

# Factors affecting Grey-headed Flying-fox (*Pteropus poliocephalus*: Pteropodidae) foraging in the Melbourne metropolitan area, Australia

E. MCDONALD-MADDEN, E. S. G. SCHREIBER, D. M. FORSYTH,\* D. CHOQUENOT† AND T. F. CLANCY

*Arthur Rylah Institute for Environmental Research, Department of Sustainability and Environment, Heidelberg, Victoria 3084, Australia (Email: dave.forsyth@dse.vic.gov.au)*

**Abstract** Factors affecting the foraging of mobile native fauna in highly fragmented urban landscapes have seldom been quantified at large spatial scales. We investigated factors affecting foraging by Grey-headed Flying-foxes (*Pteropus poliocephalus*; ‘flying-foxes’) in the greater Melbourne metropolitan area. Flying-foxes established a continuously occupied colony site in the Royal Botanic Gardens Melbourne in 1986, and the size of the colony has subsequently increased greatly. We used a stratified-random sampling design to examine the importance of six variables on the detection of foraging flying-foxes: (i) distance from the colony site (0–10, 10–20 and 20–30 km); (ii) distance from the Yarra River (0–5 and 5–20 km); (iii) the relative tree density of the municipality; (iv) whether the site was a park or street; (v) whether there was a relatively high or low density of trees at the site; and (vi) whether food was or was not detected at the site. We surveyed 240 sites within a 30-km radius of the colony site for foraging flying-foxes in both May and October 2002. The probability of detecting a foraging flying-fox declined with increasing distance from the colony site, but increased with increasing tree cover, and was higher for parks compared with streets and when food was present. Flying-foxes were observed foraging in a number of plant genera that have no species that naturally occur in the Melbourne area. Flying-foxes in Melbourne thus forage on planted resources that are widely distributed within a fragmented landscape, and are an example of a positive response by a native species to the process of urbanization.

**Key words:** flying-fox, logistic regression, optimal foraging, stratified random sampling, urban ecology.

## INTRODUCTION

The process of urbanization typically results in both a reduction in the total area of native habitat and the redistribution of the remaining habitat into small fragments within a built environment (Forman & Godron 1986; Wilcove *et al.* 1986). However, urbanization also results in the creation of new habitats, such as parks and gardens, in which both native and exotic flora may be cultivated (Gilbert 1989). Hence, although urbanization will often have a negative effect on native species (Czech & Krausman 1997), some species may be able to navigate urban landscapes and exploit remaining, or constructed, habitat patches.

Gilbert (1989) suggested that flight may enable a species to make use of the highly fragmented food resources available within an urban landscape. Because flight is one of the most energy-efficient means of travel per unit distance, commuting costs

may be negligible if a rich food source is available. Conversely, flight is expensive per unit of time, with species that forage on the wing having high energy demands (Karasov 1992). Gehrt and Chelsvig (2003) suggested that bats (Order: Chiroptera) may be one taxon that may not always be negatively affected by urbanization, and showed that industrial/commercial land uses were positively associated with bat activity in the Chicago metropolitan area. White street lamps that attract insects have been shown to be attractive to some species of insectivorous bat (review in Rydell & Racey 1995), and those species tend to be the most common bat in cities (e.g. Gaisler *et al.* 1998).

Although numerous studies have documented the relationship between the abundance of native fauna and urban land uses (e.g. for bats; Gaisler *et al.* 1998; Gehrt & Chelsvig 2003), few studies have investigated foraging in the spatially fragmented food resources that dominate urban landscapes. In this article, we investigate the factors predicting foraging by a communal-roosting herbivorous bat, the Grey-headed Flying-fox (*Pteropus poliocephalus*; ‘flying-fox’) in the greater Melbourne metropolitan area, Australia.

\*Corresponding author.

†Present address: Landcare Research, Private Bag 92170, Auckland, New Zealand.

Accepted for publication December 2004.

Flying-foxes occupy numerous colony sites in eastern Australia, some of which are in large urban centres (Parry-Jones & Augee 2001). Flying-foxes established a permanent colony site, occupied year-round, at the Royal Botanic Gardens Melbourne ('botanic gardens') in 1986 (Aston 1987). This was the only known roost in the Melbourne area at the time of this study. Estimates of population size indicated that the population has increased greatly since 1986 (van der Ree *et al.* in press). Monthly fly out counts, initiated in March 2001, indicated that the size of the Melbourne population varies seasonally, a pattern observed elsewhere in Australia (Eby 1991a; Parry-Jones & Augee 1992, 2001). The peak of abundance occurs in late summer/autumn, and the lowest abundance in winter/early spring (van der Ree *et al.* in press).

