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Diet And Ranging Behavior Of The Endangered Javan Gibbon (*Hylobates moloch*) In A Submontane Tropical Rainforest

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RESEARCH ARTICLE

Diet and Ranging Behavior of the Endangered Javan Gibbon (*Hylobates moloch*) in a Submontane Tropical Rainforest

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Key words: Javan gibbon; diet; home range size; altitude; intraspecific variation

INTRODUCTION

Primate ranging patterns are largely determined by food abundance and distribution [Lambert, 2007], although group size, topographical features, and the distribution of other resources may also affect primate ranging and activities. Ripe fruit availability can have a particularly pronounced effect on home range sizes, day ranges, and activity patterns for arboreal frugivores [Clutton-Brock & Harvey, 1977; Lambert, 2007]. Habitat structure and food availability generally vary with altitude, and accordingly, conspecific primate populations living at different altitudes often show significant differences in behavior. For example, mountain gorillas (*Gorilla beringei*) inhabiting higher elevation forests have longer daily path lengths (DPL) and larger home ranges [Ganas & Robbins, 2005] than those in lowland forests, which may reflect higher plant diversity and fruit availability at lower altitudes [Nkurunungi et al., 2004]. Solitary eastern lowland gorilla (*Gorilla graueri*) males in lowland forests travel longer distances and eat more kinds of food than males in highland forests [Yamagiwa & Mwanza, 1994]. Geladas (*Theropithecus gelada*) spend more time feeding as altitude increases, and show increasing production of stress-related glucocorticoid metabolites [Beehner & McCann, 2008]. Japanese macaque

(*Macaca fuscata*) diets and ranging patterns also vary with altitude [Hanya et al., 2003; Izumiyama et al., 2003]. However, the behavior of many primate species has been described from studies at only one or a few sites. The resulting lack of information about behavioral responses to ecological variation limits our understanding of what constitutes species-typical behavior, and may impede the establishment and implementation of effective conservation plans for endangered species.

The Javan or silvery gibbon (*Hylobates moloch*) is endemic to the island of Java in Indonesia. Java's already-dense human population almost doubled between 1941 and 2000, resulting in substantial

anthropogenic changes to the landscape. The island now retains <10% of its original forest cover [Whitten et al., 1996] and that which remains is severely fragmented, especially in lowland areas, which has resulted in the loss of most primate habitat on Java. Several endemic Javan primate species, including the Javan gibbon, are now Endangered (e.g. *Nycticebus javanicus*, *Presbytis comata*, *H. moloch* [IUCN, 2010]). Population estimates for the Javan gibbon vary widely, but recent studies have converged on estimates of about 4,000–4,500 wild individuals in ~30 forest fragments [Asquith, 2001; Nijman, 2004, 2006; Supriatna et al., 2010], of which 3,000–3,600 live in high-priority populations containing >200 individuals [Nijman, 2004; Supriatna et al., 2010]. On Java, climatic conditions, soil characteristics, and forest structure vary with altitude, and dominant tree species differ even among forests of similar elevation for both climatic and historical reasons [Whitten et al., 1996]. Javan gibbons inhabit forests of altitudes from near sea level to >1,500 m above sea level (asl). However, the vast majority of Javan gibbons remaining inhabit hill (500–1,000 m asl) and lower montane (1,000–1,500 m asl) forests [Nijman, 2006; Supriatna, 2006; Supriatna et al., 2010]. Aside from the Ujung Kulon National Park, all of the high-priority Javan gibbon habitats are comprised primarily or entirely of hill or montane forest [Nijman, 2004; Supriatna, 2006; Supriatna et al., 2010].

While forests >500 m asl comprise most of the last strongholds for the Javan gibbon, almost all information available about Javan gibbon behavior and ecology comes from Kappeler's [1981, 1984a,c] study in low-land forest at Turalak in the Ujung Kulon National Park in 1975–1976 and Malone's [2007] study in lowland forest in the Leuweung Sancang Forest Reserve in 2003–2005. While gibbon home ranges average ~40 ha [Bartlett, 2007], mean Javan gibbon home ranges at Turalak were much smaller, at ~17.4 ha [$N = 7$ groups; Kappeler, 1981], and gibbons at Turalak had the highest ratio of DPL to home range area reported for the family Hylobatidae [Chivers, 1984], suggesting especially intensive use of very small home ranges. Home range sizes in the Leuweung Sancang Nature Reserve were also very small (mean = 14.9 ha, $N = 8$) [Malone, 2007; Malone & Fuentes, 2009], and several Indonesian researchers that have conducted studies spanning a few weeks or months, often of unhabituated gibbons, have also observed or assumed small Javan gibbon home ranges [Gunung Halimun-Salak National Park, 2006; D. Rinaldi, personal communication; N. Andayani, personal communication], but few data have been published.

The densities of several gibbon species, including Javan gibbons, vary with elevation [Kappeler, 1984b; Marshall, 2009; Nijman, 2004; O'Brien et al., 2004], suggesting that habitat quality is related to elevation. Few studies of gibbon behavior have been conducted at high elevations, but Fan et al. [2008, 2009] and Fan and Jiang [2008] reported that black crested gibbons (*Nomascus concolor jingdongensis*) in high-elevation (2,000–2,200 m asl) forests on Mt. Wuliang in China have very large home ranges and include fewer fruits and more leaves in their diets than most gibbon populations do. However, Mt. Wuliang is at high latitude and displays substantial seasonal variation in food availability, so it is unclear whether the same behavioral responses should be expected in Javan gibbons living in middle- and high-elevation forests.

