

# Review of gene movement by bats and birds and its potential significance for eucalypt plantation forestry

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## Summary

Pollen- and/or nectar-feeding lorikeets and bats and nectar-feeding honeyeaters, while less frequent visitors to eucalypt flowers than insects, may make a unique contribution to eucalypt population structure because of their capacity to move pollen large distances. Birds and bats may travel upwards of 50 km day<sup>-1</sup> during feeding, and further during migration or feeding bouts over several days. Limited data suggest that they carry viable pollen. Several eucalypts have adaptations favouring bird pollinators, while some species, particularly *Corymbia* spp., have adaptations commonly found among plants pollinated by bats and other nocturnal visitors. Bats may have the capacity to carry viable pollen over greater distances than birds. We suggest that the effect of pollen transfer by birds and bats on the genetic structure of widespread eucalypt species is potentially greatest in fragmented forests where these animals can traverse gaps of several kilometres between discontinuous stands. Greater understanding of pollen movement by birds and bats in natural eucalypt forest is a prerequisite to understanding the potential for gene movement from commercial eucalypt plantations into native forests.

**Keywords:** forest ecology; geographical distribution; geographical dispersal; gene flow; nectar; pollen; pollinators; pollination; animal behaviour; feeding behaviour; forest management; birds; Chiroptera; Pteropodidae; eucalypts

## Introduction

At the current rate of establishment, eucalypt plantations will soon occupy a larger proportion of the total Australian plantation estate than softwoods (National Plantation Inventory 2000). This trend promises to reduce the overall environmental effect of commercial forestry in Australia by shifting many harvesting operations from native forests to highly productive plantations. However, there are ecological issues that arise when plantations contain non-local provenances or planting stock with reduced genetic diversity — such as seedlings from breeding programs or selected clones. The plantation revolution in Australian eucalypt forestry has drawn attention to the potential for gene movement from plantation species to related interfertile species in adjacent forests (Wardell-Johnson *et al.* 1997). The prospect of clonal eucalypt plantations and transgenic eucalypts will focus increased attention on gene movement in eucalypt plantations.

Pollen-carrying vectors are the principal agents of gene movement in eucalypt forests. Eucalypt flowers produce abundant nectar and pollen and hence attract numerous visitors, especially insects and birds. Insects vastly outnumber all other floral visitors and undoubtedly play a major role in pollen movement (House 1997). While birds and bats are less frequently recorded visitors to eucalypt flowers than insects, some species are dependent on flowers for food. These have the capacity to transport pollen over much greater distances than insects. In this paper we examine the foraging behaviour, and feeding and migratory movements, of birds and bats that feed on eucalypt flowers. We investigate their capacity to move pollen in native eucalypt forests and consider the effect of this movement on the genetic diversity of native forests and its significance for native forests in the new plantation environment.

## Eucalypts are preferential outcrossers

The breeding system of eucalypts has been reviewed previously by Pryor (1976), Moran and Bell (1983), Eldridge *et al.* (1993), and Potts and Wiltshire (1997). Eucalypts preferentially outcross but are capable of self-fertilisation, although subsequent seed set is usually severely reduced compared with that resulting from outcrossing (Eldridge *et al.* 1993; Potts and Wiltshire 1997). Progeny derived from selfing frequently suffer from severe inbreeding depression (James and Kennington 1993; Hardner and Potts 1995) and would not be expected to contribute to future generations, as the outcrossed progeny will be favoured by natural selection (Skabo *et al.* 1998). Natural eucalypt populations frequently exhibit high outcrossing rates, with mature trees showing higher than expected levels of heterozygosity (Moran and Bell 1983; Potts and Wiltshire 1997).

Other factors which may facilitate outcrossing in eucalypts include delayed receptivity of the stigma until several days after pollen shed (protandry), bending away of anthers from the style (Potts and Wiltshire 1997), stylar extension (Moncur and Boland 1989) and prolonged pollen viability (Griffin 1989). Higher rates of outcrossing have been associated with mass-flowering species (James and Kennington 1993) and higher numbers and densities of flowering trees (Sampson *et al.* 1995). Delayed production of nectar in *Eucalyptus melliodora* until after the stigma becomes receptive may also favour outcrossing (Moncur and Boland 1989).

## Seed and pollen dispersal in natural eucalypt forests

Eucalypt seed is generally dispersed by wind, with the distance travelled being related to tree height, wind velocity and seed weight (Cremer 1977). Several *Corymbia* and a small number of *Eucalyptus* species have true seed wings suitable for wind dispersal (Boland *et al.* 1980). Dispersal in animal droppings does not occur, although many birds eat eucalypt seed, because the seed does not survive passage through the alimentary canal of mammals and birds (Joseph 1986). Inadvertent dispersal of *Corymbia torelliana* seed attached to the sticky bodies of native bees has been reported over distances of up to 300 m (Wallace and Trueman 1995). The capacity for long-distance dispersal of seed or fruits by birds, floods (e.g. *E. camaldulensis*), storms, or in fire updraughts was recognised by Kirkpatrick (1977). Parrots are rather messy eaters and could disperse seed from eucalypt fruits over distances of several hundred metres as they fly from feeding sites.

