

# Responses of diurnal tree squirrels to selective logging in western Arunachal Pradesh

Aparajita Datta<sup>1,2,\*</sup> and S. P. Goyal<sup>1</sup>

<sup>1</sup>Wildlife Institute of India, Post Bag No. 18, Dehradun 248 001, India

<sup>2</sup>Present address: Nature Conservation Foundation, 3076/5, 4th Cross, Gokulam Park, Mysore 570 002, India

**The responses of diurnal tree squirrels to logging were determined by comparing their abundance in recently logged forest, 20–25-yr-old logged forest, unlogged primary forest, a relatively disturbed secondary forest and a plantation in western Arunachal Pradesh. The squirrels recorded were the Himalayan striped squirrel (*Tamiops maccllellandi*), hoary-bellied squirrel (*Callosciurus pygerythrus*), red-bellied squirrel (*Callosciurus erythraeus*) and the Malayan giant squirrel (*Ratufa bicolor*). The generalist hoary-bellied squirrel was the most common species overall. Its abundance was highest in logged forest and plantations that are characterized by low canopy cover and reduced tree density. It was the only species recorded in the plantations. The other three species were most abundant in unlogged forest. The abundance of the more arboreal Malayan giant squirrel and red-bellied squirrel was correlated to higher tree density and canopy cover, which are characteristic of unlogged primary forests. The reduced canopy cover, tree density and basal area in logged forest, and low tree species diversity and structural complexity in plantations lead to reduction or total absence of squirrels in these habitats. Degree of arboreality, diet and nesting requirements play an important role in squirrel abundance, with larger-sized or specialist species being more vulnerable to habitat modification due to logging.**

**Keywords:** Arboreality, *Callosciurus erythraeus*, *Callosciurus pygerythrus*, *Ratufa bicolor*, *Tamiops maccllellandi*.

## Introduction

ASIAN tropical forests harbour many valuable commercial timber species, and consequently logging is an important industry. 'Selective logging' involves the harvesting of a certain proportion of valuable trees from a forest<sup>1</sup> and is often regarded as being incompatible with wildlife conservation, although survival of some animal populations such as birds, squirrels and primates is possible under low-impact selective logging<sup>2–6</sup>.

Selective logging was being carried out in the lowland forests in northeast India (estimated forest loss of

1418 km<sup>2</sup> from 1989 to 1993)<sup>7</sup> until a ban in 1996. Arunachal Pradesh (26°28'–29°30'N and 91°31'–97°30'E) has great biological significance due to its high floral and faunal diversity, a result of its location at the junction of the Oriental and the Indo-Malayan realms. Although human population density is low (c. 13 km<sup>-2</sup>) and forests cover about 82% of the geographical area<sup>7</sup>, habitat loss/conversion due to logging, *jhum*, and development activities accelerated between 1989 and 1995 with a decline in forest cover of c. 381 km<sup>2</sup>. Logging has resulted in severe loss of forest cover in certain districts.

Tree squirrels constitute an important component of the animal biomass of tropical rainforests<sup>8</sup> and play an important role in seed dispersal and predation of several plants<sup>9–11</sup>. The Eastern Himalaya supports a diverse assemblage of diurnal tree squirrels (c. six species) that have been little studied<sup>12</sup>.

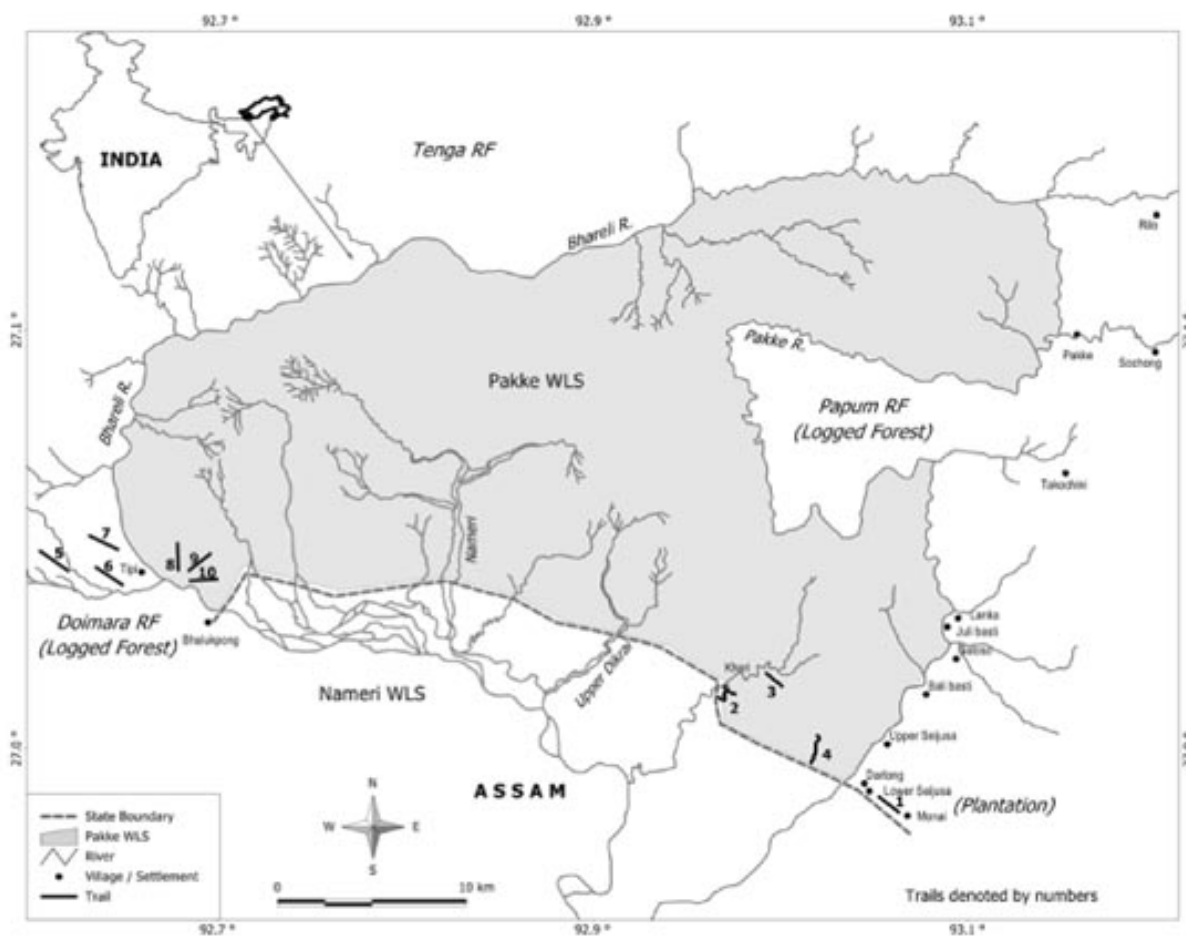
Tree squirrels are affected by the creation of canopy gaps and loss of food and nest trees during logging<sup>3,13</sup>. Selective logging can alter the distribution and abundance of resources; reduce the availability of breeding sites, nests and refuges for arboreal mammals, resulting in changes in time budgets, activity patterns and social organization of many species<sup>3,14</sup>. Many species are adversely affected during and immediately after logging<sup>3,14,15</sup>. However, studies in Amazonian and Madagascar rainforests have indicated that most wildlife could persist in areas with low levels of selective logging<sup>16</sup>.