We collected behavioral data from a population of Javan gibbons living in hill/lower montane forest (950–1,100 m asl) in the Citalahab area of the Gunung Halimun-Salak National Park to evaluate the hypothesis that Javan gibbons are characterized by small home ranges (<20 ha) and heavy reliance on ripe fruit throughout their distribution range. Our study is the first study of a habituated population of Javan gibbons involving systematic collection of data for a period spanning a full year. We describe ranging patterns, home range sizes, activity patterns, and diets and compare our observations with published data from lowland populations [Kappeler, 1984a,c; Malone, 2007; Malone & Fuentes, 2009]. We then discuss the implications of behavioral responses to variation in habitat quality for gibbon conservation management.

METHODS
Study Site

The study was conducted in the Gunung Halimun-Salak National Park (6°40′S, 106°32′E), Indonesia (Fig. 1). The park covers an area of approximately 113,357 ha (~400–2,000 m asl), and contains the largest remaining forest block on Java. The vegetation is mostly closed-canopy primary forest, surrounded or partially infiltrated by patches of secondary forest, rice fields, gardens, and tea plantations. Our research was conducted near the village of Citalahab on the slope of Mt. Kendeng, east of Mt. Halimun and immediately south of the Nirmala tea estate, which forms an enclave within the National Park. The research area (hereafter referred to as "Citalahab" after the village) is crossed by a 140-ha grid of trails at 200-m intervals (Fig. 1) and secondary trails near common gibbon travel paths, and overlaps the 3.6-km trail system associated with the Cikaniki Research Station. The study area is covered with primary forest, but is adjacent to a village and tea plantations that were established before Indonesian independence in 1945 [Whitten et al., 1996]. Some small-scale human disturbance (e.g. removal of individual trees, utilization of other forest products) has occurred in or near the study area, but the boundary of the primary forest has remained constant over the last few
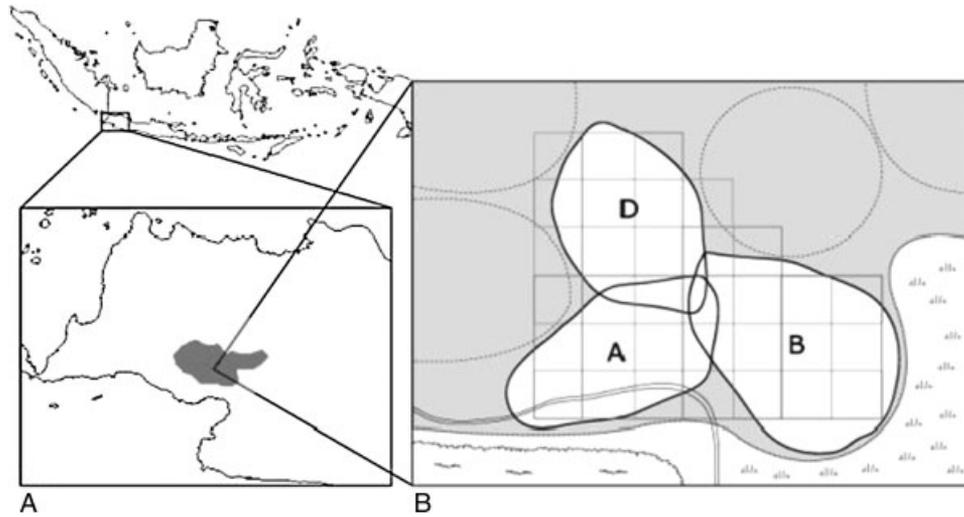
Fig. 1. The location of the study site. (**A**) The area in the enlargement on the left indicates the Gunung Halimun-Salak National Park (GHSNP). (**B**) The home ranges of the three study groups are shown in the enlargement on the right, along with the 200 × 200 m grid of trails. The approximate boundaries of unhabituated neighboring groups are also indicated with dotted lines. Group A's home range is adjacent to a tea plantation, and group B's home range borders rice paddies. The double line indicates the main Cikaniki/Citalahab trail.

decades, and human activities do not appear to have had a substantial effect on forest structure in the study area.

Study Subjects

We collected behavioral data from three gibbon groups with adjacent home ranges (Fig. 1). From July 2007–March 2008, we habituated the study groups to human observers. After habituation, which required 2–9 months for each group, the animals did not visibly respond to the presence of human observers. We systematically collected behavioral and ecological data from April 2008 to March 2009. However, group D ranged in a hilly area where the terrain made it especially difficult to follow the animals, which resulted in the collection of fewer days of behavioral data from group D (Group A: 68 days, Group B: 74 days, Group D: 31 days). The home range of group A was adjacent to a tea plantation, and that of group B was flanked on one side by wet rice fields (Fig. 1). At least three more groups occupying adjacent territories could be identified (Fig. 1).

