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A review of ecological interactions of fruit bats in Australian ecosystems

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Synopsis

The 13 species of fruit bats in Australia can be separated into five ecological groups: large-sized (>300 g) and small-sized (<60 g) specialist frugivores and nectarivores, and large-sized generalists. Each group contains only one abundant species and one or more rare species. Large nectarivores have a wide distribution which is related to the extent and species diversity of eucalypt forests and woodlands. The frugivorous species have restricted distributions that correspond to the similarly restricted and diminished distribution of rainforest. All identifiable ecological niches available in forest in Australia appear to be filled by at least one frugivorous and nectarivorous species.

Specialized frugivores locate food visually, and for one (*Pteropus conspicillatus*), the dominant dietary components are light-coloured fruits that are prominent against the dark background of the upper canopy of rainforest. The distribution of colony sites of this species is either within or adjoining tropical rainforest. The small tube-nosed bat *Nyctimene robinsoni* appears to forage only in the sub-canopy zone of rainforest and does not roost in colonies, opting rather to roost by day camouflaged within or near the last food tree used the previous night.

Reduced molariform dentition that reflects the absence of mastication of food has evolved in specialized nectarivores such as *Pteropus scapulatus* and two species of macroglossine bats. Large and highly mobile nectarivores locate food (primarily *Eucalyptus* blossom) using olfaction, with broad-scale movements over hundreds of kilometres being related to mass flowering. Eucalypt flowering patterns in north Queensland show that droughts can cause reduced nectar production or flowering failure. For *P. scapulatus* this explains occasional natural mortality coincident with migration to coastal regions. Since flowering failure occurs after 3–4 consecutive months of below-average rainfall, broad-scale migrations of this species can be predicted.

The small amount of research that has been conducted to date shows that, although a broad group of pollinators other than bats is available for them, a large suite of *Eucalyptus* species are dependent upon flying-foxes as their major

source of outcrossed pollen. Similarly, the successful regeneration of many rainforest trees is contingent upon seed dispersal by large frugivorous bats; these trees are predominantly those having light-coloured fruits. Successful seed dispersal relates to feeding territoriality; a 'raiders versus residents' concept indicates that the invasion of feeding territories results in the carriage of large propagules away from their parent tree and over long distances. This is especially important in the transmission of genes between different tracts of fragmented rainforest. It is suggested that in the long term the proportion of trees in Australia's tropical rainforest having light-coloured fruits may gradually decline. Ecological mutualism is shown to exist between pteropodid bats and the native forests of Australia.

Introduction

Bats are thought to have colonized the Australian land mass during the Pleistocene when it was connected to New Guinea and ocean barriers with Asia were shorter than they are today (Holloway & Jardine 1968; Hand 1984; Hall 1984). However, Archer, Hand & Godthelp (1991) consider that the Pteropodidae may not have entered Australia until the Quaternary, and support the theory that the primary source is undoubtedly New Guinea. The present day pteropodid fauna reflects this ancestry.

The Family Pteropodidae is represented in Australia by 13 species of fruit bats in five genera, with all but four species having an extralimital distribution into New Guinea. Of the 43 genera and 173 species of Pteropodidae in the Old World, only 12% and 7% respectively are found in Australia. There are only four endemic pteropodids in Australia (*Pteropus poliocephalus*, *P. brunneus*, *Pteropus* sp. nov. and *Nyctimene robinsoni*), less than 3% of the world's total.

Although Australia is a large continent, only a small proportion of its 7.6 million square kilometres is inhabited by fruit bats. Suitable habitat is generally found only along eastern and northern coastal regions, in subtropical and tropical environments. Much of this habitat is dominated by myrtaceous eucalypt forest and woodland, but rainforest is also present in scattered fragments. The relationship between the distribution patterns of fruit bats and these types of forests leads to the hypothesis that ecological mutualism exists between the two, a hypothesis to be tested in this review.

