Abundance patterns across months and locations, and their differences between migrant and resident landbirds in lowland subtropical eucalypt forest

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Abstract. Many migrant landbird species are winter visitors to lowland eucalypt forests of the south-east Queensland region within subtropical eastern Australia. However, neither the specific patterns of habitat use by these migrant species, nor the extent to which the temporal and spatial patterns of migration are synchronised among different species, are well understood. This paper examines the pattern and synchrony of monthly change in bird species over a nine-month period (March–November), based on counts at seven survey sites within each of three large (>600 ha) lowland eucalypt forest remnants. These were surrounded by a mostly urban matrix, and widely separated within a total area of ~1000 km^2. Species were analysed with respect to both their individual abundances and collective patterns within four *a priori* groups: winter migrants, summer migrants, complex wanderers and residents/local movers. Collectively, the numbers of winter migrants were highest from May to August, but species' broad arrival times varied from April to June, departures from July to October, and times of peak abundance also varied. Seven of eight winter migrant species that were individually analysed (Rose Robin, Yellow-faced and Scarlet Honeyeaters, Striated and Spotted Pardalotes, Grey Fantail and Golden Whistler, but not Rufous Whistler) showed large changes in abundance over the period. The abundance of these seven species did not vary among the three locations, and also showed concordant patterns of temporal change across locations. Some showed partial migration. The resident/local mover species showed little or no change in abundance over time, and eight of the 16 species analysed showed substantial abundance differences among locations. The difference in location effects between migrant and resident species may occur because the winter migrants are non-breeding visitors to the region, whilst the resident species are year-round inhabitants and are hence more selective since they are more likely to occupy long-term home ranges that must provide habitat suitable for nesting.

Introduction

A major pattern of migration among landbirds in Australia is the latitudinal movement of species that occurs within a band of country adjacent to the eastern coast (Blakers *et al*. 1984; Ford 1989; Griffioen and Clarke 2002). Birds vacate their more southerly habitats in autumn at the onset of lower temperatures and associated environmental changes, and move northward to areas that have a more benign winter climate that is accompanied by better conditions for plant growth (Nix 1976). This is followed by a return movement south in spring. Movements of this type span a north–south distance of some 4000 km from Tasmania to New Guinea, although individual birds and species typically move shorter distances (less than 1000 km: Chan 2001).

Subtropical areas of coastal eastern Australia are host to both winter migrants that mostly breed further south during summer, and summer migrants that spend the winter in northern Queensland and New Guinea. South-east Queensland supports a high regional diversity of landbird species

(Storr 1973; Taplin 1991; Catterall and Kingston 1993), due in part to seasonal turnover of different species in summer and winter. Other contributing factors are a varied topography, a wide range of local climatic conditions, and a complex regional mosaic of different vegetation types, which include eucalypt and melaleuca open-forests and woodlands, rainforest and heathlands (Catterall and Kingston 1993; Young and Dillewaard 1999).

For migrant landbirds, the open-forest and woodland areas of south-east Queensland are especially important, and provide a major over-wintering habitat (Taplin 1991; Nix 1993), during what is typically the non-breeding season. The avifauna of sites within this habitat displays a pattern of large seasonal species' turnover, coupled with local densities and species richness during winter that generally greatly exceed those in summer (Park 1994; Bentley and Catterall 1997; Catterall *et al*. 1998; Sewell and Catterall 1998). Many of the winter migrants are small-bodied, foliage-feeding species that include honeyeaters, pardalotes, fantails and whistlers

(Catterall *et al.* 1998, see also Griffioen and Clarke 2002), and these mainly use the remnant lowland forests rather than the larger tracts of reserved forest at higher elevations on the region's mountain ranges (Park 1994). The relatively mild winter temperatures, together with high moisture levels typical of the south-east Queensland lowlands, suggest that insect and nectar supplies should be available throughout the winter within eucalypt and melaleuca associations (Nix 1993).

However, little is known of the specific patterns of habitat use by these migrant birds within south-east Queensland, or of the extent to which the migration patterns (including arrival and departure times, and variation in abundance across different areas) are synchronised among different species.

Therefore, this study aimed to assess the pattern and synchrony of monthly change in abundance of migrant and other bird species in lowland eucalypt forests of the south-east Queensland region, over winter.

Methods

Study region and study design

The study was undertaken within the greater Brisbane region of south-east Queensland (centred at approximately 27°30′S, 153°E), across an area of ~960 km². The south-east Queensland region has a subtropical climate, with warm to hot summers and cool winters, and moderate to high rainfall (800–1500 mm year⁻¹), of which up to 30% occurs in winter (Young and Dillewaard 1999). Local climate varies considerably with both topography and distance from the coast. In the Brisbane region lowlands, mean monthly temperatures are lowest in July (minimum 9.5°C, maximum 20.4°C) and highest in January (minimum 20.7°C, maximum 29.4°C) (Commonwealth Bureau of Meteorology records, Brisbane weather station, 1840–1994).

The present study focuses on lowland (<160 m) eucalypt open-forests and woodlands, within which there is a complex spatial mosaic of codominant tree species from the closely related 'eucalypt' genera *Angophora*, *Corymbia* and *Eucalyptus*. A well developed shrubby understorey is often present. Since European settlement in the early to mid nineteenth century, the already heterogeneous vegetation mosaic has been further modified by deforestation and land development. At the time this study took place, some 80% of lowland areas had been cleared and converted to urban development, pasture, or cropland (Catterall and Kingston 1993; Catterall *et al.* 1997).

Data were collected from three locations (Fig. 1), each containing a large (>600 ha) remnant of lowland eucalypt open-forest and woodland: Bunyaville State Forest ('Bunya'), Brisbane Koala Bushlands ('Koala') and Toohey Forest ('Toohey'). Bunyaville State Forest covers an area of ~635 ha, 15 km north-west of the Brisbane city centre, and lies adjacent to the higher-elevation Brisbane Forest Park (>60 000 ha). Brisbane Koala Bushlands covers 1170 ha of reserved remnant forest (including Daisy Hill State Forest, Venman Bushland National Park, and the Neville Lawrie Reserve), supplemented by many contiguous patches of remnant unreserved forest, and is located ~20 km south-east of the city centre. Toohey Forest (10 km south of the city) occupies ~600 ha, of which about half is a local government conservation reserve, and is surrounded by suburban areas (see also Catterall *et al.* 2001). Strips of riparian rainforest and melaleuca forest (generally *Melaleuca quinquenervia*) occur occasionally along waterways within these eucalypt forests; riparian rainforest is most frequent at the Bunya location.

At each location, seven study sites were placed each a 200 × 30 m transect running across a gully. Hence, each included both the typically open upland vegetation and the denser, more structurally complex, gully vegetation, and encompassed known variation in bird assemblages between gullies and ridges (Bentley and Catterall 1997; Catterall *et al.* 2001). Sites were included only if they had eucalypts in the canopy vegetation, were at least 200 m from a forest edge, and were not within large Noisy Miner colonies (since miners exclude many of the migrant bird species: Catterall *et al.* 1991, 2002; Piper and Catterall 2003). Sites were located using aerial photography and 1:25 000 topographic maps, followed by ground-truthing for ease of access, and agreement with the selection criteria. Transects were generally ~800–1500 m apart within a location, and no transects were separated by less than 600 m. The approximate areas within which the transects were spaced out were 400 ha for Bunya, 3100 ha for Koala and 300 ha for Toohey.