Pollen is likely to be the major vehicle of gene movement in eucalypts. Virtually all eucalypts produce sticky pollen, a characteristic that is believed to prevent wind from being an effective agent of dispersal (Eldridge *et al.* 1993). There is, however, likely to be some movement of pollen during high winds over unknown distances. Two red gums, *E. tereticornis* and *E. blakelyi*, are the only species (Pryor 1976) known to produce dry pollen, but the importance of wind pollination with these species is not known. An important barrier to gene flow via pollen is asynchronous flowering of trees of the same species or related species capable of hybridisation.

Pollen viability under field conditions is poorly understood in eucalypts. Isolated reports suggest viability is retained for at least several days (Griffin 1989). If this characteristic is widespread in the *Eucalyptus* and *Corymbia* genera, pollinator movements over several days or during nomadic or migratory movements may be significant. Pollen transfer between vectors visiting flowers, during allopreening in the case of birds or between bees in the hive, may increase the effective distance of pollen movement.

Most visitors to flowers are insects, including numerous species of flies, wasps, ants, beetles, and native and introduced bees (House 1997). Several studies have revealed that pollen can be transferred several hundred metres by insect vectors but usually less than 100 m (Pryor 1976; Pacheco *et al.* 1986). Most pollen moved by insects is likely to be deposited close to the parent tree (Potts and Wiltshire 1997), and insects — with the possible exception of migratory moths — are unlikely to carry pollen as far as birds do between trees or populations (House 1997).

## Bird and bat pollinators of eucalypts

In general eucalypt flowers are not thought to be highly adapted to any particular pollination vector, but there are several notable exceptions. A number of mallee species in Western Australia are apparently specialised for bird-pollination, having large flowers, red or yellow stamens, pendulous or tubular flowers and synandry or aggregation of flowers (Keighery 1982; Sampson *et al.* 1989). These species, which include *E. caesia*, *E. stoatei* and *E. rhodantha*, occur as small sub-populations a few hundred metres to a few kilometres apart (Moran and Hopper 1987). Hopper and Moran (1981) suggested that specialisation for bird pollination

has evolved to maximise the likelihood of gene flow between populations.

Birds may be more important cross-pollinators of eucalypts if insect visitation is suppressed by cool conditions in the early morning or by flowering in winter (Hopper 1981). *Eucalyptus globulus* flowers during the often cold, wet and windy spring weather in Tasmania — conditions that reduce insect activity (Hingston and Potts 1998). Additionally, of the numerous insects that visit the flowers, few make contact with the stigma of the large *E. globulus* flower.

Many eucalypts have small, white and open, cup-shaped flowers that may produce modest amounts of nectar (Paton and Ford 1977) and their attractiveness to birds may vary. For instance, New England stringybark (*E. caliginosa*) flowers regularly and is a major nectar source for honeyeaters in some years, but appears to be ignored in others (H.A. Ford *pers. obs.*). This means that short-term studies may underestimate the visitation rate by birds. Other eucalypts produce copious nectar and are particularly popular with birds (*E. cosmophylla*, *E. leucoxydon*, *E. sideroxydon*: Paton and Ford 1977; Paton 1982a; Franklin *et al.* 1989; Oliver 2000).

The flowers of some eucalypts possess several characteristics found to be common amongst ‘bat-pollinated’ plants (Faegri and van der Pijl 1971; McCoy 1990; P. Birt unpubl. data). Several species produce larger volumes of nectar at night and display anthesis predominantly at night, suggesting they are capable of attracting nocturnal pollinators (McCoy 1990; P. Birt unpubl. data). Many *Corymbia* and some *Eucalyptus* species develop large terminal clumps of white flowers, which may facilitate detection at night by bats. Similar floral features have been observed in other ‘bat-pollinated’ plants (Woodside and Pyke 1995; Vieira and Decarvalho 1996; Slauson 2000).

## Pollen- and nectar-feeding parrots

There are seven lorikeet species in two genera (*Trichoglossus* and *Glossopsitta*) in Australia, which occur in woodlands and forests of northern, eastern and south-western Australia. The distribution of these species has been reviewed previously (Higgins 1999). The swift parrot (*Lathamus discolor*), the only native non-lorikeet parrot feeding on pollen and nectar, occurs predominantly in Tasmania, migrating annually to the southern regions of the mainland in autumn. All species have been observed to feed regularly on eucalypts, with the swift parrot and lorikeet species in the genus *Glossopsitta* (musk, purple-crowned and little lorikeets) preferring eucalypts (Higgins 1999).

