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Fruit availability and utilisation by grey-headed flying foxes (*Pteropodidae*: *Pteropus poliocephalus*) in a human-modified environment on the south coast of New South Wales, Australia

Abstract

Context. Extensive clearing and modification of habitat is likely to change many facets of the environment including climate and regional food resources. Such changes may result in changes in behaviour in highly mobile fauna, such as flying foxes. **Aims.** The availability of fruit resources was examined to determine whether grey-headed flying foxes (*Pteropus poliocephalus*) have feeding preferences related to habitat or dietary items, and whether human usage of the land around the colony site has affected the resources available. **Methods.** Fruit availability around a colony was monitored from December 2004 to March 2005. Night surveys and faecal analyses were undertaken to determine the distribution of feeding locations, the food species used and the food items consumed by *P. poliocephalus*. **Key results.** The amount of food available per hectare in each habitat was similar. However, we found differences in the composition of food trees and the distribution of food resources within each habitat. *Ficus* species were a major resource with flying foxes observed feeding in figs during every survey and figs identified in droppings over the whole period. Human-modified habitats were used throughout the study period with flying foxes observed in small patches of vegetation and in individual trees without any nearby vegetation. **Conclusions.** The need for maintaining vegetation, particularly *Ficus* species, in all areas where flying foxes are found, especially in human-modified habitats and rainforest remnants, is highlighted as this vegetation is of great importance to flying foxes. Other wildlife, such as birds and possums, may also benefit from the maintenance of this vegetation. **Implications.** Through management of urban resources there is the potential to prevent future conflict situations arising between humans and wildlife, such as can be seen when flying fox colonies are in close proximity to houses.

Keywords

human, *poliocephalus*, *pteropus*, *pteropodidae*, foxes, flying, headed, grey, utilisation, south, availability, australia, coast, wales, fruit, environment, modified

Disciplines

Life Sciences | Physical Sciences and Mathematics | Social and Behavioral Sciences

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Fruit availability and utilisation by grey-headed flying foxes (*Pteropodidae: Pteropus poliocephalus*) in a human-modified environment on the south coast of New South Wales, Australia

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Implications. Through management of urban resources there is the potential to prevent future conflict situations arising between humans and wildlife, such as can be seen when flying fox colonies are in close proximity to houses.

Additional keywords: diet, habitat, human impact, modification, preference, selection.

Introduction

Fauna that are highly mobile, such as flying foxes, will respond to habitat modification by changing where they forage and roost in the landscape. Thus the abundance and movements of animals are likely to reflect differences in availability of food resources. The conservation value of human-modified landscapes may be important for fauna (Goodman *et al.* 2005, 2008) although extensive modification is likely to change regional food resources as well as the local climatic conditions (Parris and Hazell 2005). It is therefore important to understand the relationship between habitat usage and the availability of food across the landscape including those habitats that have been highly modified (Petit and Petit 2003; Goodman *et al.* 2005; Radford and Bennett 2005).

Whereas some studies have documented food availability for bats (Heithaus *et al.* 1975; Banack 1998), none have investigated the availability of food resources in modified

habitats and the foraging response of bats to such modifications. In undisturbed habitats, documenting availability of fruit and relating this to flying fox behaviour or movements has been examined through studying plant phenology (McClure 1966; Medway 1972; Frankie *et al.* 1974; Opler *et al.* 1980), mapping plants and counting fruits through time (Stashko 1982; Dinerstein 1986; Funakoshi *et al.* 1993), setting seed traps (Foster 1982; Stashko and Dinerstein 1988) and monitoring removal of marked fruit (Stashko 1982).

The grey-headed flying fox *Pteropus poliocephalus* occurs along the east coast of Australia and is listed as vulnerable under the *Threatened Species Conservation Act* 1995 (NSW) and under the *Environment Protection and Biodiversity Conservation Act* 1999 (Commonwealth), largely due to habitat clearance from both urbanisation and agriculture. Although *P. poliocephalus* is a generalist nectarivore and frugivore, the species is considered a sequential specialist, that

