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OUT ON THE TOWN: WINTER FEEDING ECOLOGY OF LORIKEETS IN URBAN PARKLAND

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Rainbow *Trichoglossus haematodus* and Musk *Glossopsitta concinna* Lorikeets have increased in abundance in Melbourne, Australia in recent years. We documented the diet and feeding behaviour of these lorikeets at 20 parkland sites in autumn and winter to increase our understanding of factors facilitating this urban colonisation. Both species' diets were dominated (≥89%) by nectar and/or pollen of eucalypt species, more than two thirds of which were not native to the Melbourne area. Small numbers of invertebrates and some fruit and seeds were also consumed. Two or three of the eucalypt species used were flowering at any given time and two of the most exploited species flowered almost continuously. Introduced eucalypts have probably been important in the recent winter increase in abundance of the lorikeets in Melbourne. Both lorikeets used the same five feeding postures, perching upright (~58%) and dexterously hanging inverted (~ 40% of records) being the most common. Six other Australian native bird species exploited the lorikeets' eucalypt nectar resources, but mostly infrequently; however, they did use the same foraging substrate and exhibit similar feeding behaviour. Only 11 aggressive inter-specific interactions involving the lorikeets were observed in 4.5 months. Significant interference competition from other bird species for the lorikeets' highly abundant food resources seemed unlikely; its absence could also be facilitating the lorikeets' winter colonisation of the city. Planting more eucalypts in streets and parks, including ones native to the Melbourne area, could potentially lead eventually to further increase in lorikeet densities in the city in autumn and winter.

INTRODUCTION

Geographic range expansion of generalist and opportunist native vertebrates, often resulting from anthropogenic landscape alteration, has been common globally in the last 100 years (Garrot *et al*. 1993; Temby 2007). It can negatively affect other less adaptable, native species in the colonised area, sometimes causing local extinctions if it is accompanied by a major increase in abundance (Garrot *et al*. 1993). From a conservation perspective, such impacts are problematic because mitigation may require unpopular culling or removal of the colonising native species (Diamond 1992; Bass 1995; Major 2003). One facet of this range expansion phenomenon is the relatively recent colonisation of cities and towns by many native vertebrates, a process facilitated by human activities that alter habitats and provide abundant resources, such as breeding sites and food (Low 2000).

Several Australian cities have recently been successfully colonised or re-colonised by a suite of native bird species (Low 2000; Garden *et al*. 2006), some of which probably negatively affect other native, urban birds. For example, the Pied Currawong's *Strepera graculina* increasing colonisation of south-eastern cities is of concern, because it preys on the young and adults of many small, native bird species (Major *et al*. 1996). Recent urban colonisation by the Noisy Miner *Manorina melanocephala* is also problematic because this bird can aggressively out-compete, and sometimes kill, other native birds (Loyn 1985; Grey *et al*. 1998). On the other hand, some recent native avian urban colonisers may conceivably pose no threat to co-existing native species through resource competition, predation or the introduction of pathogens; indeed their presence may be entirely beneficial for aesthetic, educational and biodiversity conservation reasons (Platt and Lill 2006). Most inhabitants of industrialised countries now live in cities, including 85 per cent of Australians (Bridgman *et al*. 1995). Consequently there is an increasing need to understand urban ecosystems (Bridgman *et al*. 1995; Uhl 1998; Pickett and Cadenasso 2006), including the nature, causes and consequences of colonisation events by native birds.

Rainbow Lorikeets *Trichoglossus haematodus* and Musk Lorikeets *Glossopsitta concinna* have recently colonised several major Australian cities (Paton *et al*. 1994; Waterhouse 1997; Jones and Wieneke 2000; Woodall 2002; Fitzsimons *et al*. 2003). Rainbow Lorikeets inhabit lowland forests and woodlands in a broad strip of Australia fringing the northeastern, eastern and southeastern coastlines (Higgins 1999), where they consume mainly nectar and pollen from the flowers of tree species, particularly eucalypts (Cannon 1984; Franklin 1997). Musk Lorikeets inhabit eucalypt-dominated open forests and woodlands in a broad swathe of the continent fringing its southeastern coastline and including Tasmania. Their less well-documented diet resembles that of the Rainbow Lorikeet (Higgins 1999). Both species 'track' flowering and fruiting events over large areas (Emison *et al*. 1987).

