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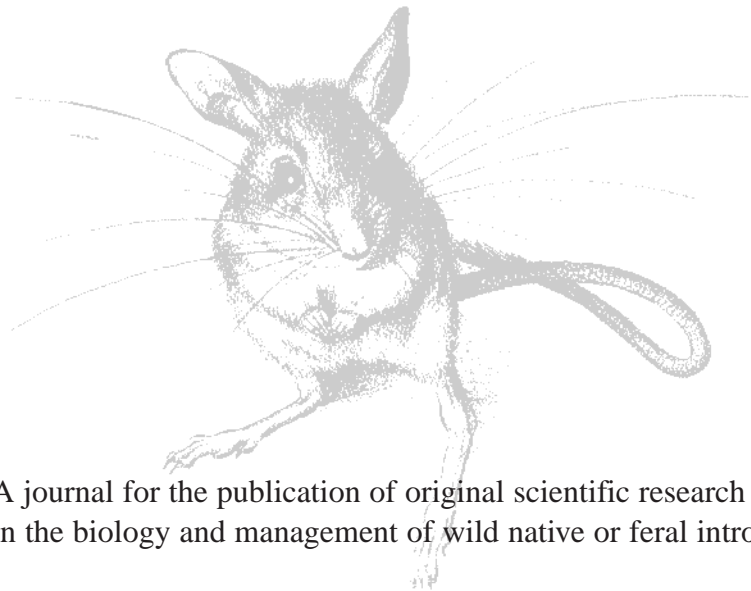
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Habitat relationships of the mahogany glider, *Petaurus gracilis*, and the sugar glider, *Petaurus breviceps*

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Abstract. Trapping data of the mahogany glider, *Petaurus gracilis*, and the sugar glider, *Petaurus breviceps*, in sympatry, in north Queensland, were analysed with vegetation variables to determine the habitat relationships of these two species. The study area contained a trapping grid (80 traps) within an area of continuous forest and trapping transects within an adjacent area of fragmented forest (44 traps). The mahogany glider was trapped more often at 43 of the 124 locations (38 in the continuous and 5 in the fragmented forest), with the sugar glider dominant at 46 locations (18 in the continuous forest and 28 in the fragmented forest). The remaining 27 trap locations where gliders were caught did not favour either species. Eight trap locations within riparian rainforest had no captures of either species. The presence of mahogany gliders was significantly correlated with the presence of *Corymbia clarksoniana*, *Eucalyptus platyphylla*, the absence of *Corymbia intermedia* and *Acacia mangium*, and a small mid and upper canopy cover. In contrast, the presence of sugar gliders was most correlated with a large number of stems. When the presence of the mahogany glider was compared with that of the sugar glider with respect to various habitat variables for the entire study area, the mahogany glider was most associated with the presence of *C. clarksoniana*, *Eucalyptus pellita*, *Lophostemon suaveolens*, *Melaleuca dealbata* and a reduced lower and upper canopy. In contrast, the sugar glider was most associated with *C. intermedia, A. mangium*, a large number of potential food species, rainforest species and a dense mid and upper canopy cover.

Introduction

The ecological niche occupied by a species is the sum of all the environmental factors acting on that species within its habitat (Hutchinson 1978; Schoener 1989). When two or more species fill similar niches and live in a habitat where resources are limited, competition can occur with one organism interfering with, or inhibiting, another, resulting in a mutual reduction in fitness (Pianka 1981). Competition is sometimes direct, as in interspecific territoriality, where direct antagonism between species occurs (termed 'interference competition') or it may be indirect, resulting from the joint use of the same limited resources ('exploitation competition') (Pianka 1981).

Differences in the body sizes of ecologically similar species may provide or reflect differences in their niches sufficient to permit coexistence (Brown and Wilson 1956). The limits to the similarity that can occur between sympatric and ecologically similar species before they effectively have the same niche has been examined by various authors including Wilson (1975), Horn and May (1977), Lewin (1983) and Tonkyn and Cole (1986), and may include differences in dietary requirements and habitat occupied. Hutchinson

(1959) proposed that the average difference between typical linear dimensions (e.g. head length) of two sympatric species necessary to prevent them from occupying the same niche is a ratio of approximately 1.3, or a doubling in weight. More recent analysis, however, has suggested that the constant proposed by Hutchinson (1959) is an artefact of the log-normal distribution of animal sizes in nature (Horn and May 1977; Maiorana 1978; Boecklen and NeSmith 1985; Eadie *et al.* 1987).

Throughout its restricted distribution in north Queensland, the mahogany glider, *Petaurus gracilis*, lives sympatrically with the smaller sugar glider, *Petaurus breviceps*. As early as 1859, Darwin noted that species of the same genus usually have many similarities in habits and constitution, and always in structure; as a result, he suggested that the struggle will generally be more severe between them if they come into competition with each other rather than with species of different genera. Competition can be reduced, however, if the resources and habitats are partitioned so that species inhabit different realised niches (Lee and Cockburn 1985). Members of the Petauridae do not appear to specialise on any food items (although the proportions and species used

may vary) and are generalist exudate and insect eaters, suggesting that there is no reason to suspect that dietary resource partitioning occurs between the different species of petaurids (Quin 1993). It has been suggested that habitat partitioning (or habitat segregation) may be a more important mechanism of resource partitioning during times of food shortage for closely related dietary generalists, such as members of the Petauridae, allowing them to coexist (Rosenzweig 1981; Quin 1993). It is generally considered that competitively dominant species exclude subordinate species from optimal habitat by some form of social dominance (Quin 1993).