Species of fruit bats in Australia

The 13 species of fruit bats recorded in Australia are shown in Table 1. One of these, *P. brunneus*, is considered to be extinct. Eight species (in the genera *Pteropus* and *Dobsonia*) are large and exceed 300 g as adults, and five species (*Nyctimene*, *Syconycteris* and *Macroglossus*) are small, weighing less

Table 1. Species of fruit bats recorded from Australia and their IUCN conservation status, as determined by Richards & Hall (in press).

Species	Status
Large fruit bats (Flying-foxes)	
<i>Pteropus poliocephalus</i>	Grey-headed flying-fox
<i>Pteropus scapulatus</i>	Little red flying-fox
<i>Pteropus alecto</i>	Black flying-fox
<i>Pteropus conspicillatus</i>	Spectacled flying-fox
<i>Pteropus macrotis</i>	Large-eared flying-fox
<i>Pteropus brunneus</i>	Dusky flying-fox
<i>Pteropus</i> sp. nov.	Torresian flying-fox
<i>Dobsonia moluccense</i>	Bare-backed fruit-bat
Small fruit bats	
<i>Nyctimene robinsoni</i>	Eastern tube-nosed bat
<i>Nyctimene vizcaccia</i>	Torresian tube-nosed bat
<i>Nyctimene</i> (cf. <i>cephalotes</i>)	Cape York tube-nosed bat
Blossom bats	
<i>Syconycteris australis</i>	Eastern blossom-bat
<i>Macroglossus minimus</i>	Northern blossom-bat

than 100 g. The two groups have distinctly different roles and interactions with forest ecosystems in Australia. Richards (1987, 1990a) concluded that *P. conspicillatus* has a specialist association with rainforest, whereas other species such as *P. scapulatus* specialize on blossom and nectar (Hall 1983a). Tube-nosed bats (*Nyctimene*) and blossom-bats (*Macroglossinae*) are principally sub-canopy fruit and nectar feeders respectively (Nelson 1964; Richards 1983a, 1986).

On the basis of dental characters and known diet, Australian fruit bats can be allocated to broad categories that reflect their general ecology (Table 2). Specialist species are those that have approximately 90% of their food as one type; generalists have a broader diet. Within each cell in Table 2, only one of the specialists has a large geographical distribution, and the remaining species in each cell have quite restricted distributions. Table 2 shows that six of the 12 extant fruit bats are apparently specialist frugivores, four are specialist nectarivores and the remaining two are dietary generalists, and include fruit, nectar and pollen in their diet.

The two extant dietary generalists, *P. alecto* and *P. poliocephalus*, appear to be competing where they are sympatric. Comparison of the distribution of *P. alecto* in eastern Australia in the 1920s (Ratcliffe 1932) with the present-day range reveals that this more aggressive species is extending southward. At the same time, both the northern and southern limits of *P. poliocephalus* have shifted southwards. These subtle changes in distribution patterns may be a reflection of the short evolutionary history of fruit bats in Australia (Holloway & Jardine 1968; McKean 1970; Hall 1981) as outlined above,

Table 2. Classification of Australian fruit bats in an ecological framework, based on dental morphology and diet. Specialists are considered to be those species with approximately 90% of their food as one type; generalists have a broader diet. Species that are abundant and widespread are indicated by an asterisk. *Pteropus brunneus* is considered to be extinct.

Frugivorous specialists	Nectarivorous specialists	Dietary generalists
Large species (weight > 300 g)		
<i>P. conspicillatus</i> *	<i>P. scapulatus</i> *	<i>P. alecto</i> *
<i>Pteropus</i> sp. nov.	<i>P. macrotis</i>	<i>P. poliocephalus</i>
<i>D. moluccense</i>		<i>P. brunneus</i>
Small species (weight < 60 g)		
<i>N. robinsoni</i> *	<i>S. australis</i> *	
<i>N. vixcaccia</i>	<i>M. minimus</i>	
<i>N. (cf. cephalotes)</i>		

and may indicate that *P. alecto* arrived in Australia much later than did *P. poliocephalus*.

Diet of Australian fruit bats

Formal dietary studies such as those of Richards (1990b), Parry-Jones (1987), Parry-Jones & Augee (1991) and Law (1992a,b, 1993) have been supplemented by a plethora of natural history observations, many of which are summarized by Marshall (1985).

