Mammal persistence and abundance in tropical rainforest remnants in the southern Western Ghats, India

Hari Sridhar[1,2,*], T. R. Shankar Raman[1] and Divya Mudappa[1]

[1]Nature Conservation Foundation, 3076/5, IV Cross, Gokulam Park, Mysore 570 002, India
[2]Present address: Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560 012, India

Occurrence and abundance of mammals were compared in five large protected rainforest patches inside the Indira Gandhi Wildlife Sanctuary and in four smaller, unprotected rainforest fragments in a plantation matrix in the Anamalai hills, southern Western Ghats using line transect distance sampling. Among the 28 mammal species found in contiguous protected rainforests, 24 persisted in unprotected fragments. For most species, population densities were similar between the two strata. Density of arboreal mammal species showed varying habitat correlates across the sites sampled; Indian giant squirrel density was negatively correlated to canopy overlap, lion-tailed macaque density negatively and Nilgiri langur positively to rainforest tree density respectively. Persistence of most mammals on private lands in a fragmented landscape may be attributed to proximity to the surrounding large tract of reserved forest areas as well as recent conservation efforts, including reduction of hunting and protection of fragments. Comparison with past estimates suggests that arboreal mammals have persisted and increased in abundance over the last decade, particularly in private fragments, possibly due to multiple factors, including the ability of the species to use matrix habitats, low hunting pressure, lack of predators and higher food availability.

Keywords: Distance sampling, habitat fragmentation, *Macaca silenus*, *Ratufa indica*, *Semnopithecus johnii*.

MUCH of the world's tropical rainforests exists today as small unprotected fragments surrounded by human-dominated land[1]. Determining how much original diversity can be conserved in them has been among the major questions in conservation biology over the last two decades[2,3]. Rainforest fragments are depauperate in diversity due to physical factors like changes in microclimate, reduced area and increased isolation[2,4,5] and biotic factors such as increased nest-predation[6]. Moreover, given that many of these fragments are not protected, human-caused disturbances such as hunting, tree-felling and forest-produce extraction also cause decline in diversity[7].

Mammals play important ecological roles in tropical forests and their removal from fragments has a cascading effect on entire communities[8,9]. It is useful to focus conservation attention on mammals in human-dominated landscapes because of their appeal to people. Two general patterns emerge across studies which have looked at fragmentation effects on mammals. First, species which use the matrix around fragments are less susceptible to extinction[10,11]. Second, hunting acts in combination with other fragmentation effects, to strongly affect mammal persistence and abundance in rainforest fragments[12]. The latter is particularly important in case of fragments on private land because they are usually not protected.

Such factors interact to determine richness, abundance and composition of mammal communities in fragmented landscape. While the overall species richness and density tend to increase with fragment area, abundances of individual species frequently show varying relationships[13,14]. In small fragments, increased density is observed in species that are matrix-tolerant[10,11] and groups such as herbivores[13]. A study has shown increase in densities of tree squirrel species in small fragments, most likely through home-range compaction[15]. Conversely, species prone to hunting may decrease in density in small unprotected fragments[13,16].

In this study, mammal occurrence and abundance in the Western Ghats biodiversity hotspot have been examined[17,18], where historical deforestation and land-use conversion have resulted in most rainforests surviving as fragments in the midst of plantations such as tea, coffee and *Eucalyptus*, and human settlements. These forested hills are home to more than 130 mammal species, including endemics such as lion-tailed macaque (*Macaca silenus*), Nilgiri langur (*Semnopithecus johnii*) and Nilgiri marten (*Martes gwatkinsi*)[19]. Earlier studies have shown that most mammal species, including endemics such as lion-tailed macaque, occur in rainforest fragments[20], but information on population status and trends remains unknown.

The specific objectives of this study were: (1) To compare the occurrence and densities of mammals between contiguous protected rainforests and unprotected rainforest fragments. (2) Determine correlates of arboreal

*For correspondence. (e-mail: hari@ces.iisc.ernet.in)

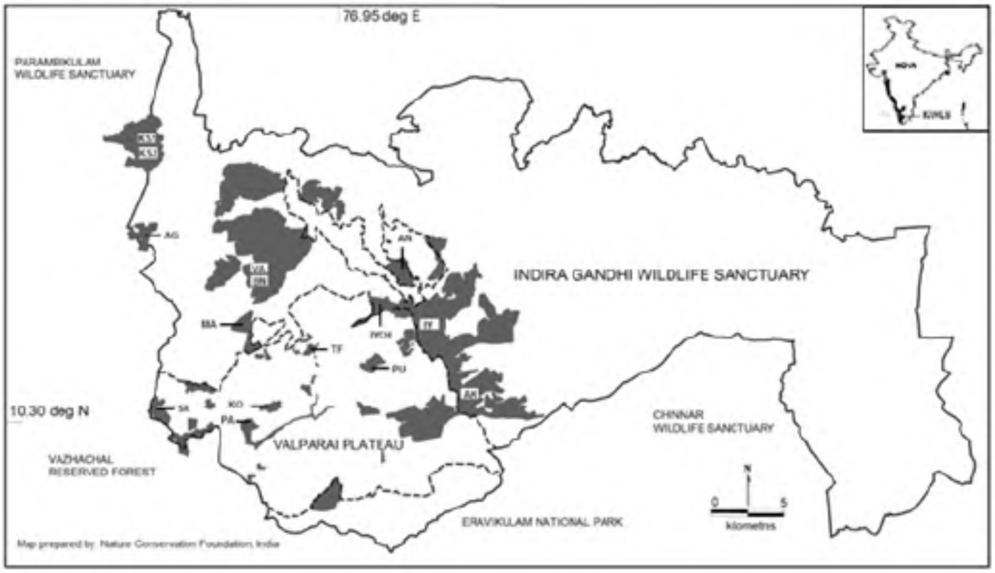

Figure 1. Map of the Indira Gandhi Wildlife Sanctuary (IGWLS) and Valparai plateau (dashed line), Anamalai hills, Western Ghats, India showing locations of transects sampled. Tropical rainforest habitat is indicated in grey. Unshaded areas indicate plantations within Valparai plateau and natural vegetation types other than rainforest within IGWLS. Transect codes are as in Table 1.

mammal densities across the sites sampled. (3) Examine temporal changes in arboreal mammal densities through comparison with estimates from 5 to 11 years earlier[20–22]. Such information is crucial for long-term monitoring of population trends in the face of continuous human pressures such as illegal felling, fuel-wood extraction and poaching on the one hand, and recent efforts to protect and restore these patches on the other[23].