In this article, we compare the richness and abundance of squirrels in logged forest, unlogged forest, old logged forest, semi-disturbed forest and plantations in Pakke Wildlife Sanctuary (PWS) and reserved forests in Arunachal Pradesh and examine their responses to changes in vegetation structure due to logging.

## Study sites

The study sites were in Pakke Wildlife Sanctuary (PWS), Doimara and Papum Reserve Forests (RFs) in East and West Kameng districts, western Arunachal Pradesh (Figure 1). PWS (862 km<sup>2</sup>, 26°54'–27°16'N and 92°36'–93°09'E) is bounded to the north and west by the Kameng river, to the east by the Pakke river and to the south by the Nameri National Park in Assam. Doimara RF and Papum RF (1280 km<sup>2</sup>) lie to the west and east of PWS

\*For correspondence. (e-mail: aparajita@ncf-india.org)



**Figure 1.** Map showing location of trails in Pakke Wildlife Sanctuary, and Doimara and Papum Reserve Forests, East and West Kameng districts, western Arunachal Pradesh.

respectively. The main vegetation type is tropical semi-evergreen<sup>17</sup>, with a high diversity of epiphytes, lianas, bamboos and canes. About 50 mammal species (excluding bats, small rodents and insectivores) are known from the area; however, three primate species and four squirrel species are the most commonly encountered mammals. The squirrel species are the Malayan giant squirrel (MGS) *Ratufa bicolour*, red-bellied squirrel (RBS) or Pallas squirrel *Callosciurus erythraeus*, hoary-bellied squirrel (HBS) *C. pygerythrus* and the Himalayan striped squirrel (HSS) *Tamiops macclellandi*.

### Survey areas

Five habitats were selected based on logging history. The habitats were recently logged forest and a mixed-species plantation in Doimara RF and Papum RF respectively, and 20–25-yr-old logged forest, semi-disturbed forest and unlogged primary forest in PWS (Figure 1). The logged forest sites were close to Tipi town with three active timber mills. Logging operations were being carried out

along two trails and had ended six months ago on the third trail.

### Methods

#### *Squirrel abundance*

Ten trails were walked in five habitats with a total of 80 replicates covering a total distance of 187.12 km during the study period from December 1995 to April 1996 (Table 1). The routes were measured using a hip-chain (Forestry Suppliers, USA) and marked every 100 m with paint. Calls and sightings of squirrels were recorded on the trails. Relative abundance was assessed by a simple measure of encounter rate, i.e. number detected per km. Calls were used only to confirm species presence in a habitat. Densities were also calculated using an optimum strip width of 30 m on both sides. The identity and number of individuals, perpendicular distance to sighting, tree species, tree height, position of squirrel (height at which sighted), activity, if feeding, the food item (fruit/seed, flower, leaf, bark, insects),

**Table 1.** Details of trails walked

Trail number	Habitat	Location	Trail length	Number of replicates	Total effort
1	Plantation	Papum RF (Monai)	3.45	10	34.50
2	Semi-disturbed secondary forest 1	Sanctuary (Khari)	2.32	7	16.24
3	Semi-disturbed secondary forest 2	Sanctuary (Khari)	2.1	7	14.70
4	20–25-yr-old logged forest	Sanctuary (Seijusa)	2.7	10	27
5	Logged forest 1	Doimara RF (Tipi)	3.0	8	24
6	Logged forest 2	Doimara RF (Tipi)	1.7	8	13.60
7	Logged forest 3	Doimara RF (Tipi)	1.96	8	15.68
8	Unlogged forest 1	Sanctuary (Tipi)	1.7	6	10.20
9	Unlogged forest 2	Sanctuary (Tipi)	2.5	8	20
10	Unlogged forest 3	Sanctuary (Tipi)	1.4	8	11.20