Data Collection

We observed the behavior of the three study groups on a rotating basis. Each group was followed from sleeping tree to sleeping tree for periods of three or more consecutive days whenever possible. We conducted scan sampling of all group members except infants at 30-min intervals, recording each animal's activity (e.g. feeding, resting, traveling, socializing, inter-group aggression and other) and location. When the animals were feeding, we recorded the food type (e.g. fig fruit, nonfig fruit, new leaves, mature leaves, flowers, shoots, insects, and

other), and identified the plant species whenever possible. We estimated the location of each individual within the grid of trails using a compass and rangefinder. Group members generally coordinated their movements and remained relatively close together, but occasionally group spreads exceeded 50 m. When it became impossible to collect data from all individuals, we prioritized a focal individual, who had been selected before beginning our daily follows. A typical observation period lasted ∼10–11 h, starting around 6:00 h and continuing until 16:00–17:00 h.

We collected information about tree densities from 25 plots (10 × 50 m) established at random junctions and with random orientations within the grid of trails. In each plot, we placed markers on all trees with diameter at breast height (dbh) ≥ 10 cm. We identified each marked tree by its species and local name with the help of local field assistants and the Herbarium Bogoriense. Plots were established before the beginning of the study, and all but two plots were located within the home ranges of one or more of the study groups. ''Food trees'' were defined as trees of species included in Javan gibbons diets either at Turalak [Kappeler, 1984a] or in this study and ''fruit trees'' were defined as trees of species from which fruits were eaten by Javan gibbons at either site. We observed gibbons at Citalahab feeding on 92% of the plant species identified as food trees, which suggests that plants eaten at Turalak were generally also eaten at Citalahab if they were available. We estimated mean tree dbh and density, mean food tree density, and mean fruit tree density and dbh, using data from the vegetation plots. We recorded rainfall and minimum and maximum temperatures daily from June 2007 to March 2009, using a standard rain gauge and an electronic temperature gauge.

Data Analysis

We used mean proportions of scan samples for each individual in which a given activity was observed for each observation day as the unit of data analysis and averaged the daily values for all individuals in a group to calculate monthly and annual activity budgets and diets. DPL was calculated as the sum of the distances traveled during each 30-min interval in a day, excluding days on which the observer lost contact with the animal for a period of an hour or more, or could not conclusively identify the sleeping tree. The structure of the forest in the areas around sleeping trees, coupled with the gibbons pre-sleep behavior [Reichard, 1998], often made it impossible to observe the actual entrance to the sleeping tree, and in many cases, it was not possible to identify the actual sleeping tree. Therefore, we were able to calculate DPL on relatively few days. However, on days when the actual sleeping tree was not known, we usually found the gibbons in the early morning within 20–30 m of the tree in which they were last seen on the previous day. As all group members generally ranged together, we included data from all individuals in calculations of mean DPL for each group. We also grouped the DPL data from groups A and B for seasonal comparisons. Home ranges (annual and monthly) and areas of overlap between groups (annual) were calculated using minimum convex polygons with ArcGIS® v.3.3 (ESRI, Redlands, CA) software with the Animal Movement extension.

We analyzed the activity data for each group and for the study population. However, we excluded group D from our analyses of seasonal variation because sampling for group D was inadequate in some months (i.e. <4 days of behavioral data were available). To evaluate gibbon diets, we calculated the percentage of feeding observations in which an individual fed on each food item for each day for each individual. The group diet on a day was the average of the values for all group members. To assess the relationships among activity variables for groups A and B, we used Pearson correlation analysis to determine whether the percentage of fruit in the diet in a given month was related to the percentage of time feeding, the percentage of time traveling, or the proportion of the home range visited in a given month. As percentages form a binomial, rather than a normal, distribution, the percentage data were arcsine-square root transformed before analysis using parametric statistical tests to approximate normality [Zar, 1996]. The DPL and home range data were normally distributed (Kolmogorov–Smirnov test, DPL: $Z = 0.115$, $P = 0.200$; home range: $Z = 0.120$, $P = 0.200$), so we used parametric statistics for these data. We divided the year into three seasons based on rainfall: dry (June–September), wet (February–May), and very wet (October–January)

and used ANOVA (Home range, DPL, dietary variables) to compare behavior among seasons.

Our research protocol was approved by the Indonesian Institute of Sciences (LIPI), the Indonesian Ministry of Research and Technology (RISTEK), the Indonesian Ministry of Forestry's Department for the Protection and Conservation of Nature (PHKA), and GHSNP. This research was conducted in compliance with Indonesian law.

RESULTS
Sampling

We followed groups A and B for a mean of 6 d/mo (range: 4–8 d/mo), resulting in a total observation time of 1,455 h (A: 617.5 hr, B: 635 hr). Group D (202.5 hr) was followed less frequently than the other groups (1–4 d/mo) as a result of the difficult terrain in its home range. Using conservative criteria for inclusion of data in our DPL calculations (see Methods), we collected 21 full day journeys for group A and 13 for group B.

Climate Conditions

From June 2007 to March 2009, rainfall averaged $321 \pm SD$ 174 mm/mo (range: 63–775 mm; Fig. 2). Annual rainfall was 4,405 mm in 2008. Rainfall was weakly seasonal, with a short dry season between June and September, but rainfall was >100 mm every month except August 2007 and July 2008. Temperatures were stable throughout the year, with maximum daily temperatures of $29.3 \pm 1.4°C$ and minimum temperatures of $16.8 \pm 0.9°C$.