Study area

Tropical rainforests of Indira Gandhi Wildlife Sanctuary (IGWLS; 987 sq. km; 10°12′–10°35′N and 76°49′–77°24′E) and adjoining Valparai plateau in the Anamalai hills, southern Western Ghats formed the study area (Figure 1). The Valparai plateau is a 220 sq. km enclave primarily covered by plantations of tea, coffee and *Eucalyptus*, roads and human settlements, abutting the IGWLS. Valparai town in the centre of the plateau and scattered settlements have a human population of around 100,000. Mid-elevation wet evergreen forests of *Cullenia exarillata–Mesua ferrea–Palaquium ellipticum* type[24] in which this study was carried out, are restricted to a few large patches in the western portion of the IGWLS and numerous fragments on private land of the Valparai plateau. Plantations were established in this region mostly between 1896 and the 1930s, and most fragments were created several decades to a century ago, although changes in size, degradation and surrounding habitats have continued till today. So far, around 40 privately-owned rainforest fragments have been identified on the Valparai plateau[23], ranging in area from 0.1 to 100 ha[23]. These fragments apart from serving as refuges for resident populations of mammals, are also used by many wide-ranging species such as the Asian elephant (*Elephas maximus*) and leopard (*Panthera pardus*) when they move through the Valparai plateau between surrounding forests. This forest–plantation landscape is surrounded by other important protected areas and reserve forests that form a regionally and globally significant conservation area. The area receives about 3500 mm of rain annually over two monsoon seasons.

Methods

Selection of study sites

Five rainforest patches were chosen within IGWLS and four privately-owned rainforest fragments in the Valparai plateau (Appendix 1). The rationale behind choosing these sites was to facilitate comparisons with earlier work[20–22] and because these sites have been identified for long-term monitoring and restoration. Three IGWLS sites which abutted the Valparai plateau were partially bordered by plantations. Apart from this, natural vegetation types (moist deciduous forests, grasslands) formed a matrix around all the IGWLS sites. All private fragments were surrounded by plantations (tea, coffee and *Eucalyptus*). The matrix elements differed in use by study species, with coffee and deciduous forest being used more than other elements. The vegetation type in all the study sites consisted of rainforests of *C. exarillata–M. ferrea–P. ellipticum* type[24]. The private fragments also included exotic trees

Table 1. Sampling effort and density of Indian giant squirrel and Nilgiri langur in the study sites in the rainforests of Anamalai hills, Western Ghats, India

Site	Effort (km)	Detections (*n*)	Mean cluster size	Density (per sq. km)				CV (%)	Population size		
				Clusters	Individuals	95% CI			Mean	95% CI	
Indian giant squirrel											
Private fragments											
KO	9.17	12	1.4	28.4	41.3	12.7	69.9	35.3	23	7	39
PA	6.00	7	1.1	27.4	31.3	6.6	56.1	40.3	21	4	37
PU	12.25	28	1.1	49.7	57.1	30.9	83.2	23.4	53	28	77
TF	5.75	12	1.2	49.0	60.3	23.2	97.4	31.4	20	8	32
Indira Gandhi Wildlife Sanctuary (IGWLS)											
AG	10.85	4	1.2	8.7	10.8	0.0	21.8	51.8	22	0	44
AN	10.40	9	1.3	20.3	27.1	8.6	45.6	34.8	50	16	84
IYAK	28.60	43	1.2	53.4	65.6	17.2	114.1	37.6	1706	447	2967
KS	28.53	17	1.2	14.0	16.3	4.7	28.0	36.4	106	31	182
VBMS	39.15	45	1.3	27.6	35.5	12.2	58.8	33.5	710	244	1176
Nilgiri langur											
Private fragments											
KO	9.17	2	4.5	2.9	13.3	0.0	34.3	81.0	7	0	19
PA	6.00	13	3.5	29.3	101.4	27.1	175.7	37.4	68	18	117
PU	12.25	1	1.0	1.1	1.1	0.2	5.7	100.1	1	0	5
TF	5.75	11	4.2	25.9	108.7	27.5	189.8	38.1	35	9	62
IGWLS											
AG	10.85	20	4.2	24.9	105.9	47.3	164.6	28.3	212	95	329
AN	10.40	15	4.6	19.5	89.7	38.3	141.1	29.2	166	71	261
IYAK	28.60	39	5.2	18.5	95.3	38.5	152.1	30.4	2478	1001	3955
KS	28.53	28	4.6	13.3	60.5	25.2	95.9	29.8	393	164	623
VBMS	39.15	48	4.7	16.4	76.7	27.7	125.8	32.6	1534	554	2516

n, Number of detections; CI, Confidence interval; CV, Coefficient of variation.

such as *Maesopsis eminii*, *Spathodea campanulata* and *Eucalyptus* sp. in the canopy. Fifteen line transects, ranging in length from 1 to 3 km were laid across the nine sites, with the three largest sites having 2–4 transects each (Table 1). The total distance covered by all transects was 32.02 km.

Field sampling

Each transect was walked five times between September 2005 and April 2006 following standard distance sampling protocol[25]. Two observers walked each transect at 0.75–1 km/h. For each detection, we recorded species, group size and perpendicular distance (measured using a rangefinder) from the transect. For animals which occurred in groups, perpendicular distances were measured to group centres. Apart from detections on transects, attempts were made to obtain group sizes of mammal species whenever incidentally detected. All transects were walked between 0630 and 1000 h. Data from temporal replicates of each transect were pooled and treated as a single sample. Indirect evidence (scat, tracks) on transects and incidental sightings (direct and indirect) of mammals were also recorded.