**Table 2.** Structural characteristics of the five habitats in Pakke Wildlife Sanctuary and adjoining reserve forests, Arunachal Pradesh

	Unlogged forest	Logged forest	Semi-disturbed forest	Old logged forest	Plantation
Tree density (ha <sup>-1</sup> )	507 ± 19.3	257 ± 16.5	686 ± 31.5	550 ± 34	284 ± 45
Large tree (≥150 cm) density (ha <sup>-1</sup> )	59	26	22	42	35
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	49	24	28	34	23
Canopy cover (%)	95 ± 0.73	50 ± 2.35	97 ± 0.33	93 ± 1.04	67 ± 2.87
Mean basal area (m <sup>2</sup> ) (per plot)*	1.53 ± 0.13	0.76 ± 0.12	0.87 ± 0.07	1.06 ± 0.08	0.73 ± 0.13
Mean no. of species/plot*	11 ± 0.37	6 ± 0.38	12 ± 0.67	10 ± 0.45	2 ± 0.36
Species diversity, <i>H'</i>	2.26 ± 0.04	1.65 ± 0.07	2.12 ± 0.08	2.09 ± 0.05	0.48 ± 0.15
GBH (cm)	81 ± 2.55	81 ± 3.22	60 ± 1.42	74 ± 2.34	93 ± 4.48
Tree height (m)	11 ± 0.16	11 ± 0.19	10 ± 0.12	12 ± 0.20	11 ± 0.26
Crown width (m)	4.45 ± 0.09	4.36 ± 0.13	3.44 ± 0.07	4.27 ± 0.10	3.17 ± 0.17
Liana density (ha <sup>-1</sup> )	748	292	765	422	35
Percentage of trees with liana	71	59	61	54	12
Weedy climber density (ha <sup>-1</sup> )	25	36	34	28	67
Mean basal area per tree (cm <sup>2</sup> )	976	959	417	626	831
Pioneer species density	83	34	62	160	No data

\*Plot = 0.031 ha.

plant species and substrate type (ground, main trunk, branch, or liana). Diet and foraging height were also recorded during opportunistic sightings. The occurrence of squirrel nests was noted in all habitats.

### *Vegetation structure and composition*

Data on vegetation structure and composition were collected in 198 circular plots of 10-m radius (0.031 ha) along the trails. All trees ≥25 cm GBH (girth at breast height, at 1.3 m) were enumerated. The species, GBH, tree height and crown width (defined as the greatest distance between diametrically opposite extremes of the crown)<sup>3</sup> of all trees were recorded in each plot. The presence of lianas, climbers, cut stumps and damage to trees was noted. Canopy cover was recorded every 50 m along the trails with a canopy densiometer.

### **Data analysis**

For relative abundance measures to be useful, there should be a monotonic relationship between the abundance index and the actual density. To test this, we examined the en-

counter rate estimates (relative abundance measures) with the density estimates using linear regression. Squirrel abundance was also related to structural characteristics to determine factors affecting abundance. The assumptions of the correlations were that squirrel abundance would respond to variation in habitat variables and that the form of the response is approximately linear. Tree and liana density, basal area, canopy cover and other structural variables were calculated for each habitat. Non-parametric statistical tests were used (due to non-normality and heterogeneity of variance) to examine differences in structural characteristics and squirrel abundance across habitats, and to correlate habitat variables with squirrel abundance.

## **Results**

### *Vegetation structure and composition*

Two hundred and thirty-five plants (58 dicot families) were recorded with the maximum representation of Lauraceae (23 species), Euphorbiaceae (19), Meliaceae (12), Sterculiaceae (8) and Myrtaceae (7). A total of 2789 individual trees were measured for structural characteristics.

## SPECIAL SECTION: ARBOREAL SQUIRRELS

**Table 3.** Per cent occurrence of the top ten plant species in old logged and unlogged forests in Pakke Wildlife Sanctuary and recently logged forest in Doimara RF, Arunachal Pradesh

Logged forest	Percentage	Unlogged forest	Percentage	Old logged forest	Percentage
<i>Magnolia hodgsonii</i>	5.3	<i>C. paniculatus</i>	7.4	<i>L. laeta</i>	12.2
<i>Chisocheton paniculatus</i>	4.8	<i>A. genticosa</i>	5.3	<i>Aporosa dioica</i>	9.2
<i>Leea indica</i>	4.6	<i>O. paniculatus</i>	5.3	<i>Pterospermum lancifolium</i>	8.6
<i>Duabanga grandiflora</i>	4.2	<i>M. hodgsonii</i>	5.2	<i>Acronychia pedunculata</i>	7.7
<i>Ostodes paniculatus</i>	3.4	<i>L. indica</i>	4.5	<i>C. roxburghii</i>	7.4
<i>Pterospermum acerifolium</i>	3.4	<i>L. monopetala</i>	4.3	<i>Syzygium syzigioides</i>	6.5
<i>Syzygium formosum</i>	3	<i>P. acerifolium</i>	4	<i>Polyalthia simiarum</i>	4.7
<i>Litsea laeta</i>	2.5	<i>L. laeta</i>	3.6	<i>Olea dentata</i>	3.2
<i>Alphonsea genticosa</i>	2.3	<i>Baccaurea ramiflora</i>	2.8	<i>Sterculia alata</i>	2.9
<i>Litsea monopetala</i>	2.1	<i>Croton roxburghii</i>	2.7	<i>C. paniculatus</i>	2.9
Per cent of total species	36		45		65

