Home Ranges, Time Budgets and Food-tree Use in a High-density Tropical Population of Greater Gliders, *Petauroides volans minor* (Pseudocheiridae : Marsupialia)

Steven S. Comport[A], *Simon J. Ward*[B] *and William J. Foley*

Department of Zoology, James Cook University, Townsville,
Qld 4811, Australia.
[A]Present address: CSIRO Tropical Forest Research Centre,
PO Box 780, Atherton, Qld 4883, Australia.
[B]Present address: Department of Zoology, University of Melbourne,
Parkville, Vic. 3052, Australia.

Abstract

The socio-ecology of *Petauroides volans* has been studied for subtropical and temperate populations, but not for the northern tropical subspecies, *Petauroides volans minor*. Data on the effects of a high population density on home ranges, time budgets and food-tree use were obtained by means of radio-telemetry. Three techniques were used to estimate home-range area (kernel, MCP and harmonic mean) and the kernel method was preferred. Estimates of home-range area (defined by the 95% kernel) gave mean values of 2·5 and 1·3 ha for males and females, respectively. Broad overlap of home ranges of males was observed, which has not been reported previously for populations of *P. volans*. Behaviour patterns for males and females were similar to those in previous studies, although the mating system may differ, possibly because of the high population density. Dietary patterns were similar to those previously reported for this species, the most important food items being young leaves and flower buds of particular eucalypt species, notably *Eucalyptus acmenoides*.

Introduction

The greater glider, *Petauroides volans,* is the largest of the gliding possums, and in the eucalypt forests of south-eastern Australia it is also among the most numerous of the arboreal mammals. Two subspecies are recognised: *P. v. volans* inhabits temperate and subtropical areas of the species' range and is extremely variable in colour, ranging from dark chocolate through grey and mottled to white, often in the same population (Ward, personal observations); *P. v. minor* occurs in the wet–dry tropical region of north-eastern Queensland, north from approximately the tropic of Capricorn to around Cairns. *P. v. minor* differs morphologically from *P. v. volans* by being less variable in colour, smaller in size (700–900 *v.* 1000–1700 g) and by having a more slender body with shorter ears and tail.

Previous studies of greater gliders have documented their reproduction and population regulatory mechanisms (Tyndale-Biscoe and Smith 1969), social organisation (Henry 1984; Kehl and Borsboom 1984), habitat requirements (Norton 1988), diet (Marples 1973; Kavanagh and Lambert 1990), population densities (Henry 1984; Kavanagh 1984; Kehl and Borsboom 1984) and digestive and energetic strategies (Foley 1987; Foley and Hume 1987a, 1987b). These studies have mostly focused on *P. v. volans* in temperate areas of Australia, with a single study of a subtropical population. No information exists for tropical populations of *P. v. minor*.

Greater gliders are selective folivores, generally consuming eucalypt species. Hence, as for many other possums and gliders, they are forest dependent. Within an area of forest they have a patchy distribution, being more abundant in areas of high soil fertility, making them a useful indicator of habitat fertility (Braithwaite 1983). These fertile zones are favoured for timber

harvesting and cultivation, often to the detriment of greater gliders (Lunney 1987; Kavanagh and Bamkin 1990).

In temperate and subtropical forests and forests, *P. v. volans* is largely solitary with a small home range (*c.* 1·2–2·6 ha: Henry 1984; Kehl and Borsboom 1984; Norton 1988) and feeds almost entirely on young eucalypt leaves and buds from favoured tree species (Kavanagh and Lambert 1990). Reported population densities, which have varied from 0·56 ha^{-1} (Henry 1984) to 1·6–2·3 ha^{-1} (Kehl and Borsboom 1984), are thought to be related to the concentration of nutrients in the foliage of particular tree species. Recent evidence suggests that some aspects of this species' social organisation may change with density (Norton 1988).

In north-eastern Queensland, in eucalypt forests north-west of Townsville, *P. v. minor* occurs at a very high population density of 3·3–3·8 ha^{-1} (Ward, unpublished data). This population is the focus of a wider study of the ecology of this tropical subspecies. This paper reports on the home ranges, time budgets and patterns of use of favoured food trees.

Methods

Study Area

The study area was on 'Taravale Station' near Paluma (19°06′S, 146°05′E) in north-eastern Queensland (Fig. 1) and encompassed *c.* 25 ha of mature eucalypt forest at an altitude of 750 m. The vegetation community was mature open forest (Specht 1981), reaching 20–25 m in height and comprising five main eucalypt species (listed here in order of numerical abundance): *Eucalyptus acmenoides, E. citriodora, E. intermedia, E. tereticornis* and *E. crebra*. Individuals of *Lophostemon suaveolens* were scattered through the study site and a small number of *Allocasuarina torulosa* were found along creek lines. The forest was lightly grazed with little understorey. The area is in the wet–dry tropics with temperatures ranging from an average minimum of 7–9°C in the dry season (typically May–October) to an average maximum of 25–34°C
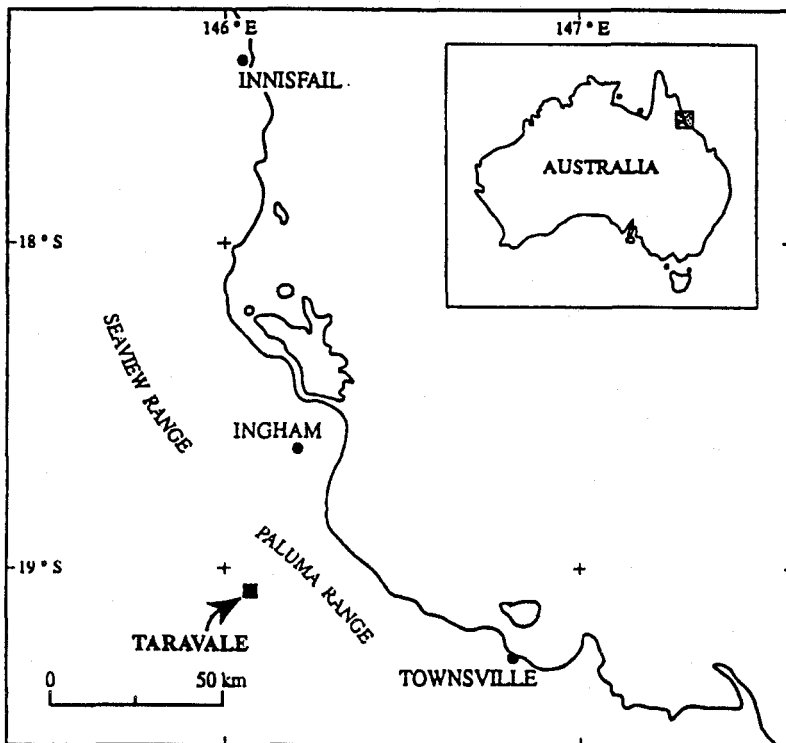

Fig. 1.   Location of study site at Taravale Station, northern Queensland.

in the wet season (November–April). Rainfall averages 1750 mm annually, most of which falls between December and March (Nix 1991). The present study was conducted on six trips (each of 6–10 days duration) in March, April, May, June, November and December 1992.

Capture and Radio-tracking Procedures

Individuals of *P. v. minor* were located by spotlighting. If an individual was in a position suitable for capture, two or more spotlights were trained on it to dazzle and disorient it. The branch on which it perched was then shaken vigorously with a hooked extendable aluminium pole. This action often forced the glider to the ground where it was caught by hand.

The weight, measurements and sex of capture individuals were determined; the animals were then collared, tagged with three fingerling eartags fitted with reflective tape (two in one ear and one in the other) and released back into the trees from which they had been taken. Gliders were fitted with a single-stage radio-transmitter (Sirtrack Electronics, New Zealand) attached to a plastic collar and fitted with two colours of reflective marking tape. The package was designed to fit under the glider's chin, with a whip antenna protruding down its back. The total weight of the transmitter package was approximately 17 g. A 'Custom Electronics' receiver, operating on the 150–152 mHz band, and a collapsible 3-element hand-held antenna were used to locate gliders.

Individual gliders were located at night in a rotational sequence, and each individual's location was recorded 4–5 times per night, with intervals between locations more than 60 min (see below), on five or six nights each trip. Locations were recorded by noting the identification number of each tree in which the glider was sighted. The exact location of each identified tree was determined later by recording its bearing and distance from marker points set at 50-m intervals on a grid across the 25-ha study site. Data were collected from six adult females and five adult males over a total of 36 nights between March and December 1992.

Den Sites

Den sites were located by tracking radio-collared gliders during daylight hours. One or more of these dens was then watched for the 1-h period around dusk in order to check time of emergence and whether dens were being shared. To minimise the level of auto-correlation in the data, den sites were not included in analyses of home-range estimates.