Habitat structure

Tree (≥30 cm girth at breast height; gbh) densities and basal area were estimated using the point-centred quarter method (PCQ)[26]. Along each transect, 25–28 PCQ plots were laid at regular intervals, at least 20 m from the transect line or any edge. From the centre of each PCQ plot, the distance to the middle of the bole of the nearest tree in each of the four quarters and their gbh (1.3 m) were measured using a measuring tape. At the centre of each PCQ plot, canopy height was measured using a laser rangefinder, and canopy overlap was also measured (Appendix 1)[27].

Analysis

Habitat structure

Tree density and basal area were calculated using KREBSWIN software[26]. Percentage of tree density contributed by exotic trees and average values for canopy height and canopy overlap index across replicate samples were calculated for each transect (Appendix 1).

Density estimation

The computer program DISTANCE 5.0 was used to estimate densities of all species (except lion-tailed macaque)[28]. Data were first visually inspected to remove outliers and detect heaping and evasive movement. Fit of different models was judged using Akaike's Information Criterion (AIC) values, visual inspection of fit, and chi-square goodness-of-fit tests to select the most suitable model to calculate cluster density (C). Average cluster size (F), based on all recorded cluster sizes for that species on and away from transects, was multiplied by cluster density to get individual density (D) of each species. Standard error of individual density (se$D$) was calculated using standard error of cluster density (se$C$) and standard error of average cluster size (se$F$) using Goodman's formula[29]: $(\text{se}D)^2 = C^2(\text{se}F)^2 + F^2(\text{se}C)^2 - (\text{se}C)^2(\text{se}F)^2$.

Analysis protocols varied between different species. For all species, other than Indian giant squirrel and Nilgiri langur, we calculated single detection functions from data across all 15 transects. This was then used to estimate and compare density of species for the two main strata – the private fragments (four sites) and the IGWLS (five sites) respectively. For Indian giant squirrel, the 15 transects were categorized into three groups based on detectability. KO and PU were distinct from all the other sites in habitat structure and therefore a detection function was calculated separately for pooled data from these sites (Appendix 1)[30]. IYAK transects (IY, AK, IYCH) were also treated separately as inspection of data revealed evidence of attraction of squirrels to the transects. Data from the remaining ten transects, were pooled for calculation of detection function. For the Nilgiri langur, a single detection function was used across all 15 transects. Using these detection functions, site-wise densities were calculated for the Indian giant squirrel and Nilgiri langur.

In the case of lion-tailed macaques, for which line transect sampling is considered inappropriate[22], complete counts were obtained of all individuals in four private fragments and one sanctuary site (AN). For other sanctuary sites, average group sizes were calculated from troops which were completely enumerated. This was multiplied by the number of troops in each site reported from an earlier study[22], to get the number of individuals of lion-tailed macaques per site. Density of individuals in each site was calculated by dividing the number of individuals by the site area.

Z tests were used to compare mammal densities between IGWLS sites and private fragments. Relationships of Indian giant squirrel, Nilgiri langur and lion-tailed macaque density to fragment area and habitat structure variables (density of rainforest trees, basal area, canopy overlap index and canopy height) were examined using stepwise multiple regressions implemented through the program SPSS[31].

Comparison with past data

To compare with past estimates, density and encounter rates were also calculated using methods used by earlier studies. To compare with the 1994 survey of arboreal mammals[20,21], Indian giant squirrel cluster densities were estimated for each transect using King's formula ($D = n/(l \times 2d)$; where n is the number of clusters seen; l the length of the transect (in km) and d the mean sighting distance (in km)). Individual densities were obtained by multiplying cluster density with average cluster size. As the earlier study did not report any measures of variance, we only compare average densities. The range in Nilgiri langur encounter rates (groups per km) across sites sampled reported by Umapathy[21] was compared with the same measure calculated from the present study. Changes in population sizes (total counts) of lion-tailed macaques in private fragments since 2001, were examined through comparison with data from an earlier study[22].

Results

Species occurrence in sanctuary sites and private fragments

Nineteen mammal species were recorded (includes visual and aural detections, and animal tracks such as pugmarks, scat, dung and pellet groups) during transect sampling in the sanctuary sites (effort = 117.5 km), and 14 species in private fragments (effort = 33.2 km; Appendix 2). When species incidentally encountered during this study or reported from earlier work[32] were included, species richness for sanctuary and private fragments overall was 28 and 24 respectively (Appendix 1). Four species (chital, Eurasian otter, Nilgiri marten and tiger) reported from sanctuary rainforest sites have never been recorded from private fragments (barring sightings of the marten and otter from a fragment less than 0.25 km from the sanctuary edge). Among these, chital typically occurs at lower elevations and in open forest habitats, including areas adjoining rainforests.

Comparison of mammal densities between sanctuary sites and private fragments

Nilgiri langur was the most abundant species in IGWLS sites (82.5 ± 47.1 CI individuals/sq. km across five IGWLS sites) and private fragments (55.2 ± 60.0 CI across four fragments). Indian giant squirrel and lion-tailed macaque were also abundant in both sanctuary sites and fragments (Indian giant squirrel: 36.9 ± 33.4 CI in IGWLS, 47.2 ± 28.1 CI in private fragments; lion-tailed macaque: 12.3 ± 6.2 CI in IGWLS, 59.1 ± 40.1 CI in private fragments). Densities of eight out of ten species were not significantly different between sanctuary and private fragments (Figure 2; Z test, $P > 0.05$). The lion-tailed macaque had significantly higher densities in private fragments compared to the sanctuary (Z test, $P < 0.05$; Figure 2). Bonnet macaques occurred only in sanctuary sites (Figure 2).