Table 2 shows that *P. poliocephalus* has been defined as a dietary generalist, a definition supported by the studies of several authors (Nelson 1965; Hall & Richards 1979; Richards 1983b; McWilliam 1986; Parry-Jones 1987; Eby 1991a). In fact, Eby (1991b) provided evidence that colonies of this species have some individuals that primarily select blossom and others that primarily select fruit. Twenty individuals from roosts in northern New South Wales were radio-tracked during nightly foraging throughout a seasonal cycle. Half of them fed primarily on subtropical rainforest fruit and had annual movements between roosts of approximately 50 km, whereas the others fed primarily on *Eucalyptus* flowers and moved up to 800 km from their origin. These annual differences in movement patterns were correlated with peaks in the fruiting and flowering phenology of forests in eastern Australia (Eby 1991b).

Fruit diets

A primarily frugivorous diet has been recorded for three flying-fox species: *P. conspicillatus* (Richards 1990a), *Pteropus* sp. nov. which is resident only in Torres Strait (L. S. Hall & G. C. Richards unpubl.), *D. moluccense*

(Dwyer 1975; Hall 1983b; Hyde, Pernetta & Senabe 1984), and one small (40 g) fruit bat *N. robinsoni* (Richards 1986). *Pteropus conspicillatus* is the largest frugivorous specialist pteropodid in Australia and has the most restricted distribution of Australia's four species of *Pteropus*. It is found only in coastal north-eastern Queensland and shows a close association with tracts of rainforest, roosting either within rainforest or never further than 7 km away (Richards 1990a).

Data on the foods eaten by *P. conspicillatus* were obtained by Richards (1990b) over a five-year period. The fruits of 26 native species were incorporated and all were rainforest canopy species. The flowers of 10 tree species were also eaten, and a single record of foraging on foliage was also reported (Richards & Prociw 1984). The overall ratio of fruit species to flower species was close to 4:1.

Van der Pijl (1957) suggested that the colour and mode of presentation of fruit may be a pattern that influences choice by fruit-eating bats. Of the sample of natural fruits in the diet of *P. conspicillatus*, 22 out of 25 were in light-coloured categories, and the majority were presented on the periphery of the tree canopy (Richards 1990b), where they were highly visible. The neurophysiological emphasis on vision and olfaction in *Pteropus* (Calford, Graydon, Huerta, Kaas & Pettigrew 1985) explains this relationship with food colour and its visibility. Möhres & Kulzer (1956) and Neuweiler (1962) also showed that the eyes of *Pteropus* are highly adapted for nocturnal vision, being particularly suited to recognizing light colours (Neuweiler 1968).

Tube-nosed bats (*Nyctimene*) forage mainly on fruit obtained from the sub-canopy stratum of rainforests, with emphasis upon the fruits of understorey shrubs, sub-canopy trees and cauliflorous upper canopy trees such as *Ficus nodosa* and *Syzigium cormiflorum* (Richards 1986).

Flower diets

The major proportion of the flower diet of Megachiroptera in Australia comes from the Family Myrtaceae, and in particular the genera *Eucalyptus*, *Melaleuca*, *Angophora* and *Syncarpia* (Ratcliffe 1932; Hall & Richards 1979; Marshall 1985; McWilliam 1986; Eby 1991a,b; Mickleburgh, Hutson & Racey 1992; McCoy 1993). *Banksia* (Family Proteaceae) are also highly important for small blossom-bats (Law 1992a,b). These plant genera have widespread distributions in Australia's forests and woodlands (Pryor 1976; Boland *et al.* 1984; Clemson 1985), have a geographic range that closely matches that of the Megachiroptera and are amongst the best nectar-producing genera in the northern tropics (Taylor & Dunlop 1985).

