

Habitat characterization of western hoolock gibbons *Hoolock hoolock* by examining home range microhabitat use

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Received: 29 March 2012 / Accepted: 12 March 2013
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Abstract Conserving a species depends on an understanding of its habitat requirements. Primatologists often characterize the habitat requirements of primates using macroscale population-based approaches relying on correlations between habitat attributes and population abundances between sites with varying levels of disturbance. This approach only works for species spread between several populations. The populations of some primates do not fulfill these criteria, forcing researchers to rely on individual-based (microscale) rather than population-based approaches for habitat characterization. We examined the reliability of using micro-scale habitat characterizations by studying the microhabitat preferences of a group of wild western hoolock gibbons (*Hoolock hoolock*) in order to compare our results to the habitat preferences of western hoolock gibbons identified during a macroscale study of populations across Bangladesh. We used stepwise discriminant analysis to differentiate between the areas of low, medium, and high usage based on microhabitat characteristics (tree species availability, altitude, canopy connection, distance from forest edge, and levels of human disturbance). The gibbons used interior forest habitat with low food tree availability most frequently for sleeping and socializing, and used edge habitat containing high food tree availability for medium periods for feeding. These results indicate that the gibbons prefer interior forest but are frequently forced to visit the forest edge to feed. Therefore,

the optimal habitat would be interior forest away from human disturbance with high sleeping-tree and feeding-tree availability. These habitat preferences are consistent with the habitat attributes of Bangladesh's largest remaining western hoolock gibbon populations, which live in areas containing low agricultural encroachment and high food-tree availability. Microhabitat use studies can be used to characterize the habitat requirements of a species, but should include multiple scales of analysis wherever possible.

Keywords Activity budget · Habitat selection · Primate · Ranging pattern · Bangladesh

Introduction

In tropical forests, pressures from increasing human populations, agricultural expansion, and logging threaten the existence of many primate species through habitat loss, degradation, and fragmentation (Johns and Skorupa 1987; Weisenseel et al. 1993; Cowlshaw 1999; Schwitzer et al. 2011). To counteract these problems, proper forest management is needed (Schwitzer et al. 2011), and, when focusing on forest-dwelling animals, one must first identify the habitat attributes which support them (Doncaster et al. 1996; Wasserman and Chapman 2003). These attributes can be studied at the micro- and macrohabitat level. Following Block and Brennan (1993), we define the macrohabitat level as landscape-scaled features that are correlated with the distribution and abundance of populations. The microhabitat level deals with specific, recognizable features of the environment that act as proximal cues to elicit a settling response from an individual or a group. For many forest-dwelling primates, researchers

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characterize their optimal (macro)habitats by finding correlations between primate population abundance estimates and vegetation variables between forests modified by different levels of disturbance, either natural or anthropogenic (Medley 1993; Worman and Chapman 2006; Hamard et al. 2010). For example, significant positive correlations between population densities of the Tana River managabey (*Cercocebus galeritus*) and forest fragment size and tree density indicate that habitat management should focus on expanding areas of high density tree cover (Wieczkowski 2004). However, such studies require the existence of several discrete populations between habitats which possessed similar vegetation structures and predation pressures before disturbance to control for intrinsic habitat variation between sites (Rovero and Struhsaker 2007). For some species, such as the dryad monkey *Cercopithecus dryas*, Natuna langur *Presbytis natunae*, and Hainan gibbon *Nomascus hainanus*, these requirements do not exist, because the only remaining populations live in single forest pockets (Lammertink et al. 2003; Hart et al. 2008; Zhang et al. 2010). In order to characterize the habitat requirements of species living in limited areas, researchers rely on individual-based (microscale) rather than population-based approaches.

We examined the reliability of using microscale approaches for habitat characterization by studying the microhabitat preferences of western hoolock gibbons *Hoolock hoolock* in Sylhet Division, Bangladesh. The western hoolock gibbon is Endangered according to the IUCN Red List criteria, and is currently on the World's 25 Most Endangered Primates list (Walker et al. 2009; Brockelman et al. 2008); in Bangladesh an estimated 300 hoolock gibbons remain, comprising 82 groups in 37 sites (Walker et al. 2009). For Bangladesh, Muzaffar et al. (2007) characterized the habitat of hoolock gibbons using a macroscale comparison of 22 forests in which gibbon populations live. Using multiple regression analyses to examine the influences of food plant species richness, forest area, and agricultural area on gibbons in these sites, they showed that gibbon numbers were positively related to the number of edible plant species, and negatively to the amount of agricultural land, but not to the area of natural forests or plantations. From this, they concluded that prime western hoolock gibbon habitat is characterized by forests with low levels of agricultural encroachment and high levels of food tree availability and variety. We examined the microhabitat preferences of one group of western hoolock gibbons in order to compare our results with those of Muzaffar et al. (2007). This allowed us to determine whether studying the microhabitat preferences of one group can predict the habitat attributes necessary for the survival of a species as a whole.

