

Home range and habitat use of a low-density population of greater gliders, *Petauroides volans* (Pseudocheiridae: Marsupialia), in a hollow-limiting environment

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Abstract. Greater gliders, *Petauroides volans*, were radio-tracked within a large tract of forest in the dry inland of southern Queensland. This forest has been commercially logged for timber for more than 100 years. Home-range estimates ranged from 1.4 ha (female) to 19.3 ha (male). Minimum convex polygon (MCP) estimates were larger for males (average, 11.5 ha) than females (average, 3.3 ha) and combined (6.8 ha, sexes pooled) were larger than estimates from other Australian populations. Gliders were located foraging in myrtaceous tree species only, using mostly *Eucalyptus moluccana*, *E. fibrosa* and *Corymbia citriodora*. *E. moluccana* was used for foraging more frequently than would be expected on the basis of its availability in the forest. *E. fibrosa* and *C. citriodora* were used in proportion to their availability in the forest. Gliders were not seen foraging in non-myrtaceous species or myrtaceous trees <20 cm diameter at breast height (dbh), preferring trees in 30–70-cm dbh classes and as ‘mature’ and ‘over-mature’ classified according to growth-stage characteristics. Den tree species included the same species used for foraging as well as dead trees (16% of den trees). *E. fibrosa* and *E. tereticornis* were preferred significantly more than expected by their availability in the forest. Non-myrtaceous species were not used as live den trees. Large (dbh >50 cm) and old living trees (in deteriorating and senescent condition: ‘late mature’ and ‘over-mature’ categories) were primarily used as den trees. Individual gliders utilised 4–20 den trees. Females utilised more den trees per unit area of home range (3.8 den trees ha⁻¹, maximum) than males (0.9 den trees ha⁻¹, maximum). Fewer den trees were used per unit area of home range than by gliders at a coastal location with approximately the same latitude. The density of live stems containing hollows suitable as dens is currently lower than 1 tree ha⁻¹ in some parts of the study forest. Gliders were two and half times less likely to be observed during standardised spotlighting surveys in the study area than elsewhere in southern Queensland. It is likely that low availability of den trees is contributing to large home ranges and the apparent low population density observed in this study.

Introduction

The greater glider, *Petauroides volans*, is distributed in eastern Australia from temperate eastern Victoria, through eastern New South Wales and Queensland, to the tropical north-east of Queensland. It is found in a range of eucalypt forest and woodland types, but prefers taller, moist sclerophyll forests (Eyre 2004; Kavanagh 2004; Van Der Ree *et al.* 2004; Winter *et al.* 2004). The species does not occur in Tasmania (Munks *et al.* 2004). Estimated densities have been variable, reaching numbers up to 2.8 ha⁻¹ in remnant vegetation corridors of fragmented landscapes (Downes *et al.* 1997) and 3.8 ha⁻¹ in tropical forest tracts (Comport *et al.* 1996). Recent reviews (Eyre 2004; Kavanagh 2004; Van Der Ree *et al.* 2004; Winter *et al.* 2004) of conservation status caution that, although greater gliders appear to be secure as a species, some populations have declined or are in decline and that measures should be taken to secure suitable forest containing food and hollow-bearing trees to prevent a decline in distribution and abundance.

Although broad in its distributional range, the greater glider is an ecological specialist. This species feeds primarily on eucalypt leaves, selecting young leaves with higher concentrations of nitrogen and lower ligno-cellulose content than mature leaves

(Kavanagh and Lambert 1990). Favoured tree species vary depending on stand composition, but gliders appear to prefer eucalypt species that have relatively higher concentrations of foliar nutrients (Kavanagh and Lambert 1990) and individual trees that have lower levels of formylated phloroglucinol compounds and terpenes, the latter of which are detected by smell (Foley *et al.* 2004).

For shelter, greater gliders rely on living ‘old growth’ trees and dead stags containing hollows. The greater glider has one of the highest known demands for hollows of any of the arboreal marsupial species that inhabit the sclerophyll forests of eastern Australia, utilising up to 20 hollows per 2 ha of home range (Kehl and Borsboom 1984; Eyre 2002).

Hollows develop extraordinarily slowly in Australian eucalypts, with figures most often quoted as minimum lag times of 150–360 years from germination to the beginning of hollow development (Mackowski 1984; Wormington and Lamb 1999; Gibbons and Lindenmayer 2002). A fall in the number of hollows below a minimum critical threshold for greater gliders could cause a decline in any local population and compromise population viability in the longer term if there is not a new

cohort of hollow trees available to replace trees lost (Lindenmayer *et al.* 1997). Wildfires may accelerate the loss of hollow trees significantly, adding further cause for concern (Possingham *et al.* 1994).

The response of a species to depletion of keystone resources is fundamental to understanding how that species will respond to forest use and different management scenarios, and requires detailed knowledge of biology and ecology of the species across the known extent of its range. Most of the ecological studies of greater gliders have been undertaken primarily along the moister eastern seaboard in relatively nutrient-rich forests (Kavanagh 1984, 1988; Kehl and Borsboom 1984; Lindenmayer *et al.* 1990, 1991a, 1991b; Comport *et al.* 1996; Eyre 2002; Wormington *et al.* 2002), although studies of greater gliders have been conducted in low-rainfall forests (e.g. Henry 1984). Studies have also been undertaken of response to landscape alteration such as forest fragmentation (Lindenmayer *et al.* 2004; Pope *et al.* 2004) and resource depletion such as declining densities of hollow-bearing trees (e.g. Wormington *et al.* 2002).

The present study used radio-tracking to examine home range, den and tree use of a low-density population of greater gliders in a low-rainfall region of southern Queensland. This is also an area that has a long history of timber utilisation and management.

Methods

Study site

This study was undertaken in Barakula State Forest (26°26'S, 150°30'E) ~45 km north of Chinchilla, in southern Queensland (Fig. 1). Barakula State Forest is ~285 000 ha in area and is aptly named after the Aboriginal word meaning tall and big timber (Cameron 1999). The forests of Barakula and surrounds have been logged since the late 1800s and early 1900s (Cameron

1999). Mainly cypress pine, *Callitris* spp., and the hardwoods *Corymbia citriodora*, *Eucalyptus crebra* and *E. fibrosa* subsp. *nubila* have been extracted for timber. Most of Barakula State Forest and surrounding state forests are under grazing lease or permit. Timber harvesting, grazing, burning to promote 'green pick' for stock, burning prescribed by forestry and wildfire have impacted on the forest's ecology. Barakula State Forest has a history of intensive selective tree harvesting, silvicultural treatment and grazing.

Barakula State Forest lies in the southern section of what is known as the Brigalow Belt bioregion (Sattler and Williams 1999). The Great Dividing Range runs westwards through northern Barakula State Forest, separating waters flowing into the Murray–Darling system (Condamine and Balonne catchments) and those flowing to the east coast (Dawson and Boyne/Burnett catchments). The topography is generally undulating with broad low ridges of dissected, Jurassic-aged sandstone and laterised sandstone hills (Sattler and Williams 1999). The geology comprises sedimentary sandstone bedrock, primarily Cainozoic and Tertiary or basalt-based clays. Igneous intrusions are scattered throughout the area, particularly to the east and north. Stony hills occur primarily in the north and west of the state forest.