The structural characteristics of the five habitats are shown in Table 2. Overall tree density was highest in semi-disturbed and old logged forest. The total basal area  $\text{ha}^{-1}$ , large tree density ( $\geq 150$  cm GBH), mean total basal area per plot, and mean number of species per plot were highest in the unlogged primary forest and lowest in logged forest (Table 2). Values of most parameters were halved in logged forest. Per cent canopy cover and woody liana density were highest in unlogged forest and semi-disturbed forest and low in the plantation and logged forest (Table 2). Only 12% of trees in the plantation had woody lianas. Weedy climbers were common in the plantation and lowest in unlogged forest (Table 2). There was a significant difference in mean GBH, mean tree height and mean crown width between the habitats (Kruskal–Wallis one-way ANOVA,  $P < 0.001$ ), but no difference between logged and unlogged forest.

Species composition was most similar between logged and unlogged forests, with eight species common to both among the ten most abundant species (Table 3). Ten species accounted for 36% and 45% of the total plant species in the logged and unlogged forest respectively, with no single species being dominant. The old logged forest consisted of species associated, with drier areas with ten species accounting for 65% of the species composition.

### Extent of logging damage

The estimated extraction rate was 6.75 trees  $\text{ha}^{-1}$  based on the number of cut stumps in logged forest. Assuming that felling girth class starts from 150 cm and that no felling had occurred before, the stand removal (trees  $\geq 150$  cm) was 21%. However, tree densities prior to logging were not known and logging appeared to have occurred in the previous years at two of the recently logged trails. Therefore, the extraction rate and the per cent stand removal may have been underestimated.

There was no difference in the distribution of girth classes between logged and unlogged forest (Kolmo-

gorov–Smirnov two-sample test, ns). The number of dead and fallen trees per ha was higher in unlogged forest ( $8.5 \text{ ha}^{-1}$ ) than logged forest ( $3.4 \text{ ha}^{-1}$ ), while more trees were found with tops broken and damaged in logged forest ( $11 \text{ ha}^{-1}$ ) than in unlogged forest ( $6.8 \text{ ha}^{-1}$ ). Thus, the total loss (cut stumps, dead/fallen trees, tops broken/damaged) was around  $21 \text{ ha}^{-1}$  in logged forest, against  $15 \text{ ha}^{-1}$  in unlogged forest (dead/fallen trees, tops broken/damaged).

### Squirrel abundance

The total number of squirrel detections was 343 (212 on transects and 131 opportunistic detections), with a total of 255 squirrels counted. The two *Callosciurus* species were sighted most frequently: HBS,  $n = 140$  detections; RBS,  $n = 115$  detections, followed by HSS,  $n = 49$  detections and MGS,  $n = 39$  detections.

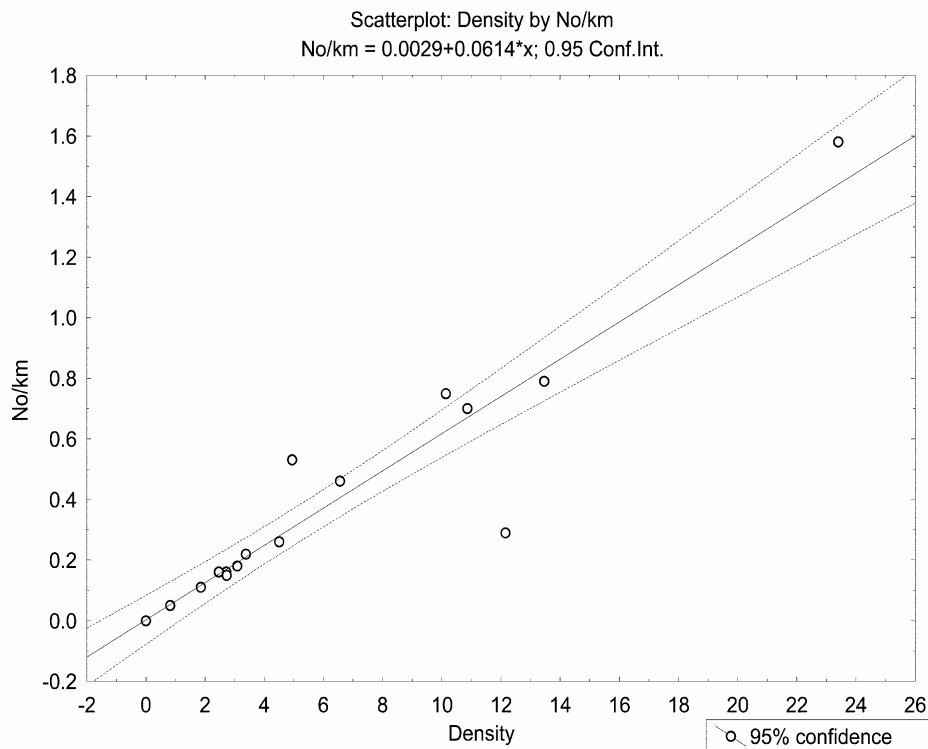
The overall squirrel encounter rate (mean  $\pm$  SE; all habitats combined) was  $1.53/\text{km} \pm 0.19$ . The most abundant species overall was HBS ( $0.63/\text{km} \pm 0.13$ ), followed by RBS ( $0.49/\text{km} \pm 0.09$ ), HSS ( $0.28/\text{km} \pm 0.06$ ) and MGS ( $0.13/\text{km} \pm 0.03$ ).