McCoy (1989, 1990, 1993) noted a wide taxonomic diversity in the flower diet of Megachiroptera in the monsoonal tropics of northern Australia, and showed that it comprised 52 species in 19 genera from 11 families, which is

similar to the diversity of this diet elsewhere in the Old World (Marshall 1983). The two *Pteropus* in this study were the 600 g black flying-fox (*P. alecto*) and the 300 g little red flying-fox (*P. scapulatus*). These bats had similar diets, with an 85% overlap in the plant species that they utilized. The diet of the sympatric 15 g northern blossom-bat (*Macroglossus minimus*) was quite different, being explained by the gross difference in body size and foraging mode between this and the *Pteropus* species, overlapping by 36% when compared with *P. alecto* (a dietary generalist), and by 46% when compared with *P. scapulatus* which is also a specialist nectarivore.

Foliage diets

The ingestion of foliage was first reported for Australian fruit bats by Ratcliffe (1932) and later by other authors (Richards & Prociw 1984; Parry-Jones & Augee 1991). The former authors observed *Pteropus* feeding on the leguminous *Albizia procera*. Marshall (1985) showed that folivory, although rarely reported, is quite widespread in the Pteropodidae. Lowry (1989) also observed folivory (upon *A. lebbek*) in *P. alecto* and calculated that the liquid fraction extracted from chewed leaves contained about 51% of the crude protein of the leaves, and was itself 36% protein (on a dry-matter basis). As a nutritional strategy, Lowry concluded that the potential attraction of tree legumes appeared to be their relatively high protein levels and lack of toxic secondary compounds.

Foraging ecology

Frugivores

As a result of studies of nocturnal territorial behaviour of *P. conspicillatus*, Richards (1990b) proposed a 'raiders versus residents' model for long-distance seed dispersal in *Pteropus*. Individuals that raid the feeding territories established early at night are inevitably evicted. They take a fruit before escaping from the aggression within the food tree and in so doing move propagules away from the parent tree. Janzen (1983) showed that seedlings growing at a distance from the parent tree had a greater chance of survival to maturity than did those growing near the parent. The 'raiders versus residents' model leads to the conclusion that *P. conspicillatus* have an integral role in the seed dispersal and regeneration of a suite of rainforest trees, particularly those having light-coloured fruit (Richards 1990c).

The carriage of fruits may be the primary dispersal role for Australian flying-foxes, but internal dispersal also has its place. The larger *Pteropus* in Australia have an oesophageal lumen distendable to 4–5 mm (G. C. Richards unpubl.), which places a limit on the size of seeds that can be transported internally. Seeds contained in *P. conspicillatus* faecal material grew to seedlings in a glasshouse, verifying that they were still viable after passing through the

digestive tract (Richards 1990b). Germination trials by Eby (1991a) of both ingested and ejected seeds showed that all but one of the species incorporated in the diet of *P. poliocephalus* were viable after dispersal by these bats.

Nectarivores

McCoy (1989, 1990, 1993) developed an 'index of advertisement' for flowers of trees, based upon eight of the main characteristics established by van der Pijl (1957) and Faegri & van der Pijl (1971) that describe bat-flowers. Those species visited by Megachiroptera had at least five of these characters; those not visited had a lower index. A review of the index of advertisement for 240 species of *Eucalyptus* in south-eastern Australia listed by Brooker & Kleinig (1983) showed that over 90% have the potential to be bat-flowers that could be utilized by *Pteropus*. By developing a 'honey index' Cocks & Dennis (1978) were able to assess the potential for viable honey production of 83 eucalypt and rainforest communities on the south coast of New South Wales. At least half of these communities had a high value for honey production and could therefore be expected to be of value as food for *Pteropus*, in particular the *P. poliocephalus* that seasonally visit this region. If, however, it can be shown that *Pteropus* have a significant role in the reproductive biology of these eucalypt communities, then there is a high proportion of coastal forests that may be dependent upon these bats.

Functional ecology of Australian fruit bats

Pollination

Most woody plants in Australian forests are obligate outbreeders, especially members of the Myrtaceae and Proteaceae (Johnson & Briggs 1975; Crome & Irvine 1986; Lamont, Collins & Cowling 1987). Outbreeding is the primary advantage that any plant species has in a co-dependent association with bats (Janzen 1970; Gould 1978; Lack 1978; Lemke 1985). Gene flow is particularly important in the genus *Eucalyptus*, which is characterized by high levels of outcrossing and reduced viability in seeds from self-pollinated flowers (Moran & Bell 1983).