Home-range Determination

The home-range areas of gliders were analysed with the RANGES IV software package (R. E. Kenward Institute of Terrestrial Ecology, Wareham, UK). This package offers several statistical and non-statistical methods to estimate home-range area, of which three were selected: the harmonic mean (Dixon and Chapman 1980); the Minimum Convex Polygon (MCP) (Mohr 1947); and the kernel method (Worton 1987). Recent studies have suggested that, because many home-range analytical techniques have a number of disadvantages, no one method is likely to be entirely satisfactory and at least two techniques should be used in any study (Worton 1987; Harris *et al.* 1990). We have adopted this approach and, for estimates of home-range area, data were analysed by the above three methods. We chose isopleths of 95 and 50% to estimate home-range areas and core areas, respectively. The inclusion of 95% of the location points is common in home-range models and is considered a close approximation of the total home-range area (Worton 1987). From preliminary analyses, the kernel method (95% isopleth) was preferred as it was more robust when sample sizes were low (see Table 1). However, since previous studies of gliding marsupials have used 100% MCP (e.g. *P. volans*: Kehl and Borsboom 1984) and 95% harmonic mean (i.e. *P. australis*: Goldingay and Kavanagh 1993), these estimators have been included to facilitate comparability between studies.

An implicit assumption of many statistical methods of home-range analysis is that successive location points form a set of independent data. If the data are temporally auto-correlated, these home-range models tend to underestimate the true home-range size, because of over-sampling in areas where animals are readily located (Harris *et al.* 1990). To test the level of auto-correlation in the data, analyses were conducted on preliminary data sets of 100 location points from each of two gliders (one male, one female) collected at intervals of 15–165 min. These analyses indicated that a minimum of 1 h between locations is sufficient to ensure independence of locations (see Fig. 2a). This result was later confirmed by home-range analyses (kernel, MCP and harmonic mean) conducted on three data sets, one consisting of the total data set (from each of eight *P. v. minor*) and two consisting of reduced data sets in which 50 and 66% of successive location points for each glider were removed. This allowed a comparison of home-range estimates for

Table 1.   Home-range estimates for 11 adult *Petauroides volans minor* at Taravale Station, northern Queensland

Estimates of the 100%, 95% and 50% home ranges for the kernel and Minimum Convex Polygon (MCP) methods and 100% and 95% home ranges for the harmonic-mean (HM) method are given. D, number of months sampled; n, total number of locations

Animal	D	n	Home-range estimates (ha)				
			Kernel		MCP		HM
			95%	50%	95%	50%	95%
			Males				
M1	6	131	2·2	0·5	2·0	0·9	0·5
M2	6	111	2·8	0·5	3·2	1·0	0·8
M3	6	120	4·2	0·8	4·1	1·3	0·7
M4	6	110	1·3	0·1	1·3	0·2	0·6
M5	2	25	1·9	0·1	1·0	0·2	—[A]
Mean			2·5	0·4	2·2	0·6	0·6
s.e.			0·5	0·1	0·5	0·1	0·06
			Females				
F6	6	121	1·1	0·1	0·9	0·7	0·2
F7	6	117	1·1	0·1	0·8	0·3	0·2
F8	6	115	1·7	0·2	1·6	0·9	0·3
F9	4	117	1·3	0·2	0·9	0·4	0·2
F10	4	113	0·9	0·1	0·9	0·1	0·3
F11	2	27	1·7	0·4	1·0	0·2	—[A]
Mean			1·3	0·2	1·0	0·3	0·20
s.e.			0·1	0·04	0·1	0·1	0·02

[A]The harmonic-mean method failed to provide stable home ranges at small sample sizes.

intervals of 1, 2 and 3 h, respectively, and confirmed that estimates derived from locations at 1-h intervals were not very different to estimates from longer intervals (Table 2).

The effect of sample size on home-range estimates was assessed with data from greater gliders for which there were more than 100 independent location points. This was determined by plotting the cumulative home-range area against number of locations and defining the minimum required sample size as the point after which additional locations resulted in a minimal increase in range size (Harris *et al.* 1990). This procedure was carried out with the harmonic-mean and kernel methods of home-range analysis in order to compare the responses of the two analytical techniques to changing sample sizes.

Use and Phenology of Trees

Preferences of radio-collared individuals of *P. v. minor* for feeding on particular plant parts, and their use of different tree species, were determined by direct observation of foraging gliders. For each observation an identity number was recorded for the tree in which it was feeding. The tree's species and phenology (see below) were then checked and recorded the following day.

To monitor the general phenology of trees at the study site, a sample of trees was assessed in each of the six sample months, with the following protocol. Four transect lines were randomly selected in the study area. Ten mature individuals of each of the five *Eucalyptus* species and *L. suaveolens* were labelled along these transect lines, and phenology (abundance of young leaves, young leaves on coppice, fruits, buds and flowers) of each was assessed with the aid of binoculars. The abundance of these phenological characters was scored as one of four classes: none (0), traces (1), abundant (2) and very abundant (3). Young leaves were recognised by size ($< 2/_3$ mature leaf size), shape, reflectance and colour (Kavanagh and Lambert 1990). Eucalypt flower buds were recognised by their characteristic cluster-type growth (small hands of 8–10 buds) and club-shaped appearance. The phenology of trees in which gliders were observed feeding was scored in the same way.
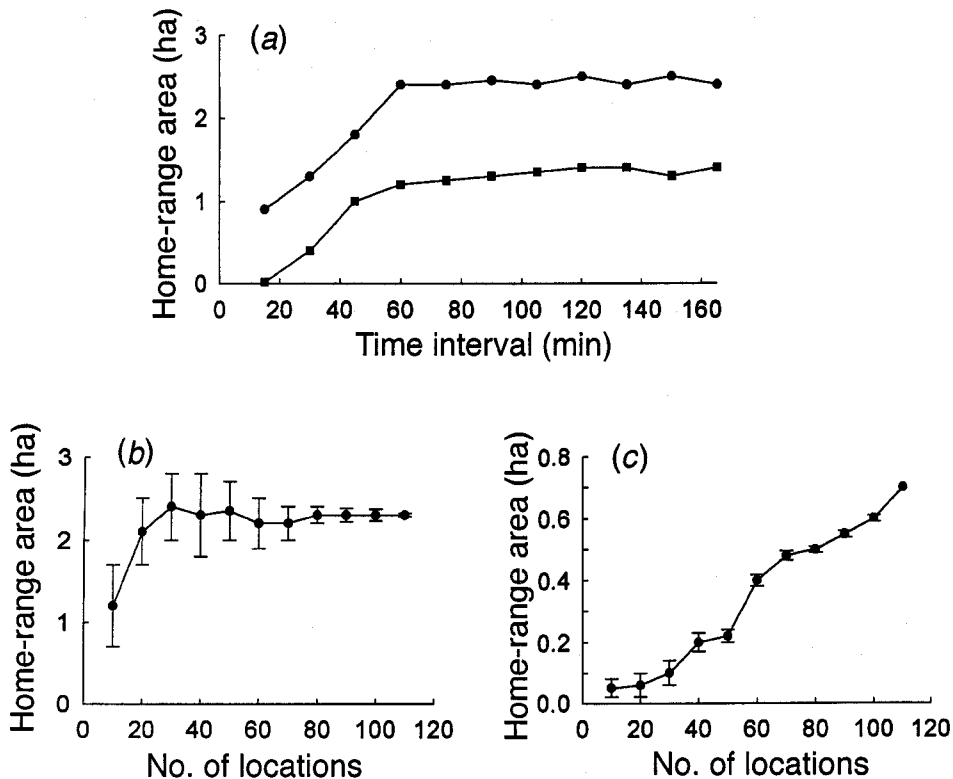
Fig. 2. Influences of time intervals between locations and total numbers of locations on estimates of home-range areas for *P. v. minor* at Taravale Station. (*a*) The influence of time interval on 95% kernel estimates for a male (●) and a female (■). (*b*) The influence of sample size on 95% kernel estimates. Values are means (± s.d.) for eight individuals. (*c*) The influence of sample size on 95% harmonic-mean estimates; values as for *b*.

For each tree species, the average of the phenology scores for a given character from the 10 sample trees was used as a phenology index. This index represents the average presence of each character across the 10 sampled trees, producing a scale of 0–3.

Preferences by gliders for feeding in particular tree species were determined by comparing the proportion of feeding observations in that tree species (*Pf*) with the frequency of occurrence of that species in the study area (*Pt*). *Pt* was estimated from censuses of all trees more than 10 cm diameter at breast height within three 0·25-ha (50 × 50 m) sample plots. These plots were positioned to overlap the home ranges of radio-collared gliders. The proportion of all feeding observations recorded in each tree species was converted to an index of feeding selectivity (*SI*) that was directly comparable between tree species, by means of the formula

$$SI = \frac{Pf - Pt}{Pt} .$$

This index produces a value of 0 when gliders use that tree species in exactly the same proportion in which it occurs on the study site, −1 when that species is totally rejected by gliders, and positive values when gliders use it in a greater proportion than it occurs on the study site.