This study had two aims. First, to identify the forest characteristics that determine the local distribution of both mahogany and sugar gliders, as the use of different forest types has important implications in managing the habitat of the endangered mahogany glider. Second, to compare the preferred habitat used by the mahogany glider with that used by the sugar glider when both species occur sympatrically.

Methods

Trapping grids

A grid was marked out in the continuous forest at Mullers Creek in north Queensland (18°26′13″S, 146°07′15″E) before the study began to trap mahogany gliders and sugar gliders. The grid contained ten transects that each contained eight traps separated by 100 m. These grids were trapped every eight weeks over 3–4 nights between February 1995 and December 1996. An area of fragmented forest, adjacent to Mullers Creek, at Porters Creek (18°26′57″S, 146°07′35″E) was trapped every eight weeks between December 1995 and December 1996. In the fragmented forest, establishing a grid was not feasible because of the linear nature of the buffer strips. This area was set up with trapping transects along the edges of the buffer strips with traps 100 m apart. Further details on the location of the study area and trapping set-up can be found in Jackson (1998, 2000).

Trapping records

Trapping records were totalled for each trap locality for the mahogany glider and sugar glider from the 10 transects within the continuous forest at Mullers Creek over a two-year period, and the five transects within the adjacent fragmented forest at Porters Creek over a 14-month period as part of a study on the population biology of the mahogany glider (Jackson 2000). The abundance of animals caught at a particular location was therefore used to indicate the species' preference for a particular forest type.

Habitat description

Each trapping area contained several distinct forest types (riparian forest along creeklines, open woodland and *Melaleuca viridiflora* swamps) with variations observed within these major forest types with respect to plant species diversity and abundance. At each trapping site, a number of vegetation attributes were recorded within a 20-m radius around the trap tree. Each tree or understorey species greater than 1 m in height within the area was recorded and classed into one of three 'diameter at breast height' (DBH) categories (0–10 cm, 10–30 cm and >30 cm). These three DBH categories were then collapsed into one variable for the multivariate analysis by multiplying the number of stems in the 0–10-cm class by 1, those in the 10–30-cm class by 2, and those >30 cm by 3, and then taking the sum of these figures. The number of stems for each size category was recorded for a total of 15 species that were potential food for both the mahogany glider and the sugar glider, including bloodwoods, eucalypts, lophostemons, melaleucas, acacias and *Albizia procera*. The total number of species that supply food at each trap location was also included. Other non-food species and rainforest species were grouped separately as additional categories. In addition to the number of trees being recorded, the average grass cover and height was estimated, and the number of grass trees, *Xanthorrhoea johnsonii*, were counted. Canopy cover was also estimated for the mid canopy and upper canopy using the procedure of McDonald *et al.* (1990), which uses a series of shaded silhouettes.

Analysis

Due to the different structures of the fragmented forest at Porters Creek and continuous forest at Mullers Creek they were treated both separately and together in order to examine whether there was a difference between the two. Habitat attributes that were most associated with the presence of the mahogany glider and sugar glider were determined by principal components analysis (PCA) and correlations (Pearson coefficients). The significance of the Pearson correlations was adjusted using a Bonferroni correction for 23 simultaneous tests, which gave an adjusted significance of 0.0022 (using an initial P value at 0.05).

The examination of any separation of habitat use between sugar gliders and mahogany gliders in the continuous forest at Mullers Creek and the fragmented forest at Porters Creek was done using canonical correlation analysis. This used the vegetation variables recorded at each trap point and the number of mahogany gliders and sugar gliders caught to examine the linear relationships between these two sets of variables. The canonical correlation analysis was also used to show which tree species were most likely to have resulted in any observed separation. Miller's test was used to calculate an F statistic for the canonical correlations, to determine whether there was a significant relationship between the habitat variables and the number of mahogany gliders and sugar gliders caught at each trap-point. The Miller's test calculation of the F statistic was determined from the following formula:

$$F = (D^2/(1 - D^2))(N - p - 1)/p$$

which approximates $F_{pq,(N-p-1)q}$ where D^2 = total variation explained by habitat variables, p = the number of animal species (2), q = the number of habitat variables (23), and N = the number of trap sites (80 in continuous forest and 44 in fragmented forest).

Results

Number of gliders caught at each trap point

A ratio of 2 : 1 in animal captures was used to separate trap locations where either mahogany gliders or sugar gliders were trapped more frequently (Fig. 1). The mahogany glider was trapped more frequently at 43 of 124 locations (38 in continuous forest and 5 in fragmented forest), with the sugar glider dominant at 46 locations (18 in continuous forest and 28 in fragmented forest). The remaining 27 trap locations in which gliders were caught did not favour either species (having a trap ratio of less than 2 : 1), with a further 8 trap locations within riparian rainforest producing no captures of either species.

