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The distribution of a flute-like dialect in territorial songs of the Superb Lyrebird *Menura novaehollandiae* in the New South Wales North Coast and New England Tableland Bioregions

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On-site recordings were made and field data obtained on the territorial songs of the Superb Lyrebird *Menura novaehollandiae* at 100+ sites in forests of the New South Wales North Coast and New England Tableland Bioregions during winter from 2009-2014. Songs were categorized as either 'flute-like' or not flute-like, and the two song types are compared. Maps are presented that define the geographical extent of the flute-like dialect. The study demonstrates that the flute-like song extends over a wider area than previously thought, but the exact place of origin remains unknown. Some interesting discontinuities in the distribution of this song dialect are discussed.

INTRODUCTION

The vocal repertoire of the Superb Lyrebird *Menura novaehollandiae* includes mimicry (mostly of other birds such as the Laughing Kookaburra *Dacelo novaeguineae*, Pied Currawong *Strepera graculina,* and Crimson Rosella *Platycercus elegans*), species-specific territorial song (typically 6-10 sec. duration) and invitation-display calls. Usually mimicry of the calls, songs, wing beats, and beak snaps of other bird species makes up 70-80% of Superb Lyrebird vocalisations, with the remainder consisting of territorial song and other signals (Robinson and Curtis 1996; Higgins *et al*. 2001). Lyrebird vocal mimicry is culturally transmitted from adult males to young birds rather than learned directly from mimicked models (Robinson and Curtis 1996). Territorial songs and mimicry repertoires are regionally distinct and typically change little over time (Higgins *et al*. 2001). Thus Powys (2006) found in a longitudinal study that geographically-distinct territorial songs were shared by all individuals in an area and changed little over a thirty-year period.

Lyrebird songs are loud and can be heard by humans from one kilometre or more away (Frith 1969; Reilly 1988; Powys 1995; Robinson and Curtis 1996). Most singing occurs during the winter breeding season (June and July) when males sing for up to 50% of daylight hours in bouts lasting 30 minutes or longer. The Superb Lyrebird's species-specific invitation-display calls include a very loud 'blick' call, as well as softer clicking, whirring, twanging, scissors-grinding, thudding, and huffing sounds (Powys 1995, 2008). These complex sounds occur over the entire range of the species, although with regional variation. They are sometimes mistaken for anthropogenic sounds, but are not mimicry. No known recording exists of a lyrebird *in the wild* mimicking mechanical or other anthropogenic sounds, although there are recordings of captive birds delivering such mimicry (Higgins *et al*. 2001; Taylor 2014).

The current study builds on the only suggested example of Superb Lyrebird imitation of a man-made sound in *territorial song* (Robinson 1975; Reilly 1988; Smith 1988; Rankin *et al*. 1999). Powys *et al*. (2013) investigated the cultural history of a Superb Lyrebird chick that was purportedly raised in captivity in the 1920s in Australia's New England Tablelands. The bird allegedly mimicked the sounds of the household's flute player, learning two tunes and an ascending scale, and when released back into the wild it is claimed that its flute-like songs and timbre spread throughout the local lyrebird population. Powys *et al*.'s (2013) research uncovered substantial primary source data, including archival and contemporaneous interviews, but was unable to confirm the veracity of the story. Thus, the flute-like song dialect's origins remain uncertain.

The sonogram in Figure 1 shows clear differences between flute-like and non-flute-like lyrebird songs in three localities. In contrast to the typically steep frequency sweeps in non-flute-like territorial songs (Fig. 1c) in our study area and in other areas of the species' range, flute-like songs are characterized by a morphology of short, discrete notes that resemble the timbre of a flute, recorder, or other similar aerophone. Individual notes of minimal frequency variation are delivered in groups of 3-5 ascending notes (Fig. 1b). In addition to the main theme, a flute-like song often begins with introductory notes (Fig. 1a and 1c). Songs at some sites attain a high degree of complexity by means of what appears in a sonogram as overlapping, ascending 'scales'. To our knowledge, no recordings outside our study area have captured such flute-like elements in the Superb Lyrebird's vocalisations.

The aim of the present study was to determine the geographical extent of flute-like songs, concentrating on a population of Superb Lyrebirds in the northeast of New South Wales (NSW).

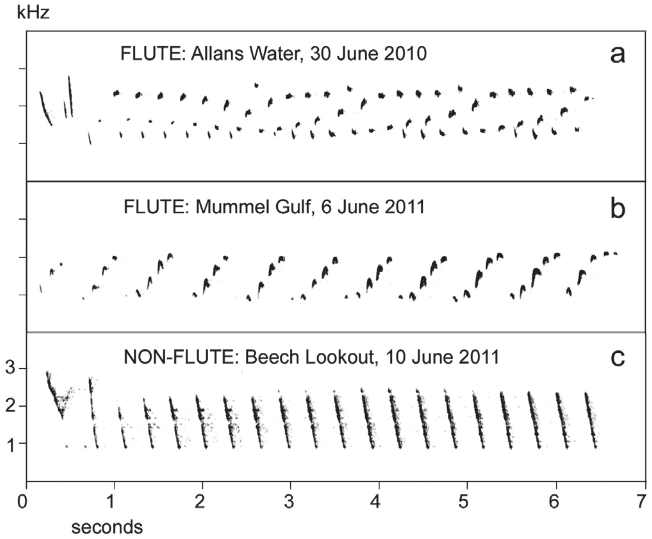

Figure 1. *A sonogram comparing three Superb Lyrebird territorial songs: a) Allans Water (site 7/subsite A11): 30 23 19.4, 152 27 09.1, 1391m, 30 June 2010 (flute); b) Enfield State Forest Road, Mummel Gulf NP (site 47): 31 20 45.7, 151 52 15.4, 1080m, 6 June 2011 (flute); and c) Beech LO, Cunnawarra NP (site 26), 30 31 06.5, 152 21 16.2, 1388m, 10 June 2011 (non-flute).*

METHODS

Study area

Fieldwork was conducted from 2009 to 2014. Most recording sites were within the NSW North Coast Bioregion, the remainder being in the New England Tableland Bioregion. Both bioregions encompass the steep slopes and gorges of the Great Escarpment and are characterized by a cool, temperate climate with no dry season. Vegetation in the study area included both *Eucalyptus* forest and rainforest, with an open forest floor that lyrebirds require for feeding. Rainforest types included cool-temperate with Antarctic Beech *Nothofagus moorei*, sub-tropical, warm-temperate, and dry. *Eucalyptus* forest types included wet and dry sclerophyll, sub-alpine, tall forests with a rainforest understorey, and woodland (Cooper and McAllan 1999).

General survey methods

The sampling protocol was designed to obtain a comprehensive coverage of song in every suitable habitat (access permitting) from the putative site of introduction to the edge of that contiguous habitat and beyond. Superb Lyrebirds are common throughout these dense forests despite the loss of nearby habitat associated with human settlement, logging and clearing of native forests, fires, agriculture, and predation. Recording sites were generally more than one kilometre apart (due to the carrying power of the lyrebird's voice), but in areas with a high density of singing birds, subsites were defined. Some remote sites had to be excluded from the survey because access was too difficult. Locations where lyrebirds were detected were documented using a hand-held GPS unit. Nine field-survey trips were undertaken, the first with two observers/recordists, the others with one observer/recordist.

The northernmost survey site was at Cloud's Creek State Forest (site 1) and the southernmost at Woko National Park (NP) (site 85), and the survey extended from Sheba Dam between Nundle and Hanging Rock in the west (site 124) to the Never Never Picnic Area in Dorrigo NP in the east (site 10). Sound recordings were made at elevations between 192 (site 12) and 1557m (site 16) above sea level.