Across the five habitats, HBS was the most abundant species in logged forest and plantation. The RBS was the most abundant species in old logged, semi-disturbed forest and unlogged forest. MGS was the most abundant in unlogged forest, very low in logged forest and absent in the plantation (Table 4).

The overall squirrel encounter rates differed significantly across habitats (Kruskal–Wallis one-way ANOVA,  $P < 0.01$ ). Overall squirrel abundance was highest in logged forest, primarily due to the large numbers of HBS sighted here. The lowest abundance of this species was in unlogged forest and it was the only squirrel species recorded in the plantation (Table 4). Unlogged primary forests had the highest abundance with regard to the other three species. The abundance of MGS, RBS and HSS was significantly lower in logged forest (Mann–Whitney  $U$ -

**Table 4.** Encounter rates (ER, number/km walk, mean  $\pm$  SE) and density (per ha, mean  $\pm$  SE) of four squirrel species in five habitats in Pakke Wildlife Sanctuary (unlogged, semi-disturbed and old logged forests) and adjoining reserve forests (logged forest and plantation), Arunachal Pradesh

Squirrel species	Unlogged forest		Logged forest		Semi-disturbed forest		Old logged forest		Plantation	
	ER	Density	ER	Density	ER	Density	ER	Density	ER	Density
Malayan giant squirrel	0.26 $\pm$ 0.09	0.45 $\pm$ 1.52	0.05 $\pm$ 0.03	0.08 $\pm$ 0.46	0.16 $\pm$ 0.07	0.27 $\pm$ 1.26	0.15 $\pm$ 0.06	0.25 $\pm$ 1.01	0	0
Red-bellied squirrel	0.79 $\pm$ 0.19	1.35 $\pm$ 3.19	0.46 $\pm$ 0.18	0.66 $\pm$ 2.56	0.53 $\pm$ 0.19	1.21 $\pm$ 4.36	0.29 $\pm$ 0.12	0.49 $\pm$ 2.02	0	0
Hoary-bellied squirrel	0.16 $\pm$ 0.06	0.27 $\pm$ 0.99	1.58 $\pm$ 0.35	2.34 $\pm$ 4.76	0	0	0.11 $\pm$ 0.06	0.18 $\pm$ 0.94	0.75 $\pm$ 0.26	1.01 $\pm$ 3.5
Himalayan striped squirrel	0.70 $\pm$ 0.19	1.09 $\pm$ 3.11	0.22 $\pm$ 0.09	0.34 $\pm$ 1.39	0	0	0.18 $\pm$ 0.08	0.31 $\pm$ 1.38	0	0
All species of squirrels	1.92 $\pm$ 0.33	3.15 $\pm$ 5.43	2.31 $\pm$ 0.47	3.42 $\pm$ 8.29	0.69 $\pm$ 0.21	1.49 $\pm$ 4.33	0.74 $\pm$ 0.19	1.23 $\pm$ 3.19	0.75 $\pm$ 0.26	1.01 $\pm$ 3.5



**Figure 2.** Scatterplot showing a significant positive relationship between squirrel encounter rates (abundance index) and squirrel density estimates (regression equation: encounter rate = 0.0029 + 0.0614  $\times$  density;  $F = 157.17$ ,  $P < 0.001$ ,  $r^2 = 0.8915$ ).

test,  $P < 0.05$ ) compared to unlogged forest. All four squirrel species were recorded in old logged forest, although with fewer detections than in unlogged primary forest.

Encounter rates and density estimates were positively correlated ( $r = 0.95$ ,  $P < 0.05$ ,  $n = 20$ ). We carried out a linear regression, which indicated a close positive relationship between encounter rate and density estimates (encounter rate = 0.0029 + 0.0614  $\times$  density;  $F = 157.17$ ,  $P < 0.001$ ,  $r^2 = 0.8915$ ; Figure 2).

Overall squirrel density ranged from 1 ha<sup>-1</sup> in plantation (only HBS) to 3.4 ha<sup>-1</sup> in logged forest (mainly HBS). MGS density ranged from 0.082 ha<sup>-1</sup> in logged forest to 0.45 ha<sup>-1</sup> in unlogged forest (Table 4). The mean sighting distance was lower in unlogged primary forest (6.3 m  $\pm$  0.91) compared to that in logged forest (8.8 m  $\pm$  0.89), but despite the lower visibility, densities of MGS, RBS and HSS were still higher in unlogged forests (Table 4). The plantation, despite being more open with the highest mean

sighting distance ( $9.5 \text{ m} \pm 1.5$ ), was the most depauperate in species richness and abundance. Squirrel nest encounter rates (mainly MGS) were highest in old logged forest ( $3.7 \text{ nests km}^{-1}$ ) and similar in semi-disturbed and unlogged forest ( $2.5 \text{ nests km}^{-1}$ ) and in logged forest ( $2.1 \text{ nests km}^{-1}$ ). No nests were seen in the plantation.