In the continuous forest at Mullers Creek the mahogany glider was clearly more commonly trapped (Fig. 2). Within the fragmented forest at Porters Creek there was an even greater difference in the number of mahogany gliders and sugar gliders caught, with this habitat clearly favouring sugar gliders (Fig. 3). Figs 2 and 3 show a clear picture of the differential trappability at each trapping location, and therefore
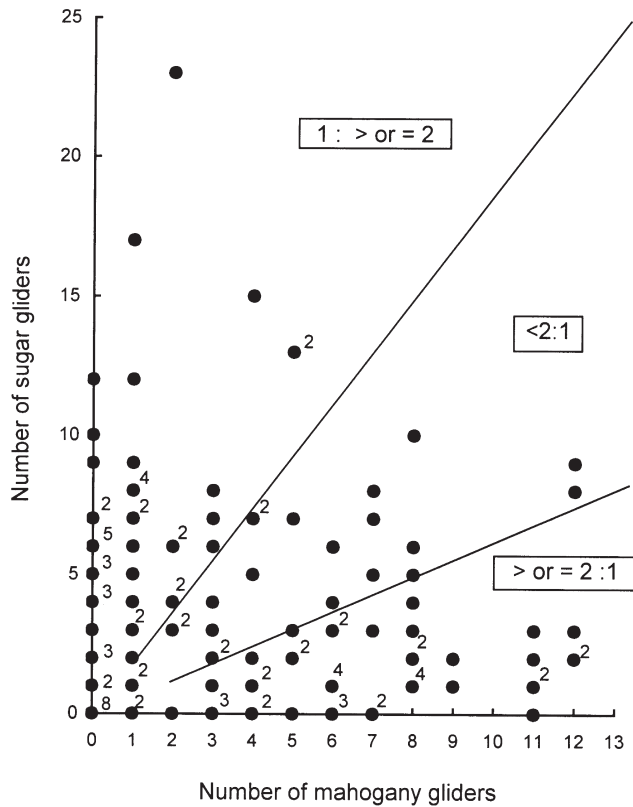
Fig. 1. A comparison of the number of captures of mahogany gliders and sugar gliders at each trap location for the entire study area. The lines separate trap localities with a ratio > 2:1 from those < 2:1. The numbers immediately to the upper right of some of the symbols indicate the number of times that that ratio occurred.

reflects the differential habitat usage of the two species over both study grids.

Habitat preference of the mahogany glider and sugar glider
The presence of the mahogany glider was significantly correlated with the presence of *Corymbia clarksoniana* and *Eucalyptus platyphylla*, the absence of *Corymbia intermedia* and *Acacia mangium*, and a small mid and upper canopy cover (Pearson correlations; Table 1). When only the continuous forest was examined, *E. platyphylla* was the only significantly correlated tree species, with a high grass cover (due to an open canopy allowing more light for the grass to grow) and a small mid and upper canopy cover being significantly correlated with the presence of mahogany gliders. When the fragmented forest was considered by itself, there was no significant correlation with any eucalypts or bloodwoods, with only *M. viridiflora* and *X. johnsonii* being significantly correlated. These two species generally occurred together as a ditypic assemblage and represented the only large areas with an open canopy within the fragmented forest. The lack of a positive correlation with eucalypts, bloodwoods, acacias or canopy cover appears to be due to
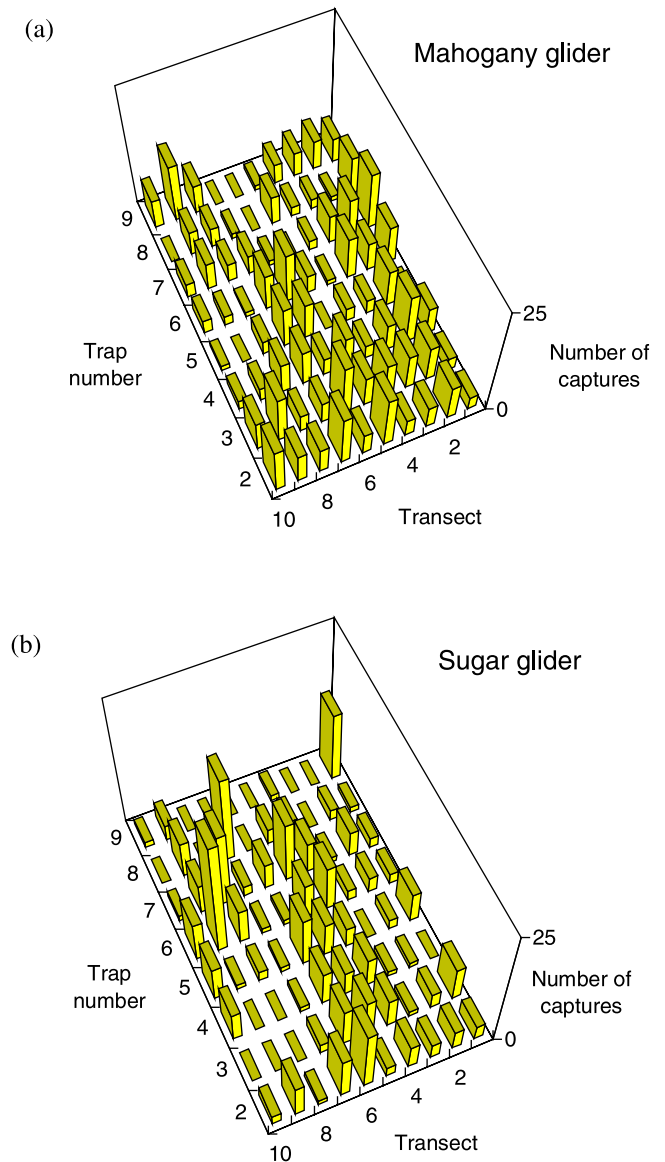

Fig. 2. Numbers of (*a*) mahogany gliders and (*b*) sugar gliders trapped at each trap-point in the continuous habitat at Mullers Creek.

the high proportion of these species throughout the entire fragmented forest (except where *M. viridiflora* and *X. johnsonii* occur).