## Feeding methods and preferences

Lorikeets are frequently observed feeding on flowers, primarily those of about 40 species of forest and urban plants, especially native species (Cannon 1984). With smaller-flowered eucalypts, the beak encloses the whole flower and nectar is obtained by projecting the tongue into receptacles. Pollen is obtained by combing the bill across the stamens (Hopper 1980; Porter 1992). With larger-flowered eucalypts, nectar and pollen are collected in separate feeding actions. Lorikeets have been observed collecting pollen from mature buds by removing the operculum and then pressing the anthers between the brush-tongue and beak.

During feeding, pollen is likely to attach to feathers on the head and chest of lorikeets, as well as other body parts where these are brushed against flowers.

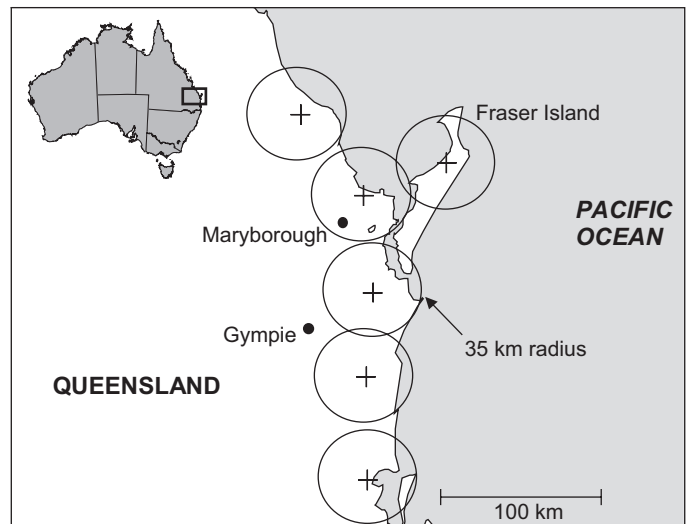
Lorikeets maintain a mixed diet throughout the year, including nectar and pollen with some fruit, seeds, vegetative parts and invertebrates (Cannon 1984; Porter 1992). As a consequence of their narrow diet, lorikeets are dependent upon flowering and fruiting cycles, and long-term observations by Porter (1992) demonstrate both a seasonal preference for particular species that flower, and shifts in the feeding preference in particular seasons as different food sources flower.

Some feeding preferences exist between lorikeet species. The rainbow lorikeet may prefer eucalypts with larger flower capsules and the spiked inflorescences of *Banksia* and *Melaleuca*, and hence is abundant in coastal lowlands where these plants dominate. Porter (1992) observed that rainbow lorikeets frequently nested in or near stands of *E. tereticornis* because it flowers reliably through winter and spring during the nesting period. Scaly-breasted lorikeets may prefer eucalypts with small flowers and tend to be more abundant on ridges and drier inland foothills along the coastal lowlands where these trees grow. Little lorikeets were recorded most frequently in tall trees, mostly *E. pilularis* and *E. microspores* in coastal southern Queensland (Porter 1992). The musk lorikeet and swift parrot are common avian visitors to *E. globulus* (Hingston and Potts 1998), which is also visited by several honeyeater species, predominantly wattlebirds. The purple-crowned lorikeet feeds almost exclusively on eucalypts (Hopper and Burbidge 1986) and is abundant during flowering in karri (*E. diversicolor*) and jarrah (*E. marginata*) forests in Western Australia (Christensen 1971; Wardell-Johnson and Williams 2000). They may even feed exclusively on pollen when nectar flow is negligible (Churchill and Christensen 1970).

### Movements in relation to foraging

Lorikeets flock in groups of two to fifty by day and roost in colonies of one hundred to several thousand birds (Higgins 1999). Communal roosts are considered to have both ecological and social significance, aiding the location of flowering areas and the breeding behaviour of the species (Porter 1992). Pairs that are nesting and feeding nestlings, while joining the roosting flocks to feed, often feed more locally. When food is scarce, lorikeets tend to disperse widely and numbers in communal roosts are lower.

Rainbow lorikeets are the most widespread species and exemplify lorikeet behaviour. Daily flights to feeding sites frequently take rainbow lorikeets up to 35 km from the roost (Fig. 1), particularly during their non-breeding phase over summer and autumn (Porter 1992). Flights to and from roosts are staged with small flocks gathering at several rest stops to preen and feed (Porter 1992). At feeding sites, most feeding occurs within a radius of 500–1000 m and individuals move regularly between trees, but movements for feeding may be much further. Lorikeets are well suited to a fragmented food source. Scouting parties frequently move distances of 5–10 km and feeding flocks may travel up to 10 km between feeding and mid-day rest areas (Porter 1992). Considering lorikeets travel at 40–50 km h<sup>-1</sup>, these distances are quickly and easily traversed. The smaller scaly-breasted lorikeet tends to have several roosts within the area served by a single rainbow lorikeet



**Figure 1.** Major rainbow lorikeet roosts (+) in a transect of the coastal lowlands of south-east Queensland as reported in Porter 1992. The circles indicate the maximal distance from the roosts that rainbow lorikeets fly during daily feeding flights.

roost, suggesting that they fly shorter distances daily. The diurnal movements of lorikeets to and from roosts and between feeding areas provide ample opportunities for pollen to be transferred over both short and long distances.