is, within one area they will use a limited number of food sources hierarchically, consuming each species in turn until it becomes used up or unavailable (Parry-Jones and Augee 1991a; Parry-Jones 1993). Major food trees include rainforest fruits and blossom of Myrtaceae, Proteaceae and a small number of species from other families (McWilliam 1986; Eby 1991; Parry-Jones and Augee 1991a). They are also known to eat leaves, bark and insect parts (Parry-Jones and Augee 1991a). However, *Ficus* species are considered very important food sources that are often available all year round and over a wide area (Banack 1998; Eby 1998; Parry-Jones and Augee 2001; Shanahan *et al.* 2001; Markus and Hall 2004). Figs are considered an easy resource to handle and consume for most animals and can be a relatively high source of protein and calcium (Shanahan *et al.* 2001; Bleher *et al.* 2003). *P. poliocephalus* are highly social animals that roost in colonies (i.e. camps or day roosts) during the day. These colonies can contain thousands of individuals. However, observations of colonies with over 200 000 flying foxes have not been recorded since before the 1990s (Ratcliffe 1931, 1932; Nelson 1963, 1965a, 1965b; Mickleburgh *et al.* 1992; Eby *et al.* 1999; Tidemann *et al.* 1999). Colonies are regularly spaced in the landscape and *P. poliocephalus* shows high seasonal fidelity to traditional sites, returning annually (Lunney and Moon 1997; Augee and Ford 1999). Modification of habitat has been shown to affect the use of traditional sites. For example, there is now a year-round camp in Melbourne, which is considered to have established in response to anthropogenic changes in the local climate (Parris and Hazell 2005).

The size of the foraging areas around colonies of *P. poliocephalus* is related to the type and availability of resources. Eby (1995) found that flying foxes can forage up to 50 km from colony sites and 20 km between feeding sites in north-eastern New South Wales when feeding on blossom resources, whereas shorter foraging flights of as little as 2.6 km are made when foraging for fruits. Short foraging distances of a maximum of 10 km were found by McWilliam (1986) also in north-eastern NSW. Thus, distances up to 10 km from colony sites should contain the available fruit for the colony.

Although the diet of *P. poliocephalus* has been widely studied (McWilliam 1986; Eby 1991, 1995; Parry-Jones and Augee 1991a, 1991b), there have been no studies conducted on the availability of fruit resources for flying foxes within a region, particularly in association with habitat modifications. Consequently, their feeding response to habitat modification is unknown. Previous studies of Australian flying foxes have alluded to the availability of food resources (McWilliam 1986; Parry-Jones and Augee 1991a, 1991b, 2001), but availability has not been quantitatively measured. Parry-Jones and Augee (1991a) found that there were restricted numbers of diet items available at one time and when preferred species diminished in availability or failed to provide food, the flying foxes would eat less desirable species or move to areas with better food supply. The measurement of availability of resources by Parry-Jones and Augee (1991a) was subjective, suggesting the need to consider such relationships in more detail.

The present study examines the availability of fruit resources for *P. poliocephalus* around a seasonal colony in temperate

eastern Australia during the period of occupation of the colony. The colony at Jamberoo is occupied during summer, when there is a scarcity of blossom elsewhere (Parry-Jones 1993; Law *et al.* 2000). While occupying this colony, *P. poliocephalus* predominantly eat fruit (Parry-Jones 1993) and leave when blossom becomes available elsewhere. Thus, the present study focussed on investigating the availability of fruit rather than blossom as the critical food resource within the landscape. We examined:

- (1) the availability of fruit in three habitat types surrounding the colony – rainforest, rural rainforest remnants and human-modified areas,
- (2) whether the distribution of flying foxes foraging throughout the study area is related to availability of fruit resources,
- (3) whether *P. poliocephalus* have feeding preferences for habitat or dietary items,
- (4) the occurrence of dietary items identified in droppings compared with the occurrence of flying foxes at feeding locations, and
- (5) whether human usage of the land around the colony site influences the resources available to *P. poliocephalus* and therefore their utilisation of those resources.

Methods

Study area

The colony is located north-east of Jamberoo (34°37'22'S, 150°47'32'E), on the south coast of New South Wales, Australia. It is situated in an east-facing gully containing rainforest vegetation and is surrounded by cleared farmland and remnant patches of rainforest. The colony was occupied from late October 2004 to the end of March 2005 and fly-out counts (Eby *et al.* 1999) were conducted monthly to determine colony size during the study.

The size of study area was determined using previous studies of the foraging patterns of flying foxes (McWilliam 1986; Parry-Jones 1993; Eby 1995; Markus and Hall 2004). The foraging area of flying foxes for fruits was defined as a 10-km radius around the colony. Within the study area we mapped the distribution of three focus habitats – human-modified, rural rainforest remnants and rainforest habitats – using vegetation maps for the Minnamurra Catchment (Harris 2002) and from Shellharbour City Council. The study area was 27 536 ha, of which 67% had been modified by humans (18 650 ha). Modified areas included cleared paddocks for grazing and low-density housing. Rainforest remnants covered 1129 ha (4% of total) and more substantial rainforest habitats covered 1247 ha (5%). These rainforest habitats were continuous with the vegetated escarpment that distinguished them from rainforest remnants, which occurred in patches within the human-modified landscape. The rest of the study area (24%) was classified as 'other' (6510 ha), which included *Eucalyptus*, *Banksia* and *Casuarina* forests, shrub-land, wetland and grassland.