Choice of recording sites was also influenced by interviews with, and recordings obtained from, the first sound recordists to document flute-like song. These localities (and specific sites when known) were visited to determine whether flute-like song producing lyrebirds were still present. Maps were created from Google terrain maps and satellite images in Google Earth. GPS coordinates were entered as location markers in Google Earth. Screen shots were processed using layers in Photoshop Elements.

Sound recording of lyrebird vocalisations

Birds were observed and recorded singing in all weathers. Recordings with Olympus LS-10 Linear PCM Field Recorders and Sennheiser ME66 and ME67 shotgun microphones covered with windshields were made opportunistically daily throughout daylight hours on each field trip. Sites initially visited during heavy rain were revisited to be certain that inclement weather had not inhibited birds from singing (Reilly 1988). All sites, but especially those where no songs were heard or recorded, were assessed for evidence of suitable lyrebird habitat, including lyrebird-raked ground.

After approximately five minutes (min) and once several territorial songs had been recorded, the recordist would either elect to continue recording or move to another individual/site. Recordings varied in length. At sites not yielding flute-like elements, we tried to record song minimally for 30 min (and up to 86 min, with a mean duration of 43 min) or to return to the site on another trip. Recordings were annotated with GPS coordinates, altitude, date, time, place, and observational notes, including behaviour and habitat. Archival recordings from six sources were collected, analysed, and incorporated into our data base; we had made no recordings at these sites prior to 2009.

RESULTS

Occurrence of flute-like song elements

In documenting how far flute-like songs extend geographically, sites close together have been combined as single symbols on the main map in Figure 2 to provide an overall visual summary of our findings. The 85 productive recording sites (1-85) are summarised in Appendix 1; 37 of these were categorised as flute-like and 48 as non-flute-like. At another 30 sites not documented here, no lyrebirds were observed or recorded, although some of the sites contained what appeared to be suitable habitat. Flute-like elements were documented at elevations from 418 (site 37) to 1557m (site 16) above sea level.

Figure 3 shows a detailed map of the area surveyed at Allans Water (sites 6-7 in Appendix 1). It includes the Jones' homestead ruins (subsite A1), alleged site of the 'original flute bird', and the site of the Manns' homestead (subsite A2) where Martha Manns lived in the 1930s. It was Manns who later recounted the story

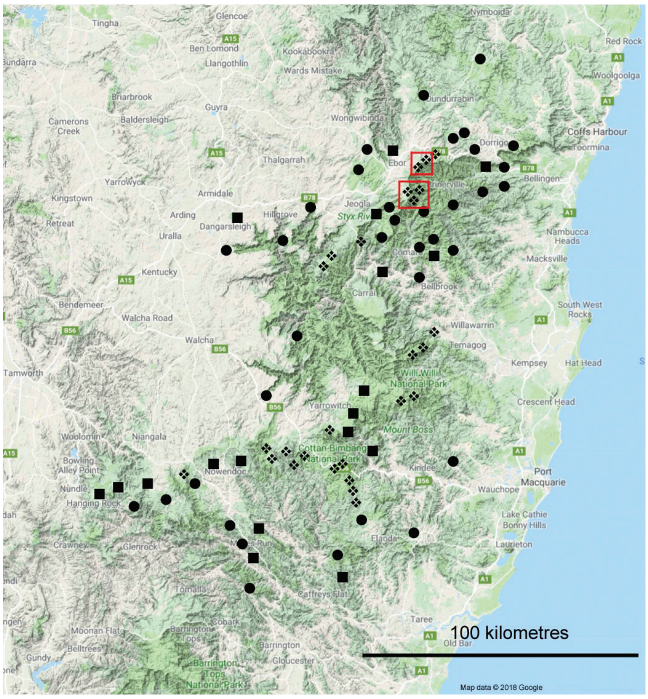

Figure 2. *The bioregions of NSW North Coast and New England Tableland showing Superb Lyrebird field sites: ❖ = flute; ● = non-flute; ■ = no songs heard/recorded. The top (more northerly) red box indicates Allans Water, the site of the 'original bird', which is detailed in Figure 3. The bottom (more southerly) red box indicates sites in and near New England NP and is detailed in Figure 4.*

of a flute player and a captive bird (Powys *et al*. 2013). Sixteen recording subsites in this area yielded lyrebird territorial songs with flute-like elements (Appendix 2); only hints of non-flute-like elements were heard or recorded at Allans Water. All the songs here achieved a high degree of complexity resembling that in the sonogram in Figure 1a. Allans Water songs with flute-like elements were longer and more complex than the flute-like songs in other areas.

However, the presence/absence of flute-like elements could not be predicted by distance from the ruins of the homestead where the 'original bird' was purportedly released at Allans Water. Radiating out from this site, our survey catalogued no flute-like elements in territorial songs to the north, east, or west. Flute-like songs were documented at Knodingbul Rd (site 56) in Doyles River State Forest (SF) (which, at 129.5 km away, was the site farthest to the south of the homestead ruins) and at Myall Creek campsite, Nowendoc SF (site 63) (the farthest to the south west). The farthest site surveyed from the homestead ruins was Woko NP (site 85), a non-flute-like site (172.5 km distant).

Another highly productive recording area was the New England NP at sites at and near Banksia Point Lookout and along Robinsons Knob Trail (Fig. 4 and Appendix 3). Fourteen recording sites here yielded lyrebird territorial songs containing flute-like elements at twelve locations (sites B1-B8 and R1-R2), and all these songs had a moderate degree of complexity. However, just to the south and almost within hearing distance of sites B1-B8 is a group of non-flute-like lyrebirds at sites R3-R6, but flute-like song populations occur again farther south in the ranges west of Kempsey, indicating that flute-like song distribution is not continuous even in contiguous habitat.

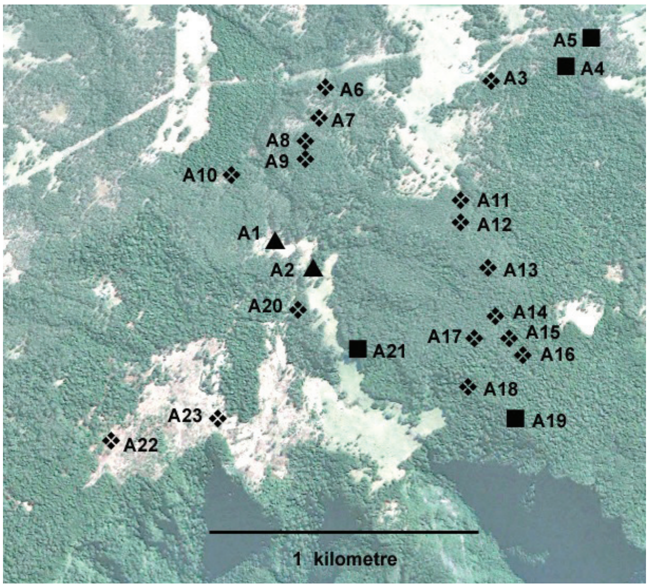

Figure 3. *The area of Allans Water near Ebor showing Superb Lyrebird field sites: ❖ = flute; ▲ = homestead sites; ■ = no songs heard/recorded.*