Density variation across sites and habitat correlates

Density of Indian giant squirrels ranged between 10.8 individuals/sq. km in a 200 ha IGWLS site (AG) and 65.6 individuals/sq. km in a 2600 ha IGWLS site (IYAK; Table 1). The latter density could have been inflated due to animals being attracted to transect lines as discussed earlier. The next three highest densities were found in private fragments. Indian giant squirrel density was not significantly related to any habitat variable or fragment area across all sites. When IYAK was excluded, Indian giant squirrel density was negatively related to canopy overlap index ($\beta = -0.798$; Adjusted $R^2 = 0.577$; $F = 10.53$; $P < 0.05$; df = 1, 6). The density of Nilgiri langur ranged from 1.1 individuals/sq. km in a 92 ha private fragment (PU) to 108.7 individuals/sq. km in a 32 ha private fragment (TF; Table 1). Nilgiri langur densities were relatively similar among all sanctuary sites (range 60.5–105.9 individuals/sq. km) compared to private fragments, among which two (KO and PU) had very low and the other two (PA and TF) very high densities. Nilgiri langur density was significantly related to density of rainforest trees ($\beta = 0.864$; Adjusted $R^2 = 0.71$; $F = 20.59$; $P < 0.01$; df = 1, 7).

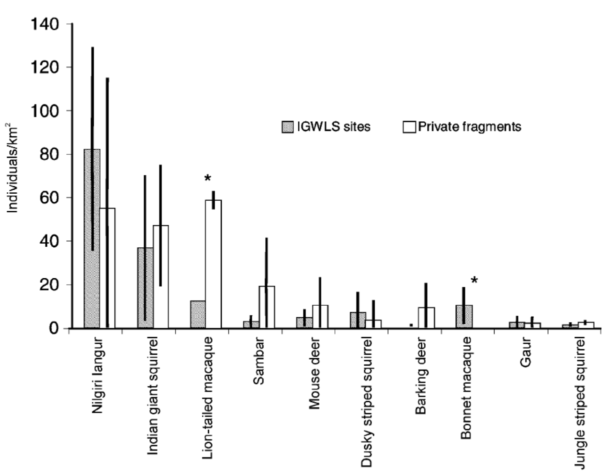

Figure 2. Comparison of densities (±95% CI) of mammal species in rainforest patches within IGWLS and private fragments on the Valparai plateau. Both visual and aural detections were used in density estimation of dusky striped squirrel ($N = 14$) and jungle striped squirrel ($N = 29$). *$P < 0.05$.

Lion-tailed macaque density was highest in the 92 ha private fragment (116.3 individuals/sq. km) and lowest in the 2600 ha IGWLS site (4.0 individuals/sq. km; Table 2). Lion-tailed macaques do not occur in Karian shola (KS), an IGWLS site, for reasons unknown. The four highest densities of lion-tailed macaques across all sites sampled were in private fragments. The density of lion-tailed macaque troops ranged from 3.1 troops/sq. km in a private fragment to 0.3 troops/sq. km in an IGWLS site. The largest IGWLS site (VBMS) had the highest number of troops (12) and total number of individuals of lion-tailed macaques (ca. 218). However, all four private fragments had higher troop density of lion-tailed macaques compared to sanctuary sites. Higher estimated densities may partly be an artefact as macaques range over a larger area, including shade-coffee plantations adjoining the fragments. Lion-tailed macaque density was negatively related to density of rainforest trees ($\beta = -0.823$; Adjusted $R^2 = 0.63$; $F = 14.645$; $P < 0.01$; df = 1, 7).

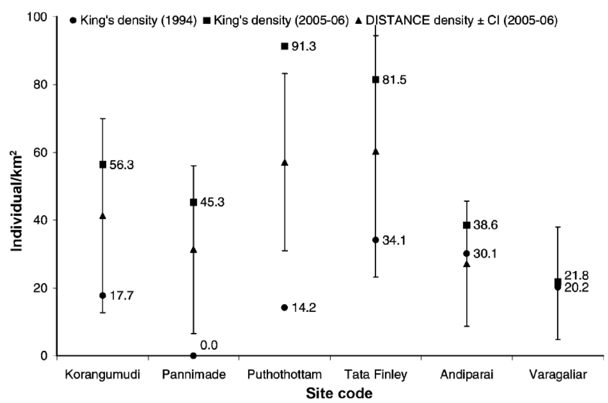

Figure 3. Changes in Indian giant squirrel density from 1994 to 2005–06 and comparison of densities obtained by distance sampling and King's method in rainforests of the Anamalai hills.

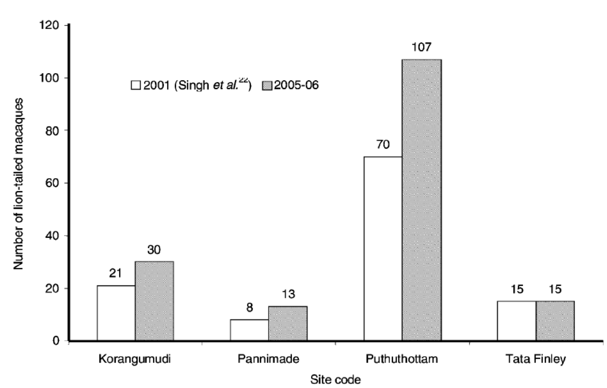

Figure 4. Temporal trend in lion-tailed macaque populations in private rainforest fragments in the Anamalai hills. Numbers over each bar correspond to the number of lion-tailed macaque individuals in each fragment.

Table 2. Count and density of troops and individuals of lion-tailed macaques in rainforest patches of IGWLS and private fragments of the Valparai plateau in the Anamalai hills

Site	Area (ha)	Number of troops	Number of individuals	Density of individuals (per sq. km)
Private fragments				
KO	56	1	30	53.57
PU	92	2	107	116.30
PA	66.7	1	13	19.49
TF	32	1	15	46.88
IGWLS				
AG	200	2	37[a]	18.50
AN	185	1	29	15.68
IYAK	2600	7	105[b]	4.04
KS	600	0	0	0.00
VBMS	2000	12	218.4[b]	10.92

[a]Data from Singh *et al.*[22]; [b]Average troop sizes obtained in this study multiplied by number of troops reported in Singh *et al.*[22].