Bird surveys

Each site was surveyed during the first fortnight of each month from March to November 2001. This period incorporated the months previously considered to be typical arrival and departure times of most migrant landbirds (Blakers *et al.* 1984; Taplin 1991). Surveys were all made 0.5–3.5 h after sunrise, in dry weather. Each transect was searched for 30 min by a single observer (mainly DF), who recorded the number of individual birds of all species seen. The observer walked a winding path from one end of the transect to the other, pausing occasionally to listen or to observe birds. Birds that were identified by their calls were recorded only if conclusively located on-transect. Birds flying high above the canopy and aquatic species were excluded from the analyses. Lorikeet species (Rainbow and Scaly-breasted) were grouped under 'lorikeet' due to difficulty with identification in mixed-species groups and fast flight, and counts of the Forest and Sacred Kingfishers were also combined.
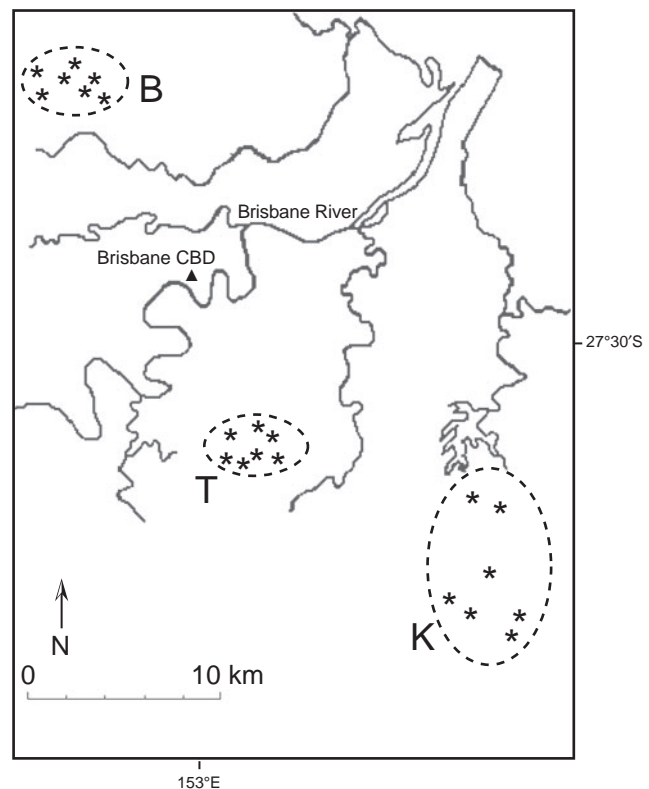

Fig. 1.   Study locations (B, Bunya; T, Toohey; K, Koala); dotted lines show broad position but not exact boundaries of each remnant lowland open-forest tract in which study sites (asterisks) were located.

We statistically tested the differences in the bird assemblages due to time (nine months) and location (three locations), using mixed-model repeated-measures analyses of variance (ANOVA). Location was the between-subjects factor, with Sites (subjects) nested within Locations. Location and Site were random effects and Month (the within-subjects factor) was a fixed effect. Sums of squares for the saturated model were calculated using PROC GLM in the SAS package (SAS Institute Inc. 1988), and relevant hypothesis tests were then conducted as described by Quinn and Keough (2002, p. 317). The Location effect was tested using Site(Loc) as the error term (df = 2,18); the Month effect was tested using Location × Month as the error term (df = 8,16). The Location × Month interaction was tested using the residual (Site(Location) × Month) term (df = 16,144). Multiple comparisons were carried out using least significant difference (LSD) tests. The incorporation of Location as a random factor in the ANOVA tested a general hypothesis about differences among lowland forest patches of the region, rather than simply comparing three specific locations by treating Location as a fixed factor.

The tested dependant variables were: (1) the log-transformed abundances of any individual species that was present at five or more of the 21 sites, and (2) the species richness and log-transformed total abundance within the following *a priori* groups of species: winter migrants, summer migrants, residents/local movers, and complex wanderers. Species' categorisations (Appendix) were based on known patterns of movement and seasonality in relation to the south-east Queensland region, from data and reviews in Bentley and Catterall (1997), Catterall *et al*. (1998), Griffioen and Clarke (2002), and references therein (see in particular Roberts 1979; Taplin 1991; Park 1994).

Habitat assessment

Structural and floristic vegetation characteristics were recorded in 10 randomly located circles of 5-m radius at each transect (Table 1). Habitat differences among the three Locations were assessed using single-factor ANOVA and LSD tests (SAS Institute Inc. 1988).

Results

Across the nine months of sampling, a total of 2308 birds from 61 terrestrial species (63 if the lorikeets and kingfisher species are separated) were recorded (Appendix). Nine species were classified as Winter Migrants, six (seven) as Summer Migrants, 30 as Residents/Local Movers, and 16 (17) as Complex Wanderers, with respect to eucalypt forests and woodlands of south-east Queensland. There were 34 species (8, 4, 16 and 6 within the respective movement categories) that occurred at five or more sites, and which were analysed individually.

Both migrant groups showed a statistically significant pattern of change over time (Fig. 2, Table 2), which was broadly consistent with expectations: numbers of winter migrant species per transect increased progressively from March to May, peaked during May to August, and then declined through to November, whereas Summer Migrants showed the reverse pattern. The Resident/Local Mover category also showed significant changes over time (Table 2), with greatest numbers of species per transect recorded during September–November (Fig. 2). This may result from a greater detectability due to actions and vocalisations related to the commencement of breeding. In contrast, the Complex Wanderers showed no significant differences in transect species richness over time (Table 2), and fluctuated somewhat erratically across the months of the study (Fig. 2). Total abundances within each group showed a very similar pattern to species richness, and are therefore not presented here.

Both the Location effects and the Location × Month interactions were relatively small, or non-significant, for all groups (Table 2), indicating that the pattern of change in numbers of species over time was consistent among the three locations, and that the three locations supported similar numbers of species within each movement class (see also Fig. 2).

Seven of the eight individual Winter Migrant species recorded at five or more sites showed a significant change

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Table 1. Habitat characteristics scored at 10 random circular plots per transect

Percentage cover scores were visual estimates. Stems were counted as different individuals if the division occurred at or beneath the ground layer. 'Variables' is the number of variables measured for each height category

Height (m)	Variables	Description of measurements
0	5	% cover of bare ground, grass, leaf litter, shrub, or other (rock, water).
	1	Index of water presence[A] (0, 1 = small amount / poolings, 2 = large volume / flow).
0.5–0.9	3	% cover of grass, shrub, and open space.
1.0–2.9	2	Number of woody stems finishing within this height range.
		% foliage cover associated with these stems.
3.0–5.9	2	Number of woody stems finishing within this height range.
		% foliage cover associated with these stems.
6.0–9.9	2	Number of woody stems finishing within this height range.
		% foliage cover associated with these stems.
>10	13	Number of trees in four diameter (cm) at breast height (dbh) classes; <20, 20–49, 50–99, ≥100.
		% foliage cover associated with all stems within this height range.
		Number of trees that were either 'eucalypt' (*Angophora*, *Eucalyptus*, *Corymbia*) or non-eucalypt. For 'non-eucalypts', the number of trees that were *Melaleuca, Glochidion, Lophostemon, Cinnamomum camphori* (Camphor Laurel), other (e.g. pines), and 'rainforest' (*Glochidion*+*Lophostemon*+*C. camphori*).