After a long period of absence or very low abundance, the Rainbow Lorikeet became re-established in Melbourne in the 1970s, initially mainly in summer (Emison *et al*. 1987; Veerman 1991; Higgins 1999). It is now present all year and has increased in abundance and distribution in the city markedly in recent years (Shukuroglou and McCarthy 2006; Temby 2007). Musk Lorikeets, more irregular and seasonal visitors, have also become more abundant in Melbourne since the 1970s (Higgins 1999). Their numbers vary annually, possibly reflecting winter flowering intensity in the remnant box-ironbark forests to the north of the city (Fitzsimons *et al*. 2003), but they are becoming more common in the city in summer. Both species occur in urban habitats ranging from woodland or forest remnants to recently developed streetscapes, but they prefer parkland and established streetscapes with native Australian trees and moderate tree cover (Fitzsimons *et al*. 2003; White *et al*. 2005; Shukuroglou and McCarthy 2006).

To help identify the factors facilitating these urban colonisation events by Rainbow and Musk Lorikeets, we documented the birds' diet and feeding behaviour in urban Melbourne parklands in the second half of autumn and throughout winter. We particularly planned to elucidate two issues encompassed by this rationale: (1) Fitzsimons *et al*. (2003) hypothesised that Australian plants that are not native to Melbourne may play an important facilitatory role in the colonisation of the city by lorikeets, so we determined the relative importance of food resources from Australian plants that are and are not native to Melbourne in the lorikeets' diet; (2) it has been argued that inter-specific competition can influence the extent and impact of avian colonisation of urban environments (e.g. Lowry and Lill 2007), so we examined whether there was evidence suggesting a significant level of such competition for the lorikeets' key winter food resources by recording firstly, their use by other urban bird species and secondly, inter-specific aggressive interactions, particularly at feeding sites, involving either lorikeet species.

METHODS

Study sites

Systematic, quantitative records of the diet and foraging behaviour of Rainbow and Musk Lorikeets were collected from mid-April to late August, 2003 in 20 public parks and golf courses. These sites were located in central, northern and eastern Melbourne, Australia (37° 48'S, 145° 00'E), extending from Royal Park South (most westerly) to Binnak Park (most northerly) to Jells and Norton's Parks (most easterly) (Appendix 1). This broad spatial focus was employed because of the spatially dynamic nature of the lorikeets' foraging behaviour (Emison *et al*. 1987). Sites were chosen mainly on the basis of their vegetation composition and the presence of known or likely food resources for Rainbow and Musk Lorikeets. They varied in area from approximately 1.3 to 180 hectares and in the relative proportion of the area that was vegetated with trees and shrubs; they also varied in vegetation composition, but the tree component of the flora was universally dominated by *Eucalytpus* or *Corymbia* species. Data were gathered every week during the study period. Each site was visited six times, alternating between the morning and the afternoon, at intervals of one to four weeks. Additionally, we collected data opportunistically from these and other northern and eastern suburban sites to broaden the documentation of lorikeet feeding ecology in Melbourne, but we distinguish these supplementary observations throughout this account. Melbourne's mean monthly minimum and maximum ambient temperatures during the study period were 7 and 16.2°C, respectively, and mean monthly rainfall was 57 millimetres.

Diet and feeding behaviour

Diet and feeding behaviour were recorded systematically whilst following a fixed route through each site. This approach facilitated sampling of the various different habitats representatively and avoided biasing observations towards lorikeets in large, conspicuous flocks. For each Rainbow or Musk Lorikeet observed feeding, we recorded: (a) the plant species in which it fed, (b) the food resource being utilized (nectar, pollen, fruit, seeds or invertebrates) and (c) the substrate (amongst foliage, on main branch or on trunk) on which and the vegetation stratum (tree canopy or shrub layer) in which it was feeding. We could rarely distinguish whether inflorescences yielded both nectar and pollen (Churchill and Christensen 1970) and so we refer throughout to 'nectar/pollen consumption'.

Both lorikeet species commonly fed gregariously. To increase the independence of the dietary and behavioural data collected during each site visit, we therefore recorded (a) only one observation per lorikeet encountered at the site and (b) from a maximum of three individuals of each lorikeet species feeding on a particular plant species, irrespective of the number of individual plants of that species at the site. When a flock of lorikeets of either species was feeding in a single tree, the three birds recorded were selected 'haphazardly', except that one was chosen from each flank and one from the centre of the flock.

The birds' posture when feeding was categorized on the basis of preliminary observation as follows:

(a) *Perching upright-reaching* – perching in an upright stance and reaching for and grasping the food item immediately in front of it with the beak or foot;

(b) *Perching upright- twisting* – perching in an upright stance, but twisting the head laterally in reaching for and grasping a food item with the beak or foot;

(c) *Perching leaning* - perching in a non-upright stance and apparently leaning on a branch for support, whilst reaching for and grasping the food item with the beak or foot;

(d) *Hanging inverted* – clinging upside-down from the foliage without other support to reach the food item with the beak;

(e) *Hanging inverted-with support* – as for *Hanging inverted*, but using other foliage for additional support.