The presence of the sugar glider correlated most strongly with the presence of a large number of other stems and the absence of *Eucalyptus tereticornis* (Table 2). When only the continuous forest was considered, *Acacia flavescens*, *A. mangium* and other stems were significantly positively correlated with the presence of sugar gliders. As mentioned above, the lack of a significant relationship with these species in the fragmented forest appears to be due to the high density of trees and canopy cover throughout the entire frag-

mented forest. The ordinated habitat data using PCA showed that none of the principal components were more strongly correlated with mahogany gliders or sugar gliders than were those derived from Pearson correlations.

Fig. 3. Numbers of (*a*) mahogany gliders and (*b*) sugar gliders trapped at each trap-point in the fragmented habitat at Porters Creek.

Habitat partitioning between the mahogany glider and sugar glider

When the presence of the mahogany glider is compared with that of the sugar glider with respect to habitat variables for the entire study area, the first two canonical variates showed significant correlation between the number of mahogany gliders and sugar gliders present and the habitat variables, with canonical correlations of 0.800 and 0.602 respectively (Wilk's tests: λ = 0.230, d.f. = 46, P < 0.01 and λ = 0.638, d.f. = 22, P < 0.01 respectively). The canonical coefficients showed a good separation between mahogany gliders and sugar gliders on the first axis, but little separation on the second axis (Table 3). The presence of the mahogany glider was negatively correlated with the first axis and separated from that of the sugar glider by the presence of *C. clarksoniana*, *Eucalyptus pellita*, *E. platyphylla*, *Lophostemon suaveolens*, *Melaleuca dealbata* and a reduced lower and upper canopy cover that is reflected in high grass height (Table 4). The presence of the sugar glider was not well correlated with the first axis although it was most associated with *C. intermedia*, *A. mangium*, a larger number of potential food species, rainforest species, a high grass cover and a dense mid and upper canopy cover. The prescence of the sugar glider was highly correlated with the second axis although,
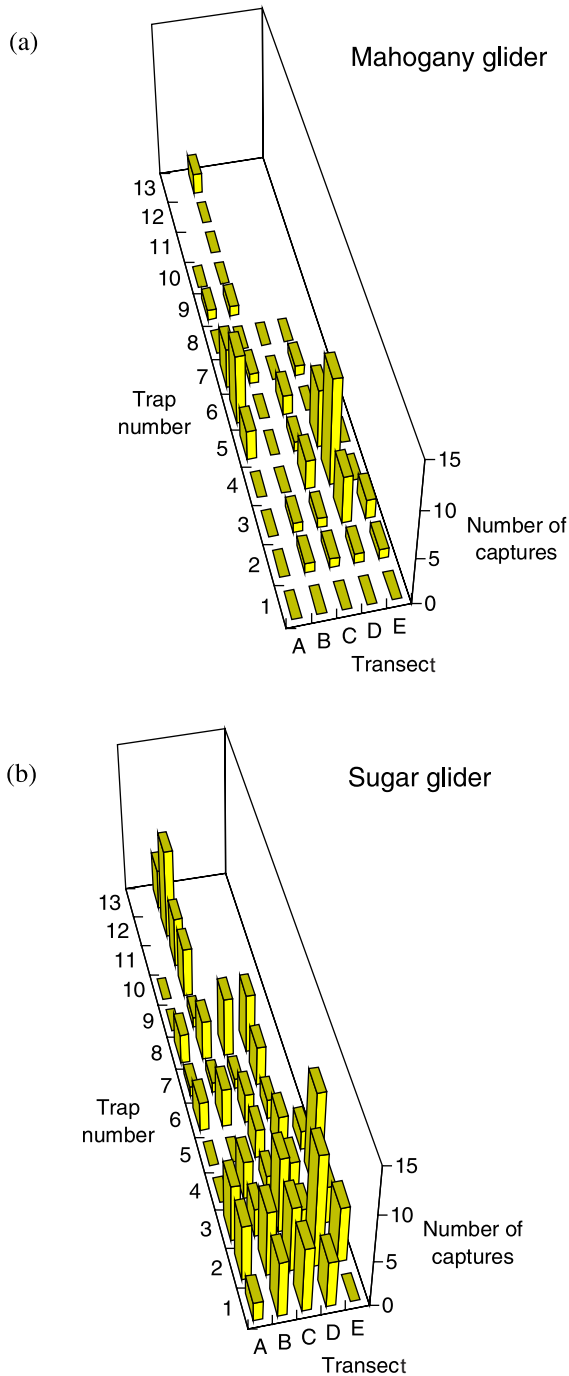
Table 1.   Pearson correlations of mahogany gliders with individual habitat variables
* indicates significance at 0.05 using the Bonferroni adjusted level of 0.0022. Non-food stems = the number of stems of non-food species, not including rainforest stems. Rainforest stems = all rainforest non-food species stems