Grey-headed Flying-foxes are dietary generalists, feeding on a combination of fruits, nectar and pollen, the composition of which varies with availability (Nelson 1965a,b; Eby 1991a,b; Parry-Jones & Augee 1991a, 1992). Flying-foxes are also highly mobile (Eby 1991a; Spencer *et al.* 1991; Webb & Tidemann 1996), and both migratory patterns and irregular campsite occupations have been associated with locations offering pulses in nectar production (Ratcliffe 1932; Nelson 1965a; Eby 1991a; Parry-Jones & Augee 1992).

Foraging decisions are based on a suite of choices that trade-off costs and benefits (Stephens & Krebs 1986). Models of optimal foraging predict that individuals should act to maximize the energetic benefits of foraging (Pyke 1978). However, foraging can be influenced by a number of other variables, including the quality and spatial arrangement of resources, the nutritional state of the animal, competition, and predation risk (Lima & Dill 1990; Shipley & Spalinger 1995; McDonald-Madden *et al.* 2000). Understanding the spatial scale at which variables influencing foraging operate is also of considerable ecological interest (Wiens 1989). We examined a total of six variables as predictors of flying-foxes foraging at two spatial scales:

#### Broad-scale variables

Broad-scale variables are not in themselves food sources, but may act as either constraints on, or cues for, flying-foxes locating food sources. We examined the role of four broad-scale variables in determining whether flying-foxes were detected at a site. First, following Pyke (1978) and Stephens and Krebs (1986), we hypothesized that distance from the colony site would be an important constraint on foraging. Second, casual observation suggested that flying-foxes leaving and entering the botanic gardens colony site used the main river flowing through Melbourne, the

Yarra River, as a flight path. We therefore hypothesized that distance from the Yarra River would be a constraint on flying-foxes foraging. Third, since flying-foxes feed mainly on the fruit, flowers and leaves of tree species (Parry-Jones & Augee 1991a,b), we hypothesized that a high density of trees within a municipality might be a cue that food resources were present within that area. Fourth, we hypothesized that parks (including golf courses and school grounds) would be more attractive foraging sites than streets, due either to greater food availability and/or less disturbance from traffic.

#### Small-scale variables

We defined small-scale variables as characteristics of individual sites likely to influence foraging by flying-foxes. We examined the role of two small-scale variables in determining whether flying-foxes were detected at a site. We first hypothesized that flying-foxes would be more likely to forage at sites where trees containing potential food resources were present compared with sites where such trees were not present. Although the diet of flying-foxes in the Melbourne metropolitan area has not been quantified, flying-foxes in the Sydney and Gosford areas of New South Wales have been recorded feeding on blossoms, fruits and leaves from a wide variety of native and introduced trees (Parry-Jones & Augee 1991a,b). As flying-foxes feed mainly in tree species the presence of relatively large numbers of trees at a site may be indicative of the availability of food. We therefore also hypothesized that sites that have a relatively high tree density would be more likely to have flying-foxes detected on them than sites with relatively low tree density.

## METHODS

#### Colony site

The botanic gardens colony site is located at 37°49'58"S, 144°58'59"E, 2.5 km from the Melbourne city centre, adjacent to the Yarra River. The number of flying-foxes roosting at the colony site varies seasonally. In the May 2002 survey period of this study an estimated 21 000 flying-foxes occupied about 7 ha of the botanic gardens, with the majority of animals occupying a 1.1 ha area known as Fern Gully. In the October 2002 survey period an estimated 16 500 flying-foxes occupied 1.5 ha of the botanic gardens, again with most in Fern Gully (I. Temby, Department of Sustainability and Environment, pers. comm., 2003). The nearest known other colony site to the

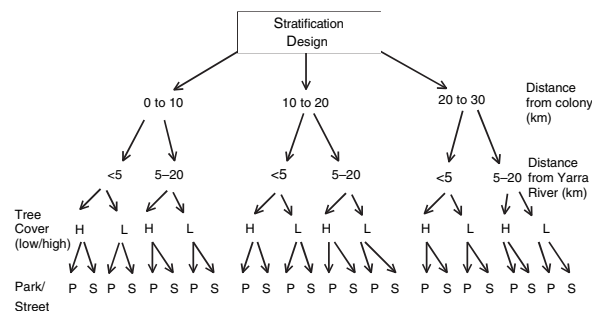
botanic gardens is at Bairnsdale, about 250 km east of Melbourne. This was not occupied by flying-foxes during our study (T. Mitchell, Department of Sustainability and Environment, pers. comm., 2003).