There is no evidence that any of the Lorinae undergo seasonal migrations, but marked local fluctuations in the size and presence of feeding flocks in all Australian lorikeets are reported, a phenomenon considered to be related to nomadic movements of populations (Blakers *et al.* 1984). Long-distance movements of rainbow lorikeets are not common, and movements of banded birds of up to 80 km may represent movements from one side to the other of feeding ranges centered on roost sites (Porter 1992). Scaly-breasted lorikeets have been recovered over longer distances (up to 230 km over 2 y), but most recoveries have been within 20 km of the banding site.

## Honeyeaters and other passerines

### Honeyeaters visiting eucalypt flowers

Honeyeaters (Meliphagidae) are the dominant family of passerines in Australia with 72 species (Christidis and Boles 1994). Almost all species of honeyeater including wattlebirds, spinebills and several of the chats, feed on nectar, and most species have been observed visiting eucalypt flowers (Pyke 1980). Honeyeaters occur in all habitats, with the exception of grassland, and ten or more species may occur in eucalypt-dominated habitats, often with replacement of congeners in different habitats (Ford and Paton 1985). In addition, a number of other passerine birds feed on the nectar of eucalypt flowers frequently (silveryeye *Zosterops lateralis*; pardalotes *Pardalotus* spp. — Paton and Ford (1977); or occasionally woodswallows *Artamus* spp. — Ford *et al.* (1986)).

A large number of species of eucalypts provide a major source of nectar for honeyeaters in many habitats in south-eastern (Ford *et al.* 1979; Paton 1986), south-western (Keighery 1982; Hopper

and Burbidge 1986) and northern Australia (Keighery 1982; Franklin and Noske 1999). There have been no reviews of the importance of eucalypt nectar to honeyeaters in north-eastern or central Australia, but the genus is certainly visited in these regions (H.A. Ford *pers. obs.*; Shurcliff 1986).

### Feeding behaviour

Honeyeaters, and other nectar-feeding passerines, probe into eucalypt flowers, either centrally or between the stamens. They extract nectar by lapping with their brush-tipped tongues. Pollen from the rings of stamens is deposited on the bill, and in the case of larger-flowered species, on the facial feathers of birds. Where flowers are numerous and close together, pollen could be liberally spread over body feathers. Pollen collected from trapped honeyeaters which were feeding on eucalypts indicates that they may carry substantial numbers of pollen grains (Paton and Ford 1977; Hopper *et al.* 1978; Paton 1982b). Eucalypt pollen, and pollen of most Myrtaceae, is small and uniform so that the species has usually not been identified, but inferred from observing where the birds are feeding (however, see Hopper *et al.* 1978). Clear proof that honeyeaters, or other passerine birds, actually deposit pollen of the correct species onto stigmas is currently lacking. However, high visitation rates and the timing and types of flowering in at least some species strongly suggest that they do. Hopper *et al.* (1978) identified natural hybrids between adjacent populations of *E. buprestium* and *E. preissiana* and observed that New Holland honeyeaters (*Phylidonyris novaehollandiae*) visited flowers and carried pollen of both species.

### Movements in relation to foraging

Inferences on pollen transfer by honeyeaters from studies of mating systems of eucalypts need to be supported by further observations of actual movements by the birds. It is common to see large honeyeaters crossing gaps of several hundred metres between patches of trees or individual trees in partly cleared habitat. Furthermore, Hopper and Moran (1981) recorded honeyeaters moving between *E. stoatei* plants up to 50 m apart, within a foraging bout. Paton (1982a) noted that honeyeaters visited, on average, at least two plants of *E. cosmophylla* per foraging bout. He made a case for significant transfer of pollen between plants. It is difficult to follow birds moving more than 100 m in woodland or forest. Limited information of greater movements comes from radio-tracking. Regent honeyeaters (*Xanthomyza phrygia*) frequently moved almost out of range (about 1 km) while foraging, even when they were feeding nestlings and fledglings (Ford *et al.* 2000). One, whose nest had just failed, moved over a few days within a home range that was 1200 m in its longest dimension and once travelled up to 1500 m beyond this range. At the time it was feeding from *E. sideroxylon* flowers. Nesting noisy friarbirds (*Philemon corniculatus*), with radiotransmitters, have also been followed over 1 km from the nest (Ford *et al.* 2000). Signals were obtained from one bird about 3 km away from its nest, though it was not found and another friarbird, whose mate was building a nest, was seen foraging in a garden about 9 km from the nest (Ford and Barrett 1995). Although these data are limited, they do indicate the distances that honeyeaters may travel within a short period while foraging. It would certainly appear that they are

capable of carrying pollen between populations of eucalypts that are several kilometres apart.