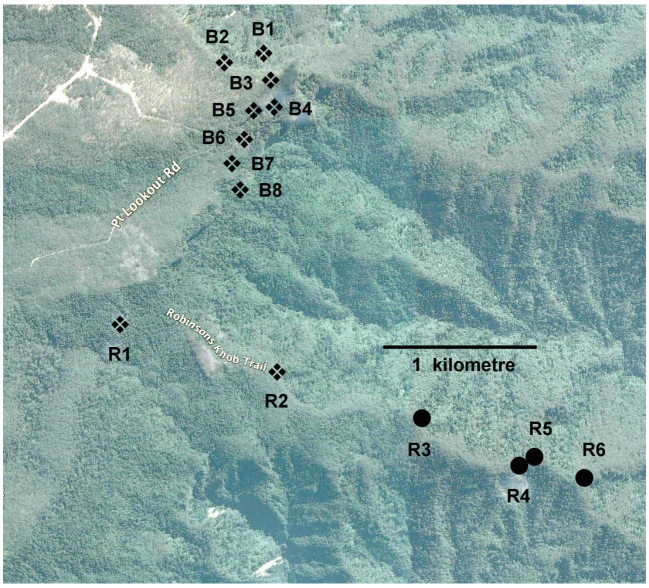

Figure 4. *Sites in New England NP at and nearby Banksia Point Lookout (B), and along Robinsons Knob Trail (R) showing Superb Lyrebird field sites: ❖ = flute; ● = nonflute.*

Some individuals delivered both flute-like and non-flute-like territorial songs. Also at site 35, several individuals delivered mimicry but no species-specific territorial songs. Revisits to this site on subsequent trips yielded similar results in recordings totalling 103 min of song. At the 17 other sites visited multiple times (shown in Appendix 1), song types were also consistent and had not changed over the years.

Song structure will be investigated more fully in a future paper, but preliminary evidence suggests that the flute-like elements at Fenwicks Rd in Cottan-Bimbang (site 44) and Mummel Gulf NPs (sites 46-48) are simpler and more consistent with the sonogram in Figure 1b than that in Figure 1a. However, both simple and more complex flute-like songs were recorded from the southerly 'flutists' at site 56 (Knodingbul Rd). Conceivably, a lyrebird's age might affect song complexity, with younger males giving simpler songs, which might explain how some areas surveyed had both simple and more complex songs (Taylor *et al*. unpubl. data).

DISCUSSION

This study has extended the previously known boundaries of the flute-like lyrebird song dialect. Initial recordists of the flute-like song focussed on Allans Water (sites 6 and 7) and Point Lookout in New England NP (site 16), which are approximately 15 km apart (Powys *et al*. 2013). However, in 1991 Ederic Slater recorded flute-like songs at Carrai (near our sites 38 or 39, approximately 65 km south of the Allans Water sites) and somewhere in, or near, Mt. Boss (possibly near our site 40, Hastings Forest Way, Willi Willi NP), which is ~85 km south of the Allans Water sites (Rankin *et al*. 1999). Slater argued that flute songs would not have 'travelled' that distance within the suggested time frame from the 1920s (the time of the alleged existence of the original flute-mimicking lyrebird at Allans Water) to 1991, although two other lyrebird experts (Sydney Curtis and Norman Robinson) believed that if there were no major habitat break, it could be possible (see Powys *et al*. 2013). In 1983, Glenn Holmes recorded the flute-like dialect occurring 'at least as far south as the Oxley Highway' (see Rankin *et al*. 1999), extending its distribution to ~120 km south of Allans Water. The present study verified Holmes' suggestion and extended the boundary another 10 km to the south (including sites 46-48, 54-56, and 82-83).

Researchers who have investigated the lyrebird's flute-like songs disagree on whether, were the 'flute lyrebird' story true, a new song could, or would be likely to, spread the extraordinary distance of 130 km in a relatively short time (from, say, 1920 to 1983). Breeding adult males and females are sedentary throughout their range, and both occupy territories. As a primarily cursorial bird, a lyrebird mainly walks and runs within its territory rather than flies. Male territories are all-purpose, maintained throughout the year and actively defended against conspecific intruders, and the maximum recorded lifetime movement of a lyrebird is only *c.* 10 km (Higgins *et al*. 2001). Given this, are lyrebirds capable of the magnitude of cultural transmission and change implied by the 'release of a captive bird' scenario?

For a new song to spread by vocal learning, presumably contiguous habitat would be required. Satellite imagery viewed on Google Earth suggests that sufficient contiguous forest habitat links all the lyrebird populations that we surveyed. Both flute-like and non-flute-like singing lyrebirds inhabit this contiguous forest area, but on the other hand flute-like songs were not found beyond any significant habitat gaps. For instance, a gap south of Knodingbul Road separates our main study area from Barrington Tops NP, where flute-like songs do not occur (Taylor *et al*. unpubl. data).

We noted that flute-like songs seemed not to carry as far as non-flute-like songs. This was confirmed by comparing the waveform peaks of territorial songs with the relative loudness of the mimicked call of the Grey Shrike-thrush *Collurincincla harmonica* from the recorded song of the same lyrebird. Non-flute-like territorial songs were louder than mimicry, whilst flute-like songs were similar to, or less loud than, mimicry (Taylor *et al*. unpubl. data). This could have implications for the relative abilities of co-occurring flute-like and non-flute-like males to attract females, although the argument is complicated by the fact that some males sing both song types.

Also of some relevance to the spread of the flute-like dialect in a relatively short time is what has happened to the vocal repertoire of the Superb Lyrebirds introduced to Tasmania from Victoria between 1934 and 1949 (Higgins *et al*. 2001). After more than 60 years of separation, 'dramatic differences' between the vocalisations of the mainland and Tasmanian lyrebirds were noted (Jordan 2007). The Tasmanian lyrebirds had begun to mimic endemic Tasmanian bird species, while continuing to produce the mimicked calls of mainland Eastern Whipbirds *Psophodes olivaceus* and Pilotbirds *Pycnoptilus floccosus*. Whipbird mimicry declined in accuracy over the years and was, by the 1980s, barely recognizable, but a more recent survey has found a range of 'whip' calls from strong to weak, as might be expected after long isolation from the original model (Jordan 2007). Whilst flute-like songs are territorial songs and may not be mimicry, the Tasmanian introduction does indicate strikingly that Superb Lyrebirds have the capacity for vocal learning from original models and not just from other lyrebirds, and the ability to retain, albeit possibly in a decaying form, the mimicked vocalizations of models to which they have long ceased to be exposed. These demonstrated vocal learning abilities perhaps make the spread of a flute-like song dialect in a relatively short time more plausible.

Three unanswered questions that seem to challenge the credibility of the flute story are: Why did the flute-like song fail to spread the 20-30 km from Allans Water to contiguous sites around Dorrigo, yet spread over 100 km to the south? Why does the distribution suddenly shift from flute-like to non-flute-like singers south of Allans Water in New England NP when flute populations occur again in the ranges west of Kempsey? Why do some males sing both flute-like and non-flute-like songs? There remain many unanswered and interesting questions about the flute-like song dialect of Superb Lyrebirds, irrespective of whether we regard the story of the original flute-mimicking lyrebird as plausible or unlikely.

CONCLUSION

The distribution map (Fig. 2) that we produced is consistent with the potential origin and cultural transmission of a flute-like song, either from the site of putative introduction or from some other contiguous site within the study area. From ground surveys and by studying Google Earth views of the terrain, we concluded that there is enough forest habitat remaining even in 2018 to connect populations of flute-like singing lyrebirds continuously from Allans Water to Knodingbul Road 130 km to the south. However, whilst habitat was continuous, flute-like songs were not geographically continuous, being separated by zones containing non-flute-like singing lyrebirds. The origins of these flute-like territorial songs remain unknown, and we still cannot discount the flute lyrebird story.