Analyses of Foliage Samples

The concentrations of total nitrogen (N), phosphorous (P) and potassium (K) were measured in foliage samples collected in six periods from December 1991 until November 1992. We chose a grid reference at

Table 2.   Comparative analysis of home-range estimates for total and edited data sets for
***Petauroides volans minor* at Taravale Station, northern Queensland**
Estimates of the 95% home ranges for total (1 h) and edited (2 and 3 h) time intervals for the kernel,
Minimum Convex Polygon (MCP) and harmonic-mean (HM) methods are given. Estimates are
mean home ranges for four males (M1, M2, M3, M4) and four females (F6, F7, F8, F9). *n*, number
of locations; M, male; F, female

Time interval (h)	*n*	Home-range estimates (ha)					
		Kernel		MCP		HM	
		M	F	M	F	M	F
1	110	2·2	1·1	2·0	0·9	0·5	0·2
2	55	2·4	1·3	2·0	0·8	0·4	0·2
3	33	2·0	1·4	1·6	0·7	0·2	0·2
Mean		2·2	1·3	1·9	0·8	0·4	0·2
s.e.		0·1	0·1	0·1	0·05	0·1	0·0

random and collected foliage from trees at each subsequent grid intersection until we had a minimum of
three samples of mature leaves for each species for each sampling period. When young leaves were present,
they were sampled and analysed separately. The samples were freeze-dried, ground to pass through a 1-mm
screen and digested in sulphuric acid and hydrogen peroxide with selenium as the catalyst. Total N was
then determined by the method of Baethglen and Alley (1989); total P (Murphy and Reilly 1962) and K
were measured by atomic absorption spectrophotometry.

Time Budgets and Social Interactions

On one night of each sample month, a single radio-collared individual (M1, M2, M3, F6, F7 or F8; see
Table 1) was followed from dusk until dawn to collect quantitative behavioural observations. Sampling
involved recording the times of changes in behaviour to the nearest minute, such that the percentage of time
spent in particular behaviours could be calculated. Behaviours were grouped into five main categories:
'feeding', 'resting', 'moving', 'grooming' and 'other' (e.g. in the den) (after Kehl and Borsboom 1984).
Social interactions were defined as any interaction between the focal glider and any other glider. These
tended to be rare and of short duration, and could occur concurrently with any of the five main categories of
behaviour listed above.

To minimise impacts of observer presence, behaviour was recorded, whenever possible, without the
assistance of artificial lights, instead from the silhouette against the moonlit sky. If this was not possible, a
small headlamp was used to illuminate the glider at close quarters or a 30-W hand-held spotlight with red
filter was used for observations to a distance of *c*. 50 m.

Results

Home-range Estimates

Estimates of home-range and core areas were determined for 11 adult individuals of *P. v.
minor* (Table 1). Home-range area at Taravale Station from the kernel method (95% isopleths)
ranged from 1·3 to 4·2 ha for males and from 0·9 to 1·7 ha for females. Males had a significantly
larger mean home-range area than females ($t = 2.51$, $P = 0.033$). The MCP method generally
produced similar but smaller estimates (although not significantly so: paired t-test, $t = 2.04$,
$P = 0.068$), approximately 70–95% of kernel estimates (Table 1). Notable exceptions were M5
and F11, in which the MCP was 53 and 59% of the kernel estimate, respectively. The harmonic-
mean method (95% isopleths) produced significantly smaller ($t = 2.24$, $P = 0.042$) estimates,
approximately 15–50% of kernel and MCP estimates.

Core areas calculated by the Kernel method ranged from 0·1 to 0·8 ha for males and 0·1 to
0·4 ha for females. MCP estimates of core areas were significantly larger (up to 55%; paired
$t = 3.35$, $P = 0.007$) than kernel estimates and showed more variation between individuals of a

given sex. Mean core areas (kernel method) of females did not differ significantly ($t = 1.64$, $P = 0.14$) from those of males. In each case, core areas represented 5–23% of home-range areas.

Analyses comparing home-range estimates from total and edited data sets indicated that the influence of auto-correlated data was minimal and did not affect home-range area in any consistent way for the three estimation techniques (Table 2). When the data set was reduced by 50% (55 points), home-range area (95% kernel) increased by 8.3 and 7.7% of the total for males and females, respectively. However, a reduction of 66% (33 points) in the data set resulted in a 16.7% decrease in home-range area of males, in all estimation techniques. No consistent pattern emerged for home ranges of females.

The influence of sample size on home-range area indicated that the number of locations required to reach a plateau in estimated area varied depending on the technique used. With the 95% kernel technique, home-range area asymptoted when approximately 25 fixes were used (Fig. 2b). However, by the 95% harmonic-mean method, the same data produced no asymptote after 110 fixes (Fig. 2c). For the latter method, this suggests that home-range area may be considerably underestimated if sample sizes of less than 100 locations are used.

Home-range Overlap

There was extensive overlap of home ranges, both within and between sexes (Fig. 3). For example, M1 displayed 75.8 and 43.2% home-range overlap with M2 and M3, respectively, and M2 had 45.2% home-range overlap with M3. This overlap was not exclusive of core areas; several gliders were often observed using the same tree, but not necessarily concurrently. The degree of overlap between females is probably underestimated in this analysis because of the presence of three, possibly four, unmarked adult females in the major area of overlap of radio-collared gliders (see Discussion).
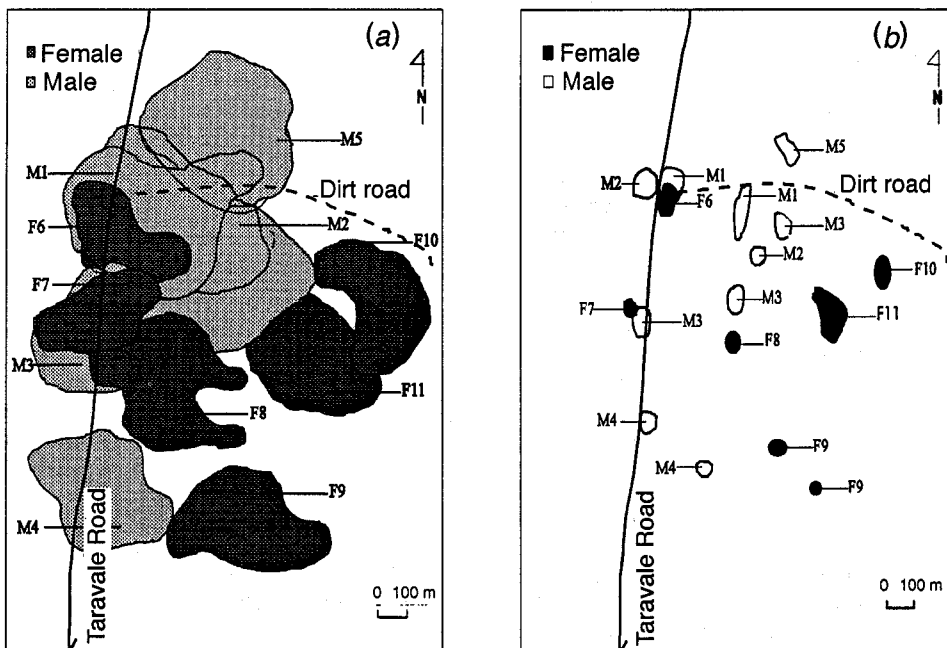

Fig. 3. Spatial arrangement of (a) home-range areas (95% isopleth) and (b) core areas (50% isopleth) of radio-collared male and female *Petauroides volans minor* at Taravale Station.

Den-site Usage

A total of 56 dens was recorded at the study site. All were hollows in trees, of which 16 (28·5%) were in *E. acmenoides*, 14 (25·0%) in *E. citriodora*, 8 (14·3%) in *E. tereticornis*, 7 (12·5%) in *E. intermedia*, 7 (12·5%) in *E. crebra* and 4 (7·2%) in dead trees of undetermined species. This distribution differs significantly from that based on the abundances of the tree species on the study site (*E. acmenoides*, 32·7%; *E. citriodora*, 28·5%; *E. tereticornis*, 5·5%; *E. intermedia*, 27·8%; *E. crebra*, 4·9%), because there were fewer dens than expected in *E. intermedia* (14·5 expected) and more than expected in *E. tereticornis* (2·9) and *E. crebra* (2·6) (χ^2 = 22·96, d.f. = 3, $P < 0.001$). There was no apparent shortage of hollow trees in the study area, and, although individual gliders showed a preference for certain dens, they regularly moved between dens in their home range. Generally, each glider utilised 4–6 different dens in any one month, with one or two dens being occupied most frequently. All primary dens were located inside core areas and only occasionally were dens situated outside core areas.

An adult female and her most recent offspring often shared dens, but only once were two adults observed to emerge from the same den (in November) from more than 50 observations. Unfortunately, only one of the pair was tagged (F11) and it was not possible to determine the sex or reproductive status of the other adult. However, the joint use of dens was probably associated with mating, given the higher number of interactions observed in November. In addition, one member of a (suspected) mated pair was observed to occupy one of its partner's primary dens while the partner used another den. This occurred on four occasions: three times in November and once in December.