	Total area	Continuous	Fragmented
Corymbia clarksoniana	0.338*	0.228	0.236
Corymbia intermedia	−0.366*	−0.231	−0.287
Corymbia tessellaris	−0.009	0.126	−0.194
Eucalyptus pellita	−0.200	−0.243	−0.082
Eucalyptus platyphylla	0.366*	0.338*	−0.153
Eucalyptus tereticornis	−0.026	−0.039	−0.105
Lophostemon suaveolens	−0.110	0.025	−0.220
Melaleuca dealbata	0.177	0.196	0.085
Melaleuca leucodendra	0.214	0.204	−0.084
Melaleuca viridiflora	0.162	0.003	0.526*
Acacia crassicarpa	0.208	0.127	0.136
Acacia flavescens	−0.257	−0.152	−0.173
Acacia leptocarpa	0.030	0.177	0.006
Acacia mangium	−0.432*	−0.299	−0.271
Albizia procera	0.211	0.129	−0.103
Xanthorrhoea johnsonii	−0.029	−0.077	0.478*
Total no. of food species	−0.175	−0.039	−0.200
Non-food stems	−0.209	−0.103	−0.126
Rainforest stems	−0.258	−0.318	−0.215
Grass cover	0.152	0.356*	0.271
Grass height	0.116	0.276	0.115
Mid canopy cover	−0.548*	−0.464*	−0.373
Upper canopy cover	−0.472*	−0.477*	−0.242

Table 2. **Pearson correlations of sugar gliders with individual habitat variables**

* indicates significance at 0.05 using the Bonferroni adjusted level of 0.0022. Non-food stems = the number of stems of non-food species, not including rainforest stems. Rainforest stems = all rainforest non-food species stems

	Total area	Continuous	Fragmented
Corymbia clarksoniana	0.027	0.060	–0.101
Corymbia intermedia	–0.011	–0.010	–0.003
Corymbia tessellaris	–0.073	–0.080	–0.070
Eucalyptus pellita	–0.076	–0.041	–0.184
Eucalyptus platyphylla	0.064	0.100	–0.103
Eucalyptus tereticornis	–0.306*	–0.330	–0.233
Lophostemon suaveolens	0.146	0.148	0.170
Melaleuca dealbata	–0.020	–0.045	0.150
Melaleuca leucodendra	0.063	0.070	–0.026
Melaleuca viridiflora	–0.003	–0.021	0.073
Acacia crassicarpa	–0.008	0.023	–0.169
Acacia flavescens	0.198	0.341*	0.007
Acacia leptocarpa	–0.003	–0.163	0.274
Acacia mangium	0.265	0.416*	–0.005
Albizia procera	–0.195	–0.214	–0.208
Xanthorrhoea johnsonii	0.145	0.205	0.086
Total no. of food species	0.180	0.187	0.193
Non-food stems	0.352*	0.446*	0.281
Rainforest stems	–0.133	–0.128	–0.165
Grass cover	–0.107	–0.174	0.040
Grass height	0.039	0.021	0.114
Mid canopy cover	0.128	0.256	–0.147
Upper canopy cover	0.062	0.127	–0.148

as the mahogany glider also had a positive coefficient, it was difficult to determine with which species of glider the habitat variables were most correlated. The first two canonical variates were a good summary of the two sets of variables, with 54% of the variation in the number of animals caught at each trap location being explained by the first two canonical variates (Miller's test: $F_{46,2783} = 62.22$, $P < 0.01$).

When only the continuous forest at Mullers Creek was considered, the first two canonical variates were significantly correlated with the number of mahogany gliders and sugar gliders present, with canonical correlations of 0.781 and 0.721 respectively (Wilk's test: $\lambda = 0.187$, d.f. = 46, $P < 0.01$ and $\lambda = 0.480$, d.f. = 22, $P < 0.01$ respectively). The canonical coefficients showed a good separation between

mahogany gliders and sugar gliders on the first axis, but little separation on the second axis (Table 3). The first axis was positively associated with mahogany gliders and negatively associated with sugar gliders. Using the first axis, the distribution of mahogany gliders was best explained by the presence of *C. clarksoniana*, *Corymbia tessellaris*, *E. pellita*, *E. platyphylla*, *E. tereticornis*, *M. dealbata*, an absence of other stems and a greatly reduced mid canopy cover, which is reflected in high grass height (Table 4). The presence of the sugar glider was best correlated with *C. intermedia*, *A. mangium*, *A. flavescens*, a high number of food plant species, other stems and a dense mid canopy cover. In total, 54% of the variation in the number of animals caught at each trap location was explained by the two canonical variates (Miller's test: $F_{46,1771} = 51.66$, $P < 0.01$).