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Appendix 1

Productive Superb Lyrebird recording sites (flute-like and non-flute-like). Sites 1-65 are from N to S; sites 66-85 re-start the N to S layout. In this and subsequent tables, the letter in column 6 denotes the observer (C=Carol, H=Hollis) and the number the trip number.

Site	Location	Flute	GPS South, East	Alt	Fieldtrip
1	Clouds Creek SF	no	30 08 53.3, 152 35 23.6	782	H2
2	Mt Hyland NR	no	30 11 17.2, 152 25 48.6	1255	C3
3	Deer Vale E of NR	no	30 19 11.8, 152 37 19.5	782	H5
4	Deer Vale NR	no	30 19 22.9, 152 35 37.9	921	C3/H5
5	Tree Fern Vale	no	30 19 51.0, 152 34 09.4	1084	C3/H5
6	Allans Water forest, NENP	YES	30 23 19.4, 152 27 09.1	1391	C4/H7/H8
7	Allans Water homestead	YES	30 23 36.6, 152 26 42.0	1330	C3
8	Native Dog RA/Guy Fawkes River NP	no	30 23 14.7, 152 16 05.8	1255	H2
9	Cathedral Rock NP walking track	no	30 25 49.3, 152 15 03.7	1481	C3
10	Never Never picnic area, Dorrigo NP	no	30 21 28.1, 152 47 29.2	748	H2
11	Waterfall Way, Newell Falls RA, Bellinger	no	30 24 07.6, 152 44 49.2	389	C3
12	Orama (Upper Thora), Diehappy SF	no	30 26 32.3, 152 42 00.3	192	C3
13	Scotchman SF, E boundary, Baalijin NR	no	30 28 13.0, 152 41 47.0	413	C4
14	Lyrebird Firetrail, Baalijin NR	no	30 28 37.1, 152 39 55.5	647	C4
15	Killiecrankie Mt	no	30 32 29.6, 152 32 29.5	883	C4
16	Pt Lookout, NENP (top of escarpment)	YES	30 29 19.4, 152 24 30.1	1557	H2/H7/H8
17	Banksia Point LO, NENP	YES	30 29 33.0, 152 24 23.6	1446	H2/C4/H5/H7/H8
18	Lyrebird Track S of Banksia Pt LO, NENP	YES	30 29 44.6, 152 24 22.9	1352	C4
19	Wrights LO, near Pt Lookout	YES	30 30 19.2, 152 23 50.9	1322	C4
20	Snowy Range 1, Wrights LO	YES	30 30 29.0, 152 24 33.3	1252	C4
21	Snowy Range 2, Wrights LO	no	30 30 39.1, 152 25 13.4	1155	C4
22	Snowy Range 3-5, Wrights LO	no	30 30 47.9, 152 25 46.4	1028	C4
23	Snowy Range 6 (S of Grasstree Ridge)	no	30 31 48.8, 152 26 55.4	882	C4
24	Snowy Range 7 (5.5km SE of Wrights LO)	no	30 31 53.2, 152 26 59.5	827	C4
25	Cunnawarra Trail, Cunnawarra & NE NPs	no	30 31 48.3, 152 21 37.1	1310	C3
26	Beech LO, Cunnawarra NP	no	30 31 06.5, 152 21 16.2	1388	C3/H5/H7
27	Forest Way/Softwood Rd, Cunnawarra NP	no	30 31 23.5, 152 20 18.1	1260	C3/H7

Appendix 1 (continued)

Site	Location	Flute	GPS South, East	Alt	Fieldtrip
27	Forest Way/Softwood Rd, Cunnawarra NP	no	30 31 23.5, 152 20 18.1	1260	C3/H7
28	Edgars LO, Oxley Wild Rivers NP	no	30 31 57.7, 152 01 34.3	1018	H2
29	Wollomombi Falls, Oxley Wild Rivers NP	no	30 32 04.3, 152 01 58.4	952	H2/H5
30	Dangars Gorge LO, Oxley Wild Rivers NP	no	30 40 28.2, 151 43 29.8	977	H2/C3
31	Long Point, Oxley Wild Rivers NP	no	30 39 58.9, 151 56 00.9	1041	C3
32	Georges Ck, Cunnawarra NP	YES	30 39 32.7, 152 12 17.7	776	C3
33	Raspberry Mtn, Cedar Rd, Styx River SF	YES	30 42 40.0, 152 06 06.3	910	C3
34	Raffertys Ck, Styx River SF	YES	30 43 56.5, 152 04 08.2	934	C3
35	O'Sullivans Gap, Pee Dee NR	no	30 47 06.4, 152 26 06.5	245	H5/H7
36	Budd's Mare/Riverside Trail	no	30 58 32.0, 151 58 24.6	937	H7
37	Mt Mystery Timber Reserve	YES	30 56 53.4, 152 24 18.1	418	C3/C4
38	Carrai Rd, Hogsback/McCoys, Carrai SF	YES	30 59 35.4, 152 21 09.4	907	C3
39	Kookaburra Forest Camp, Carrai SF	YES	31 01 27.2, 152 20 13.8	960	C3
40	Hastings Forest Way, Willi Willi NP	YES	31 09 38.8, 152 22 46.2	1012	CH1
41	Plateau Beech, 1.5 km from camp, Werrikimbe NP	YES	no signal		CH1
42	Plateau Beech camp, Werrikimbe NP	YES	31 10 48.2, 152 19 35.4	1055	CH1
43	No 1 Tower LO (Five Ways Hill), Bellangry SF	no	31 17 09.9, 152 32 08.3	661	CH1
44	Fenwicks Rd, Cottan-Bimbang NP	YES	31 16 32.6, 152 04 34.1	1029	CH1
45	Tia Falls, Oxley Wild Rivers NP	no	31 09 23.2, 151 51 29.8	1053	CH1
46	Mummel Gulf NP West	YES	31 19 07.1, 151 47 20.2	1286	C6
47	Mummel Gulf NP, New Country Swamp camp	YES	31 19 51.3, 151 51 59.9	1144	C4
48	Mummel Gulf NP, Enfield Forest Rd	YES	31 21 04.6, 151 52 09.2	1091	C4/H7/H8
49	Myrtle Scrub Scenic Dr NW end, Cottan-Bimbang NP	YES	31 20 57.0, 152 00 52.9	1154	H5/H8
50	Myrtle Scrub Scenic Drive SE end, Mt Seaview	YES	31 23 22.1, 152 03 33.6	909	H5
51	N Oxley Hwy, SE end Myrtle Scr Sc Dr, Mt Seaview	YES	31 23 20.5, 152 03 36.4	920	H5
52	Stockyard Ck	YES	31 24 13.3, 152 07 28.6	739	CH1/H8
53	Stockyard Ck Rd junction	YES	31 24 45.5, 152 08 03.0	916	CH1/H7/H8
54	Knodingbul Rd #1, Cottan-Bimbang NP	YES	31 28 06.5, 152 09 15.7	632	CH1/H8
55	Knodingbul Rd #2 + 3, Cottan-Bimbang NP	YES	31 28 50.4, 152 09 26.9	861	CH1/H8
56	Knodingbul Road #4 + 5, Doyles River SF	YES	31 29 32.3, 152 09 39.3	856	CH1
57	Knodingbul Rd/Blue Knob Rd junction, Bulga	no	31 34 41.4, 152 10 47.9	773	CH1
58	Boorganna NR	no	31 36 49.3, 152 24 39.5	690	C3
59	Dingo Tops camp, Tapin Tops NP, Dingo SF	no	31 39 58.0, 152 08 34.8	867	CH1
60	Pigeon Top, Giro SF	no	31 38 04.8, 151 46 52.4	828	C6
61	Jacky Barkers Road, Giro SF	no	31 33 22.0, 151 34 57.3	911	C6
62	Roller Road, Nowendoc SF	no	31 26 01.6, 151 34 57.3	1162	C6
63	Myall Ck campsite, Nowendoc SF	YES	31 25 43.5, 151 33 27.2	914	C6
64	Tuggolo Ck, Tuggolo SF	no	31 29 40.0, 151 29 47.0	1220	C6
65	Tomalla NR	no	31 31 53.6, 151 21 41.4	1132	C6
66	Allans Water/Rim of World	YES	30 23 54.1, 152 26 30.4	1358	C9
67	Allans Water/priv res JL	YES	30 23 49.0, 152 27 10.9	1207	C9
68	Allans Water/priv res LT/Rim	YES	30 23 57.8, 152 26 13.6	1351	C9
69	Majors Point	YES	30 25 13.2, 152 25 34.5	1513	C9
70	Majors Point escarpment	YES	30 25 13.5, 152 25 38.0	1503	C9
71	Majors Point escarpment	YES	30 25 21.6, 152 25 31.6	1504	C9
72	Johnsens Rd nr Dorrigo	no	30 20 20.0, 152 37 13.9	986	C9
73	Johnsens Rd nr Dorrigo	no	30 20 20.0, 152 37 00.9	868	C9
74	Thumb Creek SF/nr Blue Knob	no	30 41 58.4, 152 33 45.2	621	C9
75	Thumb Ck/Sheet-o-bark Rd	no	30 41 26.9, 152 33 07.9	717	C9
76	Thumb Ck/nr Kilprotay Rd	no	30 40 46.8, 152 33 10.5	723	C9
77	Nulla 5 Day SF/PostmansTrl	no	30 40 51.4, 152 26 29.3	594	C9
78	Nulla Ck Rd, nr Nulla Nulla	no	30 39 11.5, 152 28 30.1	194	C9
79	Lower Creek SF/ Petroi Rd	no	30 40 50.2, 152 14 53.9	417	C9
80	Lower Creek SF/ Petroi Rd	no	30 40 01.8, 152 15 30.1	652	C9
81	Lower Ck SF/ Petroi Rd ridge	no	30 39 42.9, 152 15 41.6	766	C9
82	Mummel Gulf/Daisy Patch Rd	YES	31 22 02.4, 151 55 54.8	1046	C9
83	Mummel Gulf/Daisy Patch Rd	YES	31 22 11.2, 151 55 53.0	1022	C9
84	Carsons PLO, southeast	no	31 40 45.9, 151 49 55.3	756	C9
85	Woko NP/Cliff Track	no	31 47 45.2, 151 47 52.4	317	C9