### Sampling design

We sampled in two time periods, autumn (May) and spring (October), and used a stratified-random sampling design based on four broad-scale variables to select 240 sites across Melbourne (Fig. 1). The four broad-scale variables were:

1. Distance from the botanic gardens. We stratified the study area into three distance classes; 0–10, 10–20 and 20–30 km from the colony site.
2. Distance from the Yarra River. Each of the three distance classes above was stratified into two further classes; 0–5 and 5–20 km from the Yarra River.
3. Broad tree density. We defined 26 municipal areas as having either high or low tree density using a GIS layer of the density of street trees per unit area within our study area (provided by E. Seager, Australian Research Centre for Urban Ecology, Melbourne). These areas were ranked into five classes according to tree density. Within each stratified distance class the two extreme classes were used to assign sites as low or high municipal tree density, with half of our sites within each grouping.
4. Parks or streets. Finally, sites were randomly selected as parks or streets using a Melbourne street directory (Melway Publishing Pty. Ltd. 2002). Golf courses and school grounds were defined as ‘parks’.

Within each stratum, 10 survey sites were randomly selected without prior knowledge of sites by observers.



**Fig. 1.** Summary of the stratified sampling design used in surveys of flying-foxes in Melbourne 2002. Stratification was based on four factors, distance from the roost, distance from the Yarra River, broad tree cover and park/streets. Ten sites were randomly selected within each final stratum ( $n = 240$ ).

### Model parameter definition

Some of the variables used for stratification were reassessed as continuous variables for modelling. Distance from the roost site and distance from the Yarra River were recalculated as the actual distance in metres. Tree cover estimates were calculated using ‘Tree25’ (Victorian Government, Australia), a presence/absence tree cover data set derived from SPOT Panchromatic imagery at a resolution of 10 m by a combination of digital classification and visual interpretation. Tree cover was defined as woody vegetation >2 m in height and with a crown cover >10%. Tree cover was calculated for each site at two spatial scales using ARCVIEW 3.2a (ESRI 2000, Redlands, CA, USA); 50 m was defined as ‘local tree cover’, and 500 m as ‘broad tree cover’.

Information on the availability of possible food resources at each site was collected during the survey process. Since there had been little work on the diet of Grey-headed Flying-foxes in the Melbourne area (Menkhorst 1995), we defined possible food resources as species within genera outlined in diet studies conducted in other parts of the range (Eby 1991a,b, 1998; Parry-Jones & Augee 1991a,b, 2001). Sites with one or more of these genera that were flowering or fruiting (see Table 1), or had new leaf growth (*Populus*), were classified as ‘food detected’. Other sites were classified as ‘no food detected’.

### Field sampling procedure

A group of sites in close geographical proximity were surveyed on the same night. An average of six sites were surveyed per night in May, and an average of nine sites per night in October. To reduce the possibility that the order of sampling influenced results, the order of sites to be sampled on a night was randomly determined.

The surveys were conducted by two and three teams of two people in May and October, respectively. A team visited each site no earlier than 2 h after sunset and no surveys continued past 1.00 hour. The two observers walked slowly along a predetermined strip of park or street for 20 min. Trials indicated that teams walked about 1 km in 20 min. Surveys ended when either a flying-fox was observed in, or taking flight from, a tree (‘detected’), or after 20 min had elapsed with no flying-foxes being observed on the site (‘not detected’). The time to detection was recorded. Bats seen or heard flying over the site were not recorded as detected.