When only the fragmented forest at Porters Creek was considered, the first two canonical variates were again found to have high canonical coefficients (0.790 and 0.665 respectively). In contrast to the results for the Mullers Creek site, the first canonical variate contained all significant correlations, with no further correlations being significant (significance of remaining axis using Wilk's test: $\lambda = 0.209$, d.f. = 46, $P > 0.05$ for the first correlation; $\lambda = 0.557$, d.f. = 22, $P > 0.05$ for the second correlation). Again, the canonical coefficients showed a good separation between the mahogany gliders and the sugar gliders on the first axis, with a less distinct difference on the second axis (Table 3). As was the case for the overall habitat, the first axis was negatively associated with mahogany gliders and positively associated with sugar gliders. Using the first axis, the distribution of the mahogany glider best correlated with that of *C. clarksoniana*, *E. pellita*, *E. tereticornis*, *M. viridiflora*, *A. crassicarpa*, *A. procera*, other stems and high grass height, which reflects the poorly developed upper canopy cover (Table 4). The sugar glider was most highly correlated with the distribution of *C. intermedia*, *A. mangium*, *A. flavescens*, *Acacia leptocarpa*, *X. johnsonii*, the number of food tree species, rainforest plants, and a highly developed upper storey. The dense understorey with which the sugar glider was associated in the continuous forest was not well correlated with either the sugar glider or the mahogany glider in the fragmented forest. Overall, 54% of the variation in the number of animals caught at each trap location was explained by the two canonical variates (Miller's test; $F_{46,943} = 24.26$, $P < 0.01$).

Table 3. **Standardised canonical coefficients for the mahogany glider and the sugar glider in the continuous habitat at Mullers Creek and the fragmented habitat at Porters Creek**

	Total area		Continuous		Fragmented	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Mahogany glider	–0.985	0.222	0.728	–0.707	–0.933	0.398
Sugar glider	0.085	1.006	–0.574	–0.837	0.239	0.985

**Table 4.   Standardised canonical coefficients for the habitat variables in the continuous habitat at
Mullers Creek and the fragmented habitat at Porters Creek**

Non-food stems = the number of stems of non-food species, not including rainforest stems. Rainforest stems =
all rainforest non-food species stems

	Total area		Continuous		Fragmented	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Corymbia clarksoniana	–0.207	–0.109	0.249	–0.017	–0.385	–0.622
Corymbia intermedia	0.145	–0.366	–0.304	0.086	0.139	–0.544
Corymbia tessellaris	–0.098	0.053	0.169	–0.193	0.050	–0.200
Eucalyptus pellita	–0.320	–0.070	0.451	–0.169	–0.411	–0.242
Eucalyptus platyphylla	–0.298	0.228	0.364	–0.180	0.081	–0.226
Eucalyptus tereticornis	–0.073	–0.548	0.216	0.410	–0.274	–0.163
Lophostemon suaveolens	–0.148	0.231	0.064	–0.524	0.050	–0.148
Melaleuca dealbata	–0.223	0.023	0.239	–0.173	–0.125	0.483
Melaleuca leucodendra	–0.116	0.153	–0.002	–0.252	0.048	–0.034
Melaleuca viridiflora	–0.123	0.224	0.068	–0.039	–0.852	0.096
Acacia crassicarpa	0.046	–0.249	–0.094	0.176	–0.326	–0.100
Acacia flavescens	0.034	0.168	–0.149	–0.112	0.163	–0.032
Acacia leptocarpa	0.125	0.061	0.041	0.079	0.439	0.321
Acacia mangium	0.301	0.255	–0.494	–0.241	0.915	0.110
Albizia procera	–0.051	–0.230	0.089	0.280	–0.582	–0.714
Xanthorrhoea johnsonii	–0.036	0.157	0.043	–0.207	0.749	0.150
Total no. of food species	0.439	–0.035	–0.262	0.534	0.427	0.208
Non-food stems	–0.023	0.368	–0.158	–0.342	–0.200	0.393
Rainforest stems	0.200	–0.161	–0.074	0.274	0.202	0.092
Grass cover	0.162	–0.547	–0.048	0.129	0.042	–0.076
Grass height	–0.198	0.219	0.191	–0.272	–0.208	0.225
Mid canopy cover	0.398	–0.066	–0.525	–0.085	0.053	–0.010
Upper canopy cover	0.189	–0.214	0.121	0.704	0.693	0.358

Discussion

Habitat use by the mahogany glider and sugar glider
Although there was significant overlap in the habitat used by
the mahogany glider and the sugar glider, a preference for
different habitat types was revealed by multivariate analysis.
The fine-scale distribution of the mahogany glider was asso-
ciated with an open canopy, poorly developed understorey
and the dominance of Myrtaceae species, including *C. clark-
soniana* and *E. platyphylla*. The preference for open forest
by the mahogany glider is similar to that of the closely
related squirrel glider, *Petaurus norfolcensis*, with records as
early as 1846 showing them to prefer more open and grassy
portions, rather than thick forest (Waterhouse 1846).

   In contrast, the sugar glider favoured forest with a more
developed mid storey and dominated by species such as *C.
intermedia*, *A. mangium* and *A. flavescens*. The preference of
sugar gliders for forest with a closed mid canopy has been
observed by Davey (1984), who found them to spend most of
their foraging time in the lower stratum, whereas the squirrel
glider prefers to forage in higher strata. The sugar glider's
preference for forest containing acacias has been observed
previously by Smith (1982), Braithwaite *et al.* (1983), Davey
(1984) and Suckling (1984), who found them across a range
of floristic communities containing *Acacia* trees.

The density of the mahogany glider in the fragmented
forest at Porters Creek is only two-thirds that in the continu-
ous forest at Mullers Creek (0.16 *v*. 0.24 ha^{-1}: Jackson 2000),
and appears to be a result of the much greater proportion of
closed habitat associated with species such as *A. flavescens*
and *A. mangium*. This, in turn, favours the sugar glider,
whose density in the fragmented forest was much greater
than in the continuous forest (0.46 *v*. 0.27 ha^{-1}). Similarly,
Suckling (1984) found the sugar glider to be highly success-
ful in roadside strips in Victoria and fragmented forest
habitat although he found much higher densities (2.9–6.1
ha^{-1}) than in this study.