Group Composition

Groups A contained four individuals and groups B and D each contained three. All groups had one adult male, one adult female, and one infant. Group A also contained a subadult female. A subadult male was loosely associated with group D, but disappeared in June 2008.

Activity Patterns and DPL

Gibbons at Citalahab spent a mean of $36\% \pm SD$ 18% (range: 34–40%) of their time feeding, a mean of $41\% \pm SD$ 18% (range: 36–44%) of resting, a mean of $14\% \pm SD$ 11% (range: 11–18%) of their time traveling, a mean of $6\% \pm SD$ 9% engaging in social behaviors (range: 4–8%), and a mean of $2\% \pm SD$ 6% (range: 1–5%) in inter-group agonistic interactions. Neither group A nor group B showed seasonal differences in any activity variable (ANOVA: Group A: Feeding: $F_{2,65} = 0.918$, $P = 0.404$; Traveling: $F_{2,65} = 0.259$, $P = 0.772$; Resting: $F_{2,65} = 0.557$, $P = 0.576$; Social: $F_{2,65} = 0.745$, $P = 0.479$; Aggression: $F = 0.520$, $P = 0.597$; Group B: Feeding: $F_{2,71} = 1.120$, $P = 0.332$; Traveling: $F_{2,71} = 0.621$,
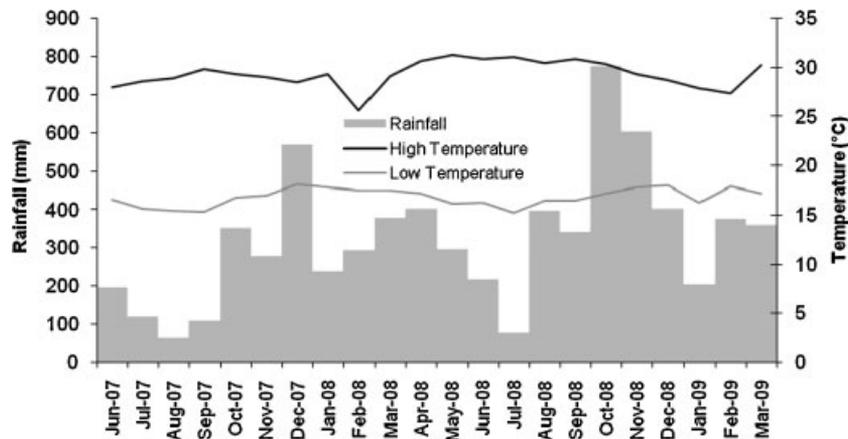
Fig. 2. Monthly rainfall and means of the daily minimum/maximum temperatures at the study site.
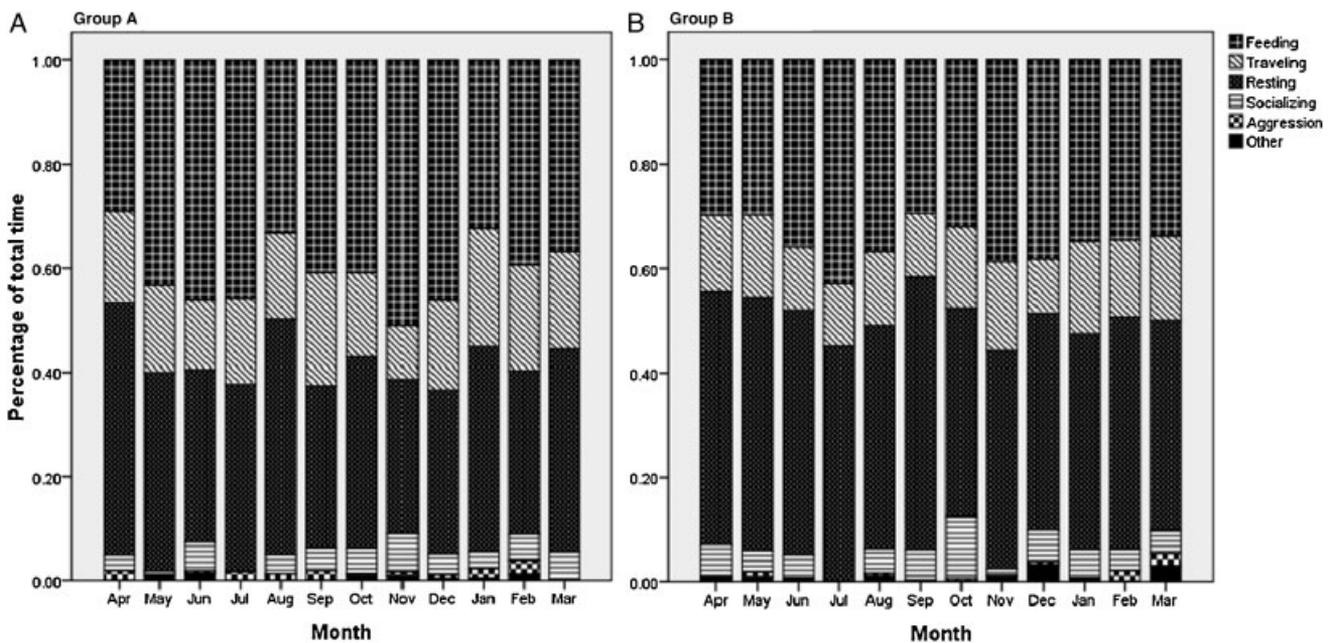

Fig. 3. Mean percentage of time spent in each activity in each study month for (**A**) group A and (**B**) group B.