Preferences for Tree Species

Radio-collared gliders were observed foraging on 477 of 1107 observations (43·0%). Of these foraging observations, 228 (47·8%) occurred in *E. acmenoides*, 101 (21·2%) in *E. intermedia*, 91 (19·1%) in *E. citriodora*, 22 (4·6%) in *E. tereticornis*, 20 (4·2%) in *E. crebra*, 14 (2·9%) in *Allocasuarina torulosa* and only one in *Lophostemon suaveolens*.

The frequencies in which gliders were observed feeding in trees of the five eucalypt species differed significantly from the frequencies of those species in the sample plots (χ^2 = 32·7, d.f. = 4, $P < 0.001$). Gliders fed selectively on particular tree species, especially *E. acmenoides*, and avoided *E. citriodora* and *E. intermedia*, in all sample months (Fig. 4). The use of *E. tereticornis* and *E. crebra* was variable, with gliders favouring species in some months and avoiding them in others. The strongest pattern of food-tree selection across all tree species occurred in November and December (Fig. 4).

Detailed analyses of phenological characters were confined to young leaves and flower buds of eucalypt species, because these items were most often eaten by gliders at Taravale Station. Previous studies (Kavanagh and Lambert 1990) also suggested that these are dominant dietary items of *P. volans*. All eucalypt species showed evidence of cyclic production of new leaves, with peak production in April, May and June (Fig. 5). The most obvious flush of leaves occurred in *E. crebra*, and the pattern was least marked in *E. tereticornis*.

Flower buds were apparent in at least some trees of each eucalypt species in all sample months (Fig. 6) and most species showed little evidence of seasonal cycles in flower-bud production.

Analyses of Foliage Samples

No significant differences occurred between sampling periods in the concentration of N, P or K in either mature foliage or young foliage of any of the six tree species analysed. The samples were thus combined; values for each species in two age-classes of foliage, mature and young, are shown in Table 3. The concentrations of elements were consistently higher in young foliage than in mature foliage for a given species, and concentrations in *L. sauveolens* were similar to those in the *Eucalyptus* spp. The highest concentrations of N and P were recorded in
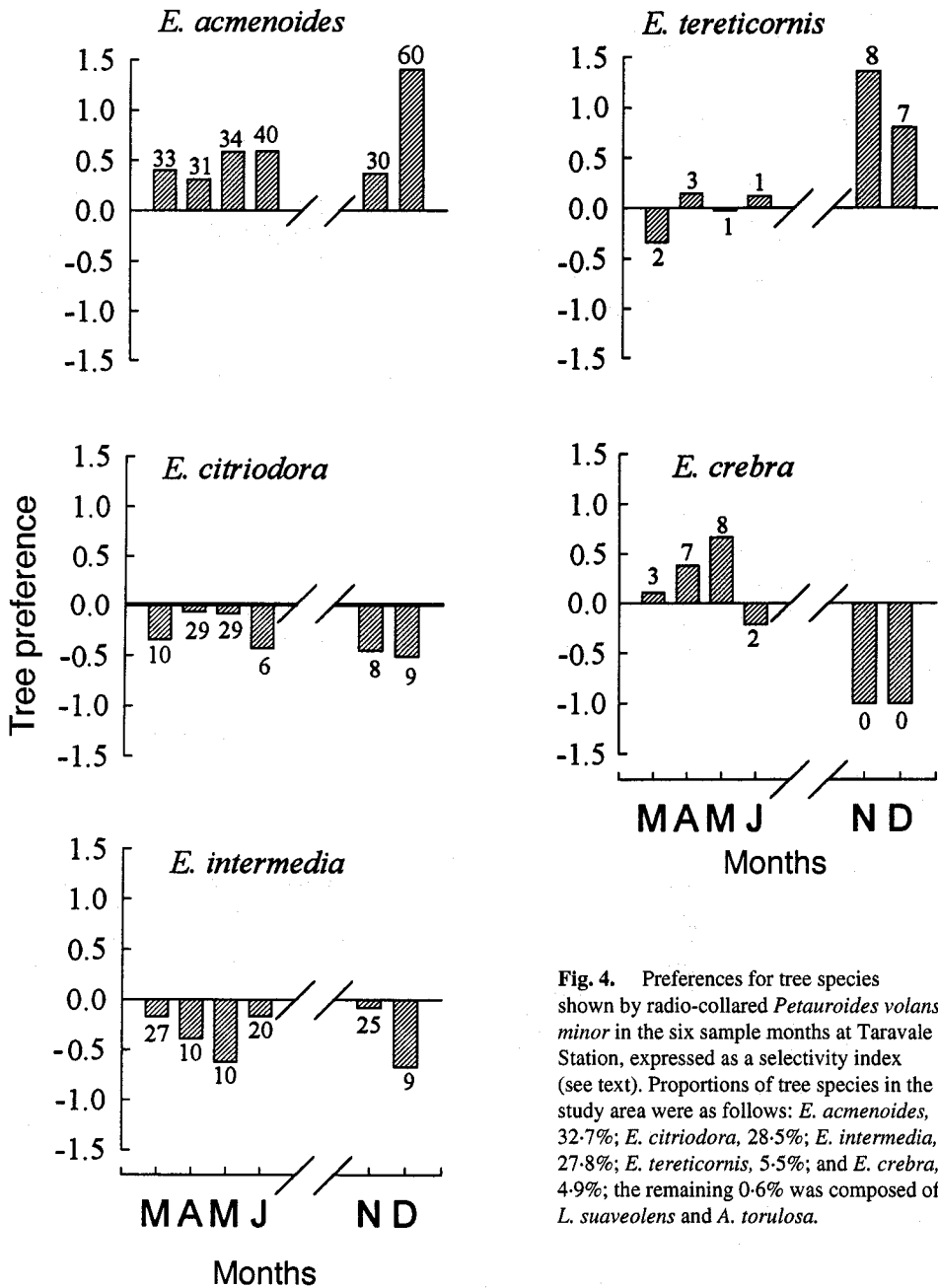
Fig. 4. Preferences for tree species shown by radio-collared *Petauroides volans minor* in the six sample months at Taravale Station, expressed as a selectivity index (see text). Proportions of tree species in the study area were as follows: *E. acmenoides,* 32·7%; *E. citriodora,* 28·5%; *E. intermedia,* 27·8%; *E. tereticornis,* 5·5%; and *E. crebra,* 4·9%; the remaining 0·6% was composed of *L. suaveolens* and *A. torulosa.*

E. tereticornis, followed by *E. citriodora;* highest K concentrations were in *E. citriodora.* The foliage of *E. acmenoides* typically contained low concentrations of all three elements: mature foliage rated fifth, equal fifth and sixth (of six species analysed), for N, P and K, respectively, and young foliage rated sixth for all three elements.
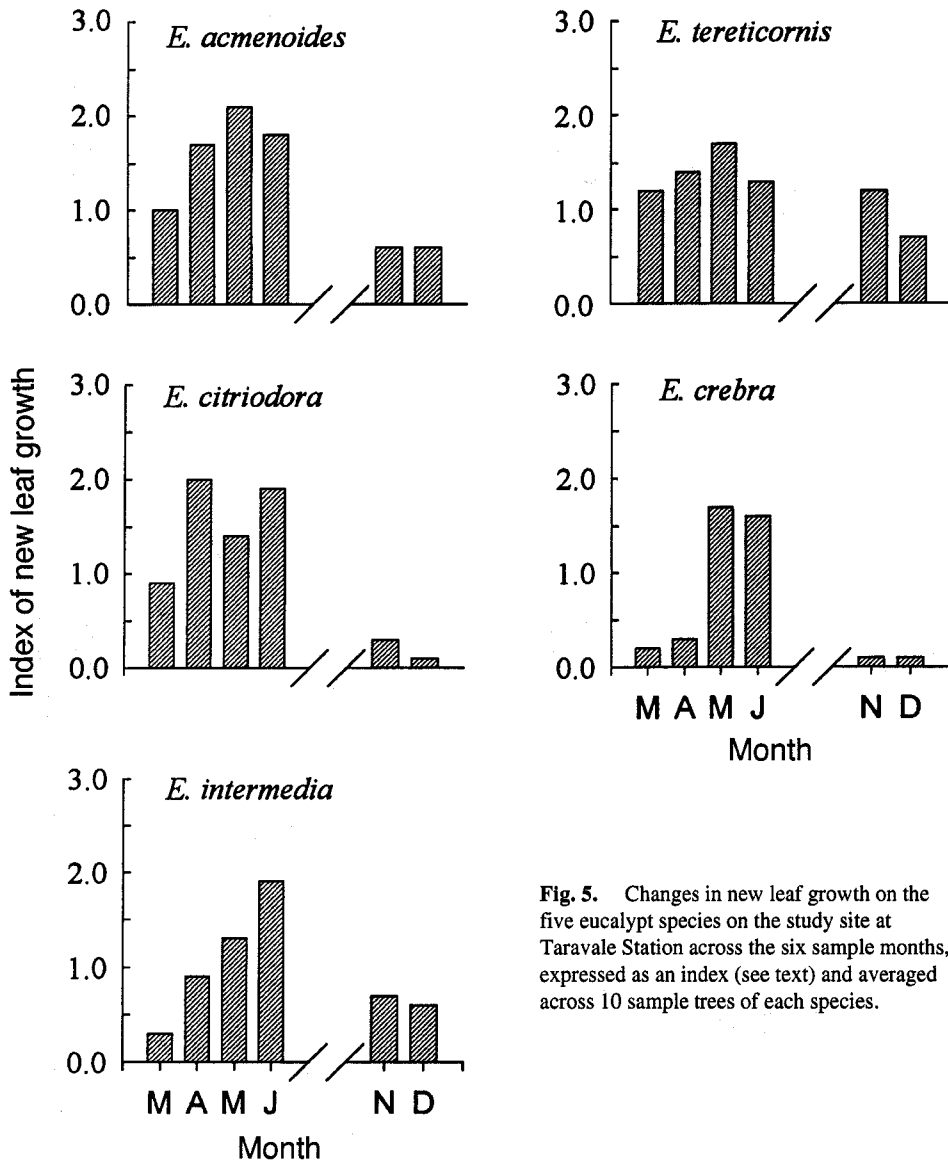
Fig. 5. Changes in new leaf growth on the five eucalypt species on the study site at Taravale Station across the six sample months, expressed as an index (see text) and averaged across 10 sample trees of each species.