Our study sites were in the eastern section of Barakula State Forest (Fig. 1). Three study sites were selected on the basis of their ease of access and known presence of greater gliders. Measured from centre to centre, Site 1 (18.1 ha) was 2.2 km from Site 2 (5.5 ha) and 4.9 km from Site 3 (19.3 ha), while Site 2 was 2.8 km from Site 3. The study sites were located in a part of the Great Dividing Range consisting of low flat alluvial systems and low, rocky ridges vegetated with cypress and hardwood forest associations. Site 1 was situated along a creek flat, while Sites 2 and 3 were on broad, low sandstone ridge country.

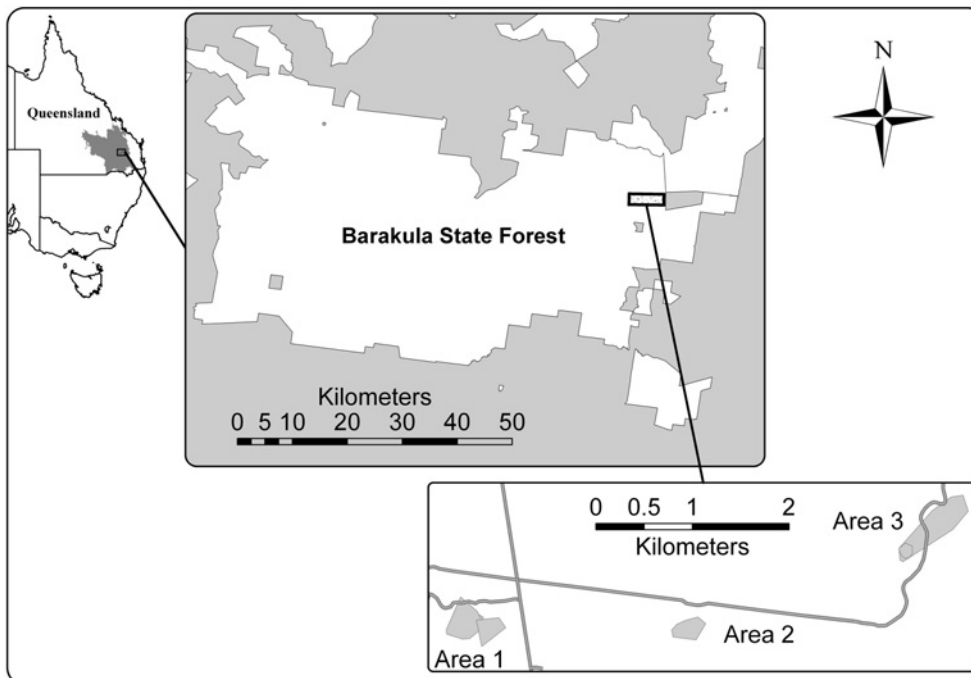


Fig. 1. Maps showing the extent of the southern brigalow belt bioregion (shaded) in Queensland, the location of Barakula State Forest and the location of the three study sites within Barakula State Forest.

Tree stand composition

Information on species, size and growth stage of trees was collected from polygons, arbitrarily located within areas occupied by gliders at each site. In total, 4 ha were sampled at Site 1, 0.7 ha at Site 2 and 3 ha at Site 3 (~10–15% of the area occupied by gliders at each site). The size of all trees was recorded using a 'dbh tape' as diameter at breast height (dbh) and trees were grouped into one of the following seven classes: 10–20 cm, 20–30 cm, 30–40 cm, 40–50 cm, 50–60 cm, 60–70 cm, >70 cm. Stems less than 10 cm dbh were not recorded. Cypress trees were recorded as either live or dead only. Myrtaceous trees (the predominant family of tree in the study area and those most typically utilised by gliders) were assigned to growth-stage categories as follows: 'regenerating' R, 'young' Y, 'early mature' E, 'mature' M, 'late mature' L, 'over-mature' O, 'indeterminate' I and 'dead' standing tree or stag DEAD according to a classification system adopted by Eyre *et al.* (2000). Trees were described by both size and growth stage because size was not always a good descriptor of growth stage and *vice versa*.

Capture, collaring and radio-tracking

A firearm was used to shoot out the branch on which each glider sat while resting or foraging at night (Kehl and Borsboom 1984; Kavanagh and Wheeler 2004; Pope *et al.* 2004). The animals were subsequently caught by hand on the ground and collared at the point of capture with Sirtrack™ (Private Bag 1403, Goddard Lane, Havelock North, NZ) two-stage transmitters with brass loop antennae. Eight animals (four males and four females) were collared. The collar from one individual was retrieved at the completion of the study. Other collars were not recovered where animals had disappeared from the study site (3 individuals), where collars had been dropped inside a hollow tree (3 individuals) or where the collar had been consumed by a python (1 individual). Animals were tracked to nocturnal (foraging) and diurnal (den) locations using hand-held 3-element Yagi antennae. Positional information was determined using Garmin™ hand-held GPS 12 XL recorders (1200 E. 151st Street, Olathe, KS, USA) in order to determine home range and use of den and feed trees. Species, size (dbh) and growth stage (Eyre *et al.* 2000) of trees used during the day as dens and at night for movement, feeding and resting (collectively called foraging locations) were recorded. The radio-tracking study was conducted from 22/8/2001 to 13/2/2003. During 26 field trips of 1–4 days duration, den locations were obtained during daylight hours, once per day for each individual and once per night for foraging locations (on a few occasions twice).

Spotlighting surveys

Spotlighting surveys were carried out within and in state forests adjacent to Barakula State Forest before and during the radio-tracking component of the study to provide an index of glider presence. Forty surveys consisting of half-hour observations by two observers, using 30-W spotlights over 200-m or 300-m transects, were conducted from 1993 to 2000. Transects were targeted primarily to eucalypt hardwood forests, which contained varying amounts of cypress. All transects were off forestry tracks and roads and were distributed at random in both space and time (i.e. not specific to a time of year).

Additional spotlighting data for other eucalypt forests within southern Queensland were obtained during a Comprehensive Regional Assessment of forest resources in south-east Queensland (Eyre *et al.* 1998) and an assessment of resources in the 'western hardwoods' forestry-allocation zone (Kelly *et al.* 2003). Rates of greater glider encounter from standardised transects (300 m long, assessed by two observers during half-hour searches) were compiled from a database containing these data for comparison with data obtained from this study.

Home-range area calculation

Minimum convex polygons (MCP: Mohr 1947) for each glider were obtained using ArcGIS™. Fixed-kernel models were used to calculate kernel home-range estimates in Arcview™, using Hooge's algorithm (Worton 1989; Hooge *et al.* 1999). Home-range area estimates were compared with published MCP and kernel estimates by Henry (1984), Kehl and Borsboom (1984), Norton (1988), Kavanagh and Wheeler (2004) and Pope *et al.* (2004). Densities for each site (Table 4) were calculated as the number of individuals observed at each site divided by the area of those sites.