$P = 0.540$; Resting: $F_{2,71} = 1.742$, $P = 0.183$; Social: $F_{2,71} = 0.915$, $P = 0.405$; Aggression $F_{2,71} = 1.631$, $P = 0.203$; Fig. 3). Our method of measuring DPL resulted in the exclusion of most days of data. The mean DPL was $1,039 \pm SD$ 320 m ($N = 21$ days) for group A, and $1,302 \pm SD$ 365 m ($N = 13$ days) for group B. For group D, we did not calculate a mean DPL, as few complete daily paths were available. Mean DPL did not differ between seasons (ANOVA: $F_{2,32} = 1.695$, $P = 0.200$).

Home Range Area

The mean home range area for the study groups was $36.6 \pm SD$ 5.9 ha ($N = 3$), and the home ranges of neighboring groups overlapped by $3.3 \pm SD$ 1.1 ha

(8%; Fig. 1). We estimate that the average area of exclusive use for a group with three to four neighboring groups would be 25–30 ha, or 67–81% of the home range. Groups A and B did not use their entire annual home ranges in most study months, but there was not significant seasonal variation in monthly home range size for either group (ANOVA: Group A: $F_{2,9} = 0.0979$, $P = 0.909$; Group B: $F_{2,9} = 0.210$, $P = 0.815$, Fig. 4).

Diet

Fruit was the most important gibbon food ($62.5\% \pm SD$ 25.9% of feeding time), followed by new leaves ($23.7\% \pm SD$ 21.9%). Flowers were also important ($11.8\% \pm SD$ 17.5%), comprising >10% of

the diets of groups A and D, and contributing more to group D's diet (18.2%±SD 28.4%) than new leaves (14.6%±SD 26.9%). Mature leaves (0.9%±SD 3.7%) and other materials (e.g. insects, shoots; 1.2%±SD 3.6%) comprised the rest of the diet. The gibbons spent similar percentages of time feeding on fig (33.4%±SD 27.5%) and nonfig (29.1%±SD 23.8%) fruit. Both groups showed seasonal differences in the proportion of fruit (Group A: $F_{2,65} = 11.986$, $P = 0.000$; Group B: $F_{2,71} = 8.194$, $P = 0.001$) and new leaves (Group A: $F_{2,65} = 6.219$, $P = 0.003$; Group B: $F_{2,71} = 9.539$,

$P = 0.000$) that they included in their diets, and Group A showed seasonal difference in flowers ($F_{2,65} = 9.197$, $P = 0.000$) and nonfig fruits ($F_{2,65} = 5.171$, $P = 0.008$) but not in mature leaves ($F_{2,65} = 0.131$, $P = 0.878$) or fig fruits ($F_{2,65} = 2.819$, $P = 0.067$). Group B showed seasonal differences in fig fruits ($F_{2,71} = 20.240$, $P = 0.000$) but not in mature leaves ($F_{2,71} = 0.343$, $P = 0.710$), flowers ($F_{2,71} = 0.274$, $P = 0.761$) or nonfig fruits ($F_{2,71} = 2.601$, $P = 0.081$; Fig. 5).

The Relationships Among Diet and Activity Patterns

There were not significant correlations between the mean monthly percentage of feeding time spent eating fruit and the mean monthly percentage of time spent feeding (Group A: $r = -0.009$, $P = 0.979$, $N = 12$; Group B: $r = 0.101$, $P = 0.775$, $N = 12$), the mean monthly percentage of feeding time spent eating fruit and the mean monthly percentage of time spent traveling (Group A: $r = -0.182$, $P = 0.571$, $N = 12$; Group B: $r = -0.365$, $P = 0.243$, $N = 12$), and the mean monthly percentage of feeding time spent eating fruit and the monthly home range area (Group A: $r = -0.014$, $P = 0.966$, $N = 12$; B: $r = 0.377$, $P = 0.227$, $N = 12$).

Food Availability

The mean density of trees with dbh > 10 cm in the botanical plots was 288±SD 107 individuals/ha, with a mean dbh of 28.2±SD 6 cm. The mean food tree density in the gibbon home ranges was 166.33±SD 29.7 individuals/ha (mean of group means). The mean fruit tree density was 62.6±SD 18.1 individuals/ha and the mean fruit tree dbh was 26.5±SD 15.4.
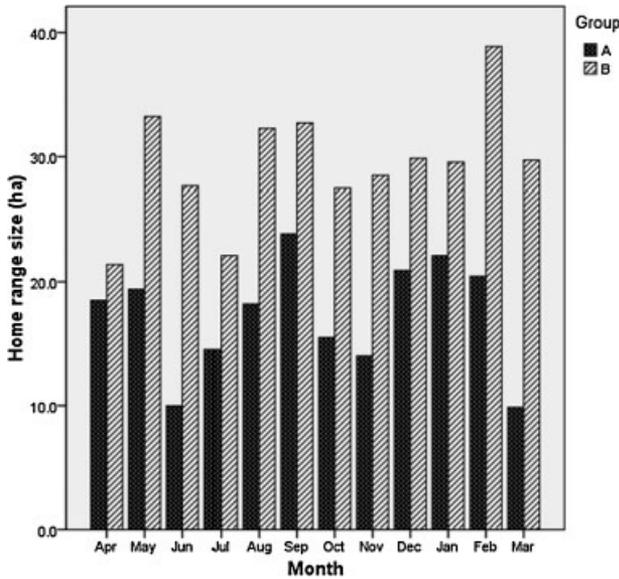