Temporal trends in arboreal mammal abundance

Densities of Indian giant squirrel obtained from distance sampling analyses correlated strongly with those obtained using King's formula (Figure 3; Pearson's $r = 0.856$, $P < 0.001$, $n = 15$). Average King's densities were higher, but fell within the 95% confidence intervals of corresponding DISTANCE estimates for all transects except KS1, PN and MA. King's densities of Indian giant squirrel from this study were higher than densities recorded in 1994 in all six sites compared[20] (Figure 3). Increase in density was higher in private fragments compared to sanctuary sites (six-fold increase in PU, three-fold in KO, two-fold in TF). Pannimade (PA), a private fragment in which Indian giant squirrel was not recorded (probably overlooked) in the previous survey, was found to support a relatively high density of the same in the present survey. Encounter rates of Nilgiri langur in the present study ranged from 0.08 groups/km (PU) to 2.2 groups/km (PA) compared to a range 0–1.03 groups/km reported in comparable-sized fragments in 1994. The number of lion-tailed macaques showed an increase of more than 30% in three private fragments (PA, PU, KO), but remained the same in one (TF) since 2001 (Figure 4).

Discussion

Species occurrence

Private fragments included almost all mammal species recorded in the IGWLS rainforests. Only three carnivore species appear to be absent from private fragments, except adjoining the sanctuary boundary. Loss of Eurasian otter could be related to lack of perennial streams in private fragments and hunting. Absence of Nilgiri marten and tiger could be due to their naturally low densities, insufficient habitat area in fragments, or avoidance of human-altered landscapes. Nilgiri martens in contiguous rainforests of Kalakad–Mundanthurai Tiger Reserve in the Western Ghats, were encountered at a rate of one animal per thousand hours of search effort[32]; in contiguous rainforests of our study area, six individuals have been sighted between 1996 and 2007.

Persistence of most mammal species in private fragments could be due to two factors. First, almost all species recorded from private fragments also used surrounding matrix habitats. Second, the relative lack of hunting pressure (no mammal traps or signs of hunting were found in any of the sites during sampling) could have allowed the persistence of mammals in our study fragments. In many fragmented tropical forests, hunting is thought to be a crucial factor in the extirpation of mammals[13,14].

Densities in protected vs private areas

Although mammal density estimation using distance sampling is widely applied, its use in rainforest habitats has so far been limited[16]. No prior estimates of mammal densities using distance sampling are available for the Western Ghats rainforests. Our results indicate that many species require larger effort (kilometres of transect) to obtain enough detections for robust density estimates[25]. Nevertheless, the present estimates are useful baselines and allow broad comparisons to be made. Densities of most species did not differ significantly between IGWLS rainforest patches and private fragments. Fragment densities could be artificially inflated because all species use fragments as daytime refuges, but also use larger areas around the fragments to forage at other times. This is especially important in the case of the lion-tailed macaque, which had significantly higher densities in private fragments compared to IGWLS, because of the way in which its density was calculated (total number of individuals divided by fragment area). In spite of this bias, the persistence of most mammals in fragments can be attributed to three reasons, in addition to low hunting pressure and ability to use the surrounding plantations mentioned earlier. Increased food availability in and around fragments is one factor. Trees such as *A. integrifolia* and *M. eminii* in coffee plantations around fragments provide fruits for arboreal mammals such as Indian giant squirrel and lion-tailed macaque. The relatively degraded private fragments also contain grass and secondary vegetation used by ungulates such as gaur and barking deer. Another reason might be lowered predation pressure in fragments for some species[15]. Encounter rates of indirect evidence of main predators in the area, leopard and tiger, were higher in sanctuary sites (0.11 and 0.05/km walked respectively) compared to private fragments (0.06 and 0.00/km walked respectively). Abundance of raptors, which are important predators of arboreal mammals, also decreases due to rainforest fragmentation[33]. Finally, at a much larger landscape level, the Valparai plateau is only a 220 sq. km enclave of plantations surrounded by several protected areas and reserved forests. Any fragment is not more than 10 km from contiguous forests and some wide-ranging species may therefore be found to use most areas of the landscape; although details of movements and source–sink dynamics need to be explored in future studies.

Density variation and habitat correlates

Arboreal mammal species showed interesting variation in densities across the study sites. Indian giant squirrel density was inversely related to canopy overlap index. This species is a generalist in terms of habitat and food, being also found in moist deciduous, dry deciduous and riparian forests and consuming a wide variety of plant parts, including seeds, leaves, flowers and bark[34,35]. The adaptability of the species probably enables its persistence even in degraded fragments. Previously, it was suggested that Indian giant squirrel density was influenced by the presence or absence of lion-tailed macaques because of interspecific competition[20]. However, recently, it has been found that niche overlap between these two species is not high[35]. It must be noted, however, that although this squirrel and other species persist in many fragments in comparable densities, their total population sizes are small and remain isolated in most fragments. The consequences of this in terms of small population biology remain unknown.