Statistical analyses

Student's *t*-tests and analysis of variance (Sokal and Rohlf 1981) were used to analyse for differences in use of den trees. The relationship between MCP and the number of position fixes obtained for each individual glider was analysed by regression analysis. Tests for 'goodness of fit' using the G-statistic (Sokal and Rohlf 1981) were used to analyse for preferences exhibited by gliders for species, size and growth stages of den and foraging trees based on expected frequencies generated from the available trees within the study forest. Data were pooled from the three study sites for these analyses.

Results

Home ranges

Eight gliders, consisting of 4 females and 4 males, were fitted with radio-collars and tracked (Table 1). Home ranges were calculated for 7 individuals on the basis of trees used, where some trees were used on multiple occasions. These comprised two females (14 locations for F1-A1 and 12 locations for F4-A1) and two males (22 locations for M2-A1 and 11 locations for M4-A1) at Site 1, there being insufficient data for a calculation for male M3-A1. Female F1-A1 disappeared during the course of tracking. The home-range estimate for Female F2-A2 at Site 2 was based on 38 locations. F2-A2 was consumed by a python ~14 months after first collaring. The snake containing transmitter and largely digested glider were located in a hollow log on the ground, inside the animal's home range. Home-range estimates at Site 3 were derived from 20 locations for Female F3-A3 and 38 locations for Male M1-A3.

Home ranges for the seven individuals are mapped as minimum convex polygons (MCP) in Fig. 2. The polyhedral MCP home ranges were roughly circular to elliptical in shape. Male M1-A3 at Site 3 had a particularly elongated, elliptical home range. Overlap between home ranges was evident between males and females (Sites 1 and 3). Much of the home range of Female F1-A1 at Site 1 was contained within that of

Male M2-A1 and the home range of F4-A1 was totally enclosed within that of M2-A1. The two females at Site 1 had exclusive home ranges. The home range of Female F3-A3 at Site 3 was contained within that of Male M1-A3. Only one female was tracked at Site 2, but another individual was seen in the same tree as this female on one occasion, indicating that there was an overlap with at least one other individual. The sex of this individual was not determined as an attempt to capture it failed.

Average MCP home range, sexes combined, was 6.8 ha (s.d. = 6.2, $n = 7$). MCP home-range polygons ranged from 1.4 ha (Female F3-A3, from 41 tracked positions) to 19.3 ha (Male M1-A3, from 64 tracked positions) (Table 1). MCP areas obtained for each individual were plotted against the number of position fixes obtained for each individual (Fig. 3). Home-range asymptotes were evident for four of the seven individuals for which MCPs were calculated (M1-A3, F1-A1, F2-A2 and F3-A3). MCP areas for the other three individuals were probably underestimates. However, a regression analysis indicated that for the sexes combined, home-range area was not dependent on the number of position fixes ($F = 2.3$, d.f. = 1,5, $P > 0.05$). It is likely that MCP areas calculated for all females were better home-range estimates than for males. Had further tracking of M2-A1 and M4-A1 been possible it is likely that MCP estimates would have been larger.

Home-range areas of males were mostly larger than those of females, but the particularly large male home range at Site 3 resulted in a high mean and standard deviation. The average male home range was 11.5 ha (s.d. = 7.2, $n = 3$) and that for females was 3.3 ha (s.d. = 2.1, $n = 4$). The difference between sexes only approached significance ($t = 2.2$, d.f. = 5, $0.05 < P < 0.1$). Mean kernel home range, sexes combined, was 6.9 ha (s.d. = 5.5, $n = 7$). Kernel estimates (95%) of home range among individuals spanned 1.8 to 17.8 ha. Kernel home ranges (95%) for males averaged 10.8 ha (s.d. = 6.7, $n = 3$) and for females averaged 4.1 ha (s.d. = 2.3, $n = 4$). Kernel home-range estimates were similar to the MCP estimates.

Stand composition at the study sites

Dominant tree species at each site were: Site 1: *Callitris* spp. (84 ha⁻¹), *Eucalyptus moluccana* (68 ha⁻¹), *E. tereticornis* (41 ha⁻¹) and *Angophora floribunda* (26 ha⁻¹); Site 2: *E. fibrosa* subsp. *nubila* (169 ha⁻¹), *Callitris* spp. (103 ha⁻¹), *C. watsoniana* (60 ha⁻¹) and *C. citriodora* (43 ha⁻¹); and Site 3: *C. citriodora* (86 ha⁻¹), *E. fibrosa* subsp. *nubila* (68 ha⁻¹) and *E. crebra* (32 ha⁻¹). The density of dead trees was similar across the sites, ranging from 41 to 46 stems ha⁻¹.

Trees of the various growth-stage categories fell predominantly into size ranges as follows: 95% of all 'regenerating' trees into the 10–20-cm dbh category, 92% of 'young' stems were in the 10–30-cm dbh, 81% of 'early' growth phase trees were in the 20–40-cm dbh, 90% of 'mature' trees were in the 30–60-cm dbh, 92% of 'late mature' trees were over 40 cm dbh and 78% of 'over-mature' trees were greater than 50 cm dbh, with no stems in the 10–30-cm size range. Growth-stage categories typically spanned size categories.

In all, 65% of trees in the study sites were 10–30 cm in diameter, and 40% of trees within the study sites were relatively small and, by corollary, were 'young' trees. 'Late mature' (4%) and 'over-mature' (2%) eucalypts (combined density of 10.9 trees ha⁻¹) and eucalypts greater than 60 cm dbh (14% of stems, density of 6.4 trees ha⁻¹) were relatively uncommon. Dead stems >10 cm dbh comprised approximately one-third of the standing stems in the forest.

Use of trees for foraging

Gliders were located foraging at night in six tree species and a hybrid, all myrtaceous species. Despite cypress comprising almost one-fifth of total forest stems, gliders were never recorded in cypress. The species used were *Eucalyptus fibrosa* subsp. *nubila*, *E. tereticornis*, *Corymbia watsoniana*, *E. moluccana*, *Angophora floribunda*, *C. citriodora* and the *E. crebra* × *populnea* hybrid (Fig. 4). Gliders were not observed in other infrequently occurring myrtaceous species (*A. leiocarpa*,

Table 1. Individual gliders tracked, with relevant tracking and home-range data

IDs refer as follows: F = female, M = male and site where tracked, A1 = Site 1, A2 = Site 2 and A3 = Site 3. n = number of locations for each glider

ID	Site	Tracking period	Days tracked	Total no. of dens or diurnal fixes (no. of dens or diurnal trees used)	Total no. of foraging or nocturnal fixes (no. of foraging or nocturnal trees used)	MCP home-range size (ha)	95% kernel estimate home-range size (ha) (Hooge's statistic, n)	Den trees ha ⁻¹ based on MCP
F1-A1	1	22.viii.2001–24.i.2002	16	16 (6)	10 (8)	4.8	5.5 (30.0, 27)	1.3
F2-A2 ^A	2	4.ix.2001–14.xi.2002	49	50 (18) ^D	26 (20)	5.5	6.5 (25.7, 76)	3.3
F3-A3	3	30.v.2002–13.ii.2003	29	29 (10)	13 (10)	1.6	1.8 (20.0, 41)	6.3
F4-A1	1	3.vii.2002–22.viii.2002	9	9 (6)	6 (6)	1.4	2.5 (20.0, 15)	4.3
M1-A3	3	30.viii.2001–13.ii.2003	49	49 (20)	18 (18)	19.3	17.8 (50.0, 64)	1.0
M2-A1	1	21.v.2002–14.xi.2002	30	30 (9)	16 (13)	10.0	10.1 (45, 43)	0.9
M3-A1 ^B	1	25.vi.2002–4.vii.2002	2	2 (2)	1 (1)			
M4-A1 ^C	1	3.vii.2002–13.xi.2002	10	10 (4)	7 (7)	5.2	4.5 (35.1, 14)	0.8

^AConsumed by python.