[A]Scored for overall site (not plots) at each of the first seven monthly visits; totalled for analysis.

in abundance over time (Table 2, Fig. 3). Most showed a clear and progressive increase over 2–3 months (presumably as individuals arrived), followed by sustained high abundance in mid-winter (sometime between June and August), and then a decline, with numbers again low in November.

However, neither the timing of the increase and decrease periods, nor the duration of peak winter abundance, were synchronised among these seven species (Figs 2, 3). For example, the Grey Fantail and Yellow-faced Honeyeater arrived in numbers earlier than the Rose Robin and Spotted Pardalote, both of which departed earlier than most (Fig. 3). None of these species showed a significant Location effect or Location × Month interaction, indicating that both the timing and magnitude of arrival, peak abundance, and departure were consistent among widely separated locations within the study region. The Rufous Whistler showed no pattern of migratory winter influx during the year of the present study. Its numbers were generally low, and its main seasonal pattern was of apparently increasing abundance into the summer months, although this occurred only at one location. The Scarlet Honeyeater showed highest abundance in October, although with high standard errors; this was due to locally high numbers visiting flowering *Melaleuca quinquenervia* trees at two of the 21 sites.

Only a small proportion of the migration cycle of the Summer Migrants was captured within the months of this study; numbers recorded were low, and generally zero during winter months (Fig. 4). The low numbers impaired our ability to detect statistically significant changes over months or among locations, although there were strong trends ($P < 0.20$) (Table 2) in both. Both the pattern of change in the group's species richness (Fig. 2) and the abundances of individual species (Fig. 4) indicate that these species began arriving around September, increasing over the next 1–2 months, and showed the reverse pattern in March–April.

Individually, the Resident/Local Mover species showed relatively few significant changes in abundance among months, although a number of them tended to increase around September–November (Table 2, Fig. 5), similar to the pattern seen in this group's species richness (Fig. 2). However, the abundances of many (8 out of 16) resident species showed significant ($P < 0.05$) effects of Location (Table 2). For example, at Toohey the White-throated Honeyeater and Torresian Crow were more abundant than at other locations, while Brown Thornbill, White-throated Treecreeper and Lewin's Honeyeater were less abundant (Table 2, Fig. 5). Apart from Lewin's Honeyeater, no species in this group showed a significant Location × Month interaction (Table 2).

The Complex Wanderer species generally lacked clear trends in numbers over the months of this study (Fig. 6, Table 2). Two of six species in this group showed significant abundance differences between locations: Spangled Drongo was most abundant at Toohey, while lorikeets were least so at

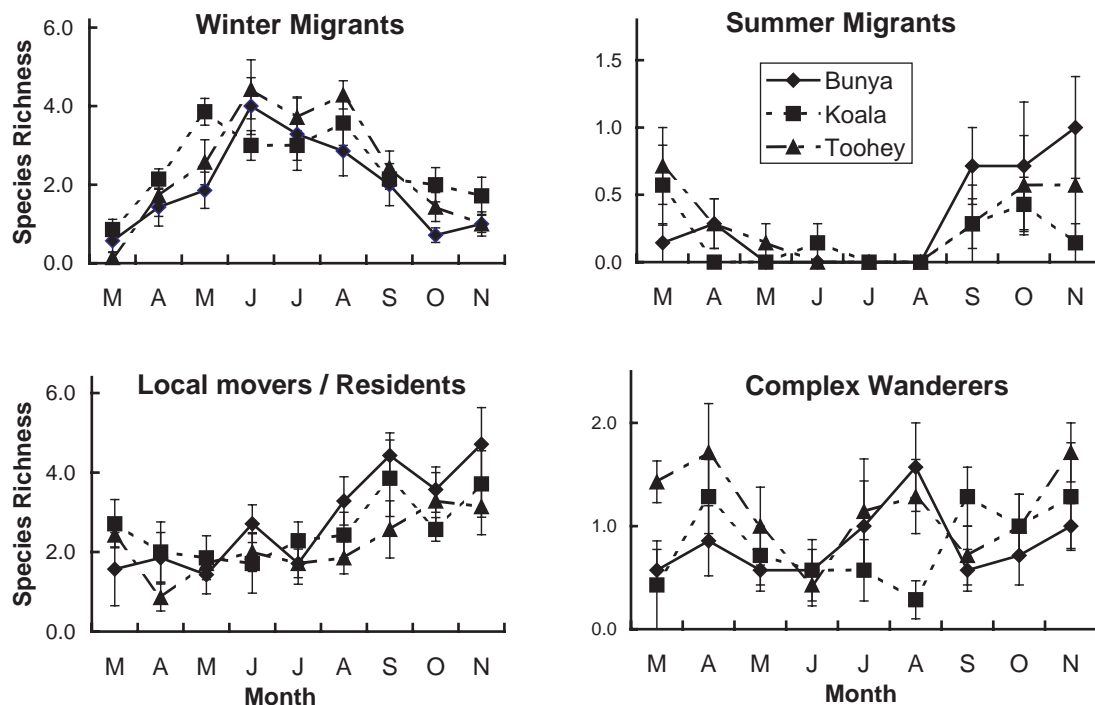**Fig. 2.** Monthly variation in species richness (number of species per 30-min visit per 30 × 200 m transect; means and standard errors; $n = 7$) within each of four *a priori* groupings of bird species based on known movement patterns (see Appendix), at each of the three locations (Bunya, Koala, Toohey) within the Brisbane region.

Koala (Table 2). None showed a significant change in abundance over time. The Fan-tailed Cuckoo was the only species of this group to show a significant Location × Month interaction. The absence of a clear pattern is evident in the varied peaks and troughs in both the individual species and the total species richness of the group (Figs 2, 6).

Of the 28 habitat characteristics (Table 1) that were statistically tested, nine differed significantly among the three locations (Table 3). The transects at each location were characterised by a slightly different set of features: Koala sites had most permanent water and a higher density of young and mature trees (stems 6–10 m and their percentage foliage cover; percentage foliage cover above 10 m, and number of stems 50–100 cm dbh) than Toohey or Bunya, whereas Bunya sites had a relatively high leaf-litter cover, a low grass cover, more Camphor Laurel trees, and a more open subcanopy (fewer stems 3–6 m) than either Toohey or Koala (Table 3). The locations did not vary significantly in their shrub cover, the density of eucalypts above 10 m tall, or the density of common riparian tree groups (*Glochidion*, *Melaleuca*, 'rainforest' trees).