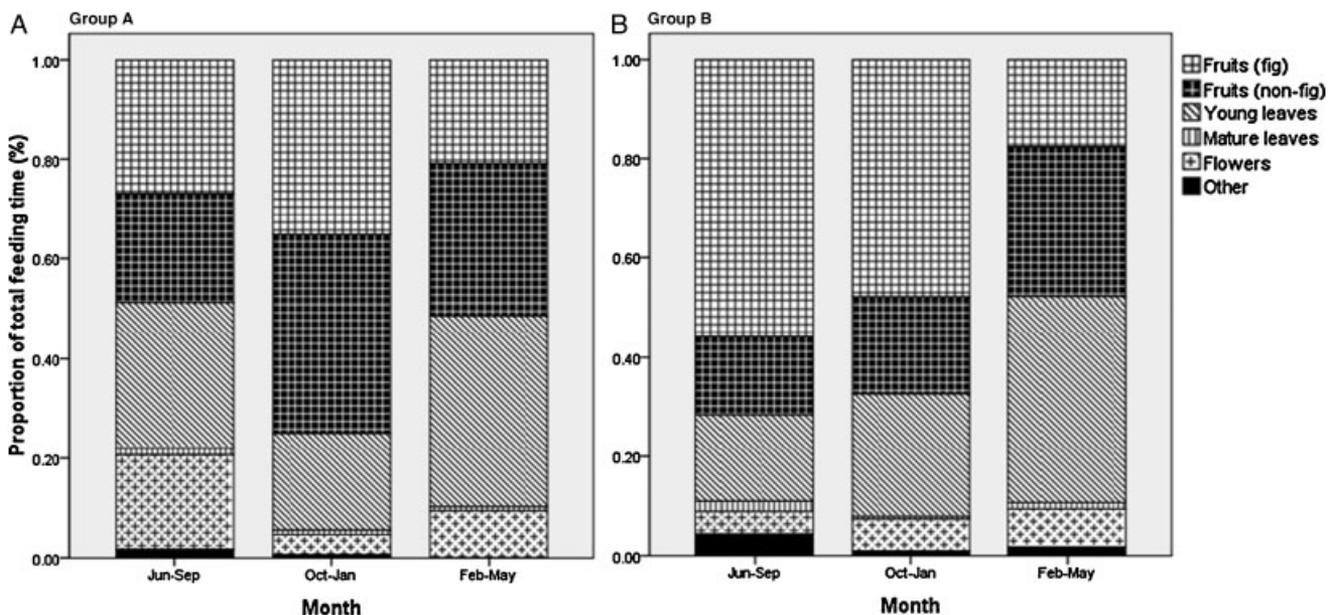Fig. 4. Monthly home range size in each study month for groups A and B.

Fig. 5. Mean percentage of time spent feeding in each plant part according to season (dry: June–September, very wet: October–January, wet: February–May) for (**A**) group A and (**B**) group B.

DISCUSSION

Gibbon densities vary among sites and habitat types [e.g. Kappeler, 1984b; Marshall, 2009; O'Brien et al., 2004], and previous studies have revealed substantial intraspecific variation in gibbon diets, ranging patterns, social organization, and mating systems [Bartlett, 2007; Malone & Fuentes, 2009]. However, most gibbon taxa have been studied at few sites, making it difficult to assess the effects of habitat characteristics on gibbon behavior. Densities of several gibbon species (e.g. *H. lar* [Chivers, 2001], *H. moloch* [Kappeler, 1984b; Nijman, 2004], *H. albibarbis* [Marshall, 2009]) vary with altitude, but the effects of altitude on other aspects of gibbon biology and the mechanisms by which altitude affects gibbon densities remain poorly understood.

Our results suggest that many aspects of gibbon behavioral biology in lower montane forests at Citalahab are similar to those reported from lowland populations, but we also noted some important differences among sites. While Marshall [2009] reported lower group sizes and reduced infant survivorship in *H. albibarbis* in higher elevation forests, Javan gibbons had similar group sizes (~3.3 individuals/group) at Citalahab and two lowland sites (Leuweung Sancang Nature Reserve and Turalak; Table I). Javan gibbons at both highland and lowland sites also spent ~60% of their feeding time eating fruit (Table I), suggesting that Javan gibbons, like other species in their genus, adopt behavioral strategies that permit them to remain heavily frugivorous across a broad range of habitat conditions. However, gibbon ranging patterns displayed substantial variation across study sites: Javan gibbons at Turalak and Leuweung Sancang had 15–17 ha home ranges, but Javan gibbon home range sizes at Citalahab were approximately twice that size (Table I). DPL also varied somewhat among sites.