### Statistical analyses

We first assessed correlations ( $r_p$ ) between all pairwise combinations of the six predictor variables. Following Booth *et al.* (1994), a threshold limit for the correlation

**Table 1.** List of genera detected as possible food resources for flying-foxes during foraging surveys in the Melbourne metropolitan area<sup>†</sup>

Resource	Family	Genus	Endemic species from food list	Non-endemic species from food list planted in Melbourne	Foraging observations in each genus	
					May	October
Flower	Myrtaceae	<i>Angophora</i>	1	1	–	–
		<i>Callistemon</i>	–	2	–	–
		<i>Corymbia</i>	1	–	–	1
		<i>Eucalyptus</i>	5	22	33	33
		<i>Melaleuca</i>	–	1	–	1
	Proteaceae	<i>Banksia</i>	1	1	1	1
		<i>Grevillea</i>	–	1	–	–
Fruit	Moraceae	<i>Ficus</i>	–	8	20	16
	Myrtaceae	<i>Acmena</i>	–	1	–	1
	Pittosporaceae	<i>Pittosporum</i>	1	–	–	–
	Ebenaceae	<i>Diospyros</i>	–	1	–	–
	Palme	<i>Phoenix</i>	–	1	–	1
	Rosaceae	<i>Malus</i>	–	1	–	–
	Rutaceae	<i>Citrus</i>	–	2	–	–
Leaves	Salicaceae	<i>Populus</i>	–	1	–	5
	Total		9	43	54	59

<sup>†</sup>Adapted from food list by G. Moore pers. comm.: see Eby 1991a,b, 1998; Parry-Jones & Augee 1991a,b, 2001). Numbers represent counts. –, not observed.

between continuous variables was set at 0.5. Local tree cover was subsequently excluded from our analyses as both tree cover factors were highly correlated (see *Results*). Box plots were used to assess the correlation between binomial variables and continuous factors. Contingency tables were used to examine the correlation between parks/streets and food detected/no food detected, with independence of these two binomial factors tested using Fisher's Exact Test (Zar 1999).

The relationship between the predictor variables and the detection of flying-foxes was examined using multiple logistic regression. Logistic regression transforms binary information into an odds ratio that indicates the probability of flying-foxes being detected at a site relative to it not being detected. An odds ratio of 1 indicates equal chances of flying-foxes being detected or not. Subsequent use of a logit transformation (link function) of the odds ratio provides a mechanism for fitting a generalized linear model (Quinn & Keough 2002).

Determining which combination of variables best explains variation in data is problematic. Even with a relatively small number of variables the potential number of models that can be considered is large (Burnham & Anderson 2002). Hence, we did not include all possible combinations of variables but rather focused on models for which there was *a priori* justification. Our analyses compared 10 models based on the four broad-scale factors and food availability (summarized in Table 2).

Akaike's Information Criterion ( $AIC_c$ ) was used to identify which of these 10 models were best supported by the data (Burnham & Anderson 2001, 2002).  $AIC_c$  assesses the model based on a trade-off between the fit of the model and the model's complexity, which is measured by the number of parameters ( $K$ ). The model with the most support has the smallest  $AIC_c$ , and models are ranked based on the difference between each model's  $AIC_c$  and the  $AIC_c$  of this model ( $\Delta AIC_c$ ). Akaike weights ( $w_i$ ) were used to provide an approximate probability that the best model is in fact the best of the candidate set. The  $w_i$  were used to

**Table 2.** Description of the 10 candidate models for predicting the detection of foraging flying-foxes at 240 sites within the Melbourne metropolitan area

Model	Variables
1	Distance roost + distance Yarra + tree cover + park + food
2	Distance roost + distance Yarra + tree cover + park
3	Distance roost
4	Distance Yarra
5	Tree cover
6	Park
7	Food
8	Distance roost + food + distance roost*food
9	Park + food
10	Distance roost + food + park

average the parameter estimates based on the candidate models whose weights equated to at least 95% probability (Burnham & Anderson 2002). The results of the model selection process are presented following the recommendations of Anderson and Burnham (2002).

We used the statistical package R version 1.9.0 (The R Development Core Team 2004) to fit the models and to obtain AIC<sub>c</sub> values, model averaged estimates of parameters, and the standard errors of these parameter estimates.

**RESULTS**

The May 2002 survey was conducted over 18 nights (30 April–27 May) and flying-foxes were detected at 93 (39%) of the 240 sites (Fig. 2). The October 2002 survey was conducted over 10 nights (7–22 October) and flying-foxes were detected at 67 (28%) of the 240 sites (Fig. 2). Flying-foxes were detected at 44 sites during both surveys.

Box plots indicated no strong correlation between food availability or park/street and distance to the colony, distance to the river, and broad or local tree cover. Box plots representative of the patterns observed are shown in Fig. 3. No correlation was observed between park/street and food availability in either May (Fisher’s Exact Test = 1.104, d.f. = 1, *P* = 0.8) or October (Fisher’s Exact Test = 0.967, d.f. = 1, *P* = 1.0). There was a strong and positive correlation between the two measures of tree cover (broad and local; *r<sub>p</sub>* = 0.826), but the *r<sub>p</sub>* estimates for all other pairwise comparisons of the continuous variables were <0.5.