Table 2. Location and time effects on species richness within *a priori* movement classes, and individual species' abundances

ANOVA was a two-factor (3 Locations (Loc), 9 Months (Mon)) mixed-model with repeated measures on seven sites in each Location (see Methods). Individual species were tested if they occurred at 5 or more sites. Statistically significant ($P \leq 0.05$) values are shown in bold. Results of LSD tests for Months and Locations are also shown: letters in common indicate pairs of means that were not significantly different, with 'a' always assigned to the month with highest mean abundance. B = Bunya, K = Koala, T = Toohey locations

	Species or group	ANOVA *P* values:			LSD Results - Month									LSD Results – Loc		
		Loc.	Mon.	Loc. × Mon.	M	A	M	J	J	A	S	O	N	B	K	T
Species richness	Winter Migrants	0.35	**0.0001**	**0.05**	f	de	bc	a	ab	ab	cd	def	ef	–	–	–
	Summer Migrants	0.50	**0.006**	0.53	ab	bc	c	c	c	c	ab	a	a	–	–	–
	Residents/Local Movers	0.19	**0.0007**	0.60	bc	c	c	c	c	bc	a	ab	a	–	–	–
	Complex Wanderers	0.26	0.24	0.15	-	-	-	-	-	-	-	-	-	–	–	–
Winter Migrant species (8 spp.)	Spotted Pardalote	0.41	**0.01**	0.40	c	c	c	abc	a	ab	bc	c	c	–	–	–
	Striated Pardalote	0.50	**0.02**	0.13	c	c	abc	a	ab	bc	c	bc	c	–	–	–
	Yellow-faced Honeyeater	0.56	**0.0001**	0.57	e	de	bc	a	a	a	b	bcd	cde	–	–	–
	Scarlet Honeyeater	0.51	**0.009**	0.26	c	c	bc	c	abc	ab	a	ab	abc	–	–	–
	Rose Robin	0.40	**0.0002**	0.85	d	d	bc	a	b	cd	bcd	d	d	–	–	–
	Golden Whistler	0.62	**0.0001**	0.76	e	bc	bc	bc	ab	a	cd	de	e	–	–	–
	Rufous Whistler	0.08	0.29	0.18	–	–	–	–	–	–	–	–	–	–	–	–
	Grey Fantail	0.35	**0.0001**	0.92	b	a	a	a	a	a	b	b	b	–	–	–
Summer Migrant species (4 spp.)	*Todiramphus* kingfishers	0.28	0.17	0.34	–	–	–	–	–	–	–	–	–	–	–	–
	Black-faced Monarch	0.80	0.10	0.72	–	–	–	–	–	–	–	–	–	–	–	–
	Leaden Flycatcher	0.07	0.15	0.65	–	–	–	–	–	–	–	–	–	–	–	–
	Rufous Fantail	0.28	0.05	0.44	–	–	–	–	–	–	–	–	–	–	–	–
Residents/ Local Mover species (16 spp.)	Pale-headed Rosella	0.28	0.08	0.63	–	–	–	–	–	–	–	–	–	–	–	–
	Laughing Kookaburra	0.22	0.29	0.13	–	–	–	–	–	–	–	–	–	–	–	–
	White-throated Treecreeper	**0.04**	0.33	0.31	ab	ab	ab	ab	b	ab	ab	a	a	a	a	b
	Variegated Fairy-wren	0.28	0.66	0.61	–	–	–	–	–	–	–	–	–	–	–	–
	Red-backed Fairy-wren	**0.02**	**0.02**	0.67	ab	c	c	c	c	c	a	bc	ab	b	b	a
	White-browed Scrubwren	0.92	0.17	0.23	–	–	–	–	–	–	–	–	–	–	–	–
	Brown Thornbill	**0.005**	**0.04**	0.75	bc	bc	c	bc	bc	bc	a	ab	ab	a	a	b
	Noisy Miner	**0.01**	0.64	0.09	–	–	–	–	–	–	–	–	–	a	b	b
	Lewin's Honeyeater	**0.003**	0.97	**0.001**	–	–	–	–	–	–	–	–	–	a	b	b
	White-throated Honeyeater	**0.0002**	0.67	0.52	–	–	–	–	–	–	–	–	–	b	b	a
	Eastern Yellow Robin	0.45	**0.007**	0.99	abc	bcd	bcd	bcd	cd	a	d	a	ab	–	–	–
	Eastern Whipbird	0.14	0.47	0.06	–	–	–	–	–	–	–	–	–	–	–	–
	Varied Sitella	**0.009**	0.90	0.20	–	–	–	–	–	–	–	–	–	b	a	b
	Grey Shrike-thrush	0.33	**0.006**	0.82	c	c	bc	bc	bc	bc	b	bc	a	–	–	–
	Torresian Crow	**0.02**	0.23	0.17	–	–	–	–	–	–	–	–	–	b	b	a
	Red-browed Finch	0.90	0.22	0.96	–	–	–	–	–	–	–	–	–	–	–	–
Complex Wanderer species (6 spp.)	Lorikeets	**0.04**	0.24	0.32	–	–	–	–	–	–	–	–	–	a	b	a
	Fan-tailed Cuckoo	0.12	0.50	**0.03**	–	–	–	–	–	–	–	–	–	–	–	–
	Spangled Drongo	**0.008**	0.10	0.38	–	–	–	–	–	–	–	–	–	b	b	a
	Black-faced Cuckoo Shrike	0.11	0.31	0.15	–	–	–	–	–	–	–	–	–	–	–	–
	Olive-backed Oriole	0.75	0.16	0.93	–	–	–	–	–	–	–	–	–	–	–	–
	Silvereye	0.56	0.81	0.59	–	–	–	–	–	–	–	–	–	–	–	–