The frequency of daily movements of pollen over moderate distances will depend on the foraging and spacing strategy adopted by the bird species. Many honeyeaters are territorial (Pyke *et al.* 1996); in extreme cases restricting most of their foraging to a single tree (Ford 1981). Other species travel greater distances between flowering plants, either because they exploit patchy, poor sources as the spinebills do (Ford and Paton 1982), or because they are driven out of defended plants (McFarland 1986). Territorial chases may continue for 100 m or more, and it is perhaps these that provide the best opportunities for moderate-distance pollen transfer. Aggression, which is often interspecific, may peak when flowering is starting or finishing (Armstrong 1991), and at such times pollen may be transferred farthest. Some nectar-feeding birds, such as brown-headed honeyeaters (*Melithreptus brevirostris*), silvereyes and woodswallows forage in flocks, which may cover some distance during a day. Woodswallows, in particular, travel a long way while foraging, though it is possible that they do most of their feeding from flowers during the early morning, before their insect prey becomes airborne.

### Migratory behaviour

Many honeyeaters and other nectar-feeding birds also perform moderate to long-distance movements on a seasonal or more irregular basis (Keast 1968). These vary from local movements among nearby habitats, as in New Holland honeyeaters, through more complex and unpredictable movements, as shown by regent honeyeaters, to the regular migrations of yellow-faced honeyeaters (*Lichenostomus chrysops*) and silvereyes. Where movements are among different habitats (e. g. between woodland and heath), there is rarely an opportunity for intraspecific pollen transfer. However, regent honeyeaters, though by no means specialists, do prefer the nectar of a small number of eucalypts, such as *E. sideroxylon* (Franklin *et al.* 1989). These trees may occur over a large range, and may show a sequence of flowering through their range. It has been suggested that regent honeyeaters, and other species, may track this flowering. We do not understand the movements of these species, but colour-banded regent honeyeaters have been sighted up to 472 km from where they were banded (D. Geering, unpubl. data).

Yellow-faced honeyeaters migrate along the coast and adjacent ranges from southern Victoria to southern Queensland every autumn, returning in spring (Liddy 1966). They are diurnal migrants, travelling especially around mid-morning, at tree-top level. They often alight on the way, and may forage from flowers before continuing. When travelling through fairly uniform habitat, they could potentially transfer pollen between trees up to 100 km or further apart within a day. A number of other honeyeaters show conspicuous migrations, such as white-naped honeyeaters (*Melithreptus lunatus*) and noisy friarbirds (Liddy 1966). Silvereyes are diurnal or nocturnal migrants, with the Tasmanian race crossing Bass Strait and reaching as far north as south-eastern Queensland (Chan and Sutton 1993). Again, it is possible that they could carry pollen for considerable distances, even between Tasmania and Victoria.

## Flying-foxes

### Flying-fox and eucalypt biology

There are four species of flying-fox (Chiroptera: Pteropodidae) on mainland Australia: little red (*Pteropus scapulatus*), grey-headed (*P. poliocephalus*), black (*P. alecto*) and spectacled (*P. conspicillatus*) (Hall 1986). Flying-foxes occur predominantly in northern and eastern subtropical and temperate coastal areas but are generally not present in Tasmania and south-western Australia (Hall 1986; Carnahan 1990). Due to their feeding on nectar and pollen, flying-foxes have been implicated in the pollination of many *Eucalyptus* and *Corymbia* species (Ratcliffe 1931; McCoy 1990; Parry-Jones and Augee 1991; Eby 1995, 1996). They have also been observed feeding on other native Myrtaceae species, such as *Melaleuca*, *Lophostemon* and *Angophora* (Ratcliffe 1931; Parry-Jones and Augee 1991, 1992; Boland *et al.* 1994; Eby 1995). When available, the nectar and pollen produced by native forest trees, particularly *Eucalyptus* species, predominate in the diet of all flying-foxes with the exception of the spectacled. Although they have been observed feeding on *Eucalyptus* nectar, spectacled flying-foxes feed predominantly on rainforest fruit (Richards 1990).