Appendix 2

Allans Water field sites used in this study (NA designates no song heard or recorded).

Subsite	Location	Flute	GPS South, East	Alt	Fieldtrip
A1	Jones' homestead ruins/priv res JU	NA	30 23 26.1, 152 26 37.8	1278	C4/H7/H8/C9
A2	Manns' homestead approx site	NA	30 23 27.5, 152 26 42 4	1301	H7
A3	New Eng NP nr gate/priv res CL	YES	30 22 56.4, 152 27 13.9	1344	H8
A4	Redman Rd	NA	30 22 54.4, 152 27 27.0	1272	C9
A5	Redman Rd, clearing beside ford	NA	30 22 48.7, 152 27 31.6	1331	C9
A6	Near access road	YES	30 23 09.4, 152 26 40.6	1329	H7
A7	Near access road	YES	30 23 11.3, 152 26 41.4	1320	H7
A8	Near access road/ravine	YES	30 23 04.7, 152 26 42.4	1342	H7
A9	Near access road/fence	YES	30 22 58.7, 152 26 43.2	1314	H7
A10	Private res DE backyard	YES	30 23 14.5, 152 26 26.8	1322	H8
A11	Forest Site 1	YES	30 23 19.4, 152 27 09.1	1391	C4
A12	Forest Site 2	YES	30 23 22.6, 152 27 09.1	1415	C4
A13	Forest Site 3	YES	30 23 30.1, 152 27 13.3	1415	C4
A14	Forest Site 4	YES	30 23 38.3, 152 27 14.6	1426	C4
A15	Forest Site 5	YES	30 23 40.5, 152 27 17.2	1434	C4
A16	Forest Site 7	YES	30 23 44.1, 152 27 19.4	1421	C4
A17	Forest Site 6	YES	30 23 41.3, 152 27 11.8	1432	C4
A18	Lyrebird Hill/priv res JL	YES	30 23 49.0, 152 27 10.9	1207	H8/C9
A19	Farthest pt walked to escarpment	NA	30 23 53.0, 152 27 18.0	1390	C4
A20	Near Jones' homestead site	YES	30 23 36.6, 152 26 42.0	1330	C3
A21	Near tank, Jones'/Manns' sites	?	30 23 42.9, 152 26 52.5	1357	C4
A22	Rim of the World, gully	YES	30 23 57.8, 152 26 13.6	1351	C9
A23	Rim of the World, escarpment	YES	30 23 54.1, 152 26 30.4	1358	C9

Appendix 3

Banksia Point LO and Robinsons Knob Trail field recording sites.

Subsite	Location	Flute	GPS South, East	Alt	Fieldtrip
B1	Eagles Nest Lookout	YES	30 29 13.0, 152 24 27.8	1350	C4
B2	Berarngutta Picnic Area	YES	30 29 15.7, 152 24 18.1	1545	H7/H8
B3	Point Lookout	YES	30 29 19.4, 152 24 30.1	1557	H2/H7
B4	Weeping Rock	YES	30 29 25.6, 152 24 30.2	1463	C4
B5	Platypus Valley Lookout	YES	30 29 26.0, 152 24 26.0	1532	H5/H7/H8
B6	Banksia Point Lookout	YES	30 29 33.0, 152 24 23.6	1478	H2/H5/H7/H8
B7	B Pt LO/Tree Fern Valley	YES	30 29 38.3, 152 24 20.6	1464	C4
B8	Lyrebird Track	YES	30 29 44.6, 152 24 22.9	1352	C4
R1	Wrights Lookout	YES	30 30 19.2, 152 23 50.9	1322	C4
R2	Snowy Range 1	YES	30 30 29.0, 152 24 33.3	1252	C4
R3	Snowy Range 2	no	30 30 39.1, 152 25 13.4	1155	C4
R4	Snowy Range 4	no	30 30 49.4, 152 25 43.4	984	C4
R5	Snowy Range 3	no	30 30 47.9, 152 25 46.4	1028	C4
R6	Snowy Range 5	no	30 30 53.2, 152 26 02.1	956	C4

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Assessment of avian site fidelity in arid *Acacia* shrubland based on a ten-year mark-recapture study in central Australia

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Mark-recapture surveys of bird communities were conducted at five *Acacia* shrubland sites near Alice Springs, central Australia, between 2001 and 2011. The primary objective was to examine the levels of site fidelity displayed by individuals to provide insight into local bird community dynamics that cannot be ascertained by visual surveying. Approximately 1800 birds from 50 species were banded and over 150 individuals were recaptured. Results for the 27 species whose members were captured and banded 10 or more times are reported and assessed for evidence of site fidelity. Eleven species were classified as sedentary based on relatively high recapture rates and individuals being recaptured over long time periods. Species with the highest rates of recapture and with individuals persisting at sites for many years included the Splendid Fairy-wren *Malurus splendens*, Redthroat *Pyrrolaemus brunneus* and Chestnut-rumped Thornbill *Acanthiza uropygialis*. The results provide new evidence of high site fidelity for a suite of species associated with *Acacia* shrubland habitat in central Australia. Conclusions about which species are sedentary and which are mobile are broadly consistent with those of previous studies in this habitat based on visual surveys and with banding data from other regions, but with some new insights being gained.