Methods

Study area and subjects

We conducted our study in a semi-deciduous forest (65 ha) within Kalachara Forest Beat, located 3.5 km north of Lawachara National Park in northeastern Bangladesh (24°22'N, 91°47'E; the altitudinal range of our study area was ~20–75 m asl). Annual rainfall is ~2000 mm, with the highest rainfall occurring during May (~550 mm) and the lowest during December (~10 mm) (Islam and Feeroz 1992). The forest comprises a teak *Tectona grandis* plantation established in 1964. The teak trees are interspersed with natural and planted trees comprised mainly of jarul *Lagerstroemia speciosa* and chapalish *Artocarpus chaplasha*. The forest is surrounded by tea *Camellia sinensis* estates, rice fields and village grounds, and is separated from its nearest neighboring forest, also a teak plantation, by a 50-m wide gap of rice fields (Fig. 1).

Local people enter the fragment during the day to collect firewood and other forest products, herd cattle, and perform religious ceremonies; teak trees are occasionally felled illegally during the night. Besides western hoolock gibbons, rhesus macaques *Macaca mulatta*, northern pig-tailed macaques *M. leonina*, capped langurs *Trachypithecus pileatus*, Phayre's langurs *T. phayrei* and Bengal slow lorises *Nycticebus bengalensis* are found in the study area.

The group of western hoolock gibbons living in the forest fragment is isolated from other gibbons living in forest to the south. Singing in gibbons often occurs in response to other groups (e.g., Ahsan 1994; Geissmann and Nijman 2006; Hamard et al. 2010), and it is important to note that the study group was in regular auditory contact with other gibbon groups. The shortest distance between the two fragments is some 40–50 m, and we anticipate that from the edge of its home range the study group is, or until recently has been, able to see and hear one or more neighboring groups in the southern fragment. At the time of the study, the study group consisted of four individuals: an adult male and female and their two offspring, a juvenile male (~4–5 years old), and an infant of unidentified sex close to weaning (~2 years old). The group was well habituated because of the daily presence of humans in the forest, allowing individual identification and daily follows.

Behavioral data collection

The group was studied during the monsoon season (May–July 2009), with follows on 47 days from 0645 and 1500 hours. Because of perceived safety concerns posed by illegal loggers, officers of the Bangladesh Forest Department did not allow us to work in the forest beyond this period. We used instantaneous scan sampling (3 min