Discussion

Changes over time

Seasonal patterns of change in abundance due to migration are greatly complicated in most parts of eastern Australia because many species are partial migrants, in which one part of the population migrates seasonally while the other does not (Nix 1993; Chan 2001). In eastern Australia, partial migrant species may include some individuals that reside permanently in the breeding or summer range, others that reside permanently (and breed) in parts of what is mainly the non-breeding or winter range, and others that migrate regularly (Nix 1993). Furthermore, the tendency to migrate may vary with the age or sex of an individual, within its lifetime
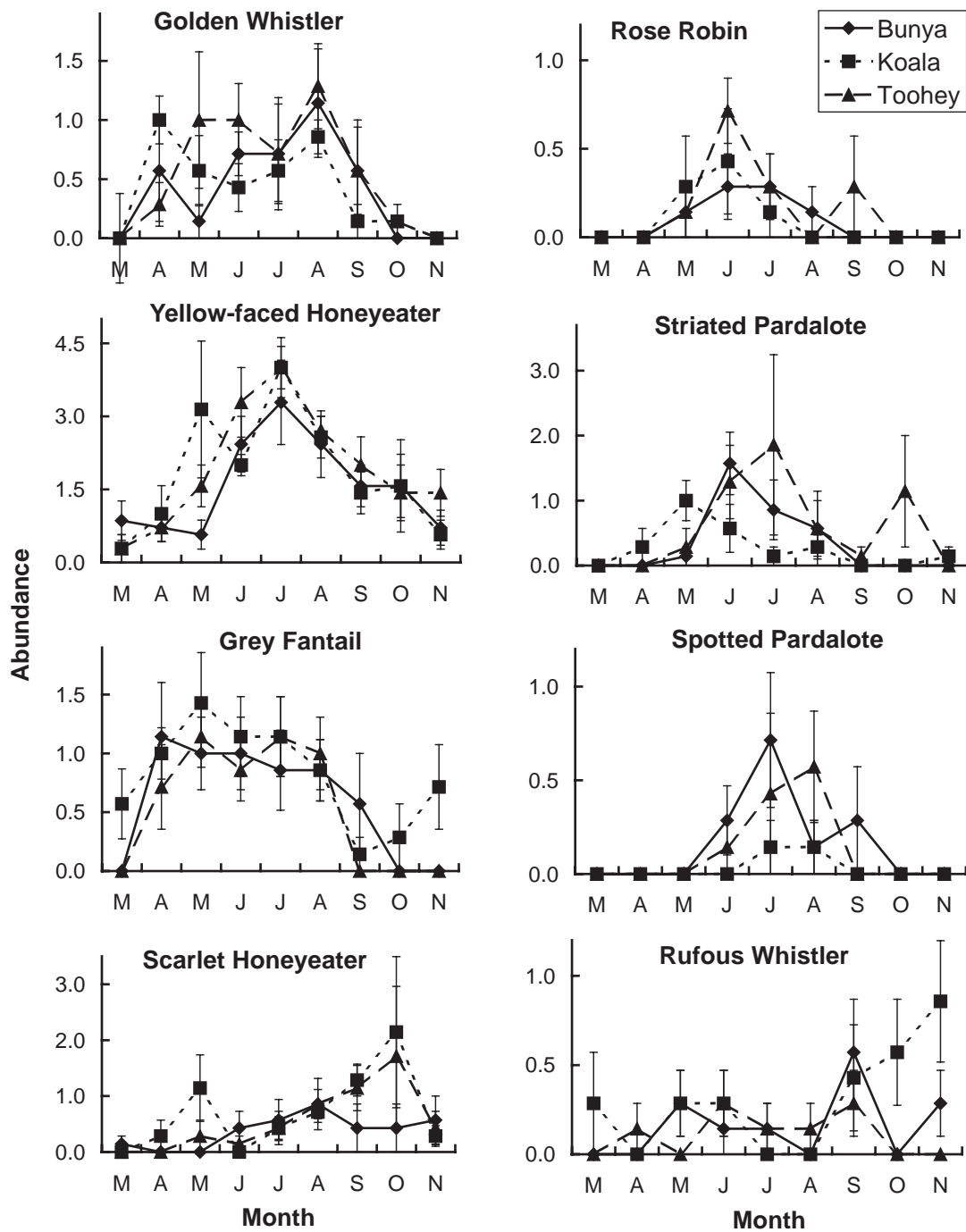
Fig. 3.   Monthly variation in abundance, at each location, of all Winter Migrant species recorded from five or more transects (number of individuals per 30-min visit per 30 × 200 m transect; means and standard errors; *n* = 7).

(cf. Gauthreaux 1982; Warkentin and Hernandez 1996). The number of migrating individuals within a species can also vary greatly between years, and this is considered to be a response to Australia's variable climatic patterns and associated resource availability (Chan 2001). Of the species analysed in the present study (Table 2), all 'migrant' species (winter and summer) are considered partial migrants (Chan 2001).

In spite of this background complexity, in the present study both winter and summer migrants showed large temporal changes in both collective species richness and the individual abundances of most species. There was a distinct pattern of monthly change during the nine months of the present study, as winter migrants arrived, increased to peak abundances, and then departed. The patterns shown by most individual species were consistent with our expectations on the basis of their *a priori* classifications. The magnitude of seasonal change also indicates that, at least within the lowland eucalypt forests, the resident part of the population was generally relatively small.

The Residents/Local Movers also behaved generally as expected for species that occupy an area year-round. There was an increase in numbers of some species (e.g. Eastern Yellow Robin, Brown Thornbill, Grey Shrike-thrush), and in overall species richness, during September–November. However, the magnitude of this increase was small compared with that of the migrating species and it is likely to be due to increased detectability associated with high activity levels during pre-breeding and breeding (accompanied by behaviours such as calling, displays, nest-building activity, feeding young), rather than actual increased abundances (see also Griffioen and Clarke 2002). Breeding activities were noted

incidentally for Eastern Yellow Robin, Noisy Miner, Lewin's Honeyeater, Rufous Whistler and Scarlet Honeyeater, during the September–November surveys. The increase in sightings of species considered resident coincided with the decrease in detections of most winter migrant species, indicating that the transect count method is reliably detecting their departure.

While the winter migrant species generally showed high abundances in mid-winter (July), they were asynchronous in their patterns of seasonal change. This is evident in both the gradual increase in species richness of winter immigrants over time (Fig. 2) and in comparisons of individual species patterns (Fig. 3). Both the times of arrival and departure and the duration of peak abundance varied among species: Golden Whistler, Yellow-faced Honeyeater and Grey Fantail were most 'reliable' in terms of high abundance combined with an extended stay across the winter months. The late arrivals, Rose Robin and Spotted Pardalote, were also the first to leave. The lack of synchrony contrasts with the predictable mass arrivals of individuals and species of migratory landbirds seen each year in some parts of the world (e.g. Keast 1980), but agrees with the variation in species' individual temporal patterns reported in detailed studies at south-eastern Australian locations (e.g. Marchant 1992; Veerman 2002).

The Rufous Whistler, although previously classified as a winter migrant to the south-east Queensland lowland eucalypt forests, behaved like a resident in the present study. Its density throughout the nine months was low. This contrasts with data presented by Bentley and Catterall (1997), Catterall *et al.* (1998), and Sewell and Catterall (1998), collected in various parts of the region during 1991–93, in which the Rufous Whistler was much more abundant in
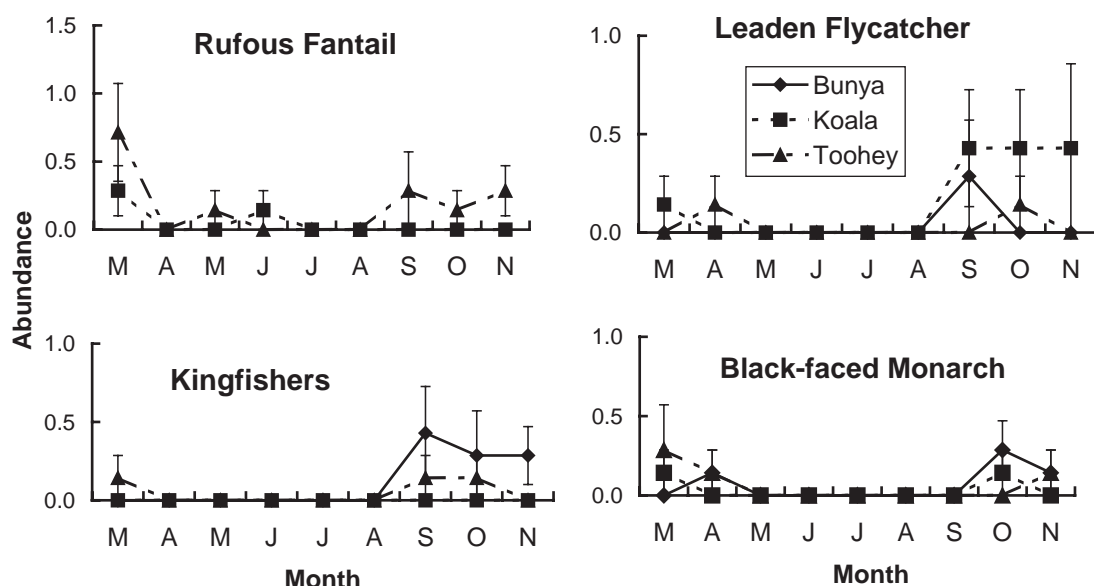