Nilgiri langur densities were similar across all sites, except two private fragments. Like the giant squirrel, this species is also a generalist in terms of habitat, but is primarily folivorous in diet[35], depending on the availability of a diversity of plant species[20]. Though plant species di-

Appendix 1. Details of line transects in the Indira Gandhi Wildlife Sanctuary (IGWLS) and fragments on private lands in the Valparai plateau, Anamalai hills, Western Ghats, India. Standard errors of habitat structural variables are indicated in parantheses

							Habitat structure				
									Tree density (stems/ha)		
Site	Site code	Area (ha)	Transect code	Transect length (km)	Altitude (m)	Matrix[a]	Canopy height (m)	Canopy overlap index[b]	All trees	% exotic trees	Basal area (sq. m/ha)
Private fragments											
Korangumudi	KO	56	KO	1.83	990	C, T	20.2 (2.0)	0.6 (0.1)	257 (23.5)	32	55.5 (11.3)
Pannimade	PA	66.7	PA	1.20	1040	E, T, W	25.7 (1.7)	1.3 (0.2)	601 (54.6)	0	104.8 (28.1)
Puthuthottam	PU	92	PU	2.45	1144	C, E, T	25.1 (2.1)	1.0 (0.2)	404 (37.1)	59	77.8 (17.6)
Tata Finley	TF	32.6	TF	1.15	1020	C, E, W	22.4 (1.9)	1.0 (0.2)	461 (43.4)	1	72.7 (23.6)
IGWLS											
Anaigundi	AG	200	AG	2.17	700	D	26.2 (1.1)	2.0 (0.2)	401 (36.7)	0	66.1 (14.7)
Andiparai	AN	185	AN	2.08	1270	G, T	21.3 (1.7)	1.9 (0.2)	505 (46.4)	0	75.2 (15.7)
Karian shola	KS	650	KS1	2.85	810	D	24.2 (0.9)	2.3 (0.1)	666 (67.8)	0	90.4 (18.7)
			KS2	2.85	810	D	20.5 (0.8)	2.2 (0.1)	579 (58.2)	0	64.4 (15.6)
Iyerpadi–Akkamalai complex	IYAK	2600	IY	2.08	1250	D, T	27.5 (1.4)	2.1 (0.2)	468 (40.8)	0	133.4 (45.9)
			AK	1.94	1540	G, T	15.1 (0.8)	1.7 (0.2)	768 (73.5)	0	65.5 (12.1)
			IYCH	1.70	1220	T	29.4 (1.0)	1.8 (0.1)	390 (35.7)	0	90.8 (13.6)
Varagaliar–Manamboli complex	VBMS	2000	VA	2.11	680	D	28.6 (1.5)	2.0 (0.2)	437 (40.3)	0	88.2 (18.7)
			BN	2.05	690	D	30.4 (1.2)	2.0 (0.1)	606 (56.1)	0	65.9 (13.5)
			MA	1.80	813	D, C	27.5 (1.3)	1.5 (0.2)	442 (40.8)	0	82.7 (14.1)
			SK	1.87	1100	D, T	30.6 (1.0)	1.7 (0.1)	577 (53.1)	0	88.2 (15.7)

[a]Matrix habitats: C, Coffee; D, Deciduous forest; E, *Eucalyptus*; G, Grassland; T, Tea; W, Water body.
[b]Average of individual samples scored as 0, if there was no foliage above the observer; 1, if canopies barely touch each other; 2, if canopies overlap but the sky is still seen, and 3, if canopies completely overlap (following Daniels *et al.*[27]).

Appendix 2. Occurrence and abundance of mammal species in rainforests of IGWLS and private rainforest fragments in the Valparai plateau, Anamalai hills. Numbers wherever present indicate visual detections of a species across all transects in a site

	Site										
	IGWLS						Private fragments				
	AG	AN	IYAK	KS	VBMS	Overall	KO	PA	PU	TF	Overall
Effort (in km)	10.85	10.40	28.60	28.52	39.15	117.52	9.17	6.00	12.30	5.75	33.22
Species											
Asian elephant (*Elephas maximus*)	p	p	p	p	1	1	1	p	p	p	1
Black-naped hare (*Lepus nigricollis*)	p*	–	–	–	–	p*	p*	p*	p*	p*	p*
Bonnet macaque (*Macaca radiata*)	5	–	–	9	5	19	–	–	p*	p*	p*
Brown mongoose (*Herpestes fuscus*)	–	–	p*	–	–	p*	–	–	–	–	p^
Brown palm civet (*Paradoxurus jerdoni*)	p*	–	–	–	–	p*	–	–	–	–	p^
Chital (*Axis axis*)	p	–	–	p	–	p	–	–	–	–	–
Common leopard (*Panthera pardus*)	p	p	p	1	p	1	p*	–	p	–	p
Dusky striped squirrel (*Funambulus sublineatus*)	3	p	2	p*	2	7	p	p	–	1	1
Eurasian otter (*Lutra lutra*)	–	–	–	p	p	p	–	–	–	–	–
Gaur (*Bos gaurus*)	p	1	p	p	5	6	1	2	p	1	4
Indian giant flying squirrel (*Petaurista philippensis*)	p*	p*	p*	p*	p*	p*	p*	p*	p*	p*	p*
Indian giant squirrel (*Ratufa indica*)	4	10	46	17	48	125	12	7	29	13	61
Barking deer (*Muntiacus muntjak*)	p*	p	p	4	p	4	5	1	p	2	8
Indian porcupine (*Hystrix indica*)	p	p*	p	p	p	p	p*	p*	–	p	p
Jungle striped squirrel (*Funambulus tristriatus*)	p	p*	p	p	2	2	p	1	2	p	3
Leopard cat (*Prionailurus bengalensis*)	–	–	–	–	p*	p*	–	–	p*	–	p*
Lion-tailed macaque (*Macaca silenus*)	4	3	1	–	5	13	1	1	7	3	12
Mouse deer (*Tragulus meminna*)	p*	1	3	p*	4	8	1	2	p*	2	5
Nilgiri langur (*Semnopithecus johnii*)	20	15	39	28	50	152	2	13	1	12	28
Nilgiri marten (*Martes gwatkinsi*)	–	–	p*	–	–	p*	–	–	–	–	–
Sambar (*Cervus unicolor*)	4	p	p	1	6	11	3	8	2	1	14
Sloth bear (*Melursus ursinus*)	p	–	p*	p	p	p	p*	p	–	p	p
Small Indian civet (*Viverricula indica*)	–	–	–	–	–	p^	–	–	–	–	p^
Stripe-necked mongoose (*Herpestes vitticollis*)	–	–	–	2	1	3	–	–	–	–	p^
Tiger (*Panthera tigris*)	p*	–	p	p	p	p	–	–	–	–	–
Travancore flying squirrel (*Petinomys fuscocapillus*)	–	–	–	p*	p*	p*	–	–	–	p*	p*
Wild dog (*Cuon alpinus*)	p*	–	p*	p*	p*	p*	p*	–	p*	p*	p*
Wild pig (*Sus scrofa*)	–	1	1	p	p*	2	–	p*	p*	1	1