Fruit availability

Within each of the three habitat types, 10 sites were randomly selected and the availability of fruit monitored monthly along an

800 × 30 m belt transect from December 2004 to March 2005. The area (m²) of fleshy fruit was estimated in a manner similar to projected foliage cover and resulted in information on the area (m²) of food provided. Every tree, shrub and vine over 2 m that was fruiting was assessed and its area estimated. The percentage of the area that was fruit was estimated into four categories: 0–30, 30–50, 50–70 and 70–100%. To calculate the estimated available fruit in terms of area, the area of canopy for each plant was multiplied by the midpoint of the percentage fruit area category.

For each month, a one-way analysis of variance (ANOVA) was used to assess the variability of food availability between habitat types. We graphically compared the variation in total area of food between months. One-way ANOVA was also used to compare the availability of *Ficus* species in each habitat, for each month. The availability of *Ficus* species was analysed as a group rather than by each individual species.

Foraging patterns

To determine the distribution of feeding locations and the food species used, night surveys were undertaken three times per month from December to March. Night surveys involved driving around the study area and stopping at random points in each habitat type to listen for the sound of flying foxes vocalising and feeding. *P. poliocephalus* are extremely vocal animals (Nelson 1964) and can be heard from some distance away. They are territorial feeders (Ratcliffe 1932; McWilliam 1986) and where more than one animal feeds on a tree, defensive behaviours and vocalisations occur (Nelson 1964). Where flying foxes were heard, the location, time, food species and the approximate number of bats were determined using spotlights. A total of 100 points were sampled. The area of each point sampled during night surveys was 7850 m²; therefore, the total area sampled was 3% of the study area. The number of stops per habitat was in proportion to the whole area of that habitat found in the study area, not on the area surveyed in the vegetation transects. Therefore, more stops were made in human-modified areas. Stops were also made in areas that had vegetation classed as 'other', to investigate usage of these areas.

To determine whether spatial distribution of foraging *P. poliocephalus* was independent of the availability of food in the three focal habitat types, the occurrence of flying foxes in habitats was tested using a Chi-square test. The expected number of bats in each habitat type was calculated using the total area of food available in each habitat, for the month in which the night survey occurred.

Diet

To determine the food items consumed by *P. poliocephalus*, 40 faecal samples and 10 spat out pellets (50 droppings in total) were randomly collected each month from under the colony using the methods of Parry-Jones and Augee (2001). Droppings were examined using a stereomicroscope and a compound microscope. There were no fresh spat-out samples collected at the end of March as the samples were collected the day after the final departure of the flying foxes and the colony was empty. The samples were frozen after collection as they consist mainly of the very soft parts of fruit. Also, as

traditional drying of the samples would render the components unidentifiable, samples were prepared and examined for food resources following the method developed by Parry-Jones and Augee (2001). Samples of fresh fruits and flowers were taken from trees in the field to attempt to identify the unknown items found in droppings.

The occurrence of each food item in a dropping was recorded and the number of droppings with that occurrence expressed as a proportion of the number of droppings analysed at a given time (frequency of occurrence), because it is not possible to determine preference for dietary items using proportion of each dropping of each food item. As bats treat food items differently (e.g. hard parts spat out) and the digestibility varies between items, the percentage of the diet made up by a food item does not equate to percentages in droppings. Furthermore, the contribution of rare, large or important items can be underestimated whereas small frequent items may be overestimated (Thomas 1988). Pollen was included as a category in assessing droppings to determine if these resources were used during the study period. However, nectar, which is a major source of high calorific input, does not show up in droppings. Pollen is generally used to determine whether nectar has been consumed (Thomas 1988). Where an item is consumed for the pollen resources, pollen grains in the droppings are 'empty' with the internal contents removed (Parry-Jones and Augee 1991a). Intact pollen grains indicate that the food resources may be used for nectar as the nitrogen content of the pollen has not been used (Parry-Jones and Augee 1991a). However, empty pollen grains do not preclude the use of that plant species as a nectar resource.

Due to a relatively fast gut transit time in pteropids, droppings collected from under colonies could represent a biased sample towards the later part of the animals' foraging period, though a retention time of >12 h has been found (Shilton *et al.* 1999). However, radiotracking studies have shown that flying foxes return to food resources they have foraged upon earlier in the evening before returning to the colony site (Banack and Grant 2003).

Results

Fruit availability

There was very high spatial variability in the food availability per hectare between transects in human-modified habitat. Some areas were totally cleared or had unsuitable vegetation and therefore provided no food, whereas other areas had individual trees that had more fruit available than all trees in some remnants or rainforest areas.