Time Budgets and Social Interactions

Resting (40·4%) and feeding behaviours (33·0%) were the most dominant individual activities (Fig. 7). Moving was the next most time-consuming activity (12·5 %), followed by 'other' activities (7·2%) and grooming (5·5%).

Social interactions between *P. v. minor* were rare. Of the 1107 behavioural observations, 1026 (92·7%) were of a single glider in a tree. Two individuals were observed together on 78 occasions (7·0%), while only three observations were made of three gliders in the same tree. Most interactions occurred in November and December, when 31–35% of all observations of resident individuals involved social contact.

Following the categories used by Norton (1988), four types of social interactions between females and males were differentiated, as follows.
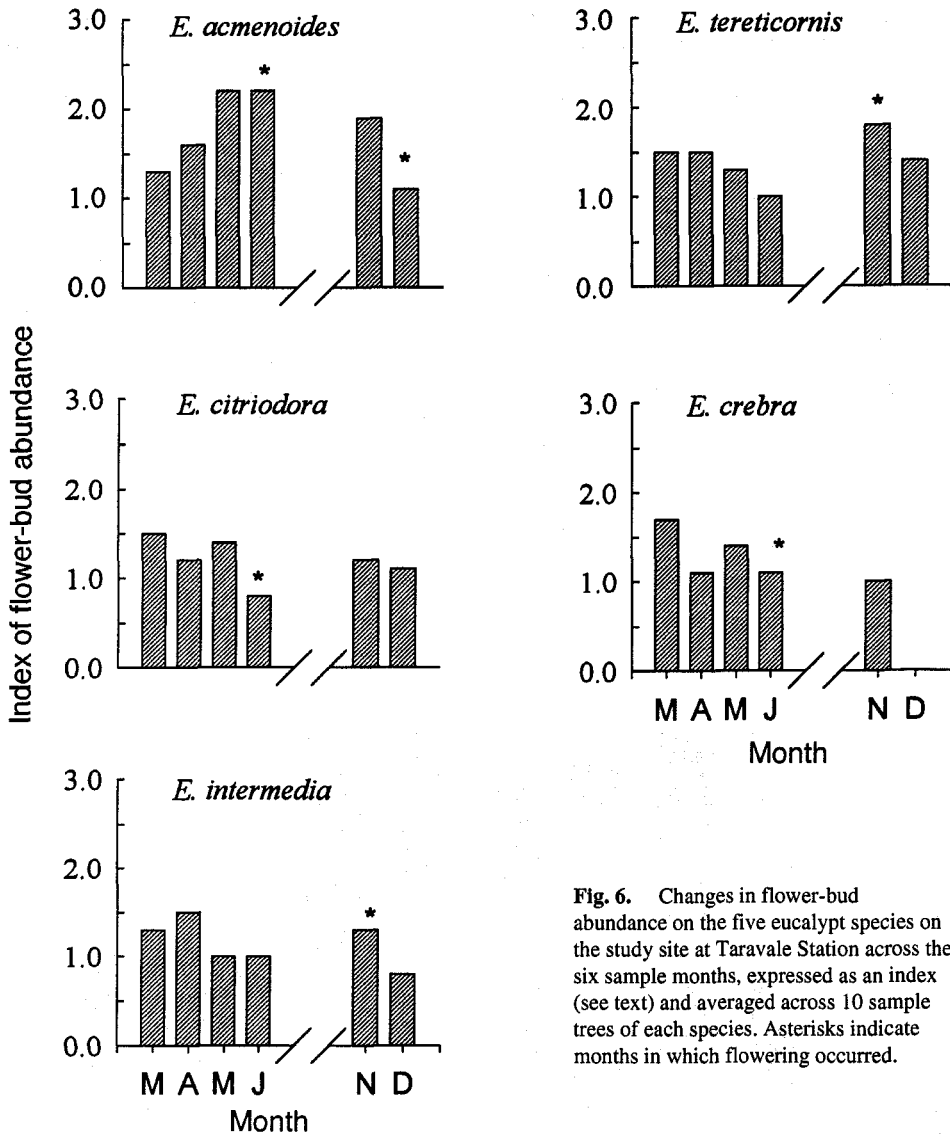
Fig. 6. Changes in flower-bud abundance on the five eucalypt species on the study site at Taravale Station across the six sample months, expressed as an index (see text) and averaged across 10 sample trees of each species. Asterisks indicate months in which flowering occurred.

1. Nasaling. This involved mutual sniffing of the snout. The male and female faced one another and briefly touched noses without any audible vocalisation. This behaviour occurred infrequently (17 occasions), usually when gliders first met during the night, or whenever frequently interacting individuals met in passing. Both sexes initiated nasaling.

2. Mutual sniffing. This behaviour, between a male and female, was noted on four occasions between regular consorts. It involved sniffing at various parts (generally the tail and flanks) of the partner's body. Males initiated this behaviour on three occasions, a female once.

3. Climbing. This involved each glider alternately climbing over the top of the other, and in so doing applying its ventral surface to the dorsal area of the other glider. Climbing was observed twice in November, both times by M3 with a female. On both occasions it was the female that initiated the behaviour, with the male subsequently returning the gesture.

Table 3.   Concentrations (% dry matter ± s.e.) of total nitrogen (N), phosphorus (P) and potassium (K) in the mature (M) and young (Y) foliage of five species of *Eucalyptus* and *Lophostemon suaveolens* at Taravale Station, northern Queensland

Values within a column and within the same leaf age class that bear the same superscripts are not significantly different ($P > 0.05$)

| Species	Leaf age	n	N	P	K
E. citriodora	M	18	0.91 ± 0.01^a	0.07 ± 0.00^d	0.67 ± 0.03^f
	Y	9	1.32 ± 0.05^k	0.12 ± 0.02^n	1.14 ± 0.08^p
E. acmenoides	M	18	0.78 ± 0.02^b	0.05 ± 0.00^n	0.30 ± 0.01^g
	Y	11	1.11 ± 0.04^m	0.09 ± 0.02^n	0.53 ± 0.04^q
E. crebra	M	18	0.72 ± 0.04^b	0.05 ± 0.00^e	0.52 ± 0.03^h
	Y	5	$1.24 \pm 0.06^{k,l}$	0.13 ± 0.01^n	0.88 ± 0.05^r
E. tereticornis	M	18	1.13 ± 0.05^c	0.08 ± 0.00^f	0.39 ± 0.03^s
	Y	5	1.64 ± 0.06^j	0.18 ± 0.02^o	0.99 ± 0.03^s
E. intermedia	M	18	0.88 ± 0.03^a	0.07 ± 0.00^d	0.35 ± 0.02^I
	Y	5	$1.21 \pm 0.04^{k,l}$	0.10 ± 0.01^n	1.13 ± 0.04^p
L. suaveolens	M	9	0.85 ± 0.03^a	$0.06 \pm 0.01^{d,e}$	0.31 ± 0.03^I
	Y	2	$1.19 \pm 0.04^{l,m}$	0.09 ± 0.01^n	0.57 ± 0.04^q
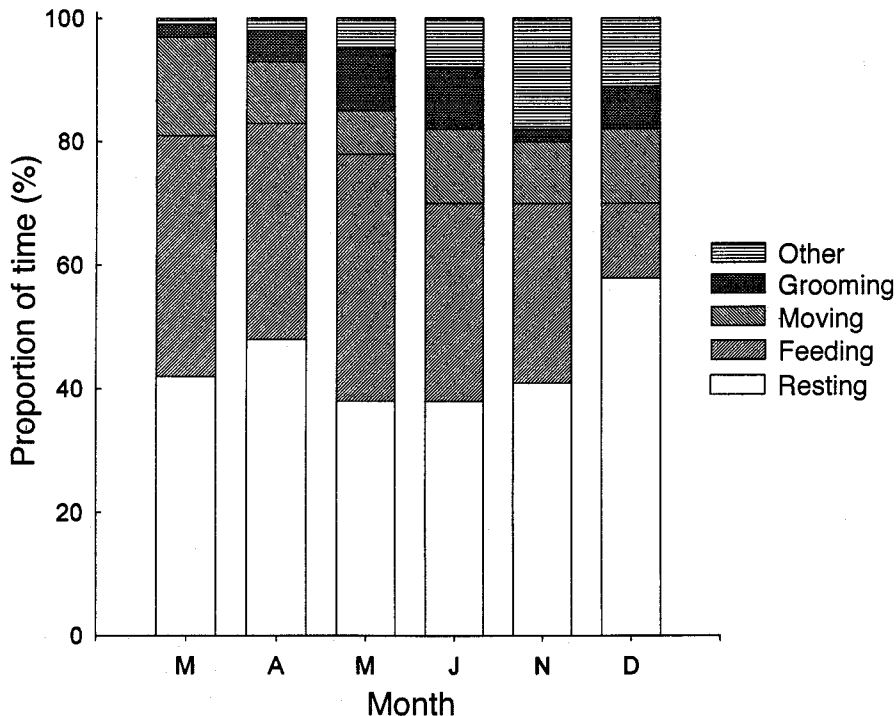
Fig. 7.   Proportions of the dusk–dawn period spent in various activities by male and female radio-collared *Petauroides volans minor* ($n = 6$) at Taravale Station. Each bar represents data from one glider for each month; females were watched in April, June and December.