Several Australian studies have identified bats as major pollen vectors. Radio-collared *P. poliocephalus* feeding on *Melaleuca quinquenervia* and blossoms of various *Eucalyptus* were highly mobile, feeding through the night on several trees within a stand as well as moving between stands of flowering conspecifics that were several kilometres apart (Eby 1991a). McCoy (1989, 1990, 1993) provided evidence that thousands of viable pollen grains collect each night on the bodies of foraging pteropodids (*P. alecto*, *P. scapulatus* and *M. minimus*). Movements of animals from plant to plant indicated that more pollen was moved a greater distance by bats than by other vertebrate flower visitors in McCoy's study area in the tropics (McCoy 1989, 1990, 1993).

Most tree species in the diet of pteropodids grow in multi-species communities and it is rare that conspecific trees grow side by side (Boland *et al.* 1984). Consequently, efficient pollinators must move 50 m or more to transport pollen to the nearest flowering conspecific. McCoy (1993) observed that 95% of movements by *P. scapulatus* from flowering tree to flowering tree were 50 m or more, but for nectarivorous birds such as honeyeaters (Family Meliphagidae), only 20% of movements between flowering plants are of the order of 50 m (Keast 1968; Hopper & Moran 1981). Although not as yet determined with necessary experimental rigidity, this evidence indicates strongly that pteropodid flower visitors are the primary donors of outcrossed pollen in Australian eucalypt forests and woodlands.

Although it is highly likely that bats have the potential to be a major pollinator in eucalypt dominated ecosystems, the question remains as to whether viable pollen can be transported. McCoy (1993) established that 78% of pollen grains removed from two *Pteropus* spp. and *M. minimus* were of high enough quality to ensure fertilization. It was also shown that pteropodid bats carry significantly greater pollen loads than those published for other bats and for all other Australian flower-visiting vertebrates. In an experiment with 568 tagged and covered flowers, McCoy also demonstrated that (for *Pteropus*) the physical act of landing and foraging upon the large inflorescences of eucalypts does in fact, ensure pollination and successful seed set by these animals.

Crome & Irvine (1986) showed that 12-g eastern blossom-bats (*Syconycteris australis*) contributed more to seed production in the myrtaceous rainforest tree *Syzigium cormiflorum* than did other visitors (Table 3). Although they were the major pollinator for this tree species, these bats spent less time foraging at the tree than did other groups that were observed (birds, possums, moths). Visiting for only a few hours after dusk and briefly before dawn, blossom bats were therefore likely to be more efficient than other pollinators.

Table 3. Pollinator effectiveness in three cauliflorous *Syzigium cormiflorum* (Myrtaceae) in night and day caging experiments. Entries are the percentage of total buds pollinated by that source (after Crome & Irvine 1986).

Tree no.	Fertilized by bats	Fertilized by birds	Fertilized by insects	Total fertilized
1	48.1	16.6	17.0	81.7
2	34.2	22.0	23.0	79.2
3	46.0	18.0	18.0	71.7
Mean	42.8	18.9	19.3	77.5

Seed dispersal

Wide-ranging seed dispersal encourages genetic exchange between fragments of forest or isolated populations of particular species, decreasing the amount of genetic subdivision of taxa (Loveless & Hamrick 1984). Since the success of self-regeneration for many tropical trees improves if their propagules are moved away from the parent tree (Baker, Bawa, Frankie & Opler 1983; Janzen 1983), those tree species that encourage visits by pteropodids ensure that such a process occurs. Crome (1975) showed that rainforest pigeons preferred to feed upon fruits that were brightly coloured, exactly the opposite colours to those selected by *P. conspicillatus*. This suggests that within Australian rainforest ecosystems, where *Pteropus* and pigeons are sympatric, it is possible that rainforest canopy tree communities may partition the suite of dispersal agents that are available. Species of pteropodids in Australia may be the only dispersal agent for many rainforest trees, and would consequently play an important role in the long-term survival of light-coloured fruiting taxa (Richards 1990b, 1991).