^BTransmitter dropped inside den tree.

^CRecollared following loss of original collar inside tree hollow.

^DOne den tree located at night as animal sought refuge from spotlight.

E. exserta, *E. populnea* and *E. rubiginosa*: comprising 26% of the ‘other’ category in Fig. 4). *E. fibrosa* subsp. *nubila*, *E. moluccana* and *C. citriodora* were the most-used foraging tree species and also the most abundant myrtaceous species across sites. However, analysis of myrtaceous tree numbers indicated that gliders did not use these species in proportion to their abundance across the sites ($G = 39.7$, d.f. = 8, $P < 0.001$).

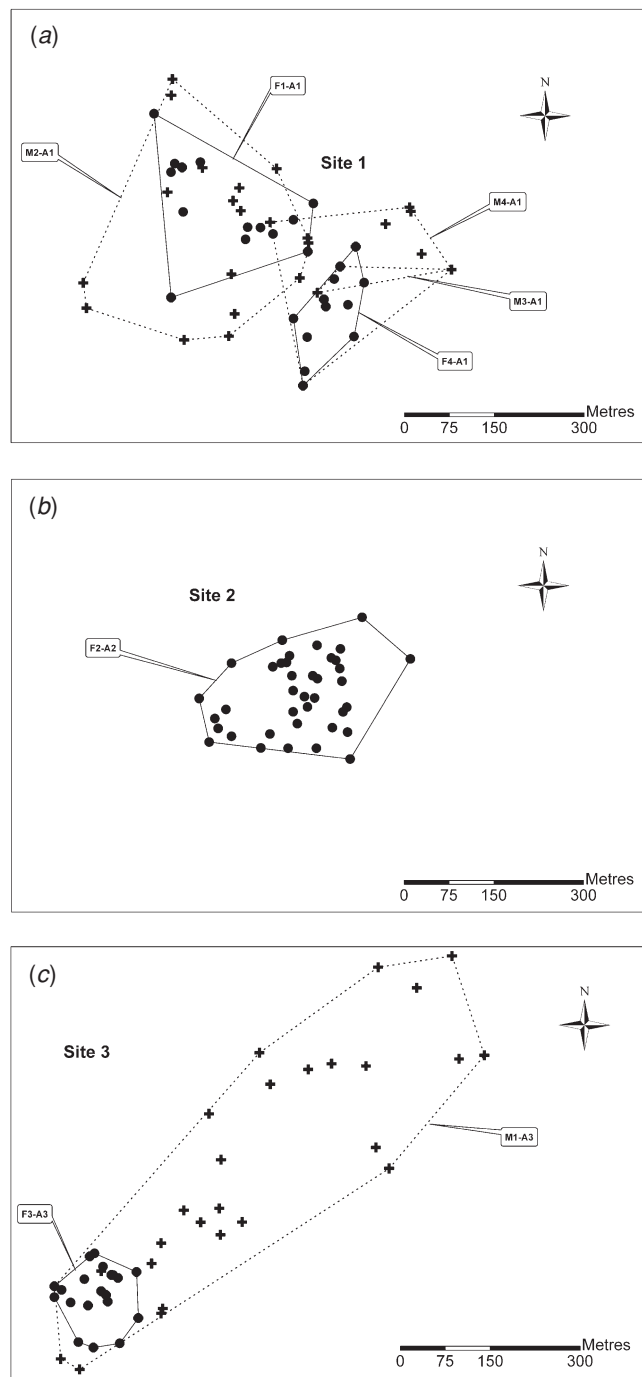


Fig. 2. Map showing the home ranges (minimum convex polygons only) of greater gliders at Sites 1–3. Male positions are shown as crosses and female positions as shaded circles.

E. moluccana was the most prevalent myrtaceous species at Site 1, where *E. fibrosa* and *C. citriodora* were absent, and therefore was used significantly more than expected as a foraging tree species ($G = 9.4$, d.f. = 1, $P < 0.01$). *E. fibrosa* ($G = 0.2$, d.f. = 1, $P > 0.05$) and *C. citriodora* ($G = 1.7$, d.f. = 1, $P > 0.05$) were used in proportion to their abundance.

Male gliders foraged in live trees of 23–74 cm dbh and females in the 20–72-cm dbh range. Fig. 5 shows use of trees for foraging according to size and age class of trees, and the overall relative availability of trees in these classes. There was a significant relationship between foraging and size class of tree ($G = 105.4$, d.f. = 6, $P < 0.001$). Trees in the 10–20-cm dbh class were significantly avoided ($G = 71$, d.f. = 1, $P < 0.001$) despite this being the most abundant size class, while foraging was recorded in all larger size classes (Fig. 5a). Lower than expected foraging was observed in trees in the 20–30-cm dbh class, based on the tree abundance in this class ($G = 7.1$, d.f. = 1, $P < 0.01$).

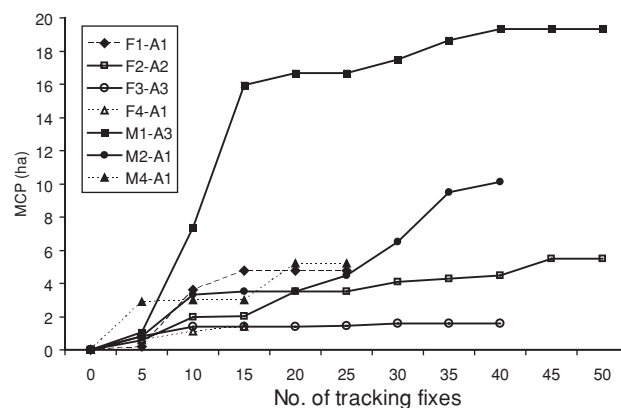


Fig. 3. MCP home-range areas for each tracked glider (except M3-A1, owing to insufficient data points) plotted against numbers of location fixes in units of five fixes for each glider. The maximum number of fixes has been cut off at 55. MCP areas did not increase any further for M1-A3 or F1-A2 beyond the cut-off.