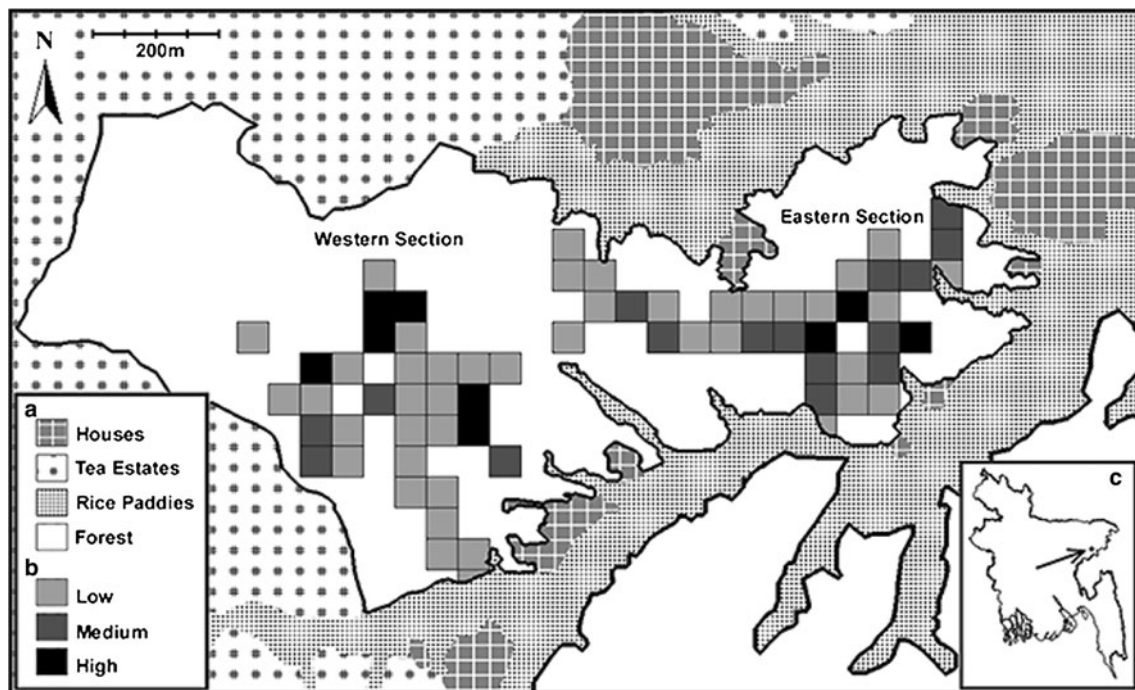


Fig. 1 Forest fragment containing the western and eastern sections of the focal gibbon group's home range, split into 0.25 ha quadrats. **a** The surrounding house sites, tea estates, rice paddy fields, and

forested areas. **b** Quadrats used low (<1 %), medium (1–3 %), and high (>3 %) percentages of the time by the gibbons. **c** The position of the study site in Bangladesh

intervals) to collect behavioral data on each visible group member (Martin and Bateson 1993; Kaplan 2001). During each scan, we recorded the behavior of each gibbon as moving (brachiating or otherwise), resting, feeding (items identified to the genus level), grooming, singing (or vocalizing), or other. We identified the trees the gibbon used to at least the genus level and visually estimated the tree's canopy connection with others. The canopy connection estimates were on a scale from 1 to 4, where 1 = 0–25 % of the tree's canopy is touching others, 2 = 25–50 %, and so on. We divided the forest fragment into 50 m² quadrats and recorded the quadrat location of each gibbon during each scan sample using a global positioning device (Garmin GPSMAP® 60Cx color map navigator). The home range of the group included all 66 quadrats in which we took a scan sample of the gibbons at least once. We measured the distance each quadrat was from the forest edge, rice paddy fields, tea estates, and houses by overlaying the gibbon's home range grid onto a satellite image (taken 4 March 2005; Google Earth™).

Vegetation data collection

We surveyed trees ≥ 10 cm diameter at breast height within and adjacent to the gibbon group's home range using plotless point-quarter sampling (Ganzhorn 2003). We chose the sample locations by randomly marking one GPS

waypoint in 66 quadrats within and 16 quadrats adjacent to the gibbon's home range. As such, the area sampled totaled 20.5 ha, equal to one-third of the entire remaining forest. We took a single vegetation sample at each waypoint, for a total of 82 sample points. When the terrain was too steep, we selected a sampling point as close to each waypoint as the terrain allowed. The quarters of each point were randomly oriented. For each tree sampled, we measured the circumference along with total height using a clinometer and identified the tree to at least genus level. We quantified levels of forest disturbance due to wood harvesting activities by tallying the number of stumps and cut trees.

Data analysis

To determine the intensity at which the gibbons used each quadrat in their home range, we counted the number of scan samples ($n = 7657$ scans) we took in each quadrat and then categorized the quadrats into areas of low (<1 % of all scans per quadrat), medium (1–3 % of all scans), and high (>3 % of all scans) relative habitat use (Fig. 1). As such, 41 quadrats were included in the low habitat use category (with a total of 1024 scans corresponding to ~51 h of observation), 16 quadrats were included in the medium habitat use category (with a total of 2505 scans corresponding to ~125 h of observation) and 9 quadrats were included in the high habitat use category (with a total

Table 1 Forest attributes used in the correlation, PCA, and stepwise discriminant analyses, with biological explanations for their importance