4. Sitting beside a consort. This behaviour (45 observations) was the most common interaction observed. Typically, two gliders would sit less than 1 m apart and either remain inactive or occasionally forage on nearby leaves. The longest observed duration of this behaviour was 2 h.

Interactions between males were rare and typically non-aggressive. On two occasions in November, two males (M1 and M2) were sitting on the same branch in a tree about 5 m apart (F6 was present in the same tree). Both males were aware of the other's presence, occasionally sniffing the branch while facing the direction of the other glider. No attempt was made to approach the other male and after several minutes the interaction ended with M1 gliding away. However, aggressive behaviour between these two male *P. v. minor* was observed on one occasion. This occurred after M1 had glided to a tree in which M2 was sitting with two unmarked *P. v. minor* (presumed female). M2 chased M1 through several trees (including several glides) for about 10 min before the interaction ended with M1 gliding away. Similar interactions were occasionally observed between unmarked *P. v. minor* on distant parts of the study site. It is assumed that these were also between males, but the details and contexts are unknown.

Discussion

Individuals of *P. v. minor* in a high-density population in the wet–dry tropics of northern Queensland differed in size and in some cases in behaviour from their temperate counterparts. Three major points emerged from this study: first, that home-range areas are similar in size to those reported in temperate populations of *P. v. volans*; second, that home-range overlap between males is extensive; and third, that social interactions were rare in this, as in other, populations of *P. volans*, but that the mating system may differ, possibly as a consequence of the high population density.

Home-range Area

The home-range areas of individuals of *P. v. minor* were relatively small and similar in size to those reported from temperate and subtropical populations of *P. v. volans* (Henry 1984; Kehl and Borsboom 1984). The area required for a home range is determined largely by the interaction of a species' body mass and the distribution of its food resources (McNab 1963). The food resources of folivores tend to be abundant, such that a folivorous animal will require a smaller area for its home range than an equivalent-sized carnivore (Harestad and Bunnell 1979). Body mass plays a role because metabolic rates of animals, and therefore their food requirements, increase with body size (Clutton-Brock and Harvey 1977; Kay and Hylander 1978). For small (<1 kg) folivorous marsupials, such as *P. v. minor*, the low energy value and high fibre content of foliage may restrict dietary intake more than does the availability of foliage. Therefore, an expansion of home-range area is unlikely to result in greater food availability, but it would increase the energy used in locomotion and is unlikely to provide substantial benefits in terms of increased fecundity. This results in relatively small home ranges for this species.

The disparity observed in home-range area between male and female *P. v. minor* is typical of many polygamous mammals and reflects the differences between the sexes in levels of parental investment. It is generally believed (Crook 1972; Emlen and Oring 1977) that, because female mammals depend strongly on the acquisition of food for enhancing reproductive success, the home range adopted will usually reflect the minimum area required to fulfil this. However, because fitness of males is enhanced by mating with as many females as possible, home ranges encompassing several females' ranges are often observed (Trivers 1972; Crook 1972). In the present study, the larger home-range area and multiple core areas of some male *P. v. minor* reflect their attempts to overlap the ranges of several females (e.g. the home-range area of M3 totally overlapped that of F7, and partially overlapped that of F6, F8 and at least one other untagged glider, presumed female).

The overlap of home-range areas of males at Taravale was extensive and has not been reported in other populations of *P. volans*. Clutton-Brock and Harvey (1979) suggested that, in arboreal folivorous primates, higher population densities led to tighter packing of individual home ranges, but that, generally, this did not lead to significant overlap of home ranges of males. Previous studies on *P. volans* have shown that at densities of 1·6–2·3 gliders ha^{-1}, males had home ranges exclusive of other males, but the ranges of females (although mainly exclusive) displayed some overlap within and between sexes (Kehl and Borsboom 1984). Studies of other arboreal folivorous marsupials, such as the common brushtail possum, *Trichosurus vulpecula* (Winter 1977), and the koala, *Phascolarctos cinereus* (Mitchell 1985), have also shown that home ranges of males are not exclusive.

An important feature of the home ranges of male *P. v. minor* is that contact between individuals was minimal, because of the way space was utilised. For example, male and female *P. v. minor* spent most of their time in a small proportion (5–23%) of their home range, thus minimising contact between individuals in adjacent home ranges. In addition, scent-marking was probably the principal method of remote communication, because this species has no loud vocalisations (Henry 1984). Both male and female *P. volans* have cloacal glands that together with urine-dribbling produce a pungent secretion that permeates the den and influences the body odour of adults (Tyndale-Biscoe and Smith 1969).

There was also overlap in the home ranges of female *P. v. minor,* but less than that observed for males. However, we have probably underestimated the degree of overlap between females because of a sampling artefact: home-range overlap could be measured between tagged gliders only but there were at least four untagged gliders in the area of highest overlap on the site. Direct observation indicated that these gliders were female adults.

Feeding Behaviour and Social Interactions

Radio-collared individuals of *P. v. minor* spent most of their time feeding or resting, which is consistent with the conservative energy budget found in this and other arboreal folivores. Cork and Warner (1983) suggested that the intake of foliage by arboreal folivorous marsupials may be limited by the gut-filling effect of the high fibre content. This constraint, together with the small gut capacity of small animals (Parra 1978) and the slow digestion times recorded for folivorous marsupials (Foley and Hume 1987a) supports the notion that gliders, as for brushtail possums, remain stationary for long periods in order to conserve energy (see MacLennan 1984).

Leaves also contain secondary compounds such as essential oils, tannins and phenols (Cork *et al.* 1983; Cork and Pahl 1984), which are thought to disrupt the digestive processes of folivores (Cork and Sanson 1990). Detoxification of these compounds is energetically expensive (Freeland and Janzen 1974). Thus, the high levels of toxins in the eucalypt leaves ingested by *P. v. minor* may aggravate energy-balance problems. Long periods of inactivity have been recorded in *Phascolarctos cinereus* (Smith 1979), *T. vulpecula* (MacLennan 1984), and common ringtail possums, *Pseudocheirus peregrinus* (Cork and Pahl 1984). All of these species rely on eucalypt leaves as their primary food source and as for *P. v. minor* may depend on behavioural mechanisms, such as inactivity, to help maintain an adequate balance of energy.

The small number of associations and interactions between individuals of *P. v. minor* described in this study shows that, despite a high population density (3·3–3·8 ha^{-1}), they are largely solitary. More than 90% of all observations were of individuals alone in a tree. Kavanagh and Lambert (1990) reported higher levels of interaction among greater gliders in south-eastern New South Wales (16%), where there is a lower population density (0·5–1·3 ha^{-1}).

Two key factors that determine group size in arboreal folivores appear to be predation pressure and food abundance and dispersion (Crook 1972; Charles-Dominique 1975). It is generally believed that, where predation is a constant threat, as in the case of diurnal arboreal monkeys subject to predation by eagles, larger group sizes are better able to detect predators (Crook 1972). However, for nocturnal arboreal animals that rely on crypsis for defence, such as *P. volans,* solitary behaviour is adopted. The influence of predation on Australian arboreal

marsupials is poorly understood. One major predator of *P. volans,* the powerful owl, *Ninox strenua,* was reported to have reduced a population of *P. volans* in south-eastern New South Wales by 90% over 46 months (Kavanagh 1988). *N. strenua* is absent from northern Queensland, but the rufous owl, *Ninox rufa,* is present in closed forest, and is a predator of arboreal mammals there (Comport, personal observations). The impact of rufous owls on mammals outside closed forest is poorly understood, but the large distance between the study site and the largest patch of closed forest likely to support rufous owls (*c.* 16 km to Paluma) makes it unlikely that these owls are a major influence on glider populations at Taravale Station.