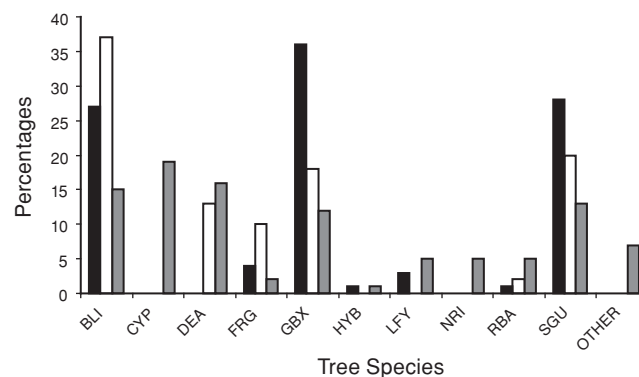


Fig. 4. Percentages of tree species used by gliders as dens ($n = 60$ den trees; open bars), tree species used for foraging ($n = 81$ foraging trees; solid black bars) and trees available (grey bars) across the three study sites. Species codes are as follows: BLI, *Eucalyptus fibrosa* subsp. *nubila*; CYP, *Callitris* sp.; DEA, dead; FRG, *E. tereticornis*; GBX, *E. moluccana*; HYB, hybrid eucalypt; LFY, *Corymbia watsoniana*; NRI, *E. crebra*; RBA, *Angophora floribunda*; SGU, *C. citriodora*.

More trees than expected were used for foraging by gliders in the 30–40-cm ($G = 16.5$, d.f. = 1, $P < 0.001$), 40–50-cm ($G = 6.1$, d.f. = 1, $P < 0.05$), 50–60-cm ($G = 8.5$, d.f. = 1, $P < 0.01$) and 60–70-cm ($G = 14.8$, d.f. = 1, $P < 0.001$) classes.

Gliders did not use growth-stage classes of live trees (excluding ‘indeterminate’) according to their availability within the forest ($G = 36$, d.f. = 5, $P < 0.001$) (Fig. 5b). Gliders were not observed foraging in ‘regenerating’ trees. Most gliders were tracked to foraging positions in ‘young’ (27% of stems used), ‘early mature’ (26% of stems) and ‘mature’ (28% of stems) trees. Although gliders foraged extensively in ‘young’ trees, they were used less frequently than expected on the basis of their relative abundance in the forest ($G = 23.8$, d.f. = 1, $P < 0.001$).

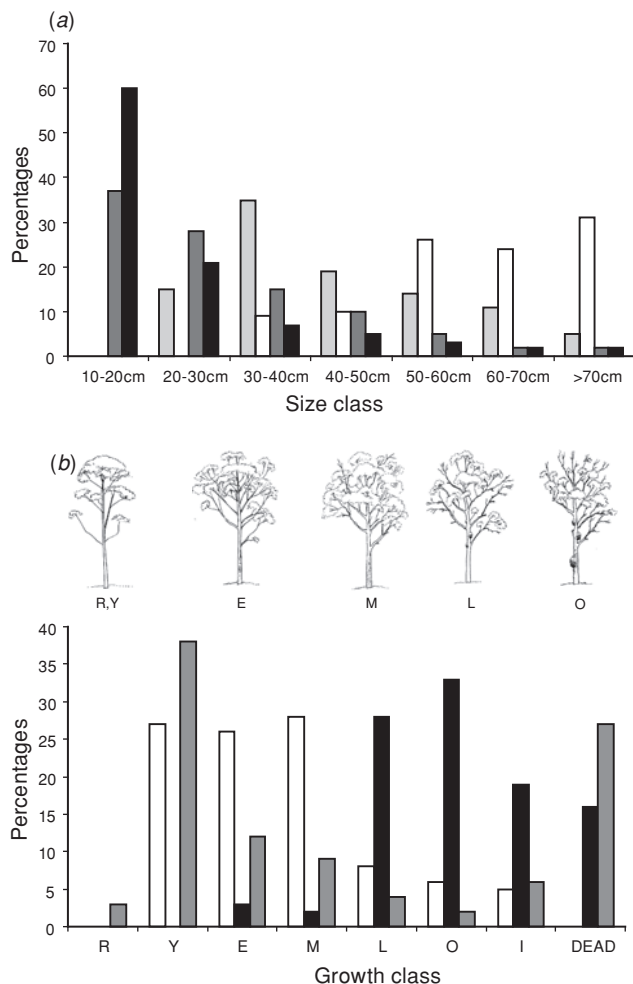


Fig. 5. (a) Percentages of live foraging trees (light grey bars) and den trees (open bars) used by gliders and available trees (live: dark grey; dead: solid black bars) plotted against diameter at breast height (dbh) categories and (b) percentages of live foraging trees (open bars) and den trees (solid black bars) used by gliders plotted together with percentages of available trees (grey bars) occurring in growth categories (as per Eyre *et al.* 2000) across the three study areas, where, on the x-axis, r = regenerating, Y = young, E = early, M = mature, L = late mature, O = over-mature, I = indeterminate, DEAD = dead standing tree or stag. Pictorial representations of categories are taken from Eyre *et al.* (2000) as reproduced from Clode and Burgman (1997).

Gliders foraged in ‘early mature’ trees consistent with their relative abundance ($G = 3.1$, d.f. = 1, $P > 0.05$). ‘Mature’ trees were selected more frequently than expected on the basis of their availability ($G = 12.9$, d.f. = 1, $P < 0.001$). There were few observations of foraging in ‘late mature’ (8% of stems) and ‘over-mature’ (6% of stems) trees. ‘Late mature’ stems were selected as foraging trees on the basis of their relative abundance ($G = 0.9$, d.f. = 1, $P > 0.05$), while ‘over-mature’ trees were used significantly more than expected ($G = 4.1$, d.f. = 1, $P < 0.05$).

Use of trees for denning

Dens were found in five myrtaceous tree species (Fig. 4). Gliders were not found to den in cypress trees, presumably because they do not form suitable hollows. In total, 16% of stems used as den trees were dead. Live den species included *E. fibrosa* subsp. *nubila*, *E. tereticornis*, *E. moluccana*, *A. floribunda* and *C. citriodora* (Fig. 4). Gliders did not den in these myrtaceous species in proportion to their abundance across the sites ($G = 37.1$, d.f. = 8, $P < 0.001$). The most common species used as den trees were *Eucalyptus fibrosa* subsp. *nubila*, *E. moluccana* and *C. citriodora*. *E. moluccana* and *C. citriodora* were used according to their availability across the sites ($G = 0.4$, d.f. = 1, $P > 0.05$ and $G = 0.1$, d.f. = 1, $P > 0.05$, respectively), while *E. fibrosa* was more likely to be used as a den species than would be expected by its availability ($G = 7.6$, d.f. = 1, $P < 0.01$). *E. tereticornis* (present only at Site 1) was also used more than expected on the basis of its availability ($G = 6.8$, d.f. = 1, $P < 0.01$).