HBS abundance was negatively correlated ( $P < 0.01$ ) with canopy cover ( $r_s = -0.95$ ) and tree density ( $r_s = -0.96$ ). MGS abundance was positively correlated ( $P < 0.05$ ) with tree density ( $r_s = 0.80$ ), basal area ( $r_s = 0.73$ ) and canopy cover ( $r_s = 0.79$ ). RBS abundance was positively correlated ( $P < 0.05$ ) with high tree species diversity ( $r_s = 0.73$ ) and basal area ( $r_s = 0.76$ ).

### Squirrel habitat use

All squirrel species were sighted primarily on trees with heights greater than 11 m (Figure 3). The larger-sized MGS and RBS foraged at significantly greater heights than did the two smaller species (Mann–Whitney  $U$ -test,  $P < 0.01$ ). The HBS (66%,  $n = 108$ ) and HSS (53%,  $n = 23$ ) mostly foraged below 10 m, while RBS (64%,  $n = 89$ ) and MGS (73%,  $n = 26$ ) foraged mainly in the mid- and upper canopy (Figure 3).

The four squirrels also differed in the use of substrate types (Figure 3), with greater use of branches and lianas

by the two larger-sized species (MGS: 94%,  $n = 35$  and RBS: 85%,  $n = 86$ ), while the two smaller-sized species mainly used the main trunk (HBS: 42%,  $n = 108$ ; HSS: 55%,  $n = 42$ ). HBS was the only squirrel species sighted on the ground (5% of sightings).

There was a significant difference in the frequency of food types taken by the four squirrels ( $\chi^2 = 13$ ,  $df = 3$ ,  $P < 0.01$ ,  $n = 68$  feeding observations). The two smaller species, HBS and HSS, were more frequently sighted feeding on bark, while the two larger species, MGS and RBS, were sighted feeding more on seeds/fruits.

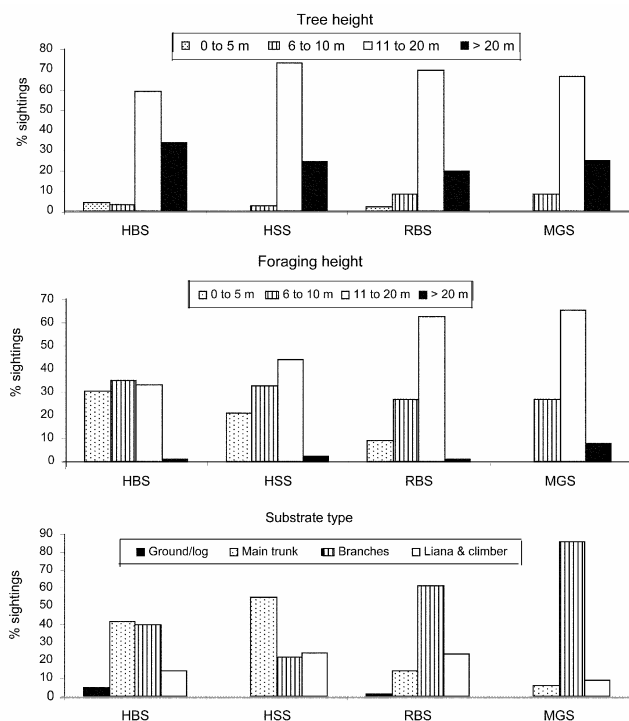
### Differences in habitat use in logged and unlogged forests

Chi-square tests were carried out to determine if there were any differences in habitat use of squirrels between logged and unlogged forests. Small sample size did not allow for comparison of each species separately. There was a significant difference in the frequency use of substrate types for all squirrels between logged and unlogged forests ( $\chi^2 = 9.92$ ,  $df = 3$ ,  $P < 0.05$ ). There was greater use of the ground and the main trunk in logged forests (39%) compared to unlogged forests (26%), while the frequency of observations on lianas/climbers was higher in unlogged forest (27%) than in logged forest (8%). There was also a significant difference in the frequency of observations in different tree height classes and in foraging heights between logged and unlogged forests ( $\chi^2 = 17.56$ ,  $df = 4$ ,  $P < 0.01$  for tree height,  $\chi^2 = 18.86$ ,  $df = 4$ ,  $P < 0.01$  for foraging height).

### Discussion

Forest structure plays an important role in the habitat selection of arboreal mammals<sup>13,18</sup> although this can be strongly affected by human disturbance. The estimated extraction rate in the forests of western Arunachal Pradesh seems moderate compared to extraction levels of  $18\text{--}25 \text{ ha}^{-1}$  in Malaysia<sup>15,19</sup>, while Neotropical and African forests yield only  $3\text{--}5 \text{ ha}^{-1}$  and  $1.1 \text{ ha}^{-1}$  respectively. However, despite relatively lower extraction rates, basal area  $\text{ha}^{-1}$  and canopy cover in logged forest was half that of unlogged forest. Other studies have also found that basal areas<sup>15,19</sup> and canopy cover<sup>20,21</sup> of regenerating forest were much lower in logged forest than unlogged forest.

The lack of a significant difference in tree girth distribution between logged and unlogged forest is indicative of the low selectivity in felling; small trees are cut, not restricting removal to large trees. Almost all studies have noted that although extraction was for only 3–7% of the stand, actual damage exceeded extraction rates and resulted in random destruction of all size classes<sup>19,20,22–24</sup>.



**Figure 3.** Comparison of tree height, foraging height and substrate type category used by the four squirrel species in Pakke Wildlife Sanctuary and adjoining reserve forests in western Arunachal Pradesh. HBS, Hoary-bellied squirrel; HSS, Himalayan striped squirrel; RBS, Red-bellied squirrel and MGS, Malayan giant squirrel.