Significance of differences in the diet and feeding behaviour of the two lorikeet species was tested with chi-squared tests of independence. However, temporal trends in these aspects of feeding ecology were not examined, given that the investigation only lasted 4.5 months.

Use of lorikeets' food resources by other bird species

To gain insight into whether there was likely to be significant inter-specific competition for the lorikeets' food resources, during the fixed route recording of lorikeet feeding behaviour we systematically recorded use by other bird species of food resources that we observed the lorikeets consuming. We

TABLE 1

Percentage of Musk and Rainbow Lorikeet systematic nectar/pollen feeding records contributed by each food plant species. Species listed in descending order of contribution to Rainbow Lorikeet's diet.

Tree species	Percentage of lorikeet nectar/pollen feeding records	
	Rainbow	Musk
Spotted Gum *Corymbia maculata*	26.8	29.1
Red Ironbark *Eucalyptus sideroxylon*	26.4	27
Yellow Gum *E. leucoxylon*[1]	16.6	12.1
Mugga *E. tricarpa*[1]	8.9	2.1
Southern Blue-gum *E. globulus*	6.8	12.8
Tuart *E. gomphocephala*	3	2.1
Pilliga Box *E. pilligaensis*	3	0.7
Flooded Gum *E. grandis*	2.1	0.7
Yellow Box *E. melliodora*[1]	1.7	1.4
Creswick Apple-box *E. aramophloia*	1.3	0
Casuarina sp.*	0.9	0
Gosford Wattle *Acacia prominens*	0.9	0
River Red Gum *E. camaldulensis*[1]	0.9	0.7
Swamp Yate *E. occidentalis*	0.4	10.6
Brush Cherry *Syzgium paniculatum*	0.4	0
Fuzzy Box *E. conica*	0	0.7

[1] indicates native to Greater Melbourne (Gray and Knight 2001).
* possibly Swamp She-oak *Casuarina glauca*

used the same recording protocol as that employed for the lorikeets. We also systematically recorded all aggressive interactions (threats and fight-chases) between the lorikeets and other birds and their outcome (spatial displacement or no displacement of one combatant) during these sessions.

Flowering phenology of lorikeet food plants

To estimate temporal availability of nectar/pollen from eucalypt (Myrtaceae) inflorescences, a major lorikeet food resource (Cannon 1984; Franklin 1997), *Eucalyptus* and *Corymbia* flowering phenology was recorded at 14-day intervals on each of eight 100 metres long × 20 metres wide belt transects distributed over five suburban parks. Four of these parks were also used in obtaining foraging observations; the two most widely separated ones, Bundoora Park in the north and Jells Park in the east, are approximately 25 kilometres apart. At Bundoora, Wattle and Jells Parks, two transects were used; at Norton's Park and Blackburn Lake Sanctuary only one transect was used because we determined that the tree component of the flora was relatively floristically homogeneous. Flowering intensity was estimated approximately by a method resembling that of Wilson and Bennett (1999). The percentage of a tree's canopy bearing fresh inflorescences (i.e. staminodes brightly coloured and 'fluffy' in appearance) was visually estimated categorically as being <10, 10–25, 26–50, 51–75 and 76–100 per cent. We refer to this percentage as the flowering intensity score (FIS). We also gathered supplementary, qualitative eucalypt flowering phenology records opportunistically in the northern and eastern suburbs by recording any species that we observed flowering during the study period. For these records we scored flowering even if only one tree was observed flowering substantially, but usually the number was much greater.

RESULTS

Lorikeets' diet and feeding behaviour

From the systematic recording we obtained 235 feeding observations for Rainbow and 141 for Musk Lorikeets. Nectar/pollen consumption accounted for very high, but significantly different percentages ($\chi^2_{(1)} = 7.697$, $P<0.01$) of the Rainbow (89.4%) and Musk (96.5%) Lorikeet's feeding records. Rainbow Lorikeets also consumed foliage-dwelling invertebrates (7.2% of records), fruit (2.6%) and seeds (0.9%) and Musk Lorikeets ate foliage invertebrates (2.8%) and fruit (0.7%), but not seeds. All feeding by both species was in the tree canopy stratum. Rainbow Lorikeets fed amongst the foliage 95.7% of the time, on main tree branches (2.6%) and on the main trunk (1.7%). Musk Lorikeets fed amongst the foliage 97.2% of the time and on main branches on all other occasions.