Movements of gliders in open and closed habitats
The preference for open habitat by the mahogany glider and
closed habitat by the sugar glider is also supported by theo-
ries related to their movement within their habitat and their
gliding ability (Jackson 1999). Although both gliders do
make short glides, Jackson (1999) found that the mahogany
glider launched and landed significantly higher in trees, and
made significantly longer glides than the sugar glider, even
though there was no significant difference in the gliding effi-
ciency (ratio of distance gained to net height loss) of the two
species. From the perspective of locomotion, open habitat

has greater air turbulence and therefore favours the larger body size of the mahogany glider, which allows them to launch higher and therefore make longer glides than smaller species such as the sugar glider. The mahogany glider's large body size, however, means that it has a decreased ability to steer, which favours open habitat. In contrast, a closed under-storey has less air turbulence and favours the smaller body size of the sugar glider. The closed canopy also favours shorter glides and the ability to make tighter turns.

Sympatry in the Australian Petauridae

There is a high degree of overlap in the diet of the species of Petauridae, with all species occupying the exudivorous/insec-tivorous dietary niche, feeding on insects, insect exudates such as honeydew, and plant exudates such as nectar, pollen, manna and sap (Smith 1982, 1984; Craig 1985; Goldingay 1986, 1990; Menkhorst and Collier 1988; Summers 1988; Van Dyck 1993; Handasyde and Martin 1996). Quin (1993) noted that, with the exception of Leadbeater's possum, *Gymnobelideus leadbeateri*, and the sugar glider, the exudi-vorous/insectivorous possums differ markedly in body size, but are otherwise remarkably similar in diet and morphology.

As diet in the Petauridae varies little between species, dif-ferential body weight and habitat selection may be an impor-tant mechanism permitting these closely related species to co-exist where resources are limiting, with the degree of habitat selectivity (and overlap) being related to the degree of specialisation of each species in the community (Brown and Wilson 1956; Hutchinson 1959; Schoener 1965, 1974*a*, 1974*b*; Quin 1993). Wilson (1975) noted the role of body size in competition and in promoting niche differentiation, with larger species being able to exclude smaller species and establishing a competitive gradient. Where species are sym-patric, the dominant species is usually considered to exclude the subordinate species from optimal habitat through some form of territorial defence (Dueser and Hallet 1980; Rosenzweig 1981; Hallet *et al.* 1983). The subordinate species is usually assumed to possess lower fitness due to the occupancy of sub-optimal habitats (Quin 1993). However, if the subordinate species is more efficient at exploiting the lower-quality patches (has higher foraging efficiency), its fitness may not necessarily be lower than that of the domi-nant species (Abramsky *et al.* 1991, 1992).

A comparison of the body length ratios of the Petauridae shows no significant difference between broadly sympatric and allopatric species ($t_{13} = 2.16$; $P > 0.05$) (Table 5). A more detailed examination of the sympatry between Australian petaurids suggests that habitat partitioning occurs on a local scale between species (see below).

The sugar glider is broadly sympatric with Leadbeater's possum in the montane ash forests of Victoria. As a result of their similar body size and niche they should face significant competition, and therefore should have difficulty coexisting unless there is a high degree of resource partitioning. Although both species have a very similar diet, feeding on arthropods, *Acacia* sap, manna and honeydew, the sugar glider also feeds on eucalypt sap, nectar and pollen (Smith 1982, 1984; Howard 1989). Despite a high degree of overlap in the height of foraging, Leadbeater's possum is most often observed at 10–15 m above the ground, while the sugar glider is most often observed at 15–20 m above the ground (Davey 1984; Lindenmayer 1997). Macfarlane (1988) found that sugar gliders occurred in the same areas as Leadbeater's possums, although they were less common in mountain ash forests than in nearby more open mixed-eucalypt forest where Leadbeater's possum was not recorded. The prefer-ence of sugar gliders for more open habitat than is required by Leadbeater's possum is suggested to be a result of its ability to glide, whereas Leadbeater's possum requires extremely dense vegetation with interlocking branches and scrub in the middle and lower storey of the forest for loco-motion (Smith 1978; Macfarlane 1988). These observations are supported by Lindenmayer *et al.* (1990), who found that Leadbeater's possum and the sugar glider never co-occupied the same trees, whereas they did share trees with other species of mammals. Indeed, Lindenmayer (1997) found dif-ferences in habitat, characteristics of trees selected for nesting, height of the entrance to the nest and method of locomotion (gliding *v.* non-volant) and suggested that these differences may enable them to co-exist in montane ash

Table 5. **Similarity ratios of the Australian Petauridae using body length**

Measurements are from Strahan (1995). Data for species that are broadly sympatric in at least part of their geographic range are shown in bold

	Leadbeater's possum	Sugar glider	Squirrel glider	Mahogany glider	Striped possum	Yellow-bellied glider
Leadbeater's possum	–	–	–	–	–	–
Sugar glider	**1.06**	–	–	–	–	–
Squirrel glider	1.31	**1.24**	–	–	–	–
Mahogany glider	1.56	**1.47**	1.19	–	–	–
Striped possum	1.64	**1.54**	1.25	1.05	–	–
Yellow-bellied glider	**1.75**	**1.64**	**1.33**	1.12	1.06	–

forests. In contrast to Macfarlane (1988), Smith *et al.* (1985) proposed that in the central highlands of Victoria, Leadbeater's possum excludes the sugar glider, as the sugar glider was found only in areas where Leadbeater's possum was absent. Unlike Leadbeater's possum, which has an extremely narrow habitat niche, being restricted to the central highlands of Victoria, the sugar glider has a very broad habitat niche, being able to exist in rainforest, tall open forest and eucalypt woodland (Winter 1997) and to co-exist with the larger squirrel glider, mahogany glider and yellow-bellied glider *Petaurus australis* (Russell 1981; Quin 1993; Winter 1997).