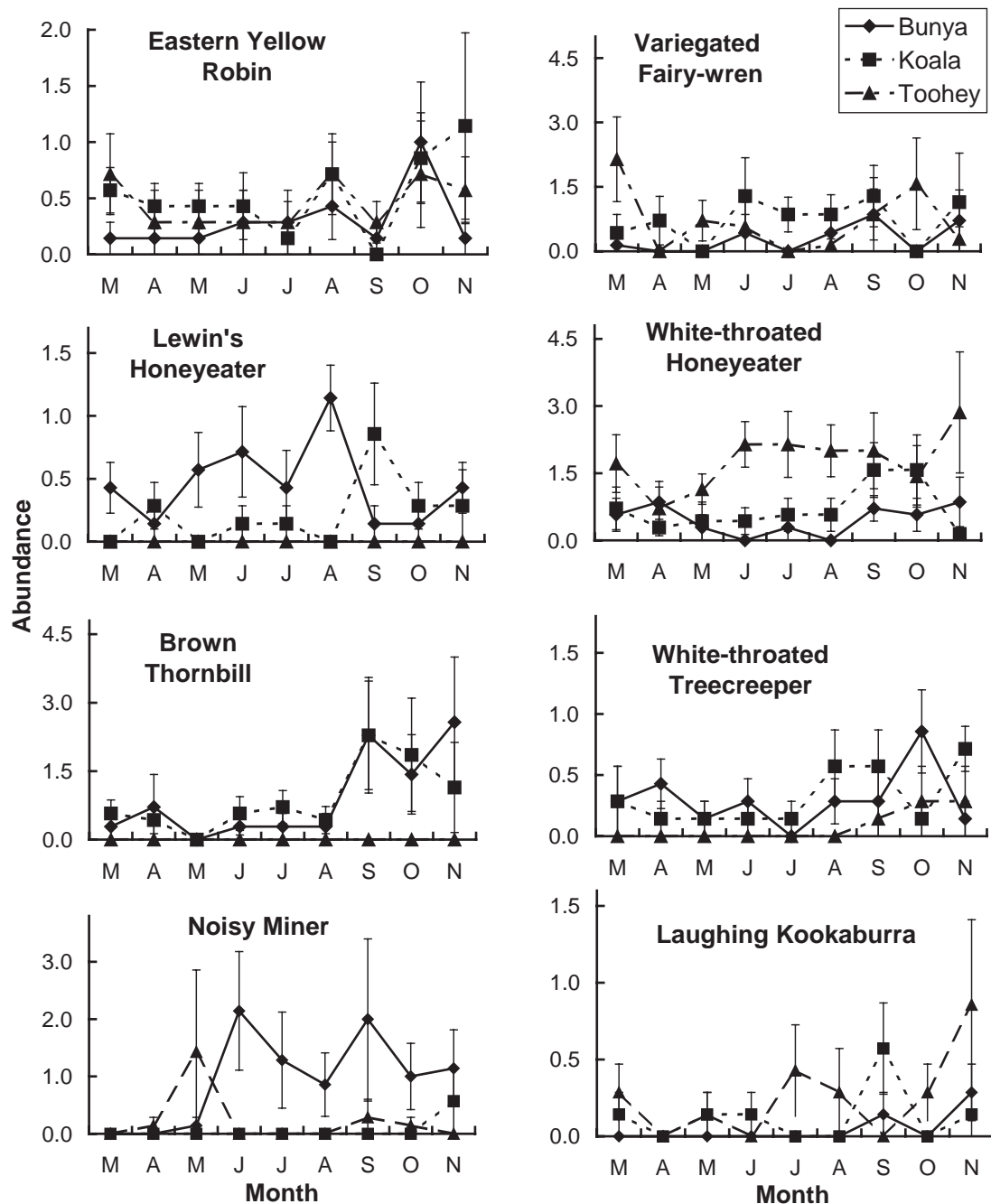**Fig. 4.** Monthly variation in abundance, at each location, of all Summer Migrant species recorded from five or more transects (number of individuals per 30-min visit per 30 × 200 m transect; means and standard errors; *n* = 7).

winter than in summer. There are three possible explanations for the relatively higher numbers of Rufous Whistler in winter in the early 1990s than in 2001: the species' continental population may have declined; many birds may have opted to remain in their breeding range during winter 2001; or they may have migrated to alternative wintering ranges, perhaps further west. Anecdotal evidence provides some support for all three possibilities. First, Veerman (2002)

described a decline in the density of Rufous Whistlers in Canberra between 1981 and 1999. Second, Mac Nally (1997) noted variation between years (1993–96) in the temporal patterning of Rufous Whistler abundance within Victorian breeding habitat (although they remained absent in winter). Third, the Rufous Whistler, unlike the coastally concentrated Golden Whistler, occurs widely in the inland, and migrates towards inland Queensland in at least some winters (Blakers

Fig. 5. Monthly variation in abundance, at each location, of selected Resident/Local Mover species recorded from five or more transects (number of individuals per 30-min visit per 30 × 200 m transect; means and standard errors; *n* = 7).

et al. 1984; Griffioen and Clarke 2002). The early 1990s were a time of severe drought in central and eastern subtropical Queensland (not the case in 2001), and this is consistent with the suggestion that the birds of the wintering Rufous Whistler population chose to become more coastally concentrated at this time.

Effects of location

During months of arrival, temporary residency, and departure, the winter migrant species did not discriminate among locations. Rather, they were spread uniformly across the study region's lowland eucalypt forests without regard to minor location-specific habitat differences. However, many of these species are selective with respect to broader habitat type within the study region; for example, the pardalotes and Yellow-faced Honeyeater avoid rainforests (Kikkawa 1968), and winter influxes appear to occur mainly in open-forests rather than other vegetation types (Roberts 1979).

Residents/Local Mover species were more selective in their habitat choices. The abundance of none of the eight winter migrant species was significantly affected by location, compared with 8 of 16 Residents/Local Movers. These proportions differ significantly (Fisher Exact $P = 0.02$; omitting Rufous Whistler gives none of seven migrants, and $P = 0.05$). While our results show that the three locations differed significantly in some of the measured aspects of their local habitat, it was not generally possible from our data to identify particular habitat features that were likely to show causal

relationships with the abundance of the particular species involved, in the light of knowledge of their biology. An exception to this is Lewin's Honeyeater, which was most abundant at Bunya (and was not recorded at Toohey) (see also Catterall *et al*. 2001). Lewin's Honeyeater is a frugivore which is especially common in rainforests (Kikkawa 1968; Roberts 1979; Green 1993), and a distinguishing characteristic of the habitat at Bunya was the greater abundance of the prolifically fruiting introduced Camphor Laurel, *Cinnamomum camphori*, an invader of former rainforest areas. Across all 21 sites the abundance of Lewin's Honeyeater was positively correlated (Pearson's $r = 0.50$, $P < 0.05$) with the abundance of Camphor Laurels.