The little red flying-fox has the most widespread distribution of all Australian flying-foxes, and is well known for its use of nectar as a principal food source, utilising fruit only when native flowering is poor (Ratcliffe 1931; Nelson 1965; McCoy 1990, 1995; P. Birt, unpubl. data). In addition to nectar, both the grey-headed and black flying-fox feed regularly on native and cultivated fruit, although they display a preference for nectar when it is available (Ratcliffe 1931; McWilliam 1986; Parry-Jones and Augee 1991; Eby 1991b, 1995, 1996). The common (*Syconycteris australis*) and northern (*Macroglossus minimus*) blossom bats utilise the floral resources of several eucalypt species, but they are considered more important pollinators of tree species belonging to the genera *Callistemon*, *Melaleuca* and *Syzygium* (Law and Spencer 1995; McKean *et al.* 1995).

Similar to other nectar-feeding animals, flying-foxes possess a tongue with a brush-like tip that is well suited for extracting nectar from flowers via capillarity. This is particularly important when the nectar is produced only as a thin film or as small droplets over the surface of the nectar container (Birt *et al.* 1997). Whilst foraging amongst the flowers for nectar, pollen adheres to the fur located on the face, chest, stomach and shoulders, and the hairs located on the underside of the wings (P. Birt, unpubl. data). The pollen is subsequently transferred to other flowers as the flying-fox moves between trees (McCoy 1990; Parry-Jones and Augee 1991; Eby 1995, 1996). At least 80% of pollen grains removed from *P. alecto* and *P. scapulatus* were found to be viable and capable of successfully fertilising receptive stigmas. In addition, flying-foxes were found to carry significantly greater pollen loads per individual than other Australian flower-visiting vertebrates (McCoy 1990).

### Movements in relation to foraging

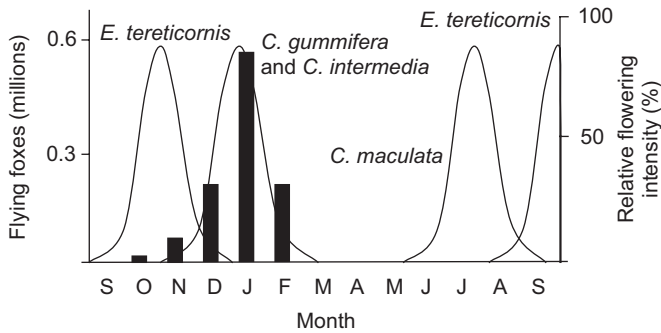
Radio-tracking studies have revealed that flying-foxes may travel more than 45 km to feeding areas and over 80 km during the night whilst foraging for nectar (Eby 1991b, 1996; Spencer *et al.* 1991;

P. Birt, unpubl. data). They are highly mobile during the night, moving between several trees within a stand, and between stands of flowering conspecifics separated by many kilometres. For instance, radio-tracking studies of grey-headed flying-foxes showed one individual foraging between three stands of flowering conspecifics in succession which were located up to 19 km apart (Eby 1991a). Little red flying-foxes were observed feeding successively between flowering conspecifics located up to 24 km apart (P. Birt, unpubl. data). Eby (1996) found that individual grey-headed flying-foxes varied in their method of foraging, due in part to their territorial feeding habits in which sub-dominant individuals were driven by dominant individuals to forage in trees further away. Similar territorial feeding habits have been observed with little red flying-foxes (P. Birt, unpubl. data). Consequently, flying-foxes are capable of moving pollen, both over large distances and to a large number of trees (Eby 1995; P. Birt, unpubl. data). Similar foraging strategies have been observed amongst other nectar-feeding bats (Howell 1979).

### Migratory behaviour

The flowering and subsequent production of nectar by eucalypts is greatly influenced by environmental factors, particularly rainfall, and tends to be patchy and irregular (Pryor 1976; Porter 1978; Clemson 1985). When environmental conditions are unfavourable, several *Eucalyptus* and *Corymbia* species, such as *C. maculata* and *C. citriodora*, may not flower for several years (Clemson 1985; Blake and Roff 1988). Alternatively, other species such as *E. crebra*, *E. platyphylla* and *E. albens* may flower intensely but produce very little nectar (Clemson 1985; Blake and Roff 1988; P. Birt, unpubl. data). Consequently, in order to survive, flying-foxes undertake large-scale migrations, moving from one area to another, depending on food availability (Eby 1991b, 1995; Parry-Jones and Augee 1991; Richards 1995). Long distance movements of radio-tracked flying-foxes frequently correlate with the flowering of *Eucalyptus* communities (Spencer *et al.* 1991; Eby 1991b, 1995, 1996). One female grey-headed flying fox, which had been fitted with a radio-tracking collar at Grafton in New South Wales, was detected one month later near Nowra, 610 km south of Grafton. The individual arrived in the area and fed on *C. maculata* until the flowering was depleted. It was next detected three days later at Wyong, 210 km north of Nowra (Eby 1991b). Another female grey-headed flying-fox which was collared at Lismore, New South Wales, in January, was detected six months later near Childers, Queensland, 450 km north of Lismore. The flying-fox was feeding on flowering *C. citriodora*. The longest distance travelled by a migrating flying-fox was greater than 800 km (Eby 1996). During migrations, flying-foxes may occupy several daytime campsites en route for short periods (Eby 1996).