'p' indicates species which were recorded through indirect evidence (tracks, calls) on transects. 'p*' indicates species not recorded on transects but incidentally encountered in a site. 'p^' indicates species not recorded during the present study but reported from that site by Kumar *et al.*[32].

versity was not measured in this study, density of native rainforest trees which is a useful surrogate, was the best predictor of density of the Nilgiri langur. The two sites with lowest densities of Nilgiri langur (KO and PU) had high percentages of exotic trees (Appendix 1).

Density of lion-tailed macaque was negatively related to rainforest tree density. Among arboreal mammals, lion-tailed macaque has the lowest niche breadth, feeding mainly on fruits supplemented with flowers and insects[35]. It is also restricted to tropical rainforest habitats. Nevertheless, this species appeared to attain high densities in relatively small degraded fragments. The reasons for this could be the availability of fruiting trees in fragments and surrounding coffee plantations combined with the fact that individuals cannot disperse out of fragments through the inhospitable matrix of tea to other forest patches. It is important to note, however, only those private fragments which contained lion-tailed macaques were sampled. This species is absent from all the remaining 30-odd private fragments in the Valparai plateau, and therefore, at the landscape level, fragmentation has had a negative effect on lion-tailed macaque densities, as noted earlier[20].

Temporal trends in arboreal mammal populations

Arboreal mammals have clearly persisted and possibly increased in numbers in private fragments over the last decade. For lion-tailed macaque, the changes revealed by this study are likely to be quite accurate since they were based on complete counts. In the case of the Indian giant squirrel, in spite of biases likely due to differences in observers and areas within the sites sampled, the magnitude of the change documented suggests that there has been a definite increase in populations in all private fragments. Uncertainty is highest in the case of Nilgiri langur, since the present study was only able to demonstrate an increase in maximum encounter rate across sites of comparable areas. Nevertheless, these trends suggest a general increase in arboreal mammals in private fragments. As already discussed, a combination of suitable conditions – low predation and hunting pressure, availability of food, ability to use resources in the surrounding matrix and proximity to contiguous forests in the wider landscape – might be causal factors for their persistence and increase.

Conservation implications

The continued occurrence of most mammal species in fragments that were mostly created decades ago, clearly highlights the value of rainforest fragments for mammal conservation in the Western Ghats. Earlier studies from other regions reported dramatic decline in populations and extinction of mammal species as a result of fragmentation associated with increase in hunting pressure[12,13]. Our study demonstrates that in a fragmented landscape with relatively low hunting pressure, a majority of mammals continue to persist and maintain populations that may even increase over time. For some species like Indian giant squirrel and lion-tailed macaque, however, this has resulted in abnormally high population densities which may have detrimental effects on their social behaviour, habitat or other species in the community[15]. For instance, in contrast to contiguous rainforests where they are highly arboreal and shy of humans, lion-tailed macaques showed greater than four-fold increase in time spent on the ground, greater dependence on non-native and pioneer plant species for food, and a greater frequency of inter-troop encounters and contact with people, in Puthuthottam, a highly degraded private fragment with densities more than 100 individuals/sq. km (ref. 36). Efforts are needed to improve habitat quality of these fragments through restoration and connectivity between them to facilitate dispersal of mammals, while reducing the likelihood of direct encounters with people and vehicular traffic. In the long-term, habitat restoration may be expected to stabilize densities of species in fragments to values found in relatively undisturbed sanctuary areas.