Construction of main access and side roads caused more damage with an estimated 13 ha affected in logged forest. Clearings were made for the loggers' camps and gaps created by felled trees widened to pull out logs for loading into trucks. Most case studies of logging impacts highlight such high incidental damage and wastage<sup>19,20,25,26</sup>.

### Responses of squirrels to logging

The estimated squirrel encounter rates and densities in these forests are higher than previous estimates from tropical forests<sup>27–29</sup>. Overall squirrel abundance was highest in logged forest, but this was due to the preponderance of a generalist common species, the HBS. The other three species were most abundant in unlogged forest.

Factors such as higher canopy cover, tree density and low human disturbance appeared to affect the abundance of MGS and RBS. Nesting requirements, degree of arboreality and diet seem to play a major role in determining species abundance. Structural characteristics of nest trees indicated that large trees were preferentially used, though most nest species were also used as timber (Datta, unpubl. data). The Indian giant squirrel (*R. indica*) also showed a preference for tall and large girth trees<sup>13</sup>. Absence of suitable nest trees in early *jhum* fallows in Mizoram has been cited as a probable reason for the absence of MGS there<sup>30</sup>. Sixty tree species were being felled in Arunachal Pradesh because of the rarity of the more valuable species and improved ability to process low-grade species. The loss of canopy cover, lianas, reduced tree density and basal area clearly led to a reduced abundance of specialist species in logged and old logged forests.

Squirrels differed in the use of substrate types between logged and unlogged forests, foraged at lower heights and used shorter trees in logged forest. This was possibly because of the destruction of travel routes and loss of emergents resulting in greater use of the ground. In logged areas, squirrels spend more time feeding on bark and sap and resting to conserve energy due to the shortage of fruits<sup>1</sup>. Logging, in addition to causing disturbance, results in habitat loss for squirrels, which ultimately suppresses breeding<sup>31</sup>.

Previous work on squirrels has indicated ecological divergence in habitat use and feeding strategies based on body size, although overlap may also be extensive<sup>28,29,32,33</sup>. In this study, we found that the two larger species generally used higher strata, and lianas and branches, while the two smaller species foraged more at lower levels and used the main trunk or ground. The smaller species were observed to feed more on bark and leaves, while the two larger species were observed to feed mainly on fruits and seeds. Most sightings of HBS and HSS were of them feeding on the bark of *Kydia calycina*, *Pterospermum acerifolium*

and *Amoora wallichii*. Giant squirrels are primarily seed predators and were observed feeding on figs, *Castanopsis* spp., *Canarium* sp. and Meliaceae species. *Callosciurus* species are known to feed more opportunistically on plant material and arthropods<sup>28,32,34</sup>. However, the HSS, despite being the smallest, was the most common in unlogged primary forest and used tall trees, though it foraged at low heights. Unlike the larger, more common, HBS, which is abundant in logged forest and plantation, this small sciurid appears to be a habitat specialist.

The responses of squirrels to logging appear to be species-specific; the generalist HBS thrives well in plantations and logged forests, while the reduced canopy cover, tree density and basal area in logged forest and the low tree species diversity and structural complexity in plantations lead to either reduced numbers or total absence of the other three species. Diet, degree of arboreality and nesting requirements are thus key factors that determine the ability of squirrels to survive in logged forests.

### Postscript

Logging was stopped in 1996 following a Supreme Court order<sup>35</sup>, which gave a much-needed respite to the forests. The Court directed that logging could re-start after territorial forest divisions drew up comprehensive working plans, that all operations should be undertaken by the Forest Department without the involvement of contractors and that the permit system should be abolished. Felling has re-started in several forest divisions since 2006–07; contractors, however, are still being used.

1. Johns, A. D., Selective logging and wildlife conservation in tropical rain-forest: Problems and recommendations. *Biol. Conserv.*, 1985, **31**, 355–375.
2. Wilson, W. and Johns, A. D., Diversity and abundance of selected animal species in undisturbed forest, selectively logged forest and plantations in East Kalimantan, Indonesia. *Biol. Conserv.*, 1982, **24**, 205–218.
3. Johns, A. D., Ph D thesis, University of Cambridge, UK, 1983.
4. Johns, A. D., Tropical forest primates and logging: Can they co-exist? *Oryx*, 1983, **17**, 114–118.
5. Johns, A. D., The use of primary and selectively logged rainforest by Malaysian hornbills (*Bucerotidae*) and implications for their conservation. *Biol. Conserv.*, 1987, **40**, 179–190.
6. Wong, M., Understorey birds as indicators of regeneration in patch of selectively logged west Malaysian rain forest. In *Conservation of Tropical Forest Birds* (eds Diamond, A. W. and Lovejoy, T. E.), Technical Publication No. 4, International Council for Bird Preservation, Cambridge, 1985, pp. 249–263.
7. State of the Forest Report, India. Forest Survey of India, Ministry of Environment and Forests, Dehradun, 1995.
8. Eisenberg, J. F., The density and biomass of tropical mammals. In *Conservation Biology* (eds Soule, M. E. and Wilcox, B. A.), Sinauer, Sunderland, Massachusetts, 1980, pp. 35–55.
9. Vandermeer, J. H., Stout, J. and Risch, S., Seed dispersal of a common Costa Rican rain forest palm (*Welfia georgii*). *Trop. Ecol.*, 1979, **20**, 17–26.
10. Stapanian, M. A., Seed dispersal by birds and squirrels in the deciduous forests of the United States. In *Frugivores and Seed Dis-*