There were no differences between habitats in the area of fruit (m²) available per hectare in any month from December to March (Fig. 1; $F_{2,29} = 0.6733 - 3.2684$, $P = 0.0536 - 0.5184$). There were also no differences between habitats in the area of *Ficus* fruit available per habitat for most months ($F_{2,29} = 0.8715 - 3.0199$, $P = 0.0655 - 0.4298$) except March ($F_{2,29} = 3.9491$, $P = 0.0313$). In March, there was significantly less area of *Ficus* species available in rainforest habitats than in rainforest remnants (Fig. 1).

The number of food trees with fruit available in the study area varied between months, with some species available in

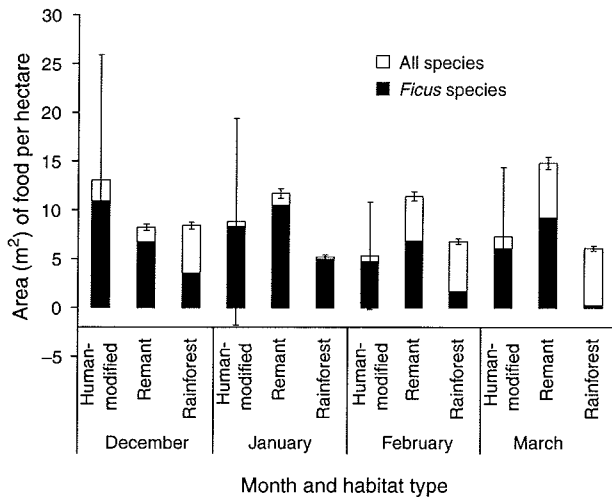


Fig. 1. Fruit available (m²) to flying foxes, *Pteropus poliocephalus*, per hectare of human-modified, rainforest remnant and rainforest habitats between December 2004 and March 2005. Vertical bars are standard deviation.

all months (e.g. *Archontophoenix cunninghamiana*, *Planchonella australis* and *Syzygium australe*; Fig. 2a, Appendix 1). The number of species available increased to maximum in February. However, fruit abundance was consistent for most of the study period with an increase in March. The number of exotic plant species with fruit was highest in December (21.4% of species available) and February (10%).

A large quantity of fruit from *Ficus* species was available in all months (Fig. 2b). *Ficus macrophylla* was abundant for the whole period whereas other *Ficus* species were available during summer but less abundant in March. *Ficus superba* only provided relatively small amounts of food in the last 3 months and peaked in March (Fig. 2).

Foraging patterns

Monthly fly-out counts determined that the colony was stable at 3500 individuals throughout the study period. Between 2

and 10% of the colony were observed foraging each night and the night surveys sampled ~3% of the available habitat within the study area, suggesting that our study area was large enough to contain all foraging individuals.

Flying foxes were observed in human-modified areas on all nights surveyed (Table 1), both in small patches of vegetation and in individual trees without any nearby vegetation. Observations of flying foxes feeding in rainforest remnants were made on all surveys in December and January, but only on one occasion in both February and March. Flying foxes were only recorded in rainforest habitat on four surveys.

During surveys in late February and March flying foxes were also observed feeding in habitats other than the three focus habitats (Table 1). Flying foxes were observed feeding on Myrtaceae species, including *Eucalyptus citriodora* and *Eucalyptus botryoides* × *saligna*. The occurrence of flying foxes feeding in 'other' habitats corresponded with the decrease in numbers seen in the three focus habitats (Table 1).

On most nights surveyed, the numbers of flying foxes seen in each habitat were different from that expected from food availability (Table 1; $\chi^2_6 = 12.022-457.007, P = 0.001$).

Overall there was a trend to preferentially forage in rainforest remnants over summer, moving to human-modified habitats towards the end of summer. Interestingly, flying foxes showed a preference for rainforest remnants at the expense of rainforest habitats in December and January, but began using rainforest at the end of January.

In the mid-February survey, flying foxes did not use rainforest remnants or continuous rainforest habitats and were only found foraging in human-modified habitats. By the end of February, flying foxes foraged in human-modified habitats and habitat other than the focus habitats where they were observed foraging on Myrtaceae blossom, and did not use rainforest remnants or rainforest habitats.

Ficus species were the main food item utilised by flying foxes (Fig. 3). Flying foxes were observed feeding on figs on every survey. The *Ficus* species used were *Ficus rubiginosa* and *F. macrophylla*. The percentage of occurrences of flying foxes feeding on *Ficus* species varied from 47 to 100% of the total observations per night (Fig. 3). The percentage of