TABLE 2

Percentage occurrence of the five feeding behaviours of Rainbow and Musk Lorikeets during systematic recording.

Behaviour	Percentage occurrence in feeding repertoire	
	Rainbow Lorikeet $n = 235$	Musk Lorikeet $n = 141$
Perching upright-reaching	43	36.9
Hanging inverted-with support	37	40.4
Perching upright-twisting	14	22
Hanging inverted	3	0.7
Perching leaning	3	0

Musk Lorikeets consumed the nectar/pollen of 12 eucalypt species; Rainbow Lorikeets consumed nectar/pollen from 11 of these species, an additional eucalypt and three other Australian plant species not native to the Melbourne area in the genera *Casuarina* (Casuarinaceae), *Acacia* (Mimosaceae) and *Syzgium* (Myrtaceae) (Table 1). Five eucalypt species accounted for the majority (85.5%) of the nectar/pollen feeding records for the Rainbow Lorikeet and four of these species plus another eucalypt species for the majority (91.6%) of the Musk Lorikeet's records. The eucalypt species concerned were Spotted Gum *Corymbia maculata*, Red Ironbark *Eucalyptus sideroxylon,* Swamp Yate *E. occidentalis*, Southern Blue-gum *E. globulus*, Yellow Gum *E. leucoxylon* and Mugga *E. tricarpa*. Whilst the first two of these species accounted for 53 per cent and 56 per cent, respectively, of the nectar/pollen consumption records for the two lorikeet species, Rainbow and Musk Lorikeets nonetheless differed significantly in their use of the six main (i.e. accounted for > 5% of records for at least one of the lorikeet species) eucalypt species that were exploited for nectar/pollen ($\chi^2_{(5)} = 32.6$, $P<0.001$). Although there were quite a few exotic plants at most study sites, we did not observe either lorikeet species feeding on any food item obtained from such plants. The feeding behaviour profiles of the two lorikeet species were indistinguishable ($\chi^2_{(2)} = 5.81$, $P> 0.05$) (Table 2). Each species exhibited five feeding postures, but *Perching upright-reaching, Hanging inverted –with support* and *Perching upright-twisting* were by far the most common, collectively comprising 94 and 99 per cent of records for Rainbow and Musk Lorikeets, respectively.

Supplementary feeding records ($n = 65$) supported the prominence in the Rainbow Lorikeet's diet of nectar/pollen from the inflorescences of *C. maculata* (30.8 % of records), *E. leucoxylon* (27.7%) and *E. sideroxylon* (10.8%) observed in systematic recording. However, three Australian plant species not native to the Melbourne area and not recorded in the systematically collected data, namely Golden Wattle *Acacia pycnantha* (Mimosaceae)*,* Weeping Bottlebrush *Callistemon viminalis* (Myrtaceae) and Sweet Pittosporum *Pittosporum undulatum* (Pittosporaceae), collectively contributed 6.2 per cent of these opportunistic records. The limited number of supplementary records for Musk Lorikeets (n =14) all involved nectar/pollen consumption from five *Eucalyptus* and one *Corymbia* species, which featured in the systematically collected data. All supplementary records for both lorikeet species involved feeding amongst the foliage in the tree canopy stratum using the postures *Perching upright-reaching*, *Hanging inverted-with support* and *Perching upright-twisting* (n = 12 per species).

Use of lorikeets' food resources by co-habiting bird species

Systematic observations (n = 64) showed that six other bird species fed on lorikeet food plant resources, namely the Noisy Miner (56.3% of records), Red Wattlebird *Anthochaera carunculata*, Little Wattlebird *A. chrysoptera*, Scaly-breasted Lorikeet *Trichoglossus chlorolepidotus*, Eastern Rosella *Platycercus eximius* and Sulphur-crested Cockatoo *Cacatua galerita* (each < 16% of records). Collectively, these species fed on 10 of the 16 plant species used for food by the lorikeets. Nectar/pollen from *Eucalyptus* and *Corymbia* inflorescences accounted for almost all of the records, with *C. maculata* (31.3% of records), *E. leucoxylon* (23.5%) and *E. sideroxylon* (23.4%) together providing more than three quarters of them. Noisy Miner feeding records for lorikeet food plants (n = 36) were distributed among these three eucalypts as follows: *E. leucoxylon* 30.6 per cent and *E. sideroxylon* and *C. maculata* each 27.8 per cent. The six bird species that used Rainbow and Musk Lorikeet food plants employed the same five feeding postures as the lorikeets when exploiting these resources and, like them, used *Perching upright-reaching* (37.5% of records), *Hanging inverted-with support* (32.8%) and *Perching upright-twisting* (14%) most frequently (n = 64). All foraging on lorikeet food plants by these co-habiting species occurred amongst the foliage in the tree canopy stratum.