INTRODUCTION

Rainfall is a dominant driver of arid ecosystems (Noy-Meir 1973; Morton *et a*l. 2011) and in the central Australian arid-zone the amount and timing of rain that falls in a year varies to a much greater extent than in many other environments (Chesson *et al*. 2004; Van Etten 2009). The availability of water is a major influence on primary productivity in this system and can determine flowering, new growth and seeding of the standing vegetation at a particular time (Bailey *et al*. 2004), thereby directly influencing the availability of food resources for nectarivorous and granivorous birds. The increase in plant-based resources also leads to increased local abundance and richness of invertebrate populations, increasing the food resources available for insectivores. The timing of high rainfall 'boom' periods is variable, and overlayed on background seasonal weather patterns which, to varying degrees, stimulate cycles of growth and senescence and flowering and fruiting in plants, and determine the life cycles and activity of invertebrates. Furthermore, the spatial distribution of rainfall can be patchy at both small and large scales, stimulating high levels of productivity in local areas while other nearby areas remain dry. This spatial variability in the resources is, in turn, overlayed on a background of distinct vegetation communities which provide a suite of distinctive habitats and are therefore associated with characteristic faunal assemblages.

In the Australian arid-zone, abundance and species richness of bird assemblages can change markedly in response to rainfall (Paltridge and Southgate 2001; Burbidge and Fuller 2007), whilst foraging assemblages also vary spatially with the dominant vegetation type (Davis and Recher 2002). Mac Nally *et al*. (2004) suggest that there is a high level of dynamism and temporal variation in rangeland bird communities compared with those in higher rainfall areas because resources are less predictable. It follows that in an environment where food resources are highly variable in space and time, the majority of bird species should be nomadic to some extent at least, but this appears not to be the case (Shurcliff 1980).

Cody (1994) found that a stable and similar suite of bird species was regularly present in Mulga *Acacia aneura* woodland at sites across Australia, suggesting that the general resources available in this habitat can support relatively stable bird assemblages. Casual or peripheral species (i.e. those that are present sometimes or rarely), although making up a large proportion of the species present in this habitat at a given time, made up a very small component of the community in terms of density (Cody 1994). Pavey and Nano (2009), using a space-for-time approach, also found distinctive bird assemblages in the vegetation types present in the Finke bioregion of central Australia. Their study was carried out during a 'boom' period, but it still found structure in bird assemblages across vegetation types.

Current understanding of the dynamics of bird communities in the Australian arid zone and how they respond to temporal variation in resource availability is based mainly on visual survey data, and surveys are often restricted to a few days at any location. These types of surveys are generally limited to identifying species composition and estimates of relative abundance, and it is not possible to determine whether the same individuals are present from one survey to the next. In contrast, mark-recapture methods provide an opportunity to establish directly whether individual birds remain resident in particular areas, and for how long, hence providing valuable information about whether birds are resident or nomadic that is complementary to the findings of visual surveys (Leishman 2000).

The degree to which individuals can remain in an area over a long period of time (i.e. the level of site fidelity) indicates the extent to which an animal is able to survive using the resources in a limited area, rendering it unnecessary to move to another part of a landscape (Giuggioli and Bartumeus 2012). Banding, like any mark-recapture technique, has limitations; a territorial shift by an individual of mere metres may result in it never being caught again. Nevertheless, long-term banding studies can identify species that display a high level of site fidelity and, conversely, those that do not appear to be sedentary (e.g. Leishman 2000; Frith and Frith 2005).

The primary aim of this study was to gather evidence through mark-recapture surveys, specifically the rate of recapture of individuals and the length of time between recaptures, to support or refute current knowledge about site fidelity of bird species associated with *Acacia* shrubland communities in central Australia.

METHODS

Data were collected at two locations in two distinct time periods. During the first period from 2001 to 2003, banding was undertaken at three sites in the Alice Valley between the Hugh River and Ellery Creek, within the Tjoritja (West MacDonnell) National Park, approximately 60 to 90 km west of Alice Springs. Sites were named after nearby topographical or man-made features: Cummings Yard (23º42'38.32"S; 133º03'38.32"E), Ryan's Dam (23º46'33.97"S; 133º 11'43.5"E) and Hugh River (23º46'33.97"S; 133º19'35.44"E). During the second period from 2008 to 2011, birds were banded at two sites on the western and eastern sides of the Alice Springs Desert Park: Alice Springs Desert Park West (23º42'22.21"S; 133º49'40.75"E.) and Alice Springs Desert Park East (23º42'34.11"S; 133º50'25.21"E.), approximately 5 km apart. All sites were within the broader area of the West MacDonnell Ranges.

Study site habitat

The habitat at all sites was *Acacia* shrubland dominated by Mulga and Witchetty Bush *A. kempeana*. Scattered trees at the banding sites included Bloodwood *Corymbia opaca* and Long-leafed and Fork-leafed Corkwoods *Hakea longifolia* and *divaricata*, and *Eremophila* and *Senna* species were occasionally present in the understorey. The ground cover was composed primarily of native and introduced grasses, with introduced Buffel Grass *Cenchrus ciliaris* being present at all sites. Specific banding sites were chosen for apparent uniformity of habitat and ease of access for equipment. To our knowledge there were no sources of water close to any of the banding sites, except for the Ryan's dam site which was approximately 200m from an old farm dam that occasionally held water.

Climatic conditions at all sites were similar, with mean maximum daily temperatures ranging between 19.7ºC and 22.7ºC in winter and 35.1ºC and 36.3ºC in summer. Mean minimum temperatures were between 4ºC and 6ºC in winter and 20.3ºC and 21.5ºC in summer. Most banding was conducted in the cooler months of the year. The average annual rainfall in the area is 283mm, and occurs mainly in summer, although it can occur at any time. During the period prior to and during this study, the area received well above average rainfall in 2000 and 2001 (664 and 741 mm) and then again in 2010 and 2011 (770 and 340 mm).

Mist netting

Mist nets used to capture birds were approximately 3m high by either 12 or 18m long. They were erected in areas that were thought to be potential flyways and out of sunlight as much as possible. Nets were opened at dawn on banding days and checked every 20-30 min (Faaborg *et al*. 2004). Sex and age of captured birds were recorded if known, and Australian Bird and Bat Banding Scheme (ABBBS) bands were applied on the right leg.

The number of nets opened at any one time varied between 6 and 12, depending on the number and experience of volunteers available. Therefore, the area within which mist nets were set up was generally between 3 and 5ha. Banding was not conducted if ambient temperature rose above 33ºC or in strong winds or rain. Length of time that nets were open also depended on the availability of volunteers and the capture rate of birds, which decreased over time as birds in the area became aware of the nets. Nets were usually operated twice at each site, but not always on consecutive days. Each day's banding was regarded as an individual sample (referred to as a 'banding event'). The timing and number of banding events at each location are outlined in Table 1.