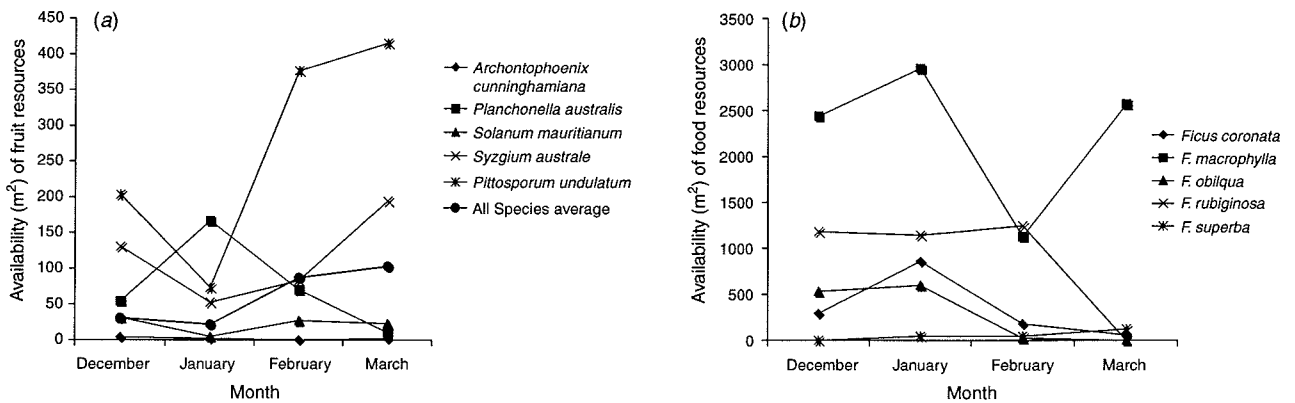


Fig. 2. Changes in the total availability of (a) specific fruits (with average of all fruit species) and (b) *Ficus* species to *Pteropus poliocephalus*, from December 2004 to March 2005 over all habitat types.

Table 1. Observed and expected (parentheses) occurrence in each habitat of flying foxes as determined by number of flying foxes observed and the availability of all plants species in the study area on each night surveyed, and Chi-square values

Observations made of flying foxes in other habitats were not compared with availability of food, but were included in this table to highlight the change in foraging patterns

Date	Human modified	Remnant	Rainforest	Other	Chi-square value	P
15 Dec	212 (232)	40 (13)	0 (7)	0	123.058	0.001
19 Dec	322 (329)	35 (18)	0 (10)	0	56.363	0.001
22 Dec	205 (258)	75 (14)	0 (8)	0	457.007	0.001
21 Jan	130 (146)	35 (12)	0 (8)	0	55.636	0.001
25 Jan	200 (198)	25 (16)	0 (11)	0	15.662	0.001
31 Jan	71 (124)	30 (10)	40 (7)	0	231.072	0.001
8 Feb	105 (152)	70 (20)	10 (13)	0	143.145	0.001
15 Feb	55 (45)	0 (6)	0 (4)	0	12.022	0.001
24 Feb	72 (59)	0 (8)	0 (5)	0	15.738	0.001
10 Mar	30 (33)	0 (4)	10 (2)	60 (0)	5.841	n.s.
18 Mar	98 (124)	20 (15)	30 (9)	45 (0)	21.662	0.001
24 Mar	30 (25)	0 (3)	0 (2)	35 (0)	5.841	n.s.

observations of flying foxes feeding on *Eucalyptus* species (for pollen or nectar) ranged from 5.4 to 53.8%.

Diet

Diet items found in the droppings included: *Ficus* species and other rainforest fruits; pollen from Myrtaceae, Proteaceae, Fabaceae and Pinaceae species; whole insects and parts; leaf cells and mangrove leaf hairs; as well as 29 unidentified items that occurred infrequently. The major items found in the droppings varied over the study period (Fig. 4) with *Ficus* species found in droppings over the whole period. Fruits were the major items found in droppings from December to February, whereas in March and the end of March pollen

occurred in higher frequency. Rainforest fruits, including *Planchonella australis*, *Maclura cochinchinensis*, *Diploglottis australis* and *Schizomeria ovata*, increased to a peak occurrence in February (74% of occurrence). The tracheal systems of larger insects were identified in faecal samples, and exoskeleton (most likely *Anoplognathus* spp. Coleoptera) was found chewed and spat out in January.

Comparison of droppings to availability of resources

The patterns of occurrence of diet items in the droppings did not follow the patterns of availability of diet items in the vegetation all the time (Fig. 5). In December and January, *Ficus* species were a major food resource and followed the changes in availability in the study site. However, in February and March this pattern became uncoupled with the availability of *Ficus* fruits decreasing in the vegetation while the flying foxes appeared to increase their consumption of *Ficus*, suggesting a preference for *Ficus* species over other resources available. Rainforest fruits occurred in the droppings following a similar pattern to availability until March when the flying foxes ate less rainforest fruits although availability increased.