The model including all five predictor variables (model 1 in Table 2) was best supported by the data in both May and October (Table 3). There was limited support for a simpler model (distance from roost, food

and park; model 10) in both seasons. There was minor support for a model including only park and food in October (model 9). In May, there was about a 99.9% probability that models 1 and 10 were the best models, whilst in October there was a 98% probability that models 1, 9 and 10 were the best models. These sets of models were averaged to obtain estimates of the five parameters and the model intercepts in May and October (Table 4).

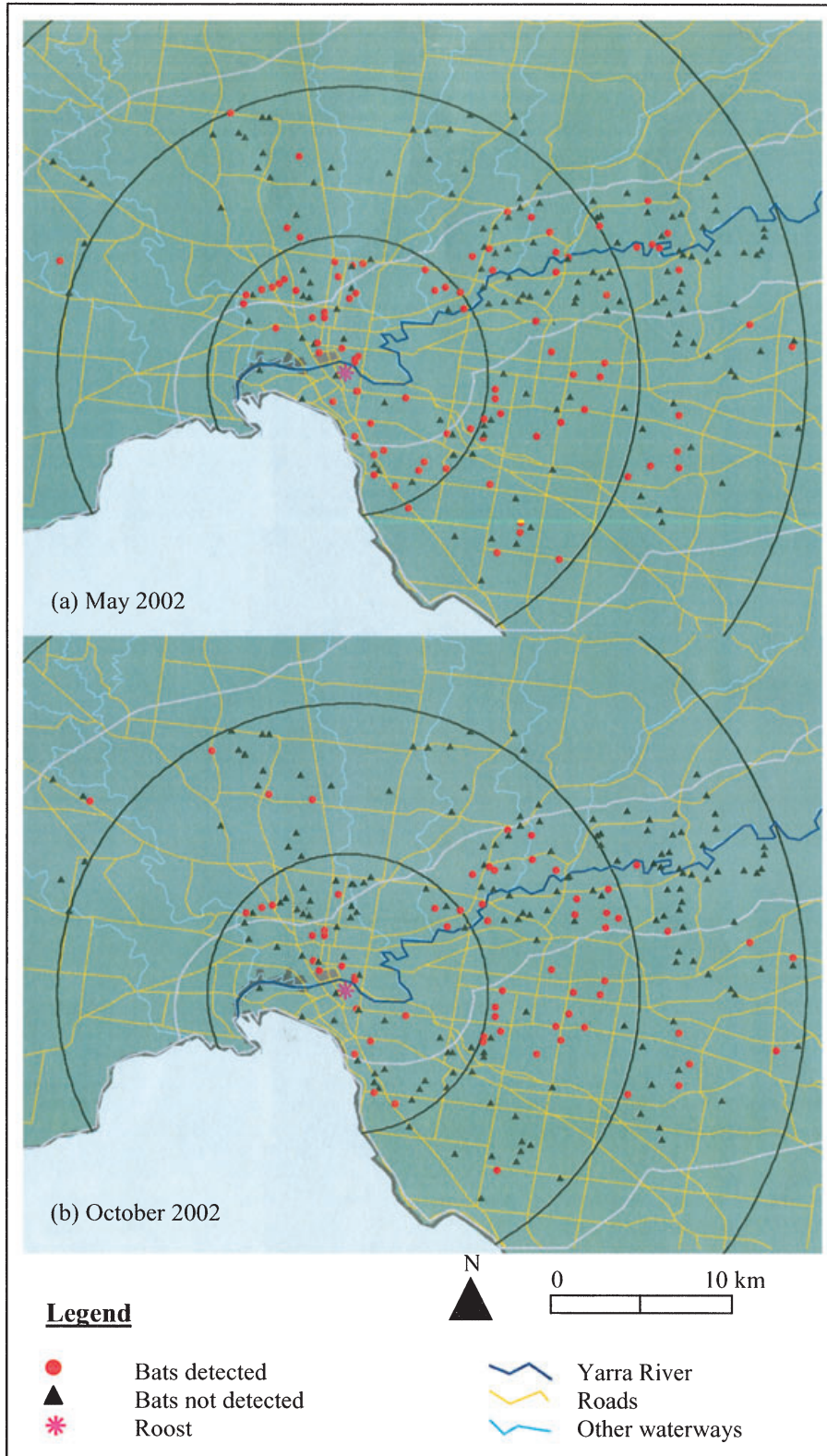
**Table 3.** Comparison of the 10 candidate models for predicting the detection of foraging flying-foxes at 240 sites, in two seasons, within the Melbourne metropolitan area