The distribution of food resources in both time and space, and the quality and abundance of those food resources, also influence animal group sizes (Crook 1972). Despite the apparent abundance of foliage, it is generally a poor-quality resource. The low energy value, high fibre and low nitrogen content of eucalypt leaves means that folivores such as *P. v. minor* must be highly selective when foraging in order to maintain an adequate intake of digestible nutrients. Such foraging is unlikely to be enhanced by feeding in groups. McNab (1978) proposed that the low availability of energy in foliage may prevent more social behaviour through constraints imposed on an individual's energy budget. It may be that larger group sizes have energy and maintenance costs above that which can be supplied on a diet of eucalypt leaves. Indeed, How (1981) noted that, for *T. vulpecula,* activity levels and home-range area increased when the proportion of foliage in the diet declined. The extents to which predation and dietary stress contribute to the solitary behaviour of *P. v. minor* cannot presently be determined.

The contact that six focal gliders kept with at least two members of the opposite sex and the absence of contact with others, even though the home ranges of males and females overlapped, is consistent with the notion of a polygamous mating system in this population. This contrasts with the facultatively polygynous mating system proposed by Henry (1984) for *P. v. volans* in a low-density population (0·56 ha^{-1}) in Victoria. Henry (1984) found that males occupied exclusive home ranges and maintained sole access to consort females by an amalgamation of female- and resource-defence. Where patches were large enough for only two gliders, the two were usually a male and female, but where patches could accommodate three gliders, a male and two females occurred (hence facultative polygyny). Norton (1988) suggested that the mating association adopted by gliders was influenced by the presence or absence of suitable concentrations of high-quality food. At sites with high-quality food, a bigamous mating system was observed, while at sites with low-quality food, gliders were monogamous. At Taravale Station, home-range areas of males overlapped broadly, and access to females appeared unrestricted. In addition, because home ranges of males were not exclusive of one another and overlapped those of females, males were not defending the habitat upon which their partners depended (i.e. resource-defence), but used female-defence. The extensive overlap would also allow opportunistic matings between a range of males and females (although this was never directly observed). Hence, a polygamous mating system may be a consequence of the high-density population of *P. v. minor* at Taravale Station. A similar mating system has been observed in *Phascolarctos cinereus,* where, at higher population densities, home ranges of males are not exclusive; copulations are opportunistic and males defend access to females (Smith 1979).

Greater gliders at Taravale Station denned only in hollow trees, unlike *T. vulpecula* and *Pseudocheirus peregrinus* elsewhere, which are less selective in their choice of den sites (Winter 1977; Munks 1990). The pattern of den-tree use showed that while greater gliders have preferred dens they may attempt to occupy many or all suitable hollows within their home range. Such behaviour may be predator avoidance by being less predictable, parasite avoidance or a mechanism to maintain their home range. The species of tree was apparently important, with *E. acmenoides* and *E. citriodora* being favoured for denning while *E. intermedia* was largely ignored. Denning studies on other species suggest den selection can be influenced by a wide range of factors, relating both to the hollow itself and to the adjacent environment (McCoumb and Noble 1981; Saunders *et al.* 1982; Lindenmayer *et al.* 1990).

Food Selection

Previous studies have highlighted the distinct preference of many arboreal marsupial folivores for restricted sets of eucalypt species (Hindell *et al.* 1985; Hindell and Lee 1988) and for young foliage (Smith 1979; Kavanagh and Lambert 1990). For example, captive koalas eat both young and old eucalypt leaves, but show a distinct preference for young foliage (Smith 1979; Ullrey *et al.* 1981). Individuals of *Pseudocheirus peregrinus* were also found to consume almost exclusively young eucalypt leaves when these were abundantly available (Pahl 1984). *P. volans* has previously been reported to prefer young *Eucalyptus* foliage, and to visit trees according to the amount of young growth present (Kavanagh and Lambert 1990). Young foliage typically has a higher concentration of available energy, moisture, N, P and K (see Table 3), and lower fibre content than mature foliage (Hladik 1978; Ullrey *et al.* 1981; Cork and Pahl 1984). However, it is clear that these fractions alone do not necessarily mean that young foliage is of higher nutritional quality.

Greater gliders at Taravale showed distinct preferences for young foliage of eucalypts and predominantly fed on one species, *E. acmenoides*. The concentrations of N, P and K in foliage of *E. acmenoides* were lower than for the other *Eucalyptus* spp. or *L. suaveolens* at the site; however, the concentrations of fibre, tannins and other polyphenols in the leaves were not examined in this study. Kavanagh and Lambert (1990) found a strong preference for *E. viminalis* by *P. volans* in New South Wales, and associated this with both high nitrogen and low fibre content of the young leaves of this species. In contrast, studies by Cork and Foley (unpublished) have shown that proximate analyses of fibre and tannins, among others, often explain little of the difference in intake and digestibility between different species of eucalypts, and that measures of nutrient concentrations are better used in comparisons at a landscape scale. Selection of *E. acmenoides* at Taravale may have occurred because of its greater and more protracted production of new leaf growth, locally.

In south-eastern New South Wales, densities of *P. volans* are low overall but gliders are concentrated in patches of nutrient-rich forest that roughly reflect differences in underlying soil parent material (Braithwaite 1984). In contrast, the high densities of *P. v. minor* at Taravale are not explainable in terms of a notably high nutrient status of the forest, since N, P and K were in concentrations similiar to those recorded for the forests of New South Wales, and, based on the nutrient models devised for the forests of south-eastern New South Wales, glider abundances would be expected to be substantially lower. Although N, P and K concentrations may be useful indices of foliage quality, they do not directly control the nutritional quality of foliage for arboreal marsupials (Cork and Foley 1991). This suggests that there are other (unknown) factors that play an important role in foliage quality. In this regard, there may be fundamental differences between tropical and temperate eucalypt forests that influence glider abundance.

This study has shown that, in the high-density population of *P. v. minor* at Taravale Station, northern Queensland, there are differences in the mating system and degree of home-range overlap when compared with temperate populations of *P. v. volans*. More data are needed on the social organisation of *P. v. minor* at high and low densities within other tropical populations before the present patterns can be understood. It would also be of interest to determine those factors that are responsible for the high population densities of gliders. This could have implications for the management of tropical forest ecosystems.

Acknowledgments

References

Baethgen, W. E., and Alley, M. M. (1989). A manual colorimetric procedure for measuring ammonium nitrogen in soil and plant Kjeldahl digest. *Communications in Soil Science and Plant Analysis* **20**, 961–9.

Braithwaite, L. W. (1983). Studies on the arboreal marsupial fauna of eucalypt forest being harvested for woodpulp at Eden New South Wales. I. The species and distribution of animals. *Australian Wildlife Research* **10**, 219–29.

Braithwaite, L. W. (1984). The indentifcation of conservation areas for possums and gliders within the Eden woodpulp concession district. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume.) pp. 501–8. (Surrey Beatty & Sons: Sydney.)

Charles-Dominique, P. (1975). Nocturnality and diurnality: an ecological interpretation of these two modes of life by an analysis of the higher vertebrate fauna in tropical forest ecosystems. In 'Phylogeny of Primates'. (Eds W. P. Luckett. and F. S. Szalay.) pp. 69–88. (Plenum: New York.)

Clutton-Brock, T. H., and Harvey, P. H. (1977). Primate ecology and social organisation. *Journal of Zoology (London).* **183**, 1–3.

Clutton-Brock, T. H., and Harvey, P. H. (1979). Home-range size, population density and phylogeny in primates. In 'Primates Ecology and Human Origins'. (Eds I. S. Bernstein and E. O. Smith.) pp. 201–14. (Garland: New York.)

Cork, S. J., and Foley, W. J. (1991). Digestive and metabolic strategies of arboreal mammalian folivores in relation to chemical defences in temperate tropical forests. In 'Plant Defences against Mammalian Herbivory'. (Eds R. T. Palo and C. T. Robbins.) pp. 133–66. (CRC Press: Boca Raton.)

Cork, S. J., and Pahl, L. I. (1984). The possible influence of nutritional factors on the diet and habit of the common ringtail possum (*Pseudocheirus peregrinus*). In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume.) pp. 269–76. (Surrey Beatty & Sons: Sydney.)

Cork, S. J., and Sanson, G. D. (1990). Digestion and nutrition in the koala: a review. In 'Biology of the Koala'. (Eds A. K. Lee, K. A. Handasyde and G. D. Sanson.) pp. 129–44. (Surrey Beatty & Sons: Sydney.)

Cork, S. J., and Warner, A. C. I. (1983). The passage of digesta markers through the gut of a folivorous marsupial, the koala (*Phascolarctos cinereus*). *Journal of Comparative Physiology* **52**, 43–51.

Cork, S. J., Hume, I. D., and Dawson, T. J. (1983). Digestion and metabolism of a natural foliar diet (*Eucalyptus punctata*) by an arboreal marsupial, the koala (*Phascolarctos cinereus*). *Journal of Comparative Physiology* **153**, 181–90.