Noisy Miners and the two wattlebird species dominated the supplementary records (n = 27) of co-habiting species exploiting lorikeet food plants. Twenty-six of these records involved the same eucalypt species which dominated the systematic records and all involved use of the same foraging substrate, stratum and principal feeding postures that dominated the systematically collected records.

Just eleven inter-specific aggressive interactions involving Rainbow or Musk Lorikeets were observed in 4.5 months of systematic observation, seven being just threats and four fight-chases. Six of these interactions were initiated by Rainbow

TABLE 3

Flowering phenology of eleven of the main lorikeet eucalypt food plants in autumn and winter, 2003 based on systematic and opportunistic observations.

Tree Species	April	May		June		July		Aug		
	W 2	W 4	W 6	W 8	W 10	W 12	W 14	W 16	W 18	W 20
Corymbia maculata		•	•	•	•	•	•	•	•	•
Eucalyptus grandis				•			•			
E. gomphocephala	•	•	•	•						•
E. occidentalis	•		•	•		•	•	•	•	
E. globulus			•	•	•	•	•	•	•	•
E. pilligaensis		•								
E. conica	•									
E. melliodora	•	•				•				
E. leucoxylon		•	•	•	•	•	•	•		•
E. sideroxylon	•	•	•	•	•	•	•	•	•	•
E. tricarpa		•	•	•	•	•	•	•	•	•

W = week from inception of study in mid-April. Month is indicated for some weeks to give a seasonal time scale.
• Black circles indicate flowering of a species in the study area.
Where circles occur in adjacent columns for a particular species, it indicates that flowering was continuous over at least a three-week period e.g. *Corymbia maculata* flowered continuously from Week 3 or 4 to Week 20.

Lorikeets, four against Musk Lorikeets and one each against an Australian Magpie *Gymnorhina tibicen* and a Noisy Miner. All resulted in the target bird's displacement, but not its departure from the site. Musk Lorikeets did not initiate any inter-specific aggressive encounters, but were the target of three encounters initiated by native species other than the Rainbow Lorikeet, two of which caused their local displacement, whilst one elicited no response.

Eucalypt flowering phenology

The five sites chosen for systematic measurement of *Eucalyptus and Corymbia* flowering phenology collectively had three of the five eucalypt species that proved to be principal food plants for the lorikeets. At these sites, *C. maculata* flowered from mid-April to early August, with a mean FIS of 5–6.5 per cent in all surveys except that in Week 9 (June) (FIS = 9%). *Eucalyptus sideroxylon* flowered throughout the study at a constant FIS of 5 per cent and *E. leucoxylon* at the same intensity, but only from mid-April to mid-June. Thus, on average, the systematic records showed that two of the lorikeets' main winter nectar/pollen sources were available for most of the study period and the third for the first half of the period.

Adding the supplementary data and expressing flowering just in presence/absence terms provided a fuller, but less rigorous, flowering phenology for 11 eucalypt species exploited by the lorikeets (Table 3). In this expanded data set, the trends apparent in the systematic data for *C. maculata*, *E. sideroxylon* and *E. leucoxylon* were broadly similar. Another fairly important food plant, *E. globulus*, flowered for approximately the last 75 per cent of the study period. *Eucalyptus tricarpa*, whose nectar was moderately important in the Rainbow Lorikeet's winter diet, flowered for all but the first two-three weeks of the study period. *Eucalyptus occidentalis*, which was significant in the Musk Lorikeet's diet, appeared to be more intermittent in its flowering, having two major flowering periods (late autumn-early winter and mid-late winter). Several of the other eucalypt species that were used relatively infrequently by the lorikeets (*E. grandis, E. pilligaensis, E. melliodora and E. conica*) also flowered much more sporadically. Overall, records showed that several eucalypt species were flowering and were exploited for nectar/pollen by the lorikeets at any given time during autumn and winter.