The contrasting effects of location between the winter migrants and the Residents/Local Movers may relate to the differing constraints associated with breeding versus feeding habitat. Resident species are able to live as sedentary pairs or groups that maintain year-round home ranges. This requires choice of a habitat that provides long-term shelter and protection from predators, a sustained food supply, and also the specific resources that are associated with successful breeding (suitable nesting sites and an adequate breeding-season supply of suitable food items for nestlings and fledglings). The latter must also be available within a distance from the nest that is economical in terms of the energy cost of feeding trips (Recher *et al*. 1987). Therefore, resident birds should be more likely than non-residents to show strong patterns of habitat selection. In contrast, the non-breeding migrants
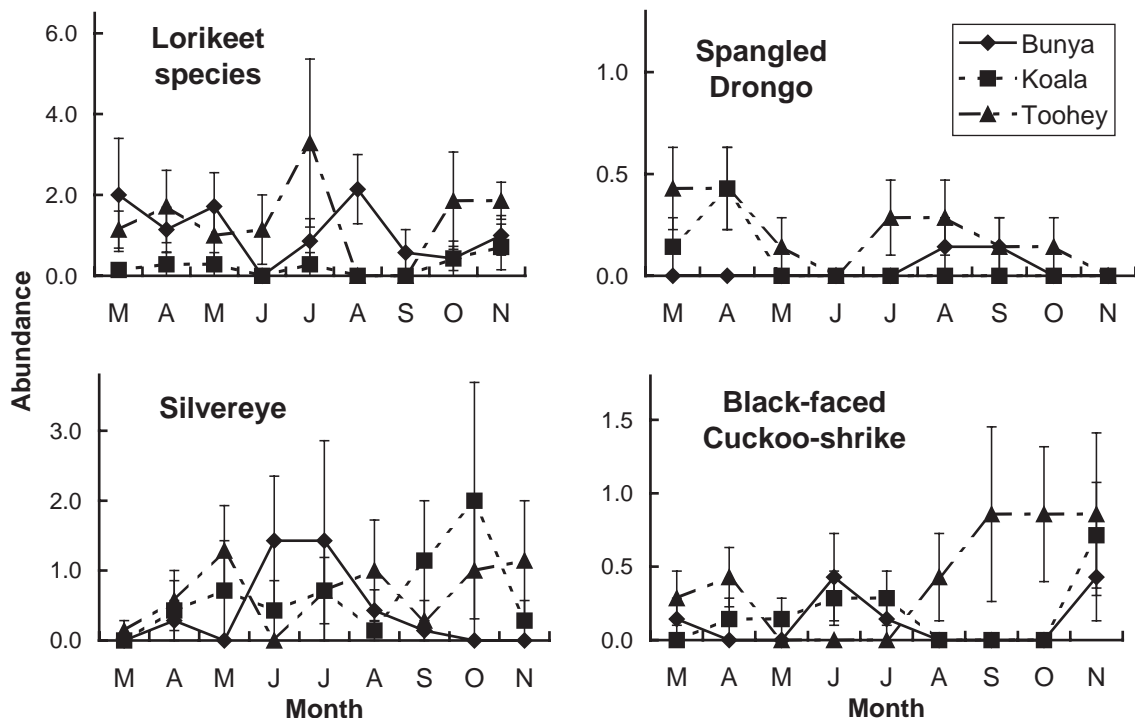

Fig. 6. Monthly variation in abundance, at each location, of selected Complex Wanderer species recorded from five or more transects (number of individuals per 30-min visit per 30 × 200 m transect; means and standard errors; *n* = 7).

require only habitat features that allow survival and feeding, and would lose less from moving elsewhere if local conditions became unsuitable. This would allow them to be more flexible in their habitat choice. Similarly, Bentley and Catterall (1997) found that the abundance of resident forest-dependent birds was reduced in small linear forest remnants 2–5 ha in size (compared with continuous forest), but that winter migrant species were unaffected.

Ecology and conservation of winter migrants

Migration is often seen as a means by which birds increase their chances of survival by leaving areas of severe cold and associated food shortage for more favourable climates and resource availability (Keast 1968; Cox 1985; Ford 1989; Chan 2001). In the Northern Hemisphere, many species make rapid and synchronous long-distance movements (Keast 1980; Griffioen and Clarke 2002), thought to be triggered by endogeneous 'clocks' based on the changes in daylength (Nix 1976; Gwinner 1996). However, Australian landbird migration covers shorter distances, and the winters are not so harsh that small birds cannot survive (Keast 1968). It is therefore plausible that Australian migrants respond less to 'migratory clocks' and more to climatic changes, such as temperature and rainfall, and the availability of food resources (Chan 2001). The two winter migrant honeyeaters within this study, the Yellow-faced Honeyeater and the Scarlet Honeyeater, both showed peaks in abundance coincident with mass flowering of *Melaleuca quinquenervia* in parts of the Koala location in May. However, there is still little information to explain the external environmental influences that trigger the various different migration times of the insectivorous species such as the whistlers, pardalotes and Rose Robin.

The alternative ranges used at other times of the year are also unclear. All eight Winter Migrants of this study show some evidence of latitudinal movements in eastern Australia (Blakers *et al.* 1984; Griffioen and Clarke 2002), suggesting that many have summer ranges further south. Some indi-

viduals and species may also have alternative winter ranges, that are used in different years, or in different months within a year (as suggested above for the Rufous Whistler). At least part of the wintering population of Scarlet Honeyeaters in the study region also breeds at this time (authors' personal observations). The other listed Winter Migrant species are all also known to breed in south-east Queensland (Roberts 1979; Blakers *et al.* 1984), but this may be confined to the non-migratory part of the local population. The Golden Whistler is common year-round in rainforests of the study region (Kikkawa 1968), but is also clearly a non-breeding migrant to lowland eucalypt forests, where a large proportion of wintering birds are brown-plumaged immatures (CPC, unpublished data). Roberts (1979) noted the species to be 'Common. Rainforest and other forests with thick understorey. Open forest in winter'. In south-east Queensland the Rose Robin also appears to be a breeding resident in upland rainforests, and a non-breeding winter migrant to lowland eucalypt forests. These species are probably not migrating between altitudes or habitats, but rather the south-east Queensland region supports both a resident subpopulation in upland and/or wetter forests, and a transient winter migrant subpopulation in the lowland open-forests, that mostly spends the summer months further south (see also Park 1994).