Microhabitat variables	Hypothesized relationship to microhabitat use by gibbons	References
Spatial attributes		
Forest edge distance	Negative: western hoolock gibbons are forest dwelling primates who are strictly arboreal, suggesting they would avoid edge habitat	Gupta (2001), Pachuau and Nijman, unpublished data
Rice paddy field distance	Negative: large populations of western hoolock gibbons are found in areas of low agricultural disturbance, suggesting they would prefer areas away from cultivated land	Muzaffar et al. (2007)
Tea estate distance	Negative: as above	Muzaffar et al. (2007)
House distance	Negative: unhabituated gibbons usually avoid humans, suggesting the gibbons would prefer areas away from high concentrations of humans	Raemaekers et al. (1984), Williamson and Feistner (2003)
Altitude	Positive: the remaining western hoolock gibbon populations in Bangladesh inhabit hilly areas, suggesting they would prefer higher altitudes; gibbons disproportionately use trees on ridges (i.e., areas of high elevations) as sleeping sites; gibbons use valley bottoms (i.e., areas of low elevation) disproportionately for foraging	Islam and Feeroz (1992), Peng-Fei and Xue-Long (2008a, b), Tenaza and Tilson (2005), Nijman (2006), Kim et al. (2011)
Disturbance attributes		
Cut tree count	Negative: western hoolock gibbons are strictly arboreal, suggesting they would avoid areas where trees have been cut down	Gupta (2001), Pachuau and Nijman, unpubl data
Canopy connection	Positive: western hoolock gibbons are strictly arboreal, suggesting they would favor areas of high canopy connectivity	Gupta (2001), Pachuau and Nijman, unpublished data
Resource attributes^a		
Chapalish (<i>Arcocarpus chaplasha</i>)	Positive: important feeding tree	Muzaffar et al. (2007)
Fig (<i>Ficus</i> spp.)	Positive: as above	Muzaffar et al. (2007), Ahsan (1994), Pachuau (2011)
Dawa (<i>Artocarpus lakoocha</i>)	Positive: as above	Muzaffar et al. (2007), Pachuau (2011)
Bolos (<i>Sapium baccatum</i>)	Positive: as above	Islam and Feeroz (1992)
Kakra (<i>Aporosa dioica</i>)	Positive: as above	This study
Jarul (<i>Lagerstroemia speciosa</i>)	Positive: Jarul trees are native to Bangladesh, suggesting they may be structurally important in the forest	Ahmed et al. (1999)
Garjan (<i>Dipterocarpus turbinatus</i>)	Positive: as above	Ahmed et al. (1999)
Sal (<i>Shorea robusta</i>)	Positive: as above	Leuschner and Khaleque (1987)
Ton (<i>Toona ciliata</i>)	Positive: as above	Ahmed et al. (1999)
Ironwood (<i>Xylia dolabriformis</i>)	Negative: ironwood trees are exotic to Bangladesh, suggesting the gibbons would not naturally use them; fruit are very hard	Hossain and Pasha (2001)
Teak (<i>Tectona grandis</i>)	Negative: as above; fibrous and desiccated fruits	Hossain and Pasha (2001)

^a Proportion of the scan samples taken in each quadrat for which the gibbons were located in the tree species. They were arcsine transformed before statistical analysis

of 4128 scans corresponding to ~206 h of observation). There were two “gaps” in the recorded home range (i.e., quadrats that were used by the gibbons but where we did not record them. These could have been included in the low habitat use category, but given that it was not possible to determine exactly which quadrats were used, these were not included. We used chi square goodness-of-fit tests to determine whether the gibbons displayed different activity budgets in the areas of low, medium, and high use compared to their expected overall activity budget.

Table 1 lists the 18 microhabitat attributes we collected for each quadrat within the gibbon home range. The microhabitat attributes are categorized as spatial, disturbance, or resource attributes. We included the 11 most frequently used tree taxa as resource attributes because this list includes all the trees the gibbons used as food sources along with the non-food trees the gibbons used at least as frequently. We computed correlations between selected spatial attributes and carried out a principal component analysis (PCA) on the microhabitat attributes to aid in data

reduction. We used the 8 extracted principal components in a stepwise discriminant analysis to create a model to discriminate between quadrats used by the gibbons in low, medium, and high amounts, based on the microhabitat characteristics of the quadrats. We used SPSS Statistics 17.0 to complete all statistical analyses; we present averages ± 1 standard deviation, and all statistical tests were two-tailed with significance accepted when $P < 0.05$.