Crook, J. H. (1972). Sexual selection, dimorphism and social organisation in the primates. In 'Sexual Selection and the Descent of Man, 1871–1971'. (Ed. B. G. Campbell.) pp. 231–81. (Aldine: Chicago.)

Dixon, K. R., and Chapman, J. A. (1980). Harmonic mean measure of animal activity area. *Ecology* **61**, 1040–4.

Emlen, S. T., and Oring, L. W. (1977). Ecology, sexual selection and the evolution of mating systems. *Science* **197**, 213–15.

Foley, W. J. (1987). Digestion and energy metabolism in a small arboreal marsupial, the greater glider (*Petauroides volans*), fed a high terpene *Eucalyptus* foliage. *Journal of Comparative Physiology B* **157**, 355–62.

Foley, W. J., and Hume, I. D. (1987a). Passage of digesta markers in two species of arboreal folivorous marsupials—the greater glider (*Petauroides volans*) and the brushtail possum (*Trichosurus vulpecula*). *Physiological Zoology* **60**, 421–50.

Foley, W. J., and Hume, I. D. (1987b). Nitrogen requirements and urea metabolism in two species of arboreal marsupials—the greater glider (*Petauroides volans*) and the brushtail possum (*Trichosurus vulpecula*), fed *Eucalyptus* foliage. *Physiological Zoology* **60**, 421–50.

Freeland, W. J., and Janzen, D. H. (1974). Strategies in herbivory by mammals: the role of secondary compounds. *American Naturalist* **108**, 269–89.

Goldingay, R. L., and Kavanagh, R. P. (1993). Home-range estimates and habitat of the yellow-bellied glider (*Petaurus australis*) at Waratah Creek, New South Wales. *Wildlife Research* **20**, 387–404.

Harestad, A. S., and Bunnell, F. L. (1979). Home-range and body weight—a revaluation. *Ecology* **60**, 389–402.

Harris, S., Creswell, W. J., Forde, P. G., Trewella, W. J., Woolard, T., and Wray, S. (1990). Home-range analysis using radio-tracking data: a review of problems and techniques as applied to the study of mammals. *Mammalian Review* **20**, 97–123.

Henry, S. R. (1984). Social organisation of the greater glider (*Petauroides volans*) in Victoria. In 'Possums and Gliders'. (Eds A. P. Smith, and I. D. Hume.) pp. 221–8. (Surrey Beatty & Sons: Sydney.)

Hindell, M. A., and Lee, A. K. (1988). Tree use by individual koalas in a natural forest. *Australian Wildlife Research.* 15, 1–7.

Hindell, M. A., Handasyde, K. A., and Lee, A. K. (1985). Tree species selection by free ranging koala populations in Victoria. *Australian Wildlife Research* 12, 137–44.

Hladik, A. (1978). Phenology of leaf production in rainforests of Gabon: distribution and composition of food for folivores. In 'The Ecology of Arboreal Folivores'. (Ed. G. G. Montgomery.) pp. 235–7. (Smithsonian Institute Press: Washington, DC.)

How, R. A. (1981). Population parameters of two congeneric possums, *Trichosurus* spp. in north eastern N.S.W. *Australian Journal of Zoology* 29, 205–15.

Kavanagh, R. P. (1984). Seasonal changes in habitat use by gliders and possums in south-eastern New South Wales. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume.) pp. 221–8. (Surrey Beatty & Sons: Sydney.)

Kavanagh, R. P. (1988). The impact of predation by the powerful owl *Ninox strenua*, on a population of the greater glider, *Petauroides volans*. *Australian Journal of Ecology* 13, 445–50.

Kavanagh, R. P., and Bamkin, K. L. (1990). Distribution of nocturnal forest birds and mammals in relation to the logging mosaic in south-eastern New South Wales, Australia. *Biological Conservation* 71, 41–53.

Kavanagh, R. P., and Lambert, M. (1990). Food selection by the greater glider: is foliar nitrogen a determinant of habitat quality. *Australian Wildlife Research* 17, 285–99.

Kay, R. F., and Hylander, W. L. (1978). The dental morphology of mammalian folivores with special reference to primates and Phalangeroidea. In 'The Ecology of Arboreal Folivores'. (Ed. G. G. Montgomery.) pp. 173–91. (Smithsonian Institute Press: Washington, DC.)

Kehl, J., and Borsboom, A. (1984). Home-range, den tree use and activity patterns in the greater glider (*Petauroides volans*). In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume.) pp. 229–36. (Surrey Beatty & Sons: Sydney.)

Lindenmayer, D. B., Cunningham, R. B., Tanton, M. T., Smith, A. P., and Nix, H. A. (1990). Habitat requirements of the mountain brushtail possum and the glider glider in the montane ash–type eucalypt forests of the central highlands of Victoria. *Australian Wildlife Research* 17, 467–78.

Lunney, D. (1987). Effects of logging, fire, and drought on possums and gliders in the coastal forest near Bega, N.S.W. *Australian Wildlife Research* 14, 263–74.

MacLennan, D. G. (1984). The feeding behaviour and activity pattern of the brushtail possum (*Trichosurus vulpecula*) in an open eucalypt woodland in south-east Queensland. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume.) pp. 155–61. (Surrey Beatty & Sons: Sydney.)

McCoumb, W. C., and Noble, R. E. (1981). Nest-box and natural-cavity use in three mid-south forest habitats. *Journal of Wildlife Management* 45, 93–101.

McNab, B. K. (1963). Bioenergetics and the determination of home-range size. *American Naturalist* 97, 133–41.

McNab, B. K. (1978). The comparative energetics of neo-tropical marsupials. *Journal of Comparative Physiology B* 125, 115–28.

Marples, T. J. (1973). Studies on the marsupial glider, *Schoinobates volans* (Kerr). Feeding biology. *Australian Journal of Zoology* 21, 213–16.

Mitchell, P. (1985). The home-ranges and social activity of koalas — a quantitative analysis. In 'Biology of the Koala'. (Eds A. K. Lee, K. A. Handasyde and G. D. Sanson.) pp. 129–44. (Surrey Beatty & Sons: Sydney.)

Mohr, C. O. (1947). Table of equivalent populations of North American small mammals. *American Midland Naturalist* 37, 223–49.

Munks, S. A. (1990). Ecological energetics and reproduction in the common ringtail possum. Ph.D. Thesis, University of Tasmania, Hobart.

Murphy, J., and Riley, J. P. (1962). A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta* 27, 31–6.

Nix, H. A. (1991). Biogeography: pattern and process. In 'Rainforest Animals, Atlas of Vertebrates endemic to Australia's Wet Tropics'. (Eds H. A. Nix and M. Switzer.) pp. 13–15. (Australian National Parks and Wildlife Service: Canberra.)

Norton, T. (1988). Ecology of greater gliders (*Petauroides volans*) in relation to variations in habitat quality in eucalypt forests in south-east New South Wales. Ph.D. Thesis, Australian National University, Canberra.

Pahl, L. (1984). Diet preference, diet composition and population density of the ringtail possum (*Pseudocheirus peregrinus cooki*) in several plant communities in southern Victoria.   In 'Possums and Gliders'. (Eds. A. P. Smith and I. D. Hume.) pp. 253–60. (Surrey Beatty & Sons: Sydney.)

Parra, R. (1978). Comparison of foregut and hindgut fermentation in herbivores.   In 'The Ecology of Arboreal Folivores'. (Ed. G. G. Montgomery.) pp. 305–13. (Smithsonian Institute Press: Washington, DC.)

Saunders, D. A., Smith, G. T., and Rowley, I. (1982). The availability and dimensions of tree hollows that provide nest sites for cockatoos (*Psittaciformes*) in Western Australia.   *Australian Wildlife Research* **9**, 541–6.

Smith, M. (1979). Behaviour of the koala, *Phascolarctos cinereus*, in captivity. 1. Non-social behaviour. *Australian Wildlife Research* **6**, 117–29.

Specht, R. L. (1981). Foliage projective cover and standing biomass.   In 'Vegetation Classification in Australia'. (Eds A. N. Gillison and D. J. Anderson.) pp. 10–21. (Australian National University Press: Canberra.)

Trivers, R. L. (1972). Parental investment and sexual selection.   In 'Sexual Selection and the Descent of Man, 1871–1971'. (Ed. B. G. Campbell.) pp. 136–79. (Aldine: Chicago.)

Tyndale-Biscoe, C. H., and Smith, R. F. C. (1969). Studies on the marsupial glider (*Schoinobates volans*). II. Population structure and regulatory mechanisms.   *Journal of Animal Ecology* **38**, 637–49.

Ullrey, D. E., Robinson, P. T., and Whether, P. A. (1981). Comparison of preferred and rejected eucalypt browse offered to captive koalas, *Phascolarctos cinereus* (Marsupialia).   *Australian Journal of Zoology* **29**, 839–46.

Winter, J. W. (1977). The behaviour and social organisation of the brushtail possum (*Trichosurus vulpecula*: Kerr). Ph.D. Thesis, University of Queensland, Brisbane.

Worton, B. J. (1987). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**, 164–8.