Lowland (<160 m) eucalypt forests in south-east Queensland have been extensively cleared and fragmented, with less than 20% remaining, and clearing is on-going, especially in the urbanising greater Brisbane and coastal subregions (Catterall and Kingston 1993; Catterall *et al.* 1997). Only 6% of land is reserved as national park or state forest (Catterall *et al.* 1997). The winter migrant species of the present study do not persist in cleared and urban parts of the south-east Queensland landscape (Catterall *et al.* 1998; Sewell and Catterall 1998). Furthermore, in the present study, the avoidance of Noisy Miner densities was a criterion used in site selection. Small fragments and thinned or partly cleared areas of lowland eucalypt forest are at high risk of being

Table 3. Significant (*P* < 0.05) ANOVA results showing among-location differences in habitat characteristics
s.e. = standard error; means with the same LSD letter are not significantly different

Height (m)	Characteristic[A]	ANOVA *P*	Bunya Mean	s.e.	LSD	Koala Mean	s.e.	LSD	Toohey Mean	s.e.	LSD
0	% grass	0.004	20.3	4.74	b	43.2	3.07	a	43.8	6.09	a
	% leaf litter	0.006	55.4	3.65	a	33.1	5.54	b	34.1	4.86	b
	Water	0.006	2.7	1.25	ab	5.9	1.40	a	0.1	0.14	b
3–5.9	No. of stems	0.01	4.3	0.47	b	8.2	1.04	a	7.0	0.91	a
6–9.9	No. of stems	0.006	3.5	0.31	b	5.7	0.83	a	3.0	0.37	b
	% cover	0.02	19.9	2.34	ab	26.1	3.26	a	13.6	2.86	b
>10	% cover	0.02	26.0	1.85	ab	33.0	2.47	a	20.7	3.44	b
	Trees 50–99 cm dbh	0.006	0.4	0.07	ab	0.6	0.05	a	0.2	0.06	b
	Camphor Laurel	0.05	0.1	0.03	a	0.0	0.00	b	0.0	0.00	b

[A]See Table 1 for full list and descriptions of variables.

occupied by Noisy Miners, which results in the exclusion of the smaller-bodied winter migrant species (Catterall *et al.* 1991, 2002; Piper and Catterall 2003; Catterall 2004). Therefore, the winter habitat of a wide range of common Australian migrant landbird species is at risk of disappearing before its significance for within- or between-year sustenance of the eastern Australian populations of these birds is understood.

Acknowledgments

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Appendix.   All terrestrial bird species recorded, the number of sites (total 21) at which each was recorded, the total individuals (abundance), and each species' category of movement with respect to the study region (movement class)

MS, Summer Migrant (regularly migratory, mainly inhabiting the study region in spring/summer); MW, Winter Migrant (regularly migratory, mainly inhabiting the study region in winter); RL, Resident/Local mover (individuals known to typically inhabit the same local area year-round, but may undertake some local movements); CW, Complex Wanderer (apparently undertakes some long-range movements, but these are poorly known or variable in relation to the study region) (see text for sources)

Common name	Scientific name	No. of sites	Abundance	Movement class
Australian Brush-turkey	*Alectura lathami*	1	1	RL
Pacific Baza	*Aviceda subcristata*	2	3	CW
Brown Goshawk	*Accipiter fasciatus*	1	1	CW
Collared Sparrowhawk	*Accipiter cirrhocephalus*	1	1	RL
Brown Cuckoo-dove	*Macropygia amboinensis*	3	6	RL
Galah	*Cacatua roseicapilla*	4	14	RL
Sulphur-crested Cockatoo	*Cacatua galerita*	3	7	RL
Lorikeets	*Trichoglossus haematodus, T. chlorolepidotus*	18	168	CW
Australian King Parrot	*Alisterus scapularis*	1	2	RL
Pale-headed Rosella	*Platycercus adscitus*	9	30	RL
Fan-tailed Cuckoo	*Cacomantis flabelliformis*	10	14	CW
Shining Bronze-Cuckoo	*Chrysococcyx lucidus*	2	2	CW
Tawny Frogmouth	*Podargus strigoides*	1	4	RL
Laughing Kookaburra	*Dacelo novaeguineae*	12	27	RL
Todiramphus kingfishers	*Todiramphus macleayii, T. sanctus*	5	10	MS
Rainbow Bee-eater	*Merops ornatus*	1	3	CW
Dollarbird	*Eurystomus orientalis*	1	1	MS
White-throated Treecreeper	*Cormobates leucophaeus*	14	44	RL
Variegated Fairy-wren	*Malurus lamberti*	13	108	RL
Red-backed Fairy-wren	*Malurus melanocephalus*	12	53	RL
Spotted Pardalote	*Pardalotus punctatus*	9	20	MW
Striated Pardalote	*Pardalotus striatus*	17	76	MW
White-browed Scrubwren	*Sericornis frontalis*	9	34	RL
Large-billed Scrubwren	*Sericornis magnirostris*	1	1	RL
Weebill	*Smicrornis brevirostris*	1	1	RL
White-throated Gerygone	*Gerygone olivacea*	4	8	CW
Brown Thornbill	*Acanthiza pusilla*	12	113	RL
Noisy Friarbird	*Philemon corniculatus*	4	14	MW
Noisy Miner	*Manorina melanocephala*	8	78	RL
Lewin's Honeyeater	*Meliphaga lewinii*	10	43	RL
Yellow-faced Honeyeater	*Lichenostomus chrysops*	20	337	MW
Yellow-tufted Honeyeater	*Lichenostomus melanops*	2	3	RL
Fuscous Honeyeater	*Lichenostomus fuscus*	1	1	CW
White-throated Honeyeater	*Melithreptus albogularis*	21	186	RL
White-naped Honeyeater	*Melithreptus lunatus*	2	2	CW
Scarlet Honeyeater	*Myzomela sanguinolenta*	17	103	MW
Rose Robin	*Petroica rosea*	13	22	MW
Eastern Yellow Robin	*Eopsaltria australis*	18	82	RL
Eastern Whipbird	*Psophodes olivaceus*	5	12	RL
Varied Sittella	*Daphoenositta chrysoptera*	9	33	RL
Golden Whistler	*Pachycephala pectoralis*	20	88	MW
Rufous Whistler	*Pachycephala rufiventris*	16	36	MW
Grey Shrike-thrush	*Colluricincla harmonica*	12	24	RL
Black-faced Monarch	*Monarcha melanopsis*	6	10	MS
Spectacled Monarch	*Monarcha trivirgatus*	3	5	MS
Leaden Flycatcher	*Myiagra rubecula*	7	14	MS
Rufous Fantail	*Rhipidura rufifrons*	9	23	MS
Grey Fantail	*Rhipidura fuliginosa*	20	121	MW
Spangled Drongo	*Dicrurus bracteatus*	12	19	CW
Black-faced Cuckoo-shrike	*Coracina novaehollandiae*	16	45	CW
White-bellied Cuckoo-shrike	*Coracina papuensis*	1	2	CW
Olive-backed Oriole	*Oriolus sagittatus*	10	21	CW

Appendix.   (*continued*)

Common name	Scientific name	No. of sites	Abundance	Movement class
Grey Butcherbird	*Cracticus torquatus*	2	6	RL
Pied Butcherbird	*Cracticus nigrogularis*	1	1	RL
Australian Magpie	*Gymnorhina tibicen*	4	9	RL
Pied Currawong	*Strepera graculina*	1	1	CW
Torresian Crow	*Corvus orru*	13	69	RL
Double-barred Finch	*Taeniopygia bichenovii*	1	1	CW
Red-browed Finch	*Neochmia temporalis*	10	31	RL
Mistletoebird	*Dicaeum hirundinaceum*	2	4	RL
Silvereye	*Zosterops lateralis*	12	110	CW