Model	<i>K</i>	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	Rank	<i>w<sub>i</sub></i>
May					
<b>Model 1</b>	<b>6</b>	<b>257.00</b>	<b>0</b>	<b>1</b>	<b>8.34E-01</b>
Model 10	4	261.00	3.23	2	1.66E-01
Model 8	4	274.00	16.14	3	2.61E-04
Model 9	3	277.00	19.15	4	5.79E-05
Model 2	5	278.00	20.51	5	2.93E-05
Model 7	2	287.00	29.06	6	4.09E-07
Model 3	2	288.00	30.69	7	1.81E-07
Model 6	2	313.00	55.97	8	5.84E-13
Model 4	2	322.00	64.86	9	6.88E-15
Model 5	2	324.00	66.57	10	2.92E-15
October					
<b>Model 1</b>	<b>6</b>	<b>209.00</b>	<b>0</b>	<b>1</b>	<b>7.88E-01</b>
Model 10	4	212.00	3.64	2	1.27E-01
Model 9	3	214.00	4.91	3	6.76E-02
Model 8	4	217.00	8.74	4	9.98E-03
Model 7	2	218.00	9.45	5	7.00E-03
Model 3	2	276.00	67.53	6	1.71E-15
Model 2	5	277.00	68.31	7	1.16E-15
Model 6	2	284.00	74.96	8	4.15E-17
Model 4	2	287.00	78.84	9	5.98E-18
Model 5	2	288.00	79.35	10	4.63E-18

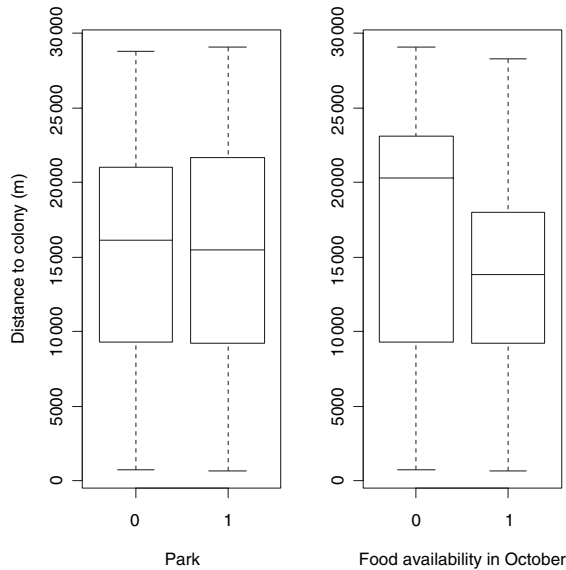
Model number corresponds to those in Table 2. *K* is the number of parameters in the model and *w<sub>i</sub>* are the Akaike weights. The best model in each season is highlighted in bold. AIC<sub>c</sub>, Akaike’s Information Criterion.

**Table 4.** Parameter estimates based on model averaging (May: Models 1 and 10, October: Models 1, 9 and 10)

	Estimate	SE	Lower 95% CI	Upper 95% CI
May				
Intercept	-0.7910000	0.5620000	-1.8910000	0.3090000
Distance roost	-0.0001440	0.0000381	-0.0002187	-0.0000693
Distance Yarra	0.0000795	0.0000442	-0.0000071	0.0001661
Tree cover	3.0600000	1.4100000	0.3000000	5.8200000
Park	1.0100000	0.3260000	0.3710000	1.6490000
Food	1.5400000	0.3500000	0.8540000	2.2260000
October				
Intercept	-4.1400000	0.9970000	-6.0900000	-2.1900000
Distance roost	-0.0000730	0.0000348	-0.0001412	-0.0000048
Distance Yarra	0.0000464	0.0000449	-0.0000416	0.0001344
Tree cover	3.7400000	1.7900000	0.2300000	7.2500000
Park	0.7110000	0.3560000	0.0130000	1.4090000
Food	3.8100000	0.7190000	2.4000000	5.2200000



**Fig. 2.** The location of sites sampled for flying-foxes in Melbourne and where they were detected in (a) May and (b) October 2002. The black concentric circles indicate 10, 20 and 30 km from the botanic gardens roost and the pale grey lines 0–5 km and 5–20 km strata, from the Yarra River.