- persal* (eds Estrada, A. and Fleming, T. H.), Dr W. Junk Publishers, Lancaster, 1986, pp. 225–236.
11. Smythe, N., Seed survival in the palm *Astrocaryum standleyanum*: Evidence for dependence upon its seed dispersers. *Biotropica*, 1989, **21**, 50–56.
12. Corbet, G. B. and Hill, J. E., *The Mammals of the Indo-Malayan Region: A Systematic Review*, Natural History Museum Publications, Oxford University Press, Oxford, 1992.
13. Datta, A. and Goyal, S. P., Comparison of forest structure and use by the Indian giant squirrel (*Ratufa indica*) in two riverine forests of Central India. *Biotropica*, 1996, **28**, 394–399.
14. Johns, A. D., Effects of selective logging on the behavioral ecology of West Malaysian primates. *Ecology*, 1986, **67**, 684–694.
15. Johns, A. D., Effects of 'selective' timber extraction on rain forest structure and composition and some consequences for frugivores and folivores. *Biotropica*, 1988, **20**, 31–37.
16. Johns, A. D., Forest disturbance and Amazonian primates. In *Primate Responses to Environmental Change* (ed. Box, H. O.), Chapman and Hall, London, 1988, pp. 115–135.
17. Champion, H. G. and Seth, S. K., *A Revised Survey of the Forest Types of India*, Manager of Publications, Government of India, New Delhi, 1968.
18. Lemos de Sa, R. M. and Strier, K. B., A preliminary comparison of forest structure and use by two isolated groups of woolly spider monkeys, *Brachyteles arachnoides*. *Biotropica*, 1992, **24**, 455–459.
19. Johns, A. D., Economic development and wildlife conservation in Brazilian Amazonia. *Ambio*, 1988, **17**, 302–306.
20. Thiollay, J.-M., Influence of selective logging on bird species diversity in a Guianan rain forest. *Conserv. Biol.*, 1992, **6**, 47–63.
21. Uhl, C. and Vieira, I. C. G., Ecological impacts of selective logging in the Brazilian Amazon: A case study from the Paragominas region of the State of Pará. *Biotropica*, 1989, **21**, 98–106.
22. Uhl, C., Verissimo, A., Mattos, M. M., Brandino, Z. and Vieira, I. C. G., Social, economic, and ecological consequences of selective logging in an Amazon frontier: The case of Tailândia. *For. Ecol. Manage.*, 1991, **46**, 243–273.
23. Woods, P., Effects of logging, drought, and fire on structure and composition of tropical forests in Sabah, Malaysia. *Biotropica*, 1989, **21**, 290–298.
24. Johns, A. D., Vertebrate responses to selective logging: Implications for the design of logging systems. *Philos. Trans. R. Soc. London*, 1992, **B335**, 437–442.
25. Robertson, J. M. Y. and Soetrisno, B. R., Logging on slopes kills. *Oryx*, 1982, **16**, 229–230.
26. Skorupa, J. P. and Kasenene, J. M., Tropical forest management: Can rates of natural treefalls help guide us? *Oryx*, 1983, **18**, 96–101.
27. Marsh, C. M., Johns, A. D. and Ayres, J. M., Effects of habitat disturbance on rainforest primates. In *Primate Conservation in the Tropical Rainforest* (eds Marsh, C. W. and Mittermeier, R. A.), Alan R. Liss, Inc., New York, 1987, pp. 83–103.
28. Mackinnon, K. S., Stratification and feeding differences among Malayan squirrels. *Malay. Nat. J.*, 1978, **30**, 593–608.
29. Payne, J. B., Competitors. In *Malayan Forest Primates* (ed. Chivers, D. J.), Plenum Press, New York and London, 1980, pp. 261–277.
30. Raman, T. R. S., Impact of shifting cultivation on diurnal squirrels and primates in Mizoram, Northeast India: A preliminary study. *Curr. Sci.*, 1996, **70**, 747–750.
31. Joshua, J. and Johnsingh, A. J. T., Impact of biotic disturbances on the habitat and population of the endangered grizzled giant squirrel *Ratufa macroura* in South India. *Biol. Conserv.*, 1994, **68**, 29–34.
32. Payne, J. B., Abundance of diurnal squirrels at the Kuala Lompat post of the Krau Game Reserve, Pahang, peninsular Malaysia. In *The Abundance of Animals in Malaysian Rainforests* (ed. Marshall, A. G.), University of Hull, 1979, pp. 37–52.
33. Emmons, L. H., Ecology and resource partitioning among nine species of African rain forest squirrels. *Ecol. Monogr.*, 1980, **50**, 31–54.
34. Setoguchi, M., Food habits of red-bellied tree squirrels on a small island in Japan. *J. Mammal.*, 1990, **71**, 570–578.
35. Anon., <http://www.forestcaseindia.org/>, accessed on 27 September 2007.

**ACKNOWLEDGEMENTS.** We thank the Director and Dean, Wildlife Institute of India, Dehradun for their support and the Arunachal Pradesh Forest Department for granting permission, and forest officers D. N. Singh, Pratap Singh and P. Ringu for their help. We thank Japang Pansa and Narayan Mogar for invaluable field assistance. We also thank T. R. Shankar Raman and Charudutt Mishra for comments on earlier drafts and R. Raghunath for preparing the map.