1. Wade, T. G., Riitters, K. H., Wickham, J. D. and Jones, K. B., Distribution and causes of global forest fragmentation. *Conserv. Ecol.*, 2003, **7**, 7.
2. Turner, I. M., Species loss in fragments of tropical rainforest: A review of the evidence. *J. Appl. Ecol.*, 1996, **33**, 200–209.
3. Debinski, D. M. and Holt, R. D., A survey and overview of habitat fragmentation experiments. *Conserv. Biol.*, 2000, **14**, 342–355.
4. Saunders, D. A., Hobbs, R. J. and Margules, C. R., Biological consequences of ecosystem fragmentation: A review. *Conserv. Biol.*, 1991, **5**, 18–32.
5. Laurance, W. F. and Vasconcelos, H. L., Ecological effects of habitat fragmentation in the tropics. In *Agroforestry and Biodiversity Conservation in Tropical Landscapes* (eds Schroth, G. *et al.*), Island Press, Washington, 2004, pp. 33–49.
6. Chalfoun, A. D., Thompson III, F. R. and Ratnaswamy, M. J., Nest predators and fragmentation: A review and meta-analysis. *Conserv. Biol.*, 2002, **16**, 306–318.
7. Tabarelli, M., Cardoso da Silva, J. M. and Gascon, C., Forest fragmentation, synergisms and the impoverishment of neotropical forests. *Biodivers. Conserv.*, 2004, **13**, 1419–1425.
8. Laurance, W. F. *et al.*, Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conserv. Biol.*, 2002, **16**, 605–618.
9. Asquith, N. M. and Mejía-Chang, M., Mammals, edge effects and the loss of tropical forest diversity. *Ecology*, 2005, **86**, 379–390.
10. Laurance, W. F., Ecological correlates of extinction proneness in Australian tropical rainforest mammals. *Conserv. Biol.*, 1991, **5**, 79–89.
11. Viveiros de Castro, E. B. and Fernandez, F. A. S., Determinants of differential extinction vulnerabilities of small mammals in Atlantic forest fragments in Brazil. *Biol. Conserv.*, 2004, **119**, 73–80.
12. Peres, C. A., Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. *Conserv. Biol.*, 2001, **15**, 1490–1505.
13. Chiarello, A. G., Effects of fragmentation of the Atlantic forest on mammal communities in south-eastern Brazil. *Biol. Conserv.*, 1999, **89**, 71–82.
14. Pattanavibool, A. and Dearden, P., Fragmentation and wildlife in montane evergreen forests, northern Thailand. *Biol. Conserv.*, 2002, **107**, 155–164.
15. Koprowski, J. L., The response of tree squirrels to fragmentation: A review and synthesis. *Anim. Conserv.*, 2005, **8**, 369–376.
16. Chiarello, A. G., Density and population size of mammals in remnants of Brazilian Atlantic forest. *Conserv. Biol.*, 2000, **14**, 1649–1657.
17. Myers, N., Mittermeier, R., Mittermeier, C. G., daFonseca, G. A. B. and Kent, J., Biodiversity hotspots for conservation priorities. *Nature*, 2000, **403**, 853–858.
18. Kumar, A., Pethiyagoda, R. and Mudappa, D., Western Ghats and Sri Lanka. In *Hotspots Revisited – Earth's Biologically Richest and Most Endangered Ecoregions* (eds Mittermeier, R. A. *et al.*), CEMEX, Mexico, 2004, pp. 152–157.
19. Nameer, P. O., Molur, S. and Walker, S., Mammals of Western Ghats: A simplistic overview. *Zoos' Print*, 2001, **16**, 629–639.
20. Umapathy, G. and Kumar, A., The occurrence of arboreal mammals in the rainforest fragments in the Anamalai hills, south India. *Biol. Conserv.*, 2000, **92**, 311–319.
21. Umapathy, G., Impact of habitat fragmentation on the arboreal mammals in the wet evergreen forests of Anamalai hills in the Western Ghats, south India. Ph D dissertation, Bharathiar University, Coimbatore, 1998.
22. Singh, M., Singh, M., Kumar, M. A., Kumara, H. N., Sharma, A. K. and Kaumanns, W., Distribution, population structure and conservation of lion-tailed macaque (*Macaca silenus*) in Anamalai hills, Western Ghats, India. *Am. J. Primatol.*, 2002, **57**, 91–102.
23. Mudappa, D. and Raman, T. R. S., Rainforest restoration and wildlife conservation on private lands in the Valparai plateau, Western Ghats, India. In *Making Conservation Work* (eds Shahabuddin, G. and Rangarajan, M.), Permanent Black, New Delhi, 2007.
24. Pascal, J. P., Wet evergreen forests of the Western Ghats of India: Ecology, structure, floristic composition and succession. Institut Français de Pondichéry, Puducherry, 1988.
25. Buckland, S. T., Anderson, D. R., Burnham, K. P. and Laake, J. L., *Distance Sampling: Estimating Abundance of Biological Populations*, Chapman and Hall, London, 2003.
26. Krebs, C. J., *Ecological Methodology*, Harper and Row, New York, 1989.
27. Daniels, R. J. R., Joshi, N. V. and Gadgil, M., On the relationship between bird and woody plant species diversity in the Uttara Kannada district of south India. *Proc. Natl. Acad. Sci. USA*, 1992, **89**, 5311–5315.
28. Thomas, L. *et al.*, Distance 5.0. Release Beta 5. Research Unit for Wildlife Population Assessment, University of St Andrews, UK, 2005; http://www.ruwpa.stand.ac.uk/distance/

29. Goodman, L. A., On the exact variance of products. *J. Am. Stat. Assoc.*, 1960, **55**, 708–713.
30. Raman, T. R. S., Effects of habitat structure and adjacent habitats on birds in tropical rainforest fragments and shaded plantations in the Western Ghats, India. *Biodivers. Conserv.*, 2006, **15**, 1577–1607.
31. SPSS Inc., *SPSS Base 8.0 for Windows User's Guide*, SPSS Inc., Chicago, 1998.
32. Kumar, A., Chellam, R., Choudhury, B. C., Mudappa, D., Vasudevan, K., Ishwar, N. M. and Noon, B. R., Impact of rainforest fragmentation on small mammals and herpetofauna in the Western Ghats, South India. WII–USFWS collaborative project. Final report, Wildlife Institute of India, Dehradun, 2002.
33. Thiollay, J.-M., Distribution patterns and insular biogeography of South Asian raptor communities. *J. Biogeogr.*, 1998, **25**, 57–72.
34. Borges, R., A nutritional analysis of foraging in the Malabar giant squirrel (*Ratufa indica*). *Biol. J. Linn. Soc.*, 1992, **47**, 1–21.
35. Sushma, H. S. and Singh, M., Resource partitioning and interspecific interactions among sympatric rainforest arboreal mammals of the Western Ghats, India. *Behav. Ecol.*, 2006, **17**, 479–490.
36. Singh, M., Kumara, H. N., Kumar, M. A. and Sharma, A. K., Behavioural responses of lion-tailed macaques to a changing habitat in a tropical rainforest fragment in the Western Ghats, India. *Folia. Primatol.*, 2001, **72**, 278–291.

ACKNOWLEDGEMENTS. We are grateful to the Tamil Nadu Forest Department for research permits and private plantation companies (Puthuthottam Estates Limited and Tata Coffee Limited) for access to their rainforest fragments. This research was carried out as part of the Rainforest Restoration Project funded by UNDP–GEF Small Grants Programme, India; Conservation, Food and Health Foundation, USA; Barakat, Inc., USA, and Ford Foundation, India. We thank Krishnan, Vena Kapoor, M. Anandakumar and Atul Joshi for help during fieldwork, Ajith Kumar and G. Umapathy for sharing data.

Received 20 September 2007; revised accepted 12 February 2008