Den trees used by males ranged from 43.2 cm to 156.5 cm dbh, while those for females ranged in size from 30 to 91.7 cm dbh. Fig. 5a shows den use according to the size of trees, and the overall relative availability of trees in these classes across sites. Gliders did not use trees within size classes according to their availability ($G = 216.4$, d.f. = 7, $P < 0.001$). Dens were not recorded in trees up to 30 cm dbh in size. Numbers of den trees within the 30–40-cm and 40–50-cm dbh classes of myrtaceous and dead trees occurred as expected relative to their availability ($G = 0.9$, d.f. = 1, $P > 0.05$ and $G = 0.1$, d.f. = 1, $P > 0.05$, respectively). The most common size of live and dead trees used for den trees were assigned to classes greater than 50 cm dbh (81% of stems). Significantly more trees than expected were used as den trees within the 50–60-cm, 60–70-cm and >70-cm dbh classes based on availability ($G = 29.5$, d.f. = 1, $P < 0.001$; $G = 43.2$, d.f. = 1, $P < 0.001$; and $G = 72.8$, d.f. = 1, $P < 0.001$, respectively).

The live component of den trees comprised primarily ‘late mature’ or ‘over-mature’ stems (92% of live trees excluding ‘indeterminate’ category or 71% including ‘indeterminate’ trees) (Fig. 5b). ‘Regenerating’ and ‘young’ growth classes did not provide dens for gliders and very few ‘early mature’ and ‘mature’ trees were used as dens. Overall, gliders did not use live trees from the various age classes (excluding ‘indeterminate’) according to their availability across sites ($G = 169.1$, d.f. = 5, $P < 0.001$). ‘Early mature’ and ‘mature’ classes were utilised significantly less than expected by their availability within the forest ($G = 5.6$, d.f. = 1, $P < 0.05$ and $G = 5.1$, d.f. = 1, $P < 0.05$, respectively). ‘Late mature’ and ‘over-mature’ trees were used more than expected by their availability ($G = 43.8$,

d.f. = 1, $P < 0.001$ and $G = 86.7$, d.f. = 1, $P < 0.001$, respectively). Although large old trees in senescing condition were scarce in the study forest, gliders selected these rare stems as den trees, presumably because of the hollows they contained.

Dens and den use

Male greater gliders used 4–20 separate den trees (mean = 11, s.d. = 8.2, $n = 3$); male M3-A1 was excluded from this statistic as data were limited. Females utilised 6–18 den trees (mean = 10, s.d. = 5.6, $n = 4$) (Table 1). The number of den trees used by individuals was positively related to tracking effort (Fig. 6a). Female home ranges contained, on average, 3.8 den trees ha^{-1} (s.d. = 2.1, $n = 4$), which was greater than the 0.9 den trees ha^{-1} (s.d. = 0.1, $n = 3$) recorded in male home ranges (Table 1). The difference between the sexes approached statistical significance ($t = 2.4$, d.f. = 5, $0.05 < P < 0.1$).

Approximately one-third of all dens were visited only once by an individual during the study. Visits per individual per tree did not increase significantly in relation to increased search effort (Fig. 6b). There were two outliers: Male M2-A1 used an *E. moluccana* (dbh 50.6 cm) on 12 occasions and Male M1-A3 occupied an *E. fibrosa* subsp. *nubila* (dbh 61.1 cm) on 10 occasions. Both were clearly the primary dens for these individuals. The *E. fibrosa* subsp. *nubila* occurred at the centre of the home range occupied by Female F3-A3 and she shared this den tree with M1-A3 on four concurrent occasions. A total of 12 den trees on Sites 1 and 3 were shared serially or concurrently by individuals within each site.

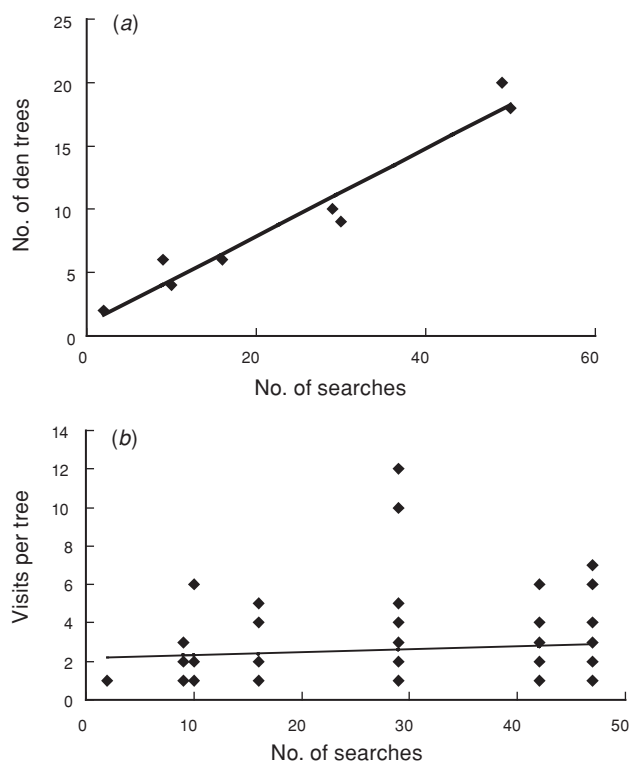


Fig. 6. (a) Den tree numbers per individual plotted against number of search days and (b) visits per den tree per individual plotted against number of search days.

Table 2. Mean visits per den tree per individual by size of tree

Tree dbh category	Mean visits per tree (s.d., n)
30–40 cm	3.2 (1.3, 5)
40–50 cm	1.5 (0.8, 6)
50–60 cm	2.9 (2.6, 19)
60–70 cm	2.8 (2.4, 16)
>70 cm	2.4 (1.6, 23)

Visits per individual per den tree were assigned to size and growth stage of trees (Tables 2, 3). The data on visits per individual per tree were square-root transformed to test for significant differences between size and growth categories. No significant differences were detected in rates of visitation per individual between either size ($F = 0.92$, d.f. = 4,64, $P > 0.05$) or growth categories ($F = 0.48$, d.f. = 3,54, $P > 0.05$).

Greater gliders encountered on broad spotlighting surveys

Greater gliders were present at 14% of sites ($n = 40$ sites) surveyed for arboreal marsupials in Barakula and forests in the immediate vicinity. These forests have had a history of forestry activity similar to that outlined for Barakula. Surveys over a broader area of the ‘western hardwoods region’ comprised less intensively managed forests. Overall encounter rate from 190 transects conducted over the wider area of the southern brigalow belt (comprising the ‘western hardwoods region’) was 36% (Queensland Government database; T. Eyre, pers. comm.).