Discussion

Differences in fruit availability and foraging between habitats

Although the majority of the vegetation around the Jamberoo flying fox colony has been modified, the amount of food available per hectare in each habitat was similar. Differences between habitats were in the composition of food resources and the distribution of food resources through each habitat as the season progressed. Thus, within the study area, food was available in both modified and natural habitats. The human-modified habitats had a higher component of non-native species, including exotic species and species planted out of

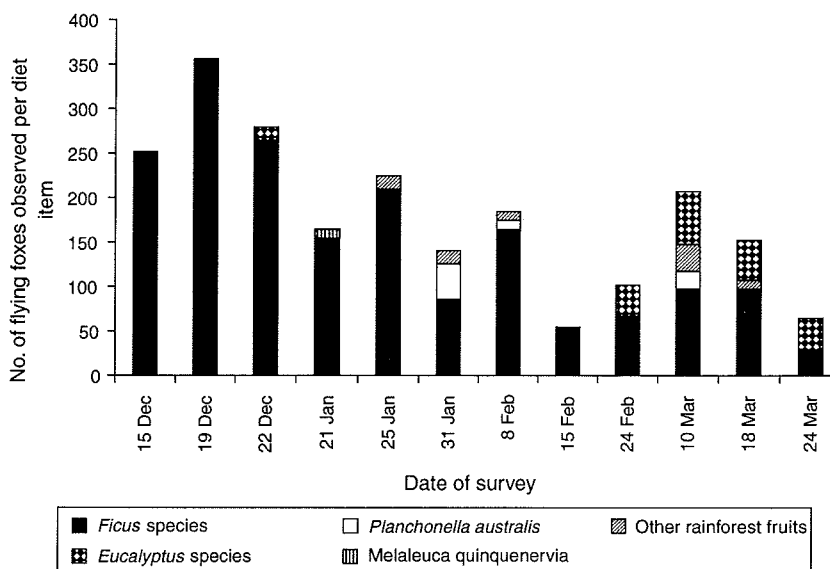


Fig. 3. Flying fox sightings in food resources on each night survey around the Jamberoo colony site from December 2004 to March 2005.

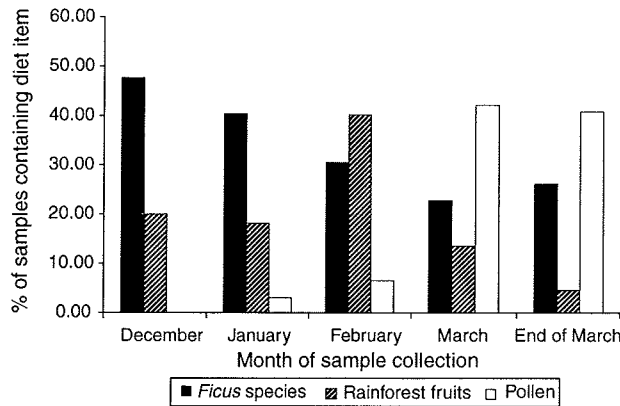


Fig. 4. Change in occurrence of diet items observed in flying fox droppings from December 2004 to the end of March 2005.

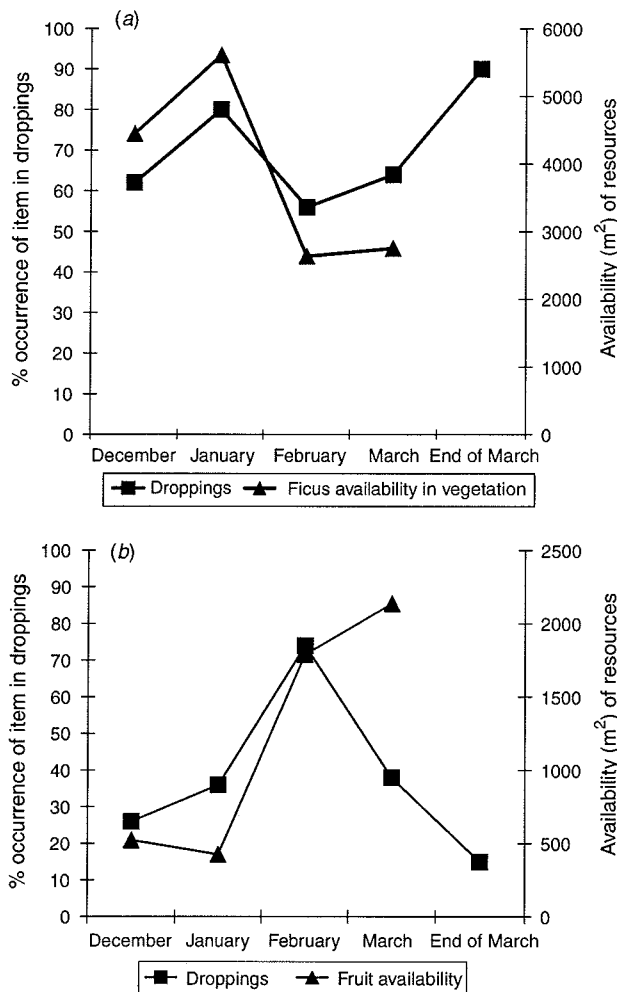


Fig. 5. Occurrence of selected diet items in droppings of flying foxes over the study period compared with the availability of each item in vegetation around the Jamberoo colony for (a) *Ficus* species and (b) rainforest fruits.

their natural distribution, than the other habitats. Furthermore, they provided dense patches of resources (large individual trees) often surrounded by cleared land or areas with no resources.