Results

The forest had a canopy height of 18 ± 10 m, with emergent ironwood *Xylia dolabriformis* trees of 32 ± 10 m; the basal area of the trees was 0.1 ± 0.1 m² with a significant positive correlation between tree basal area and tree height ($r_s = 0.5$, $N = 304$, $P < 0.01$). There was no significant difference between the tree heights or mean basal areas of trees within the quadrats that received zero, low, medium, and high usage by the gibbons (tree height, $\chi^2 = 4.8$, $df = 3$, $P = 0.186$; basal area $\chi^2 = 2.5$, $df = 3$, $P = 0.479$). The average altitude of the quadrats was 47 ± 4 m asl. The gibbons displayed significantly different activity budgets than expected based on their overall activity budget in the areas of low, medium, and high use (Table 2; low: $\chi^2 = 89.1$, $df = 4$, $P < 0.001$; medium: $\chi^2 = 33.4$, $df = 4$, $P < 0.001$; high: $\chi^2 = 62.5$, $df = 4$, $P < 0.001$). Feeding took place disproportionately in quadrats of low and medium use, and moving took place disproportionately in quadrats of low use. More social activities, such as singing, grooming, and resting (with the members of the group in close proximity) were done preferentially in areas of high use. One reviewer expressed concerns about a lack of independence of behavioral data because of the arguably short 3-min sampling interval used in the study. Pooling data from 2 or 3 scans (thus creating 6- or 9-min intervals) while reducing the sample size leads to very similar results. When strictly applying a 0.05

threshold and using a 9-min sample interval, the activity budgets in areas of medium use no longer differ from a uniform distribution ($\chi^2 = 10.89$, $df = 4$, $P = 0.056$). Furthermore, because of smaller sample sizes, grooming is no longer conducted significantly more or less in any of the low-, medium-, or high-use quadrats (Table 2).

For the spatial attributes, significant positive correlations existed between distance to the forest edge and distance to houses, rice paddy fields, and altitude (edge and houses: $r_s = 0.442$, $N = 100$, $P < 0.01$; edge and rice: $r_s = 0.711$, $N = 100$, $P < 0.01$; edge and altitude: $r_s = 0.655$, $N = 100$, $P < 0.01$). A significant negative correlation existed between distance to the forest edge and distance to tea estates ($r_s = -0.325$, $N = 100$, $P < 0.01$).

Data reduction through principal components analysis reduced the 18 forest attribute variables to 8 principal components with eigenvalues > 1 . The 8 principal components together explained 78.0 % of the variance in the original variables. Table 3 lists the amount of variance in the original variables explained by each principal component, along with the variables that are most highly correlated with each principal component.

Stepwise discriminant analysis extracted two canonical variates (CV₁ and CV₂) that were able to discriminate significantly better than chance between the low-, medium-, and high-use areas based on the microhabitat attributes of those quadrats (CV₁, Wilks' lambda: $\chi^2 = 24.5$, $df = 6$, $P < 0.001$; CV₂, Wilks' lambda: $\chi^2 = 7.1$, $df = 2$, $P < 0.05$). CV₁ accounted for 73.3 % of the variance in the discrimination (canonical correlation 0.576, eigenvalue 0.497), while CV₂ accounted for the remaining 26.7 % of the variance (canonical correlation 0.391, eigenvalue 0.391). The model correctly classified 68.1 % of the quadrats into their original groupings, i.e., 92.3 % of the low-, 38.5 % of the medium-, and 37.5 % of the high-use quadrats. CV₁ was highly negatively correlated with PC₁ (discriminant function coefficient -0.744) and highly positively correlated with PC₆ (discriminant function

Table 2 Observed behavioral frequencies in areas of high, medium, and low use compared to the expected frequencies calculated from percentages of the total activity budget

Behavior ^a	Number of observations of each behavior						Total %			
	Low-use area		Medium-use area		High-use area					
	Observed	Expected	Observed	Expected	Observed	Expected				
Resting	↓	262	332.8	–	816	817.0	↑	1412	1345.4	32.6
Moving	↑	335	253.2	–	623	621.5	↓	936	1023.5	24.8
Feeding	↑	124	76.6	↑	208	188.0	↓	243	309.5	7.5
Singing	↓	5	19.4	↓	9	47.6	↑	130	78.4	1.9
Grooming	↓	2	11.2	–	27	27.6	↑	58	45.4	1.1

↓, Observed significantly less than expected; ↑, observed significantly more than expected; –, no significant difference between observed and expected frequencies