Discussion

The ecology of the greater glider has been investigated along the east Australian seaboard, from the southern forests of Victoria (Henry 1984; Lindenmayer *et al.* 1990, 1991a), along the coasts of New South Wales (Davey 1984, 1989; Kavanagh and Lambert 1990; Kavanagh 2000; Kavanagh and Wheeler 2004), through the open coastal forests of south-east Queensland (Kehl and Borsboom 1984) and on the Paluma Range in north Queensland (Comport *et al.* 1996). Information on the ecology of this species is therefore available from a broad geographic region, but studies have largely focussed on populations living in more productive, higher-rainfall environments at the high end of the population density spectrum (Table 4). These studies provide information on key life-history and ecological attributes which we have used to compare with the results of the current study of greater gliders living in the drier inland of southern Queensland. For the purposes of our comparison we have focussed on home-range size, social interactions between individuals, use of habitat for foraging and denning and population density. We have attempted to explain differences in ecological

Table 3. Mean visits per den tree per individual by growth-stage categories

Tree ‘growth’ stage	Mean visits per tree (s.d., n)
Early	1.7 (0.6, 3)
Mature	0.0 (0, 0)
Late maturity	2.9 (2.5, 18)
Senescing	3.1 (2.4, 26)
Dead	2.4 (1.3, 11)

parameters between populations in terms of geography, climate, forest composition, the history of forest utilisation and trends in use and forest condition.

Home range

The influence of sample size on home-range estimates for gliders is well documented. Kavanagh and Wheeler (2004) found that ~110–210 tracking positions and 150 tracking positions of greater gliders were required to reach a 90% estimate of eventual home-range area when undertaking MCP and adaptive kernel estimates, respectively. Comport *et al.* (1996) found that as few as 25 positions yielded reasonable estimates of a 95% kernel home range, but that more than 110 tracking fixes were required to undertake a 95% harmonic mean analysis of home range. Pope *et al.* (2004), working in small native forest remnants around Tumut, found that home-range estimates for many of their greater gliders reached an asymptote at ~13–15 tracked positions, while for a few individuals home-range estimates continued to increase after 22 position fixes. It is possible that fewer positions were necessary to achieve asymptotes in small remnants because of limited habitat availability. The home-range estimates of this study were based on sample sizes of 15–76 tracking fixes and some individuals had clearly reached a home-range asymptote while others had not. Even so, home ranges of greater gliders in Barakula were, in general, larger than any of those previously reported elsewhere (Table 4).

Explanations for this could include low nutrient availability in the available eucalypt trees, a paucity of suitable feed trees for reasons other than nutrient availability, a low density of individuals requiring more exploratory movements to locate mates or an absence of available hollow trees in which to den at Barakula.

Home-range overlaps at Barakula were common, particularly between males and females, but less so within the sexes. Henry (1984) did not record direct encounters between males, but recorded overlapping female home ranges; he noted, though, that females tended to use overlapping parts of their ranges at different times. Kehl and Borsboom (1984) similarly found that adult male home ranges did not overlap and that female home ranges were mostly mutually exclusive. Overlapping home ranges among males at Taravale in north Queensland was extensive (Comport *et al.* 1996). It is clear that spatial organisation is variable between populations, but the nature of relationships between resource availability, population density and social organisation remain unclear.

Habitat use – foraging and denning

Like populations studied elsewhere, gliders in Barakula used primarily live myrtaceous trees for foraging activities and live myrtaceous trees and dead stags as dens (cf. Davey 1989; Kavanagh 1984; Lindenmayer *et al.* 1990, 1991a; Cunningham *et al.* 2004; Eyre 2005). Other southern Queensland glider populations (Kehl

Table 4. Comparative site and home-range data from seven studies of greater gliders

Site description and location	Average annual rainfall (as cited or from nearest weather station)	MCP mean home-range areas (s.d.) and range (ha)	Kernel mean home-range areas (s.d.) and range (ha)	Population densities (individuals ha ⁻¹)	Study
Upland moist sclerophyll forest, south-eastern Victoria	700 mm (cited)	2.08 (0.66) polygynous male; 1.36 (0.19) monogamous male; 1.25 (0.46) female; 1.48 (0.59) all residents. Range 0.7–2.94 (modified minimum area of Harvey and Barbour (1965)).	–	0.56	Henry (1984)
Coastal lowland forest, south-eastern Queensland	1150.1 mm (Maryborough)	2.6 (1.7) male; 2.5 (1.2) female. Range not cited. Minimum area of Hayne (1949) and modified minimum area.	–	1.6–2.3	Kehl and Borsboom (1984)
Morton and Deua National Parks, south-east New South Wales	–	1.4 to 1.8 male; 0.9 to 1.5 female. Range not cited.	–	0.88–1.67	Norton (1988)
Tropical sclerophyll forest, north Queensland	1750 mm (cited)	1.9 (0.1) male; 0.8 (0.05) female. Means are estimates from 4 males and 4 females using 3 different sample sizes. Range not cited.	2.2 (0.1) male; 1.3 (0.1) female. Means calculated from data provided. Range 0.9–4.2.	3.3–3.8	Comport <i>et al.</i> (1996)
Moist sclerophyll forest, south-east New South Wales	1167 mm (cited)	2.03 (0.69) male; 0.81 (0.21) female; 1.35 (0.78) all. Means calculated from data. Range 0.47–2.25.	1.92 (0.83) male; 0.76 (0.25) female; 1.27 (0.82) all. Means calculated from data.	–	Kavanagh and Wheeler (2004)
Sclerophyll remnant forest in pine plantation matrix, ACT	906.3 mm (Tumut)	–	2.6 (0.8) male; 2.0 (0.6) female. Range not cited.	0.24–1.66	Pope <i>et al.</i> (2004)
Dry sclerophyll forest, southern Queensland	660.8 mm (Barakula Forest Station)	11.5 (7.2) male; 3.3 (2.1) female; 6.8 (6.2) all. Range 1.4–19.3.	10.8 (6.7) male; 4.1 (2.3) female; 6.9 (5.5) all. Range 1.8–17.8.	0.1–0.36	This study

and Borsboom 1984; Eyre 2002; Wormington *et al.* 2002) gliders have, like Barakula, been found to utilise *Eucalyptus tereticornis* and *C. citriodora* where available, although *E. moluccana* and *E. fibrosa* were also used at Barakula.

From a foraging perspective, foliar nutrients are known to have a significant effect on the distribution of greater gliders because they prefer to feed on high-nutrient eucalypt leaves (Braithwaite *et al.* 1983, 1984; Kavanagh and Lambert 1990). They have been reported to visit trees with a high proportion of young foliage (Kavanagh and Lambert 1990; Comport *et al.* 1996) and although young foliage is not necessarily restricted to any particular size class of tree, Kavanagh and Lambert (1990) found that they preferred to feed in larger (≥ 80 cm dbh) trees even though these comprised a small proportion of the overall stem composition of the forest. The current study suggested that gliders avoided smaller trees (10–20 cm dbh), showed lower use of trees in the 20–30-cm dbh class (in comparison with their availability), and preferred trees in the 30–70-cm dbh range for their foraging activities. Trees > 70 cm dbh were not selected preferentially. Preferential selection of trees in ‘mature’ and ‘over-mature’ growth categories was apparent, although most foraging records were of animals in ‘young’, ‘early mature’ and ‘mature’ growth classes. Harvesting and treatment of large old stems > 70 cm dbh in Barakula has led to a paucity of these stems and probably explains why gliders fed on trees smaller than those preferred in the Kavanagh and Lambert (1990) study.