Data Analysis

Analysis of recaptures was designed to identify degrees of site-fidelity and two recapture measures were calculated. One was the percentage of banded individuals of each species that were recaptured. The second percentage calculated (referred to as 'recapture rate') included every recapture for each species (i.e. including multiple recaptures of the same individual). Other measures used to assess site-fidelity were the time-intervals between captures of the same individual, and the frequency at which species occurred at the different sites. As the number of individuals banded varied among species and the likelihood of recapturing individuals depends partly on the number of individuals banded initially, we conducted additional analyses to account for these effects. We first tested whether the predicted positive relationship between the number of individuals banded and the number of recaptures made was significant, and described this relationship using linear regression. We also examined how species deviated from the expected relationship by examining the residual values from the regression for each species.

Activities were undertaken with approval from the Charles Darwin University Animal Ethics Committee (project # A08007) and under Scientific Permit (# 39155) issued by the Parks and Wildlife Commission of the Northern Territory. The project had ABBBS approval (Authority 2392 Project 1).

RESULTS

Between 2001 and 2011, 1803 individual birds of 50 species were captured and banded. In addition, 169 individual birds were recaptured, some on multiple occasions, resulting in a

Table 1

Dates and locations of mark-recapture activities. Numbers of banding events are shown in parentheses.

Year	Cummings Yard (8)	Ryans Dam (9)	Hugh River (9)	Desert Park E (37)	Desert Park W (20)
2001	Oct (1)	Oct (1)	Oct (1)	Sep (2) Dec (2)	
2002	Feb (1) May (2) Sep (2)	Feb (1) May (2) Sep (2)	Feb (1) May (2) Sep (2)	Mar (2) Jul (2) Aug (2)	Jul (1)
2003	Jan (2)	Jan (2) Sep (1)	Jan (2) Sep (1)	Jan (2) Mar (3) Jun (1) Jul (1)	Sep (1)
2004	–	–	–	Jun (2)	–
2005	–	–	–	–	–
2006	–	–	–	–	–
2007	–	–	–	May (1)	–
2008	–	–	–	Jun (2) Dec (2)	Jun (2)
2009	–	–	–	May (2) Aug (2) Nov (1) Dec (1)	Apr (2) Jul (2) Sep (2)
2010	–	–	–	May (2) Oct (1) Nov (2)	Mar (2) Apr (2) Aug (2) Nov (2)
2011	–	–	–	Apr (2)	Mar (2)

total of 222 recaptures (10% recapture rate). Six hundred and twenty-one individuals of 37 species were caught in the Alice Valley and 1182 individuals of 45 species near the Alice Springs Desert Park.

Our focus was on the 27 species in which ten or more individuals were banded during the project (Table 2), because the likelihood of recapturing species in which very few individuals are banded is very low (even if the species is highly sedentary), and therefore not informative with respect to our research question. Data for the 28 species in which fewer than ten individuals were banded are provided in Appendix 1. Of the 27 most commonly banded species, 20 included individuals that were recaptured (Table 2). The 7 species with no recaptures all had relatively low (<30) numbers of individuals that were banded; however, other species with similarly low numbers of banded individuals, such as the Redthroat *Pyrrolaemus brunneus*, White-plumed Honeyeater *Lichenostomus penicilatus* and Southern Whiteface *Aphelocephala leucopsis*, had high recapture rates (Table 2). In some species, such as Splendid Fairy-wren *Malurus splendens* and Redthroat, individuals were caught on multiple occasions. Although only a small number of Redthroats were caught, they were proportionally the most recaptured species, with over 50% of trapped individuals being re-trapped at the initial point of capture (Table 2).

The time between original trapping and recapture provides an indication of the level of site fidelity for a species, with the maximum time between recaptures representing the minimum time that an individual is present at the site. When compared among species, the maximum time between recaptures for any individual and the mean maximum time between recaptures of individuals provide information about relative levels of site fidelity (Table 3). It is important to consider when interpreting these data that the number of days between recaptures is partly dependent on the time between banding events and that data suggesting long-term site fidelity will be biased toward longer-lived species (Table 3).

Species such as the Yellow-rumped Thornbill *Acanthiza chrysorrhoa* and Diamond Dove *Geopelea cuneata* (near the bottom of Table 3) were only ever recaptured within a few days of their initial capture when there were multiple banding events within a month, whereas individuals of other species (near the top of Table 3), such as the Splendid Fairy-wren, Spiny-cheeked Honeyeater *Acanthagenys rufogularis* and Chestnut-rumped Thornbill *Acanthiza uropygialis*, were caught at the same location years after initial capture (Table 3).

As predicted, for each species the number of individuals recaptured depended partially on the number of individuals banded. Thus, recaptures were more likely for species in which many individuals were banded and less likely in species in which very few individuals were banded ($R^2 = 29.2\%$; df = 1.25; $P = 0.004$) (Fig. 1). The regression line in Figure 1 is described by the equation *Recaptures = 2.6 + 0.08 Birds Banded*. This equation predicts the number of recaptures that could be expected based on the number of birds banded at our sites, assuming no differences in site fidelity. The residual values from the regression for each species (Table 4) represent the position and distance of each species in Figure 1 relative to the fitted regression line. Species with positive residuals are those that were recaptured more than expected (i.e. evidence of relatively high site fidelity), whilst those with negative residuals (points below the line) were recaptured fewer times than expected based on the number of individuals banded (i.e. evidence of relatively low site fidelity). From these analyses, the species with the strongest evidence of site fidelity were the Splendid Fairy-wren, Redthroat, Singing Honeyeater *Lichenostomus virescens* and Spiny-cheeked Honeyeater; species with the weakest evidence of site fidelity, suggesting high mobility, were the Diamond Dove and Zebra Finch *Taeniopygia guttata*.

There was variation in the regularity with which species were captured among the study sites. Some species were not captured at every study site or on every sampling occasion, but others were regularly caught at all sites. Table 5 illustrates the rate at which species were encountered in both spatial and temporal terms in the study sites. Notably, some species with relatively low recapture rates (e.g. Zebra Finch) were encountered very regularly at all sites, whereas other less abundant species with low recapture rates (e.g. Willie Wagtail *Rhipidura leucophrys*) or that were never recaptured (e.g. Mistletoe Bird *Dicaeum hirundinaceum*) were still encountered across all sites.

Table 2

Capture and recapture data for species with 10 or more individuals banded. Species are ordered according to percentage of banded individuals that were recaptured, from highest to lowest.