DISCUSSION

Diet and feeding behaviour of urban Rainbow and Musk Lorikeets

The smaller sample size for Musk Lorikeets reflected their low abundance in Melbourne until well into winter, which may have resulted from abundant flowering in the box-ironbark woodlands to the north of the city in winter, 2003 (A. Bennett, personal communication). One important issue concerning what Blair (2001) calls 'urban adapters' is whether their colonising is facilitated essentially by replication of their natural 'niche' in cities or by their inherent ecological adaptability or flexibility. In a six-month period spanning the wet and dry seasons, the diet of Rainbow Lorikeets in monsoon woodland at Berry Springs, N.T. comprised 94 per cent nectar and pollen, mostly obtained from three *Eucalyptus* species native to the area, plus some fruit and leaf material. Eighty-three per cent of foraging was done amongst foliage and all of it whilst perching (Franklin 1997). On the Queensland–New South Wales border over a one-year period, Rainbow Lorikeets fed mainly (87%), and particularly in winter, on nectar/pollen; forty-one per cent of this resource was obtained from ten eucalypt species native to the area (Cannon 1984). Some nectar was also obtained from *Melaleuca* (Myrtaceae), *Callistemon*, *Banksia* (Proteaceae) and *Tristania* (Myrtaceae) species and small amounts of fruit, leaf buds, bark and insects were also consumed, particularly outside of winter. Some of Cannon's (1984) observations were made in natural woodland habitat, but 59 per cent were in urban areas. The Musk Lorikeet's diet in its natural habitat is not known in much detail, but comprises mainly eucalypt nectar and pollen, with small amounts of fruit, seeds and insects (Higgins 1999; Courtney and Debus 2006).

These observations accord with our findings for Melbourne parkland in autumn and winter, where the dominant food (89–97% of records) of both lorikeets was *Eucalyptus* and *Corymbia* nectar/pollen, supplemented by small quantities of invertebrates, fruit and, in Rainbow Lorikeets, seeds. Both species foraged predominantly amongst foliage and exclusively in the tree canopy stratum. Thus in a general sense urban Melbourne parkland contained the natural feeding 'niche' (i. e. food resources, foraging substrates and vegetation stratum) of these two lorikeet species. Most of the trees exploited were part of the huge range of eucalypts planted in Melbourne's streets and parks in, and since, the 1970s; their presence and maturity now greatly increase the spatiotemporal availability and diversity of nectar and pollen sources for avian and mammalian consumers (Fitzsimons *et al.* 2003; Shukuroglou and McCarthy 2006; Williams *et al.* 2006).

However, one factor distinguishing the lorikeets' diet in Melbourne from that in their ex-urban habitats was the greater proportion (Rainbow Lorikeet 72%, Musk Lorikeet 84%) of the nectar/pollen component obtained from Australian plant species that are not native to the area (cf. Franklin 1997 on ex-urban Rainbow Lorikeets). Only four of 13 eucalypt species exploited by the lorikeets in Melbourne in autumn and winter, namely *E. melliodora, E. tricarpa, E. leucoxylon and* River Red Gum *E. camaldulensis*, are native to the area (Gray and Knight 2001). The flowering seasons of most of the introduced eucalypts encompass autumn and/or winter in their ex-urban ranges and our phenological data for Melbourne broadly reflected this timing. Williams *et al.* (2006) also found from a literature search that *E. sideroxylon* usually flowers throughout late autumn and winter in Melbourne, but they report a much shorter season for *E. globulus* than we observed in 2003.

In contrast, only approximately 43 per cent of the eucalypt species native to Melbourne have flowering periods strongly encompassing these seasons (Walsh and Entwistle 1996; Gray and Knight 2001). Fitzsimons *et al.* (2003) showed that in winter in Melbourne, Rainbow and Musk Lorikeets' preferred habitat was established streetscape with Australian native trees, many of which do not occur naturally in the area. They also noted that the eucalypts which are native to the city are not generally recognized as profuse winter nectar producers. These eucalypts may have a greater arthropod biomass than introduced species (Bhullar and Majer 2000), but invertebrates comprised only about 3–7 per cent of the lorikeets' winter diet in the city. Thus the urban lorikeets' strong focus on these introduced eucalypts in our study was predictable and consistent with the hypothesis that the maturation of individuals of these tree species planted mostly as ornamentals in Melbourne in the 1970s has been important in the recent increase in Rainbow and Musk Lorikeets' abundance in suburbia in autumn and winter (Fitzsimons *et al.* 2003; Shukuroglou and McCarthy 2006). Williams *et al.* (2006) advanced a similar argument for the Grey-headed Flying Fox *Pteropus poliocephalus*, which consumes a lot of nectar from introduced eucalypts in Melbourne.