**Fig. 3.** Representative box plots of the correlation between binomial variables and continuous variables. The example represents food availability and park, with the continuous variable, distance to the colony (m).

In both seasons, the probability of detecting foraging flying-foxes declined with increasing distance from the botanic gardens. All other parameter estimates were positive, and their 95% CI did not include zero, except for the estimate of distance from the Yarra River. The 95% CI for this estimate included zero, indicating that this variable had little effect. The magnitude of the effect of distance to the roost on detecting foraging flying-foxes was small relative to the coefficients for tree cover, park/street and food availability. This pattern was true in both seasons, with only small differences in the parameter estimates between seasons (Table 4).

In both survey months, 63% of sites at which flying-foxes were detected were parks. The presence of food resources did not differ between parks and streets in either month (May,  $\chi^2 = 1.12$ ,  $P = 0.77$ ; October,  $\chi^2 = 7.68$ ,  $P = 0.053$ ), nor were flying-foxes detected any earlier at parks compared with streets (May, mean time to detection in parks = 8 min 0 s  $\pm$  5 min 0 s, mean time to detection in streets = 9 min 0 s  $\pm$  6 min 0 s,  $t = 1.07$ , d.f. = 91,  $P = 0.29$ ; October, mean time to detection in parks = 7 min 13 s  $\pm$  6 min 52 s, mean time to detection in streets = 7 min 50 s  $\pm$  4 min 30 s,  $t = 0.44$ , d.f. = 63,  $P = 0.66$ ).

Flying-foxes were detected foraging in a number of different plant genera throughout Melbourne (see Table 1). From a full list of Australian species (119 species) that flying-foxes have previously been known to feed in throughout their range (see Eby 1991a,b, 1998; Parry-Jones & Augee 1991a,b, 2001), only 10 species from 7 genera are endemic to the Melbourne

area (G. Moore pers. comm., 2003). The majority of observations in both May (61%) and October (56%) were in *Eucalyptus* species (see Table 1). Although eucalypts were rarely identified to the species level, only five dietary species are endemic to Melbourne, whilst a further 22 known dietary eucalypts are not endemic to the area (see Table 1). An additional 21 species of eucalypt, not previously listed as food trees, are known to be planted in Melbourne (G. Moore pers. comm., 2003). Flying-foxes were observed feeding in species from Western Australia on at least one occasion (*Eucalyptus conferruminata*). In May and October, 37% and 32% of observations, respectively, were in genera of which no species are endemic to Melbourne.

## DISCUSSION

Our results show that, in both May and October, four variables predicted whether flying-foxes were detected foraging at a site in the Melbourne metropolitan area. In both seasons the probability of detecting foraging flying-foxes declined with increasing distance from the botanic gardens, but increased with increasing tree cover, and was higher for parks compared with streets and also higher when food was present.

Under the assumptions that flying-foxes were acting to maximize their energetic balance and that distance travelled is an index of energy expended during foraging, foragers such as flying-foxes should minimize the distance that they travel to forage (Pyke 1978; Stephens & Krebs 1986). Hence, since we assume that the primary activity of flying-foxes when away from the colony site is foraging (Palmer & Woinarski 1999; Palmer *et al.* 2000; Banack & Grant 2002), our findings confirm that distance from the colony is a constraint on foraging, as predicted by foraging theory. However, distance from the colony was not as important as broad-scale tree cover, whether the site was a park or street, or whether food was available (Table 4). There are several possible explanations for this finding.

First, flying-foxes may have been foraging >30 km from the botanic gardens. Although small numbers of flying-foxes have been observed foraging in apple orchards approximately 40 km from the botanic gardens, there were no reports of flying-foxes in those orchards during this study (I. Temby, Department of Sustainability and Environment, pers. comm., 2003). Several studies have reported foraging behaviour of radio-collared Grey-headed Flying-foxes (e.g. McWilliam 1986). Spencer *et al.* (1991) reported a 'feeding range' of 25 km for one flying-fox at Lismore, and up to 17 km for two flying-foxes in Sydney. Eby (1991b) reported that distances from day roosts to initial feeding trees ranged from 4 to