When considering the larger petaurids, current records indicate that the distribution of the squirrel glider in North Queensland surrounds that of the mahogany glider with no known overlap, with records showing them to occur within 25 km (Jackson and Claridge 1999). It is suggested that these two species would find it difficult to exist unless character displacement occurred, and it appears that the squirrel glider replaces the mahogany glider outside its limited distribution (*sensu* Brown and Wilson 1956; Grant 1972). The distribution of the squirrel glider and the yellow-bellied glider do not appear to overlap in Queensland, as Winter (1997) found the yellow-bellied glider to occupy an extremely narrow habitat niche in the wet sclerophyll forest on the western boundary of the wet tropics rainforest in North Queensland, with the squirrel glider having a slightly broader habitat niche, occupying drier areas immediately adjacent to the yellow-bellied glider.

The striped possum, *Dactylopsila trivirgata*, the yellow-bellied glider and the mahogany glider are similar in body size, and although the striped possum lives in close proximity to both of these species over part of its range, there appears to be very little overlap between its distribution and those of the other two species. The striped possum occurs in tropical rainforest, gallery forest and adjacent woodlands (Handasyde and Martin 1996), whereas the yellow-bellied glider occurs in wet sclerophyll forest in North Queensland (Winter 1997), and the mahogany glider occurs in open woodland (Van Dyck 1993). Although all of these species consume insects (Smith and Russell 1982; Henry and Craig 1984; Van Dyck 1993; Handasyde and Martin 1996; Jackson 1998), the striped possum appears to consume more insects and has specialised cranial morphology and an elongated fourth finger for feeding on wood-boring insects, so it appears to be able to consume insects unavailable to the other two species. As the striped possum lacks a patagium and therefore does not glide, it would further enable them to co-exist due to different movement, and therefore utilisation, patterns of their habitat.

The limits to similarity that allow co-existence appear to be quite conservative among the petaurids as even species with large differences in body size, and which appear to be sympatric, show habitat separation, as shown by the mahogany glider and the sugar glider, and between the

yellow-bellied glider and squirrel glider in north Queensland. The habitat partitioning observed by Menkhorst *et al.* (1988) for the squirrel glider and the sugar glider appears to be far more severe than that observed between the mahogany glider and the sugar glider. Although the sugar glider and the squirrel glider are broadly sympatric, Menkhorst *et al.* (1988) found them to be syntopic at only one site and suggested that habitat partitioning was occurring. In contrast, Traill and Lill (1997) observed considerable interspecific overlap in the use of hollows and nest-boxes by sugar gliders and squirrel gliders, with both preferring hollows and nest boxes with narrow entrances (<50 mm diameter); the sugar glider preferred nest boxes and possibly natural tree hollows with entrances too narrow for the larger squirrel glider (Traill and Lill 1997). Trail and Lill (1997) found an increase and then a decrease in numbers of sugar gliders when nest boxes were added and then removed, suggesting that the larger squirrel glider monopolises the best available hollows. They concluded that numbers of sugar gliders may have been limited by a lack of suitable hollows.

In contrast to the sugar glider, which has a broad habitat niche, the mahogany glider, the yellow-bellied glider, the non-gliding Leadbeater's possum, the striped possum and, to a lesser degree, the squirrel glider are far more specialised and therefore restricted in the habitat niche they can occupy. Their larger body sizes (except for Leadbeater's possum) and the associated energy needs may restrict the range and types of habitats they can occupy (Quin 1993).

Management implications of habitat preference for the mahogany glider

The preference for open habitat shown by the mahogany glider has several major implications for the management of this species' habitat, particularly along corridors provided for the mahogany glider to move between fragments of habitat. As corridors are generally only narrow strips of habitat, they have a high tendency to have a well-developed understorey compared with areas in larger patches of habitat. This is due to edge effects, as exotic and some native plant species (such as *A. flavescens*) favour the disturbed habitat along the edge of fragments, resulting in an increased mid-storey canopy cover. Nonetheless, despite trapping records that show the density of mahogany gliders along corridors to be much lower than in continuous forest (Jackson 2000), these results show that corridors do allow individuals to move between patches of habitat. As corridors are generally along creek-lines, which invariably have at least a partial riparian rain-forest component, the corridors are particularly vulnerable to rainforest invasion and further increases in the density of both the understorey and upperstorey. If rainforest covers the complete width of the corridor, then the use of this habitat as a corridor is likely to be reduced or stopped. The use of fire to control the understorey and rainforest expansion along key corridors, and potentially some areas of closed forest within

continuous habitat, should be examined to successfully manage the habitat of the mahogany glider.

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