Comparison of the availability of food resources to the number of foraging flying foxes found in each habitat shows that *P. poliocephalus* have a preference for foraging in rainforest remnants although this varied through the season. From January to March, rainforest remnants had the highest food availability per hectare and more flying foxes were seen in the remnants until mid-February, when more foraging occurred in human-modified habitats and rainforest habitats. From the end of March, flying foxes also foraged in habitats other than the focus habitats. Flying foxes utilised rainforest remnant more often than expected, highlighting the importance of this habitat until blossom resources become available.

Observations of flying foxes in trees were based on vocalisation to pinpoint location, followed by spotlighting to count animals. The intensity and number of vocalisations may differ between habitats in relation to the density of the food resources. In human-modified habitats, food resources are available in small dense patches, so that often a high number of flying foxes were found in one tree, perhaps resulting in an increase in the number of vocalisations, compared with remnant habitats. This may result in an underestimation of numbers in the rainforest although we were aware of this while surveying and spent extra time listening and searching in rainforest habitats. Thus the usage of rainforest may be greater than measured in this study but unlikely to be appreciably higher.

Feeding preferences

The diet of the flying foxes in the Jamberoo colony changed over the course of the study. The major diet items consumed by the flying foxes changed from rainforest fruits to pollen and nectar of Myrtaceae and Proteaceae species from the beginning of December to the end of March. The change in diet could not be predicted by the availability of fruit in the three focus habitats of this study as the amount of rainforest fruits had increased during this time period. We therefore suggest that there is a preference for pollen and nectar, which causes foraging to change when this dietary item is available. Habitats in which the majority of myrtaceous species (e.g. eucalypts) are found were not monitored for availability and therefore changes in availability over the study of large-scale myrtaceous resources are not known. Previous studies have specified Myrtaceae species as preferred diet items (Parry-Jones and Augee 1991a), so the absence of pollen in the droppings from December to February suggest that myrtaceous resources were not available to flying foxes, although the possibility that bats prefer fruit during this summer period cannot be ignored.

Importantly, *Ficus* species are a staple part of the diet of bats in the Jamberoo colony and provide food throughout occupancy. Observations of feeding showed similar patterns to the occurrence of diet items. *Ficus* species was the most common fruit found in the droppings of this study; however, other fruits were also eaten and a drop in *Ficus* species occurrence in the

droppings coincided with a large amount of *M. cochinchinensis*, also from the Family Moraceae.

Insects have also been found to be used as a protein source by flying foxes (Courts 1998). *P. poliocephalus* has been known to consume insects in the wild (Parry-Jones and Augee 1991b, 1992; Parry-Jones 1993). The presence of the taenidida spirals in the droppings along with the exoskeleton in the spat-out pellet shows that *P. poliocephalus* will eat large beetles.

The conclusions of the present study support the findings of previous studies (McWilliam 1986; Eby 1991; Parry-Jones and Augee 1991a, 1991b, 2001) where quantitative data on the availability of food resources was not collected. Whereas other studies have analysed diet in relation to habitat usage (Parry-Jones and Augee 1991a; Banack 1998; Parsons *et al.* 2006), this study was the first attempt in Australia to physically quantify the availability of food resources to flying foxes.

Value of human-modified habitat as a resource for flying foxes

The findings of the present study highlight the need for maintaining vegetation in human-modified habitats and rainforest remnants, as this vegetation is important for flying fox food resources. The NSW Threatened Species Scientific Committee (2001) has identified clearing and modification of habitat as a key threatening process to *P. poliocephalus*. The present study has shown that in the Shellharbour and Kiama area, human-modified habitats provide important additional food resources to areas of natural vegetation, and that the flying foxes will use resources in human-modified habitats when available. Human-modified habitats will only help continue to support flying foxes if the trees providing food resources are kept, and added to, in order to maintain food supply. If the large trees, such as *F. macrophylla*, are removed, human-modified areas will not provide resources to flying foxes and will further reduce the habitat available to the flying foxes at this colony. Management of the vegetation in human-modified habitats, remnants and rainforest habitats is required to maintain the present level of essential food resources for *P. poliocephalus* at Jamberoo. Fruit resources in human-modified areas are used by a wide variety of wildlife, such as birds and possums, as well as flying foxes; therefore, the maintenance of urban vegetation for flying foxes would benefit additional species.