Furthermore, it is possible that some tree species dispersed only by pteropodids may be *pivotal* taxa (keystone mutualists), in accordance with the concept of Howe (1984): 'Although most species of trees produce when other fruits are readily available in the forest, others ... [species listed] ... bear fruits during annual periods of fruit scarcity, and consequently maintain species of fruit-eating birds and mammals which are critical for the dispersal and ultimate recruitment of many tree species at other times of the year.' Howe & Westley (1988) expand further on this concept.

Broad-scale migrations: influences and effects

Several studies have shown that the movement patterns of flying-foxes (*Pteropus*) are related to the local availability of food; a decline in food supply causes migration out of one area to another with an abundant food source (Nelson 1965, 1989; McWilliam 1986; Eby 1991a,b; G. C. Richards unpubl.).

Availability of food resources

What little is known about the broad-scale availability of native fruit as food for bats in Australia indicates that nowhere are flowers or fruit in continuous supply, year after year. Nelson (1965) noted that the amount of blossom produced by any one species varies, observing that in some years most of the trees of a species in an area flower at the same time, in other years most of the trees flower individually at different times over a period of 4–5 months, and in other years only a few trees may flower. This study was the first to identify the unpredictable nature of the food supply available to pteropodid bats.

Phenological studies of fruit production in rainforests indicate high seasonality by most species, with the greatest number of species fruiting in summer (Holmes 1987; Innis 1989). The latter author also showed that winter was a period of low fruit availability. Some genera such as *Ficus* and *Solanum* have fruit throughout the year (Eby 1991a; G. C. Richards unpubl.). In the rainforests of north Queensland, many tree species have a sequential fruit set and ripening related to altitude, where the fruit in coastal populations ripens earlier than that in the cooler uplands (Crome 1975). Thus, frugivorous pteropodids may be faced with a food supply that is highly predictable in its seasonal availability.

Although the majority of *Eucalyptus* species have extensive distributions in Australia (Boland *et al.* 1984), their flowering patterns show some seasonality and often occur sequentially along latitudinal and altitudinal gradients (Pryor 1976). In many species, individual trees or populations do not flower annually, and flowering is patchy throughout the range of some tree species (Clemson 1985; Eby 1991a,b). Therefore, nectarivorous pteropodids may differ from frugivorous ones by having a food supply that is highly variable in its availability, and it can be shown that migration patterns differ between the different food specialists (Eby 1991b). Eby also classified the intensity of flowering by Myrtaceae and Proteaceae communities to allow regional mapping of food resources and correlation with movements and migrations of *P. poliocephalus* in New South Wales.

Many eucalypts in tropical Queensland flower synchronously, but the month of first flowering and the period of flowering vary, so that a range of food is provided throughout the year when environmental conditions are good (G. C. Richards unpubl.). In the monsoonal tropics of the Northern Territory, the flowering period for food trees averaged five months, but in tropical Queensland it averaged only three months. The Queensland tree species could be grouped into winter-flowering or summer-flowering species and had flowering times averaging 3.9 and 2.8 months.

Food availability appeared to be virtually continuous and therefore more reliable for nectarivorous bats in the Northern Territory than in Queensland. This is reflected in the migratory patterns of *Pteropus* when the two regions are compared: McCoy (1993) noted that in the Northern Territory tropics *P. alecto* and *P. scapulatus* were always present and occupied colony sites for long periods, and the movements that occurred were small and local. Conversely, G.C. Richards (unpubl.) recorded the occupation time of 22 colony sites in Queensland's tropical Gulf of Carpentaria region as ranging from two weeks to two months, and 21 sites were occupied only once in 410 inspections. During six years of study, three large-scale migrations of *P. scapulatus* colonies were recorded. These migrations could be related to the failure of winter-flowering food trees during droughts. *Eucalyptus* trees will have poor flowering when rainfall is lower than normal (Pryor 1976; Landsberg 1986) or, if in flower, may have reduced nectar production during

droughts (Clemson 1985). Species such as *E. maculata* that hold buds for long periods may abort them during periods of climatic stress, and other species such as *E. albens* may still flower but with reduced amounts of nectar (Clemson 1985). The circumstances surrounding the migrations by *P. scapulatus* in north Queensland were related to variations in rainfall and food supply, and were correlated with approximately four consecutive months of below-average rainfall.