37 km, with individuals visiting multiple trees located several km apart in one night. Assuming that the flying-foxes detected in this study all roosted at the botanic gardens, some individuals flew at least 30 km to forage. Maximum foraging distances approaching 30 km were recorded by Palmer and Woinarski (1999) for radio-tracked Black Flying-foxes (*Pteropus alecto*) in the Northern Territory. White-necked Flying-foxes (*Pteropus tonganus*) roosting on the west side of American Samoa have been recorded flying similar distances [mean  $22.8 \pm 8.3$  (SE) km], although distances were much shorter for individuals roosting on the east side of the island ( $4.8 \pm 0.6$  km; Banack & Grant 2002). Hence, 30 km is about the maximum foraging distance recorded for *Pteropus*. Our results are consistent with these data. Second, the costs of flying to 30 km may have been small relative to the quality and quantity of resources available there (see Karasov 1992).

It had previously been suggested that the Yarra River was an important flight-path for flying-foxes leaving and returning to the botanic gardens colony. We found that distance from the Yarra River was not an important predictor of flying-foxes being detected at a site. The Yarra may initially be an important flight-path to navigate to and from the colony, but then the extensive network of roads and waterways in Melbourne may enable flying-foxes to navigate more widely in search of food.

Because local and broad tree cover were strongly correlated, it was not possible to include them both in our analyses. The probability of detecting foraging flying-foxes increased with increasing broad tree cover. We suspect that this relationship derives from the availability of food increasing with the density of trees at a site. The probability of detecting foraging flying-foxes at a site also increased when food was present. Although the presence of food did not differ between parks and streets in either month, our method of estimating the presence of food was crude in this study. However, we note that quantifying the quality and quantity of the food of flying-foxes would be difficult.

Flying-foxes were detected more often in parks than in streets during both May and October, despite food availability being similar. There was no difference in the time to detection between parks and streets in either month, suggesting that bats were equally likely to be detected in both. One possibility is that flying-foxes prefer park sites to street sites for reasons unrelated to foraging, perhaps because the former were darker and quieter.

Our results were broadly similar in both seasons, suggesting that the rules governing flying-fox foraging in the Melbourne metropolitan area did not vary between seasons. However, we did detect flying-foxes at more sites in May than October, reflecting the trend observed in the number of flying-foxes counted at the

colony site in those months (van der Ree *et al.* in press).

Whereas previous studies have investigated the behaviour of individual flying-foxes, either by radio-tracking (Palmer & Woinarski 1999; Banack & Grant 2002) or direct observation (Banack 1998), the network of streets and parks in the Melbourne metropolitan area provided the opportunity to implement a stratified, random sampling design to test hypotheses about the variables governing flying-foxes foraging at the whole colony scale. Our inferences thus apply to the whole population of flying-foxes roosting at the botanic gardens in May and October 2002.

Flying-foxes have established several other large colony roosts in urban areas in eastern Australia (Eby 1991a). Although the reasons for the recent (1986) establishment of a colony in Melbourne are unclear, the steady increase in the number of flying-foxes using this colony is evidence that this species can utilize fragmented food resources. Interestingly, a number of the observations of foraging flying-foxes in this study were in species that are not endemic to Melbourne (see Table 1). Furthermore, there seems to be many eucalypt species planted in Melbourne that may be food for the flying-foxes. Hence, whereas other studies have shown that white street lamps appear to be beneficial for some insectivorous bats in urban areas (Rydell & Racey 1995; Gaisler *et al.* 1998), our study shows that the planting of trees during the process of urbanization has been beneficial to flying-foxes (*sensu* Gilbert 1989). Flight enables flying-foxes to utilize forage trees in a highly fragmented urban landscape with few remaining areas of natural habitat.

## ACKNOWLEDGEMENTS

Funding for this project was provided by the Department of Sustainability and Environment, Victoria. We thank Linda Bendall, Simon Hart, Andrew Kleinig, Mark Padgem, Andrew Vance, Matt West, Nick Clemann, Lou Grgat and Simon Scott for conducting the nocturnal surveys. We also thank Emma Seager and Rodney van der Ree (Australian Research Centre for Urban Ecology, Melbourne) and Greg Moore and Jill Kellow (School of Botany, University of Melbourne) for providing information, Andrew Bearlin for assistance with GIS, and Michael Scroggie and Joanne Potts for advice and assistance with analyses. Comments by Lindy Lumsden, Ian Temby, Rodney van der Ree, Peggy Eby, Michael Bull, Allen Paul McIlwee and one anonymous reviewer greatly improved this article.

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