Table 3 Eight extracted principal components

Principal component	% of variance ^a	Highly correlated variables ^b	Component score ^c
PC ₁	21.5	Distance to forest edge	0.901
		Distance to rice field	0.896
		Altitude	0.881
		Distance to houses	0.787
		Distance to tea plantation	-0.663
PC ₂	12.6	Canopy connectivity	-0.687
		Dawa proportion	0.618
		Ton proportion	0.573
		Cut tree count	0.481
PC ₃	9.6	Chapalish proportion	0.521
PC ₄	8.2	Bolos proportion	-0.543
		Sal proportion	0.504
PC ₅	7.5	Jarulul proportion	0.602
		Ironwood proportion	0.550
PC ₆	6.8	Fig proportion	0.527
		Kakra proportion	0.476
PC ₇	6.4	Teak proportion	0.562
PC ₈	5.6	Garjan proportion	0.615

^a Percent of variance in the original variables explained by the principal component

^b The original variables that are most highly correlated with the principal component

^c Component score showing the level of correlation of the variable to the principal component

coefficient 0.724). PC₁ was most highly correlated to the 5 spatial habitat attributes and PC₆ was most highly correlated to fig *Ficus* spp. and kakra *Aporusa dioica* proportions (Table 3), so CV₁ distinguished forest edge from forest interior and areas with low fig and kakra availability from areas with high availability (Fig. 2). CV₂ was highly positively correlated with PC₅ (discriminant function coefficient 0.915), which was positively correlated with ironwood and jarul proportions (Table 3), indicating that CV₂ distinguished areas of low ironwood and jarul availability from areas of high availability (Fig. 2).

CV₁ discriminated the medium-use areas from the low- and high-use areas, while CV₂ discriminated the high- and medium-use areas from the low-use areas (Fig. 2). The low-use group centroid was negative for both CV₁ and CV₂, indicating that areas that received low use by the gibbons were generally in the forest interior, with low fig, kakra, ironwood and jarul availability. The medium-use group centroid was positive for both CV₁ and CV₂, indicating that areas that received medium use were generally near the forest edge, with high fig, kakra, ironwood, and

jarul availability. The high-use group centroid was negative for CV₁ and positive for CV₂, indicating that areas that received high use were generally in the forest interior, with low fig and kakra availability and high ironwood and jarul availability (Fig. 2).

Discussion

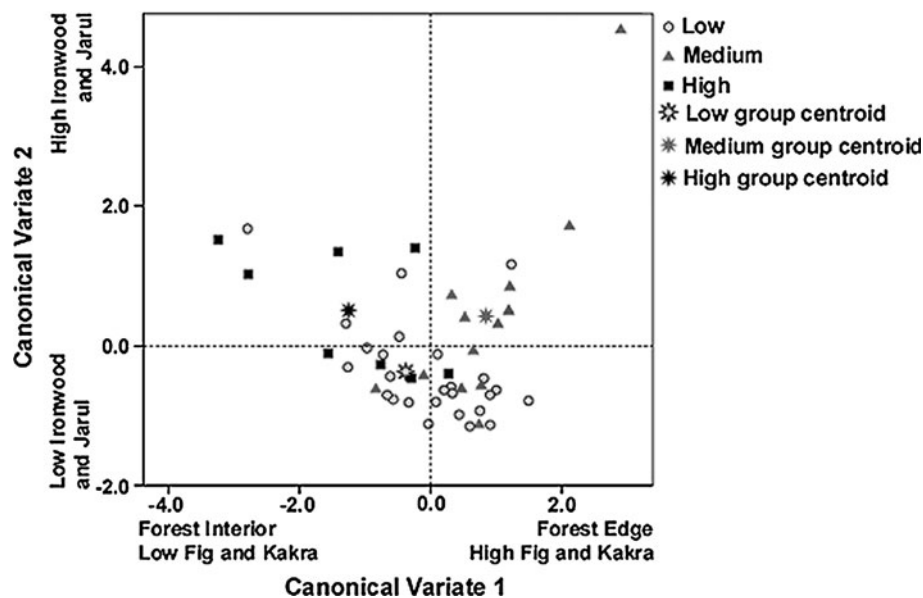
The stepwise discriminant analysis created a model that successfully categorized a quadrat within the gibbon's home range into the correct use category 68.1 % of the time. The model was better at correctly categorizing the low-use quadrats (91.3 % correct) than categorizing the medium- and high-use quadrats (38.5 % and 37.5 % correct, respectively). The model was conservative in its identification of quadrats as suitable for medium and high levels of use by the gibbons. It incorrectly predicted 0 % of the medium-use quadrats as high-use quadrats and incorrectly predicted 3.8 % of the low-use quadrats as medium- and high-use quadrats. The conservatism of the model is favorable. If the model categorized a habitat as suitable for medium or high levels of use by the gibbons there was a high probability the model was correct.