Migrations by frugivorous species

Studies of *P. conspicillatus* showed that this species is a specialized frugivore (Richards 1990b), distributed only in north-eastern Queensland (Hall & Richards 1979), and roosting either within or adjacent to tropical rainforest.

The occupancy of traditional roost sites by *Pteropus conspicillatus* in Queensland was either a continuous or a seasonal residence. Colonies resident along the coastal section of the study area were most likely to occupy roost sites continuously, whereas traditional sites on the Atherton Tableland were only occupied on a winter or summer basis, without continuity. The winter versus summer occupancy of traditional *Pteropus* roost sites has also been noted by many authors (Ratcliffe 1932; Nelson 1965; Hall & Richards 1991; Eby 1991b).

Differences in fruiting seasons and in types of rainforest (Tracey 1982; Tracey & Webb 1975) have some influence on the pattern of seasonal movements by *P. conspicillatus*. The altitudinal difference between the north Queensland coast and adjacent uplands (over 700 m) accounts for differences in rainforest species composition, as well as for differences in the fruiting seasons of species that are common to both regions (Crome 1975; Tracey 1982). It is possible that some colonies of *P. conspicillatus* utilizing a particular rainforest type may have to accommodate a greater variability in food supply, whereas others do not, especially during the young-rearing phase when energetic demands are high. In lowland areas, and possibly upland areas as well, Crome (1975) observed that the late dry-season months (August and September) constituted the period of overall peak fruiting in rainforest. The birth period of *P. conspicillatus* lags behind this fruiting peak by one month. Crome also observed that the late wet-season months (March to May) were the period of least fruit abundance, corresponding with the period when colonies have left their traditional maternity roosts on the Atherton Tableland.

Migrations influenced by differential ripening of fruit also occur in the Torres Strait region of north Australia, an area located between Cape York and the New Guinea mainland and containing approximately 40 islands and atolls. L. S. Hall & G. C. Richards (unpubl.) gathered evidence that *P. alecto* leave New Guinea in September each year and progressively infiltrate islands southward, following the progressive ripening of native

fruits and others such as mangoes. By the following March these animals have disappeared from the area and are presumed to have returned to New Guinea.

Radio-tracking studies of *Nyctimene robinsoni* show that these bats reduce the effort of searching for food at dusk by roosting during the day in the food tree last visited (C. Tidemann, J. E. Nelson & G. C. Richards unpubl.). For an animal that has an apparently high metabolic rate (body water turnover has been measured at over $1000 \text{ ml}^{-1} \text{ kg}^{-1} \text{ d}^{-1}$ —G. C. Richards unpubl.—and is one of the highest for any mammal), this strategy provides immediate savings in the energetic cost of commuting to and from permanent roost sites and foraging grounds.

Migrations by nectarivorous species

The migrations by *P. scapulatus* mentioned above ended at the Atherton Tableland, a region where they were not normally distributed (G.C. Richards, unpubl.), and were correlated with food availability (the failure of inland eucalypt flowering caused by below-average rainfall). During one migration (in 1986), many individuals were emaciated and dying.

Migrations by dietary generalists

Long-distance migrations by *P. poliocephalus* were suggested in the early research of Ratcliffe (1932), whereas the studies of Nelson (1965) and McWilliam (1986) indicated that localized movement patterns were perhaps more typical of this species. Recent work by Eby (1991a,b) demonstrates that both long and short migrations occur during the annual cycle of this species. However, L. S. Hall (unpubl.) has gathered evidence that during the last decade, populations of some *Pteropus* species have become reduced in size, large colonies have disappeared completely or have fragmented into smaller groups and migration pathways have been broken. The implications of these problems are as yet not well defined, but they may have a major significance due to the apparent dependence of a myriad of tree species upon fruit bats for their successful reproduction.