Migrations are particularly evident during mass flowering (Ratcliffe 1931; Eby 1995), which occurs every 4–10 y for some eucalypt species (Clemson 1985). During such events, large numbers of flying-foxes, sometimes exceeding 500 000 (Fig. 2), congregate to feed on the available nectar (Ratcliffe 1931; Eby 1991b, 1996; Parry-Jones and Augee 1992; P. Birt, unpubl. data). The ability of flying-foxes to detect flowering Myrtaceae, often hundreds of kilometres away, is not well understood, but demonstrates their reliance on these plants for food. Although they utilise a large variety of *Eucalyptus* and *Corymbia* species,



**Figure 2.** Little red flying-fox numbers (solid bars) at a camp in southern Queensland during 1996/97 coinciding with flowering of two bloodwood species (P. Birt, unpubl. data).

there are species for which flying-foxes will undertake large-scale migrations, including *C. maculata*, *C. citriodora*, *C. intermedia*, *C. gummifera*, *E. tereticornis*, *E. moluccana*, *E. populnea*, *E. albens*, *E. melliodora*, *E. melanophloia*, *E. cloeziana* and *E. pilularis* (Ratcliffe 1931; Nelson 1965; Eby 1991b, 1996; Hall and Richards 1991; P. Birt, unpubl. data).

Due to the fact that flying-foxes have been observed with large quantities of pollen on their fur, they are considered to be pollen vectors for a large variety of *Eucalyptus* and *Corymbia* species. Furthermore, most of the pollen attached to the fur has been found to be viable and thus capable of successful fertilisation should it come into contact with the receptive stigma of a flower. Limited data exist on the rate of successful pollination by flying-foxes. Exclusion experiments involving *Syzygium cormiflorum* (Myrtaceae) demonstrated that visitation by the Queensland blossom bat (*Syconycteris australis*) resulted in more seed production than visitation by birds, possums or insects. Of particular interest was that these bats spent less time foraging in the trees than did other pollinator groups (Crome and Irvine 1986). In light of these findings, it would appear that flying-foxes may contribute significantly to long-distance movement of eucalypt pollen. Flying-foxes may have the capacity to move pollen over greater distances than birds.

### Bird and bat pollinators and eucalypt genetic diversity

Indications of the impact of long-distance gene flow in eucalypt forests may be deduced by observing patterns of genetic diversity of widespread species throughout their geographical distribution. Typically most of the genetic variation in widespread eucalypts is observed within rather than between populations. Clustering of related populations within a species frequently occurs over geographic regions spanning distances up to 600 km (Moran 1992). However, most widespread eucalypts do not occur as continuous distributions but as fragmented populations reflecting the influence of a wide range of factors including aspect, slope, climatic conditions and fire, and the physical, nutritional and biological status of the soil (Florence 1996). In some cases the conservation of genetic diversity within disjunct populations may reflect the survival of remnant populations from earlier more

continuous distributions under different climatic conditions. It would appear, however, that significant gene movement between fragmented populations or stands does occur. Birds and bats may play an important role in this gene movement.

*Eucalyptus grandis* and *E. saligna* occur as overlapping and fragmented populations over large distances along the east coast of Australia (Boland *et al.* 1994). The two species are genetically distinguishable, but the correlation between genes and geography within each species was low (Burgess and Bell 1983). Two *E. grandis* populations, which clustered closely together, occurred at the extremes of the disjunct species range separated by almost 2000 km. Little geographic structure in *E. urophylla* populations was observed between populations on several islands in eastern Indonesia throughout a range of almost 500 km (House and Bell 1994). These populations are frequently separated by stretches of sea tens of kilometres across. Populations on an outlying island separated by about 100 km showed a higher degree of genetic differentiation. Outlying populations of *E. delegatensis*, *E. marginata* (Moran and Hopper 1987) and *E. diversicolor* (Coates and Sokolowski 1989) separated by 50–200 km from the main species range still retained most (>87%) of the total species genetic diversity.

Strong regional divergence has been detected in *E. nitens*, a species that occurs in a few widely separated (100–400 km apart) populations over an extensive geographical range from central Victoria to northern New South Wales (Byrne *et al.* 1998). The Tasmanian and mainland populations of *E. delegatensis* are also genetically distinct; but markedly less divergence occurs within the regional distributions found either side of Bass Strait, which span distances of 200 and 600 km respectively (Moran 1992). Like many eucalypts, the distribution of *E. delegatensis* throughout these regions is patchy, with frequent gaps of 10–50 km between stands. *Eucalyptus pellita* populations in Australia and New Guinea are genetically distinct, while considerably less divergence was observed in trees dispersed over a range of about 700 km in northern Queensland (House and Bell 1996). Research on the genetic structure of *E. globulus* native forests suggests gene flow at a scale of several kilometres (Skabo *et al.* 1998). Similar levels of relatedness were observed between family clusters separated by as little as 25 m or as much as 14 km. While some *E. globulus* populations appear to cluster geographically, a number of genetically similar populations occurred at extremes of the natural distribution (Nesbitt *et al.* 1995).