Our study was a 'snapshot' of lorikeet feeding in urban Melbourne parkland in one autumn and winter. Eucalypts vary in their flowering intensity and timing among years (Mac Nally and McGoldrick 1997; Courtney and Debus 2006) and therefore we need to establish whether introduced eucalypts provide more than 70 per cent of the lorikeets' nectar/pollen resources every winter in this habitat and in a broader range of urban habitats. Our supplementary records added nectar/pollen of some non-eucalypt species to the lorikeets' known winter diet in urban parkland; in streetscapes and gardens, foods other than nectar (e.g. fruit) may feature more prominently (Higgins 1999). It is also pertinent to determine whether as much as 72–84 per cent of the nectar/pollen consumed by Rainbow and Musk Lorikeets in parks in central, northern and eastern Melbourne in spring and summer is similarly obtained from introduced eucalypts, because there is more flowering of eucalypts native to the area and other Australian native (and exotic) plant taxa then.

With respect to the recent, large-scale re-colonisation of Sydney by Rainbow Lorikeets (Burgin and Saunders 2007), Waterhouse (1997) documented a very different situation in the southern part of the city to the one described here for Melbourne. Lorikeets there also fed mainly on nectar/pollen, but only three eucalypt species featured prominently in the diet overall and only the introduced *C. maculata* in winter. Instead there was a strong dependence in winter on the nectar of introduced Australian native plants in other families, notably the Coral Tree *Erythrina variegata* (Fabaceae), and exotic plants. Therefore the specific factors that facilitate urban colonisation by lorikeets may differ among Australia's eastern seaboard cities.

Lorikeets are primarily nectar and/or pollen consumers, which have evolved a brush-tipped tongue and simplified gut that facilitate nectar ingestion and processing (Richardson and Wooller 1990). Rainbow and Musk Lorikeets in Melbourne obtained over 50% of their nectar/pollen by simply perching upright close to eucalypt flowers and reaching or twisting to access the food. However, they accessed flowers that could not be reached by perching through dexterously hanging upside down, approximately 40 per cent of nectar acquisition being achieved in this way. Unlike many more granivorous and frugivorous parrots (del Hoyo *et al.* 1997), they did not grasp food with the feet whilst feeding. Presumably inflorescences do not require detaching and manipulating to facilitate efficient nectar/pollen extraction and a selective advantage would accrue from leaving such a renewing resource *in situ.*

Are urban lorikeets involved in inter-specific food competition in winter?

Classical trade-off and stochastic niche theories both acknowledge inter-specific competition as one important factor probably involved in contemporary and historical structuring of animal communities, even though its role is difficult to prove, particularly in an evolutionary context (Tilman 2004; Begon *et al.* 2006). Interference competition among co-habiting species can involve members of one species preventing individuals of other competing species obtaining critical, limiting resources, often by overtly aggressive behaviour (Case and Gilpin 1974). Rainbow and Musk Lorikeets frequently fed simultaneously on the same individual food plant with negligible inter-specific aggression. Grey-headed Flying Foxes consume the nectar/pollen of some of the lorikeets' food plants (e.g. *E. leucoxylon* and *C. maculata*) at night in Melbourne (Williams *et al.* 2006), but relatively few other bird species significantly exploited the nectar/pollen of the prominent eucalypt species in the lorikeets' diet and when they did, there was little overt aggression with the lorikeets. This extremely limited involvement of the lorikeets in inter-specific aggression whilst feeding did not accord with the characterization of such urban matrix-occupiers as behaviourally aggressive (Garden *et al.* 2006). It is worth noting that Rainbow Lorikeets do interact aggressively with other lorikeets at artificial feeding stations in Sydney (Burgin and Saunders 2007).

Aggressive inter-specific interference competition for shared nectar resources could also theoretically be manifested in learned avoidance, in which case the incidence of inter-specific, resource-focused aggression should be fairly low. Nonetheless, we would still have expected to see more inter-specific aggression than the 11 encounters recorded if learned avoidance was operating, because it would likely be the aggression that triggered and maintained it. If learned avoidance was occurring, one might also predict that the incidence of members of the subordinate species feeding on the shared food resources when the dominant species was absent might be quite high. This possibility warrants quantitative investigation for Rainbow and Musk Lorikeets in Melbourne.

Whilst there was little indication of overtly aggressive, inter-specific interference competition for food involving the lorikeets, competition for limited food resources among co-existing species with similar dietary modes (e.g. nectarivory) can also theoretically be reduced and their co-existence facilitated on an evolutionary timescale by resource partitioning (Begon *et al.* 2006). One facet of such partitioning involves the use of different feeding behaviours and/or substrates (Vestjens 1975; Bell 1985) by morphologically differing competitors, affording them differential access to components of the same broad food resource type (e.g. nectar of different flowering plant species). However, both lorikeet species foraged mainly amongst the tree canopy foliage and their feeding behaviour profiles were statistically indistinguishable. Other bird species exploiting the lorikeets' main nectar sources also always foraged in the tree canopy, mostly amongst foliage (92% of systematic records) and using the same feeding postures in similar proportions as the lorikeets. Thus the two lorikeet species did not obviously appear to be involved in resource partitioning with respect to nectar/pollen in Melbourne parklands in autumn and winter, 2003.