Some of the observed inter-population differences may have resulted from methodological differences among studies. However, the mean home range size in our study was more than twice the size of those reported by Kappeler [1981] and Malone [2007], a difference that is difficult to attribute simply to differences in sampling effort or methods. Previous studies do not suggest pronounced seasonal variation in range use in gibbons in tropical evergreen habitats [Whitten, 1982] and Javan gibbon DPL and monthly range size did not differ among seasons at Citalahab, so the differences between home range estimates resulting from differences in study duration in studies spanning more than a few months should be incremental. In addition, several gibbon home ranges at Leuweung Sancang were located on habitat edges, and the entire circumference of the smallest home range was bounded by habitat edge or other gibbon home ranges [Malone, 2007], suggesting that there was little or no

TABLE I. Comparisons of Javan Gibbon Population Characteristics at Citalahab, Leuweung Sancang Nature Reserve (CALS), and Turalak

Site	Group size	Density (gp/km²)	Home range (ha)	% overlap (area)	DPL (m)	% Time Feed	% Time Travel	% Feed time Fruit	% Feed time Leaves	References
Citalahab	3.2	3.8ᵃ	36.6	8.3% (3.3 ha)	1,171	36	14	63	24	This study
CALS	3.3	1.33	14.9	12% (2.1 ha)	835	38	13	–	–	Malone [2007]; Malone and Fuentes [2009]
Turalak	3.3	6.7	17.4		1,400	32	23	61	38	Kappeler [1984a] and Chivers [1984]

ᵃDensity estimates for Citalahab are derived from Iskandar's [2006] surveys at Cikaniki, which included the Citalahab area.

additional habitat available in the area, and gibbons at Turalak occupied contiguous home ranges with areas of overlap similar to those observed in our study [Kappeler, 1981, 1984a]. Therefore, our results suggest that Javan gibbon home ranges are indeed substantially larger at Citalahab than Turalak or Leuweung Sancang.

Differences in ranging patterns in groups of similar size are often caused by differences in the distribution or abundance of food resources [Isbell, 1991; Lambert, 2007]. In territorial animals, home range sizes are affected by temporal and spatial variation in resource availability, and viable home range sizes may approximate the smallest area within which the group is likely to be able to obtain sufficient resources throughout the year [Carr & MacDonald, 1986; MacDonald & Carr, 1989]. Frugivores are particularly sensitive to variation in food availability [Clutton-Brock & Harvey, 1977; Lambert, 2007], and the high fruit consumption by Javan gibbons at Turalak and Citalahab (Table I) suggests that Javan gibbons, like several other *Hylobates* species [Bartlett, 2007; McConkey et al., 2003] employ behavioral strategies that allow them to maintain high fruit intake in most months.

At many sites, gibbons eat more fruit when more fruit is available [Ahsan, 1994; Bartlett, 1999; Chivers, 1972; Raemaekers, 1980], and these seasonal differences appear to drive differences in other aspects of their behavior [Bartlett, 2003, 2009; Raemaekers, 1980]. For example, at Khao Yai in Thailand, white-handed gibbons (*H. lar*) traveled substantially less [Bartlett, 2009] and ate less fruit [and dramatically less nonfig fruit; Bartlett, 1999] during the months of lowest fruit availability. However, we did not find significant seasonal variation in DPL or home range use at Citalahab, and there was no correlation between the percentage of time that Javan gibbons spent eating fruit and travel time or home range area. In addition, while each group's diet varied across seasons, peaks in total fruit-feeding, nonfig fruit-feeding, and fig fruit-feeding occurred in different seasons for different groups (Fig. 5). These observations suggest that variation in overall fruit availability associated with seasonal temperature and rainfall regimes at higher latitude sites causes discernible and predictable seasonal shifts in gibbon ranging behavior, but that at some lower-latitude, less-seasonal sites such as Citalahab, temporal variation in gibbon diets and ranging patterns may be driven primarily by the local distribution and fruiting (or flowering) phenology of preferred species, rather than seasonal variation in overall fruit availability. Lappan [2010] reported significant temporal and spatial heterogeneity in the diets of five neighboring siamang (*Symphalangus syndactylus*) groups at Way Canguk, another low-latitude site, and McConkey et al. [2003] did not find a correlation between overall fruit availability and the fruit component of hybrid Bornean gibbon (*H. muelleri × agilis/albibarbis*) diets, both of which are consistent with this argument.

Overall tree density and food tree density were substantially lower at Citalahab than Leuweung Sancang, while mean tree dbh was similar (Table II). Tree dbh is generally a reasonable predictor of the size of the fruit crop [Chapman et al., 1992]. Therefore, these differences suggest that fruit abundance is likely to be higher at Leuweung Sancang than Citalahab. Tree size and forest complexity generally decline with increasing altitude on Java [Whitten et al., 1996], which suggests that the differences between gibbon home range sizes at these sites may represent an general pattern of increasing home range sizes with altitude. Similar patterns of altitudinal variation in home range size have been reported in gorillas [Ganas & Robbins, 2005]. However, data from additional sites and more information about the relationship between altitude and resource abundance and distribution and habitat heterogeneity will be required to rigorously examine the relationship between Javan gibbon home range sizes, altitude, and habitat quality. Other geographic factors, including latitude and rainfall regimes, may also affect food availability. However, as wild Javan gibbons inhabit only wet forests within a very narrow latitudinal band, it is unlikely that differences in latitude or rainfall are the primary causes of the differences observed in this study.