This genetic evidence suggests long-distance gene movement may occur between widely fragmented populations of certain eucalypt species. Given the feeding behaviour of birds and bats, it is possible that they may play a significant role in the maintenance of genetic diversity across fragmented populations within large regions. It is unlikely that other eucalypt pollen vectors could transfer pollen over such distances at a similar scale. In some cases, flowering asynchronicity will limit effective gene movement, while genes from very distant populations may also be less suited to local selection pressures than genes carried by more local outcrossed pollen. The data tend to indicate localised specialisation superimposed upon a significant degree of regional genomic homogenisation.

## Conclusion

Data on both local and long-distance movements of birds and bats feeding on eucalypts are still very scanty, but it is likely that viable pollen could be transferred between conspecific or related eucalypt species many kilometres apart. Most eucalypt pollen is likely to be deposited on flowers of the same tree or trees in the immediate vicinity, predominantly by the numerous insect visitors. However, eucalypts frequently exhibit high levels of outcrossing, indicating that less abundant non-self pollen is more likely to achieve fertilisation due to a level of self-incompatibility. This biological favouritism and the increased vigour of the resulting outcrossed individuals may serve to magnify the importance of less frequent pollen transfer from more distant trees. Bird and bat long-distance transfer of genes has been going on for thousands (if not millions) of years, and may contribute significantly to the maintenance of genetic diversity within eucalypt species with disjunct native populations.

Measuring the scale and significance of low-frequency movement of eucalypt pollen by birds and bats over many kilometres is technically challenging. In highly fragmented forests where species distributions are precisely known, it may be possible to gain some measure of the extent and distance of paternal gene flow using molecular markers. Molecular studies on progeny of important target tree species growing in the vicinity of current or past roost sites may help confirm the role of bats and birds in maintaining genetic diversity in situ in species with widespread distributions.

Our understanding of bird and bat pollen vectors of the major commercial eucalypt species is particularly poor. Plantation species are generally among the largest eucalypts, naturally occurring in closed forests. It is therefore a challenge to observe floral phenomena. Studies of small fast-moving (e.g. little lorikeets) or nocturnal (e.g. little red flying-fox) visitors are particularly challenging. It is imperative that there is greater understanding of the pollination biology of major commercial eucalypt species. More comprehensive radio-tracking studies of bird and bat species are required in targeted locations where plantations occur, so we can fully appreciate the potential of these vectors to move genes from plantations into surrounding native forests.

There remain significant gaps in our understanding of eucalypt pollen biology. The number of species with dry pollen that may be wind dispersed is not known, and reports on eucalypt pollen viability are largely anecdotal. Pollen stickiness varies widely in eucalypts (Moncur and Boland 1989) and affects the clustering of pollen grains. Clustered pollen grains may be more effectively transported than isolated pollen. Further studies on the pollen presentation mechanisms of eucalypts, and the capacity of bats and birds to carry it, are required in order to appreciate fully the likelihood of long-distance transfer.

The shift to eucalypt plantations offers significant environmental benefits by withdrawing forestry operations from native forests, but it has raised ecological concerns (Wardell-Johnson *et al.* 1997) due to the likely transfer of genes from plantation species into local native stands. *Eucalypt* species (e.g. *E. globulus* in Western Australia and *E. nitens* in Tasmania) and provenances are now grown in Australia in plantations outside their natural range.

Frequently these plantations are adjacent to forests in which related interfertile species are present. Evidence has been found of hybridisation between plantation-grown *E. nitens* and adjacent native *E. ovata* (Barbour *et al.* 2002). While most eucalypts currently being planted are derived from seed from native forests, pressures for increased productivity from plantations will result in an increasing proportion of the plantation estate being selections from breeding programs and inevitably improved clones. These trends are likely to increase ecological concerns.

Application of biotechnology in eucalypt forestry offers significant opportunities to further increase productivity, but has increased concerns about the potential for transgene flow into native forests. The capacity of bat and bird pollinators to travel considerable distances highlights the obvious impracticality of gene containment in transgenic eucalypt plantations by the use of buffer zones of non-transgenic trees. Consequently, a major objective of eucalypt biotechnological research is to develop transgenes that confer sterility. While current sterility research is focussed on containment of transgenes, it may also have wider application in alleviating ecological concerns of plantations per se.

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