The apparent absence of significant inter-specific competition for food involving the lorikeets may reflect the fact that the combined winter nectar and pollen resources provided by introduced eucalypts and eucalypts native to the area were extremely abundant and thus not limiting. Moreover, these resources were patchily dispersed, an individual patch usually comprising just one or a few flowering trees. Cannon (1979) estimated that a Rainbow Lorikeet would have to exploit about 5,000 flowers daily to satisfy its nutritional requirements. If this estimate is realistic, many of the patches in our study sites probably could not have consistently supported a single Rainbow Lorikeet and thus would not have been economic for an individual to aggressively defend (Carpenter *et al.* 1983). The phenological data show that there were two to three key food plant species flowering at many of our study sites at any given time during the investigation. Cannon (1984) showed that there were about six lorikeet food plant species flowering at any given time in the Queensland–New South Wales border region and little obvious competition for nectar/pollen between Rainbow and Scaly-breasted Lorikeets. She also attributed the lorikeets' lack of inter-specific resource defence to resource superabundance and patchiness. In Melbourne, the apparent lack of involvement of the lorikeets in intense, aggressive, inter-specific competition for eucalypt nectar/pollen in autumn and winter may have been important in facilitating their recent colonisation of the urban environment.

Management and research implications

Although the inter-specific food competition issue needs more empirical investigation, it seems likely that Rainbow and Musk Lorikeets did not strongly negatively affect other native birds in Melbourne in autumn and winter, 2003 in this way. However, Rainbow Lorikeets apparently compete with other native and exotic birds (and other vertebrates) for limited tree-hollows for nesting in spring and summer in Canberra and Sydney (Pell and Tidemann 1997; Waterhouse 1997; Burgin and Saunders 2007). Whether such competition occurs in Melbourne where tree-hollow availability is also relatively low (Shukuroglou and McCarthy 2006) requires investigation. The extent to which Rainbow and Musk Lorikeets deplete garden and, to a lesser extent, commercial fruit and seed crops in Melbourne also requires quantitative evaluation. In Auckland and Perth, introduced Rainbow Lorikeets have acquired pest status partly because they are perceived as a threat to such crops (Ell 1999). These two possible negative impacts could somewhat offset the obvious aesthetic, educational and biodiversity conservation benefits stemming from the occurrence of colonising lorikeets in Melbourne. If these benefits outweigh possible negative impacts on the breeding success of other native bird species and the productivity of domestic (and commercial) fruit and seed crops in Melbourne, our study suggests that further planting in parks and streets of eucalypts native to, and introduced into, the area would lead eventually to even greater densities of Rainbow and Musk Lorikeets in the city in autumn and winter. Although we observed two other lorikeet species, Scaly-breasted and Little *Glossopsitta pusilla* Lorikeets, feeding in Melbourne on some of the eucalypt nectar/pollen resources used by Rainbow and Musk Lorikeets, their numbers were very small. The reason for this is unclear and warrants detailed examination, particularly as Scaly-breasted and Rainbow Lorikeets have both colonised Brisbane in large numbers in the last 25 years (Woodall 2002).

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APPENDIX 1

Study sites used to obtain feeding records and score flowering phenology (marked with an asterisk) in urban Melbourne. Map references give page number and grid square (e.g. 2 : K6) in Melway Street Directory of Greater Melbourne, edition 27.

Site	Map References	Site	Map References
Bellbird Picnic Area	44 : K3	Norris Bank Reserve	9 : G12
Binnak Park	10 : D11	Norton's Park*	71 : K2
Blackburn Lake Sanctuary*	48 : C11	Partington Flat	10 : J12
Bundoora Park*	19 : F2	Pioneer Reserve	20 : K1
Edwards Lake Park	18 : D4	Royal Park South	43 : E2
Fairfield Park	30 : H12	Strathallan Golf Course	19 : K4
Greensborough Park	20 : K1	Studley Park Boathouse	44 : H4
Jells Park*	71 : K7	Wattle Park*	60 : K3
Kalparrin Gardens	10 : H12	Waverley Public Golf Course	71 : J4
Monash University Clayton Campus	70 : E10	Whatmough Park	20 : J1