The studies of McWilliam (1986) in north-eastern New South Wales revealed a seasonal migration of *P. poliocephalus* from the coast to inland areas. This was attributed to both climate (temperature) and food availability, but the influence of the weather is an as yet unknown influence on the ecology of this species. There is strong taxonomic evidence indicating that two races may exist, separable by fur length and density: a southern (cold-adapted) form and a northern (subtropical) form. McWilliam's (1986) study may have included the northern form, affected to an unknown degree by temperature when at the southern limit of its range. However, there is stronger evidence that food availability is the driving force for movements and migrations of dietary generalist species.

As outlined above, Eby (1991a) provided strong evidence from radio-tracking studies that colonies of *P. poliocephalus* have individuals that primarily select blossom and others that primarily select fruit. Those feeding primarily upon fruit had annual movements between roosts of approximately 50 km, whereas those that fed primarily on *Eucalyptus* flowers moved up to 800 km during the annual cycle, following the mass flowering of eucalypt communities. One individual in the latter category moved 210 km in three nights to a new feeding area. The sequential flowering southward of *E. maculata* was the predominant reason for migration (Eby 1991a).

The mutualism hypothesis

Megachiropteran bats have shared a long association with angiosperms, these plants probably evolving in the South-East Asian region around 130 million years ago and achieving world-wide dominance over gymnosperms about 90 million years ago. Furthermore, the first recognizable rainforest formations were in existence 60 million years ago, and megachiropteran bats have been in existence for 35 million years (Mickleburgh *et al.* 1992). Frugivory in this suborder arose before nectarivory (Marshall 1983). Although it would stand to reason that, given the period of evolution, a strong association between bats and plants would exist, a review of evidence is necessary before this conclusion can be attained for the Australian Pteropodidae. Evidence supporting the concept of a mutualistic relationship between Australian forest trees and megachiropteran bats includes:

- the correlation between the distribution patterns of fruit bats and myrtaceous forest, and the fact that Myrtaceae blossom is the primary food of many pteropodid taxa;
- 10 of the 12 extant pteropodid species are dietary specialists and all ecological niches in forest in Australia available to pteropodids are filled by at least one common specialist and several less abundant specialists;
- that eucalypt flowers have most of the characteristics that support the bat-pollination syndrome of Faegri & van der Pijl (1971), particularly their odour and colour;
- that the Australian Pteropodidae have innumerable sensory, morphological and anatomical adaptations for locating or utilizing plants;
- the pattern of mass flowering by many of the Myrtaceae taxa, which draws large populations of *Pteropus* as potential pollen vectors from long distances;
- that several common and widespread pteropodids have been shown to be competent pollen vectors and satisfy the requirements of the Myrtaceae for outcrossing; a large proportion of pollen is carried undamaged and pollen transferred by pteropodids will cause fertilization to occur;
- that most of the fruits known to be eaten by pteropodids fit the bat-plant

syndrome of van der Pijl (1957), particularly their light colour and presentation on the periphery of the tree;

- that pteropodids in Australia may be the only dispersal agent for many rainforest trees and may therefore play an important role in the long-term survival of some taxa;
- the 'raiders versus residents' model for the dispersal of large fruits and seeds by *Pteropus*, and a paucity of other dispersal agents, both suggest that some trees are totally dependent upon pteropodids for their regeneration;
- and that germination trials of both ingested and ejected seeds of approximately 60 species showed that all but one was viable after dispersal by pteropodids.

The evidence that a mutually advantageous system is in existence appears to be conclusive. The Myrtaceae appear to be highly dependent upon pteropodids in Australia for outcrossed pollination; a large suite of rainforest tree species are dependent upon pteropodids for seed dispersal, yet without these food sources this family of bats would not exist. Until further research is conducted, the effect upon ecosystem function of current conservation problems is unknown. One of these problems, the culling of at least 240 000 individuals in the period 1986–1992 (D.E. Wahl unpubl.) by fruit-growers in north coastal NSW alone, must be having a major effect.

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