Habitat disturbance may also affect gibbon population parameters. Gibbon densities generally vary with food availability [Chivers, 2001], and density is usually positively correlated with group size or negatively correlated with home range size, or both, but the gibbon density at Citalahab was intermediate between those at the two lowland sites, although gibbons at all three sites had similar group sizes and gibbons at the lowland sites had smaller home ranges. This discrepancy likely results from reduced occupancy of forest fragments at Leuweung Sancang caused by recent habitat disturbance or hunting [Malone, 2007], leading to very low gibbon density in this area. Habitat disturbance can also affect gibbon ranging patterns. For example, gibbons in fragmented forest in Assam, India and western Sumatra, Indonesia have shorter DPL in fragmented than continuous forests, although their home range sizes do not differ [Kakati, 2004; Yanuar & Chivers, 2010]. Can the difference in home range sizes between the lowland sites sampled and Citalahab also be attributed entirely or largely to differences in their degrees of anthropogenic habitat disturbance? The overall pattern of variation suggests that it cannot. The average gibbon home range sizes at Turalak, the least-disturbed site considered in our comparisons, and Leuweung Sancang, the most-disturbed site, were very similar, while gibbon home ranges at Citalahab were substantially larger.

TABLE II. Comparisons of Javan Gibbon Habitat Characteristics at Citalahab, Leuweung Sancang Nature Reserve (CALS), and Turalak

Site	Elevation (m asl)	Annual rainfall (mm)	Tree density (ind./ha)	Mean tree dbh (cm)	Food tree density (ind./ha)	Habitat type	Reference
Citalahab	950–1,100	4,405	288±107	28.2	139	Primary, adjacent to human settlement	This study
CALS	0–150	3,686	465±42	27.4	241	Primary and secondary, substantial disturbance	Malone [2007]; Priatna et al. [1989]
Turalak	~50	3,249	–	–	–	Primary	Kappeler [1981, 1984a]

Therefore, while gibbon density is correlated with the degree of habitat disturbance in the three study sites, gibbon home range sizes was correlated with altitude, but not with the degree of habitat disturbance. As Javan gibbons are territorial, their ability to respond to changes in their environments by shifting to new areas is limited. Therefore, habitat disturbance resulting in the loss of essential food resources may tend to lead to the loss of whole gibbon groups, and only incremental shifts in the boundaries of existing home ranges, at least in the short term. These observations highlight the fact that food availability, food distribution, habitat patchiness, anthropogenic habitat disturbance and hunting, and recent historical changes must all be considered when evaluating the relationships among ecological factors and primate group sizes, home range sizes, and population densities. It is also important to note that gibbon researchers do not choose their sites randomly, often selecting study sites with unusually high or low primate densities. Therefore, population parameters from behavioral studies may tend to reflect gibbon behavior in better-than-average (or worse-than-average) habitats.

Estimates of the total wild Javan gibbon population vary dramatically [e.g. Asquith & Sinaga, 1995; Nijman, 2004; Supriatna, 2006], in part because population estimates are typically extrapolated from data collected during brief surveys using a variety of different methods and analyzed using different sets of simplifying assumptions. For example, some researchers have assumed that gibbons do not occupy habitats <1 km from the forest edge [e.g. Nijman & van Balen, 1998; Supriatna et al., 1994]. However, the gibbon density in edge habitat at Citalahab is substantially higher than average densities reported or assumed for forests at similar elevations. This result and those of other studies [Geissmann & Nijman, 2006; Malone, 2007] suggest that densities near habitat edges may be as high as densities in interior forests. In addition, the high densities of gibbons at Citalahab and Turalak and the low density at Leuweung Sancang relative to sites of similar elevation suggest that extrapolations using altitude as the sole index of habitat quality may result in poor estimates of gibbon populations, especially in human-altered landscapes.

Several researchers and organizations [e.g. Campbell et al., 2008; Supriatna, 2006; Supriatna et al., 1994; but see Asquith & Sinaga, 1995; Nijman, 2006] have suggested that a high conservation priority should be placed on reintroduction of captive Javan gibbons. Identifying appropriate areas for reintroduction can be difficult, however. Gibbons may be able to survive for some time in fairly small habitat fragments, but two recent demographic studies suggest that the ability of adult gibbon pairs to survive in habitats of marginal size or quality does not indicate that the habitats are sufficient to

support breeding pairs or populations [Marshall, 2009; O'Brien et al., 2003]. Our results suggest that wild Javan gibbons may require substantially larger home ranges in hill and montane forests than in lowland forests to guarantee sufficient food availability throughout the year. Therefore, we suggest that in the absence of detailed information about Javan gibbon dietary preferences and fallback strategies, conservative estimates about gibbon ranging needs should guide decisions about acceptable sizes for release habitats, especially those in hill or montane forests, to ensure that reintroduced gibbons have the best possible opportunity to survive and reproduce in the wild without ongoing food supplementation.

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