The gibbons used the interior forest most frequently (Fig. 1). These results support our hypothesis that the gibbons would avoid edge habitat near houses and rice paddy fields (Table 1). The largest remaining gibbon populations in Bangladesh live in areas of low agricultural encroachment, indicating that the species as a whole suffers from such disturbance (Muzaffar et al. 2007; cf. Molur et al. 2005; Gupta 2005; Das et al. 2009). The forest interior was low in fig and kakra availability compared to the forest edge (Fig. 2). Figs and kakra fruit are two important food sources for western hoolock gibbons (figs: Islam and Feeroz 1992; Pachuau 2011; Ahsan 1994; Kakra, this study). The low availability of fruit sources in the forest interior may have forced the gibbons to visit the forest edge for medium amounts of time to feed (Table 2). For periods of resting and socialization (such as grooming and singing), when the gibbons did not need access to food, they preferred using areas of high use in interior forest (Table 2).

The gibbons frequently used ironwood trees for resting and socialization, probably because of their height. In line with other gibbon species, western hoolock gibbons use tall trees relative to the surrounding canopy for sleeping (Ahsan 2001; Reichard 1998; Peng-Fei and Xue-Long 2008a, b; Phoonjampa et al. 2010).

The results of the discriminant analysis indicate that the optimal western hoolock gibbon microhabitat is interior forest containing high availabilities of trees used for resting and feeding. These preferences match the habitat

Fig. 2 Stepwise discriminant analysis graph using 47 home-range quadrats that saw low (●, $N = 26$), medium (▲, $N = 13$), and high (■, $N = 8$) usage by the gibbons. Group centroids for the areas of low (⊛), medium (⊛), and high (⊛) use are marked



requirements of western hoolock gibbons identified by Muzaffar et al. (2007), who found that the largest gibbon populations in Bangladesh live in areas of low agricultural encroachment and high food-tree availability, indicating that microhabitat studies can characterize the habitat requirements of primate species. While we were only able to follow a single group for a limited period of time, and some of our findings may be site- or group-specific, and we caution against extrapolation to beyond the dry season, some management recommendations can be made. While at first glance the interior of the forest seems to be of prime importance (with most high habitat use quadrats), it is clear that maintaining connectivity to the edge of the forest is paramount. The daily, or at least regular, movement from the interior to the edge allows gibbons to maximize the (limited) resources available in the forest fragment. From a management perspective, it is also important to note the relatively high usage of quadrats at the forest edge close to the adjacent fragment with other gibbons: this suggest interactions between groups, highlighting the importance of establishing connectivity between these fragments.

Animals use a hierarchical decision-making process during territory and home-range selection. First they choose the appropriate general habitat, then they assess how to use the various habitat patches (microhabitats) within it, and they finally choose an area to inhabit (Orians and Wittenberger 1991). Examining this hierarchy reveals that animals sometimes use different criteria for habitat selection at different scales (Mayor et al. 2009). Contrary to our findings, animals do not necessarily possess the same micro- and macrohabitat preferences. This reveals that, rather than limiting analysis to a single scale, where possible, researchers should make habitat characterizations across multiple scales in order to detect the intricacies of

species' habitat requirements. Using multiscale approaches reduces the likelihood of implementing incomplete conservation schemes that improve/protect several components of species' habitats but ultimately fail due to unintentional omissions of key habitat attributes.

Acknowledgments This research was supported by grants from the American Society of Primatologists and Oxford Brookes University. We thank the Bangladesh Forest Department for granting us permission to work on their land, and Enayetullah Khan, the Chairman of the WildTeam, for granting us permission to work with WildTeam to research the gibbons, and Sarah B. Karr, Shyamol Deb Barma, Gawsia W. Chowdhury, Jayanta Das, and Sam V. Pachuau for information and support. The research complied with Oxford Brookes University's research ethics protocols and the legal requirements of the People's Republic of Bangladesh. We thank the reviewers, including Thomas Gray and Tommaso Savini, for constructive comments and suggestions for improvement.

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