Highly mobile fauna, such as flying foxes, are likely to respond to changes in food supply by changing the areas in which they feed across the landscape. Such movements are likely to occur at a range of scales, with animals moving to resource-rich trees within a patch, resource-rich patches within a region, or resource-rich regions across the landscape. For flying foxes, changes in food supply may change the rate of occupation of colony sites, for example with an increase in numbers using historically temporary sites, for longer occupation periods. This can lead to an increase in human–flying fox interaction and possible conflict. Where significant local changes in food supply occur, a reduction in regional populations is likely as animals move to resource-rich areas within a region or resource-rich regions. This may have flow-on effects to total population

size if there are inadequate resources across the landscape. Thus for flying foxes, regional changes in food availability are likely to be important determinants of overall population sizes. Extensive clearing and modification of habitat is likely to change regional food resources and may result in changes in feeding behaviour in flying foxes. Conservation of food resources at the regional level is critical for this species to prevent a further decline in population size and an increase in human–flying fox conflict.

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Appendix 1. Plant species providing fruit food for flying foxes and the amount of food resources available (m²) in each month and habitat over the study area

Scientific name	Common name	December	January	February	March	Human	Remnant	Rainforest
Fruit								
<i>Acmena smithii</i>	Lilly pilly	0.00	71.67	152.45	48.42	0.00	0.00	272.53
<i>Alphitonia excelsa</i>	Red ash	0.00	44.73	263.30	730.62	0.00	218.89	819.76
<i>Archontophoenix cunninghamiana</i>	Bangalow palm	4.18	2.06	0.12	2.00	8.36	0.00	0.00
<i>Cassine australis</i>	Red-fruited olive plum	0.00	2.83	45.55	128.41	0.00	108.66	68.13
<i>Cissus antarctica</i>	Water vine	0.00	1.88	141.14	446.38	0.00	184.10	405.30
<i>Diploglottis australis</i>	Native tamarind	0.00	0.00	45.24	150.44	0.00	150.44	0.00
<i>Elaeocarpus reticulatus</i>	Blueberry ash	101.87	0.00	0.00	0.00	0.00	28.43	73.43
<i>Ficus coronata</i>	Sandpaper fig	293.07	859.81	182.96	58.75	0.00	543.02	851.57
<i>Ficus macrophylla</i>	Morton Bay fig	2437.95	2960.36	1129.80	2570.22	4607.34	4040.36	450.62
<i>Ficus obilqua</i>	Small-leaved fig	532.03	598.16	26.51	0.00	249.29	0.00	282.74
<i>Ficus rubiginosa</i>	Port Jackson fig	1181.79	1145.15	1247.49	0.00	811.47	3466.15	266.72
<i>Ficus superba</i>	Deciduous fig	0.00	47.12	47.12	125.66	0.00	219.91	0.00
<i>Maclura cochinchinensis</i>	Cockspur thorn	0.00	0.00	345.93	0.00	0.00	288.63	57.29
<i>Melia azedarach</i>	White cedar	0.00	29.65	0.00	0.00	0.00	0.00	29.65
<i>Morus nigra</i>	Mulberry (E)	1.06	0.00	0.00	0.00	1.06	0.00	0.00
<i>Passiflora</i> spp.	Native passionfruit	0.24	0.00	0.12	0.59	0.00	0.59	0.24
<i>Pennantia cunninghamii</i>	Brown beech	0.00	0.00	97.19	2.95	0.00	20.22	100.14
<i>Phoenix canariensis</i>	Canary Island date palm (E)	0.74	1.06	0.47	0.00	2.27	0.00	0.00
<i>Pittosporum undulatum</i>	Sweet pittosporum	203.46	73.20	376.53	415.32	73.29	479.49	529.44
<i>Planchonella australis</i>	Black apple	54.23	166.82	70.18	10.49	0.00	206.52	95.19
<i>Polysoma cunninghamii</i>	Featherwood	0.00	0.00	0.00	1.06	0.00	0.00	1.06
<i>Schizomeria ovata</i>	Crabapple	0.00	7.54	169.14	7.85	0.00	0.00	175.93
<i>Solanum mauritianum</i>	Wild tobacco (E)	31.69	5.07	27.33	23.05	30.47	25.76	30.91
<i>Syzygium australe</i>	Brush cherry	130.81	52.62	83.03	194.43	43.52	280.39	56.86
No. of species available		13.00	17.00	20.00	17.00	9.00	16.00	19.00
Total food resources (m ²)		6780.58	6343.96	4576.57	6071.56	7274.63	10722.52	5938.95