With regard to the suitability of species as den trees, Gibbons and Lindenmayer (2002) reported that the physiological traits among tree species determined the rates at which hollows developed. Greater gliders are not normally associated with cypress forest so the occurrence of gliders within a mixed eucalypt–cypress forest at Barakula is thought to be unusual (R. Kavanagh, pers. comm.). However, although cypress was abundant within study sites, gliders were not seen in cypress trees, nor did they den in cypress, which do not become hollow like the eucalypts.

Dens occurred mainly in older, large ‘late mature’ and ‘over-mature’ live trees (dbh 50+ cm) and stags. It is the dead stags and the larger, older live trees that are more likely to contain hollows, owing to their age and extent of decay. Use of larger and older trees within forest stands by greater gliders has been reported elsewhere (e.g. Davey 1989; Lindenmayer *et al.* 1991b; Kavanagh and Wheeler 2004; Kehl and Borsboom (1984), so the Barakula gliders present nothing new in this regard. However, what was notable was the overall use of trees by gliders at Barakula across a broad range of sizes and growth characteristics. Use of trees among size and growth-category stages was strongly bimodal, with one modal peak on mid-range-size trees, (corresponding to trees used for feeding) and the other on larger, older trees (used for denning).

For many of the gliders in our study it is likely that den numbers may have been underestimated. Lindenmayer *et al.* (2004) found that with increasing search effort den number per individual generally increased over time. Despite the considerable search effort of Kavanagh and Wheeler (2004) gliders used as few as 1–7 den trees per glider, typically fewer than our estimate (4–18 den trees per glider with sufficient data) and another estimate of 4–18 den trees per glider from Wongi, in southern Queensland (Kehl and Borsboom 1984).

Although estimates of den tree use were similar between our study and that of Kehl and Borsboom (1984), average home range in this study was ~ 2.5 times (sexes combined) greater. Therefore, den densities were lower than those recorded by Kehl and Borsboom (1984). Average den tree density calculated from MCP estimates (this study) was 2.6 den trees ha^{-1} (s.d. = 2.1, $n = 7$), although this may be biased, either because MCPs or numbers of dens utilised for some individuals had not reached an asymptote.

While suitable food availability is likely to be an important determining factor of greater glider density, it is likely that den trees, at densities as low as 0.8 trees ha^{-1} , have become a limiting resource in Barakula, particularly compared with densities in other areas such as Wongi, where Kehl and Borsboom (1984) and J. Kehl (pers. comm.) recorded up to 20 den trees per home range (average home range 2.6 ha). Analysis of male and female home ranges and den tree availability within home ranges at Barakula also showed that while male and female home ranges contained similar numbers of den trees, females were more restricted in their home range to areas where there were at least 3.8 den trees ha^{-1} (average). Males, on the other hand, utilised larger areas with lower den tree density overall. This would suggest that females may be restricted to parts of the forest where den density is high enough to support them and that this may be the limiting factor controlling whether greater gliders do or do not occur. Males, on the other hand, ranged over wider areas in order to satisfy their social needs and although they utilised similar numbers of den trees within their home range, their home ranges were larger and therefore density of den trees lower.

Den sharing and serial den use recorded at Barakula might be expected on the basis of the low density of den trees. However, even in an area of abundant hollow trees, Kehl and Borsboom (1984) reported concomitant and serial den sharing, with the latter more common. Lindenmayer *et al.* (2004) also recorded concurrent den sharing but noted that occurrences were uncommon (5% of all records).

Population density and potential threats

Surveys in the south-east Queensland bioregion undertaken during a regional assessment of resources indicated encounter rates of 20% (when rainforest sites were excluded, $n = 212$ sites), while Eyre (2004) cites a reporting rate from southern Queensland (combined south-east Queensland and southern brigalow belt bioregional records) of 23.5%. On the basis of spotlighting returns, greater gliders within the Barakula State Forest were encountered less commonly than elsewhere in southern Queensland. Low encounter rates of greater gliders during spotlighting in Barakula compared with coastal populations and elsewhere in the southern section of the brigalow belt bioregion were symptomatic of low population density (Table 4). While we acknowledge that spotlighting surveys can underestimate actual population size of greater gliders (Lindenmayer *et al.* 2001), our standardised surveys in Barakula, and surrounding forests yielded encounter rates of 14% compared with 36% for the same standardised surveys in other locations within the southern section of the brigalow belt bioregion and 23.5% from the same standardised spotlighting surveys from southern Queensland (Eyre 2004). If the low rate of encounter within the study forest is a sign of low population

density, then it is likely that low density results from low den resource availability and the presence of non-suitable food and den trees, such as *Callitris* sp. It is also likely that traits such as home-range size are concomitantly affected. Numerous studies have demonstrated inverse relationships between home-range size and population density for a range of species. This includes several predatory carnivores (Dahle and Swenson 2003; Marker and Dickman 2005; Benson *et al.* 2006), primates (Glessner and Britt 2005), ungulates (Kilpatrick *et al.* 2001; Kjellander *et al.* 2004) and small mammals (Wolff 1985).

While greater gliders appear to be persisting in low abundance in areas with low den tree density, we are concerned that gliders may be in population decline across the southern section of the brigalow belt bioregion and particularly at Barakula, where den tree numbers are critically low. It has been shown that greater gliders can rapidly disappear from an area (Kavanagh 1988; J. Kehl, pers. comm.). The tall eucalypt forests of Queensland historically contained abundant den trees suitable for greater gliders. Ross (1999) estimated that up to 22 den trees ha⁻¹ could have been the norm in southern Queensland forests in the past. More recently, the silvicultural treatment of forests, timber extraction and clearing of forests for agricultural land and urbanisation have led to diminished hollow and food resources (Ross 1999; Eyre 2004). Ross (1999) reports that in inland forests, such as those contained within the southern section of the brigalow belt bioregion, the mean number of live and dead hollow trees suitable as dens and greater than 10 cm diameter to be ~3 and 2.6 trees ha⁻¹, respectively. Like forests in south-east Queensland (Eyre 2004), approximately half of the hollow resource in Queensland's western forests available to greater gliders occurs in dead trees or stags.

We are concerned that the availability of hollow trees in the study region is below that currently recommended by a code for maintenance of viable populations of the glider and that a considerable part of the den tree resource exists as stags with potentially shorter life than live den trees (Ross 1999; Queensland Government 2002; this study). Lindenmayer *et al.* (1997) reported declines in Leadbeater's possum populations through loss of stags, a scenario that could easily be replicated in the forests of western Queensland.

This study is the first of its kind to examine the ecology of the species in the context of den tree availability within a selectively harvested, inland dry sclerophyll forest comprising mainly cypress and eucalypt species. While this study did not unravel environmental and social impacts on glider populations, there is an indication that in low-rainfall areas of the greater glider's range where the availability of hollows is limiting, populations exist at low density, with subsequent effects on home-range size and tree use. Without careful forest management, fecundity, longevity and recruitment may be lowered, with possibly disastrous consequences for the persistence of greater gliders in these forests.

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