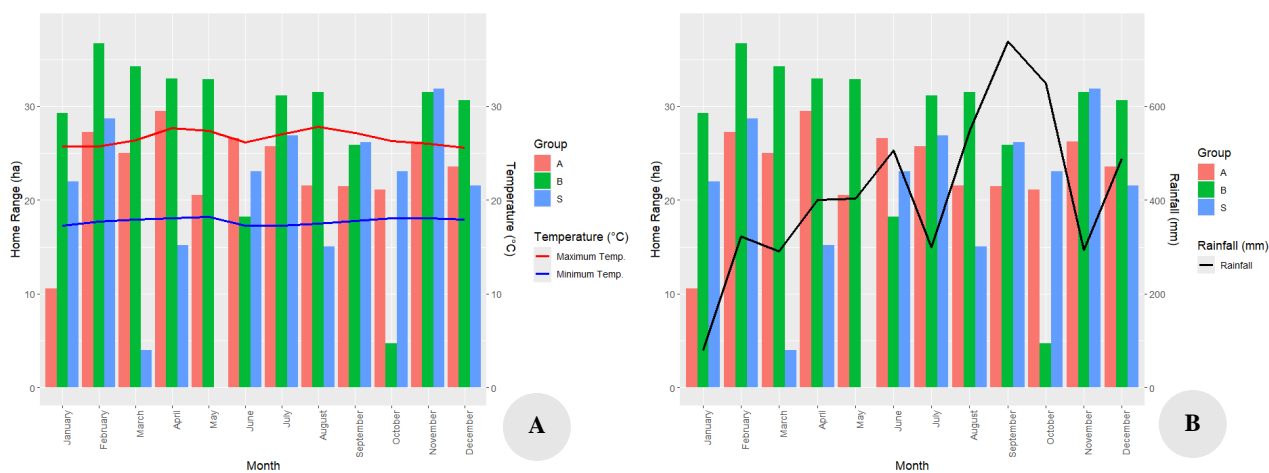


Figure S2. Home range size changes of each Javan gibbon (*Hylobates moloch*) group. A. Average maximum and minimum daily temperature, B. Monthly rainfall during the research period from January to December 2022