Species		No. banded (No. recaptures)	No. individuals recaptured	% Banded individuals recaptured	% Recapture rate
Redthroat	*Pyrrholaemus brunneus*	17 (12)	9	52.9	70.5
Chestnut-rumped Thornbill	*Acanthiza uropygialis*	33 (10)	9	27.2	30.3
White-browed Babbler	*Pomatostomus superciliosus*	38 (11)	9	23.6	28.9
Splendid Fairy-wren	*Malurus splendens*	198 (63)	41	20.7	31.8
White-plumed Honeyeater	*Lichenostomus penicillatus*	21 (4)	4	19.0	19.0
Southern Whiteface	*Aphelocephala leucopsis*	16 (3)	3	18.7	18.7
Grey-crowned Babbler	*Pomatostomus temporalis*	38 (7)	7	18.4	16.6
Singing Honeyeater	*Lichenostomus virescens*	113 (19)	16	14.1	16.8
Spiny-cheeked Honeyeater	*Acanthagenys rufogularis*	136 (21)	19	13.9	15.4
Rufous Whistler	*Pachycephala rufiventris*	87 (13)	12	13.7	14.9
Western Bowerbird	*Ptilonorhynchus guttata*	16 (2)	2	12.5	12.5
Inland Thornbill	*Acanthiza apicalis*	51 (8)	6	11.7	15.6
Red-capped Robin	*Petroica goodenovii*	78 (9)	7	8.9	11.5
Yellow-throated Miner	*Manorina flavigula*	24 (2)	2	8.3	8.3
Hooded Robin	*Melanodryas cucullata*	30 (2)	2	6.6	6.6
Brown Honeyeater	*Lichmera indistincta*	97 (4)	4	4.1	9.7
Willie Wagtail	*Rhipidura leucophrys*	26 (1)	1	3.8	3.8
Zebra Finch	*Taeniopygia guttata*	425 (15)	12	2.8	3.5
Yellow-rumped Thornbill	*Acanthiza chrysorrhoa*	40 (1)	1	2.5	2.5
Diamond Dove	*Geopelia cuneata*	93 (2)	2	2.1	2.1
Budgerigar	*Melopsittacus undulatus*	29 (0)	0	0	0
Western Gerygone	*Gerygone fusca*	14 (0)	0	0	0
Pied Honeyeater	*Certhionyx variegatus*	23 (0)	0	0	0
Grey-headed Honeyeater	*Lichenostomus keartlandi*	22 (0)	0	0	0
Crimson Chat	*Epthianura tricolor*	12 (0)	0	0	0
White-winged Triller	*Lalage sueurii*	24 (0)	0	0	0
Mistletoebird	*Dicaeum hirundinaceum*	26 (0)	0	0	0

Table 3

Data on the times between recaptures, with species ordered by the longest time between banding and recapture of any individual.

Species	Mean maximum time between recaptures of individuals (days)	% of recaptures >180 days	% of recaptures >360 days	% of recaptures >730 days	Longest time between recapture of any individual (days)
Splendid Fairy-wren	292	14.0	8.3	1.5	2151
Spiny-cheeked Honeyeater	369	6.9	5.7	3.2	1947
Singing Honeyeater	271	6.1	2.3	0.7	1825
Chestnut-rumped Thornbill	378	13.3	11.1	2.2	1521
Rufous Whistler	319	7.2	3.1	2.1	1338
Grey-crowned Babbler	319	4.5	4.5	4.5	1125
Redthroat	333	29.6	11.1	7.4	882
Inland Thornbill	331	10.3	5.2	3.4	852
Red-capped Robin	246	7.1	3.5	0.0	608
Western Bowerbird	324	5.9	5.9	0.0	547
White-browed Babbler	276	12.2	12.2	0.0	517
Southern Whiteface	155	5.3	5.3	0.0	456
Hooded Robin	229	6.3	0.0	0.0	336
Yellow-throated Miner	370	3.8	0.0	0.0	334
Zebra Finch	73	0.2	0.0	0.0	213
Brown Honeyeater	77	0.0	0.0	0.0	168
White-plumed Honeyeater	93	0.0	0.0	0.0	122
Diamond Dove	11	0.0	0.0	0.0	13
Willie Wagtail	4	0.0	0.0	0.0	4
Yellow-rumped Thornbill	1	0.0	0.0	0.0	1

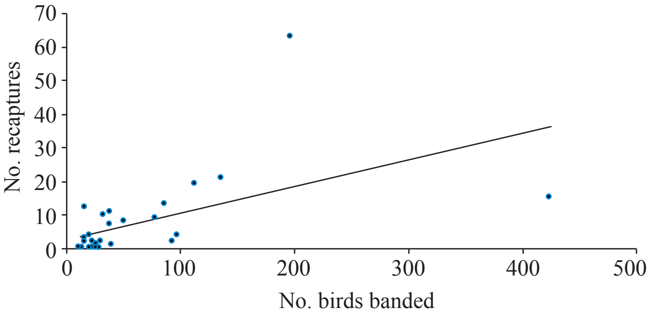

Figure 1. *Regression plot showing the relationship between the number of individuals banded and the number recaptured. Recaptures = 2.6 + 0.08 Birds Banded (R^2 = 29.2%, P = 0.004).*

DISCUSSION AND SYNTHESIS

Classification of species as sedentary or mobile based on mist netting

The capture and recapture rates and times between recapture of individuals that we have presented can be used to draw conclusions about the level of site fidelity of species. For example, some species, such as Splendid Fairy-wren and Chestnut-rumped Thornbill, had high recapture rates and long intervals between recaptures. These patterns of recapture are compelling indicators of site fidelity and sedentary behaviour (Leishman 2000; Frith and Frith 2005). These species were also regularly encountered at several sites throughout the year, indicating that they can be regarded as sedentary in *Acacia* shrubland. Other species exhibited a contrasting pattern; they were captured irregularly and some were never recaptured. It is impossible to draw conclusions for some species because few individuals were banded. However, for species in which many individuals were banded, low rates of recapture and short intervals between recaptures indicate that they are mobile and that individuals do not stay at a site for long. Such species may still be strongly associated with *Acacia* shrubland and occur predictably at many sites and times, but there is no evidence that they exhibit sedentary behaviour within this habitat. Based on the results of 10-years of banding surveys that we have presented, we have assigned the species trapped into three categories: sedentary, mobile and unclassifiable (insufficient data, the results are inconclusive) (Table 6). Our classification is compared to those of other authors who have presented data on the status of birds in Mulga communities, and to reported ABBBS recapture rates in Table 6.

Sedentary species

Of the 21 species encountered in >10 % of our banding events (see Table 6), 13 were among the 18 species listed by Cody (1994) as 'core' to *Acacia* habitat, four were considered peripheral, three casual, and one was unlisted by Cody. Eighteen of our 21 commonly encountered species were considered resident in *Acacia* shrubland in the Finke bioregion in central Australia by Pavey and Nano (2009). Our data for encounter rates therefore generally support the findings of Cody (1994) and Pavey and Nano (2009) with respect to species that are strongly associated with *Acacia* shrubland habitat. Notable exceptions are the Brown Honeyeater *Lichmera indistincta* and Redthroat, which we encountered relatively commonly but which were not recorded in Pavey and Nano's (2009) surveys and were classified as peripheral species by Cody (1994).

Table 4

Residual values for each species from the regression: Recaptures = 2.63 + 0.08 Birds Banded. Positive residuals indicate that more individuals than expected were recaptured and negative residuals that fewer individuals than expected were recaptured, when accounting for the number of birds of each species that were banded.

Species	Residual
Splendid Fairy-wren	44.12
Singing Honeyeater	8.28
Redthroat	8.00
Spiny-cheeked Honeyeater	7.27
White-browed Babbler	5.31
Chestnut-rumped Thornbill	4.55
Rufous Whistler	3.37
Grey-crowned Babbler	1.31
Inland Thornbill	1.19
Red-capped Robin	0.10
White-plumed Honeyeater	-0.32
Southern Whiteface	-0.92
Western Bowerbird	-1.92
Yellow-throated Miner	-2.56
Hooded Robin	-3.04
Crimson Chat	-3.60
Willie Wagtail	-3.72
Western Gerygone	-3.76
Grey-headed Honeyeater	-4.40
Pied Honeyeater	-4.48
White-winged Triller	-4.56
Mistletoebird	-4.72
Budgerigar	-4.96
Yellow-rumped Thornbill	-5.01
Brown Honeyeater	-5.59
Diamond Dove	-8.11
Zebra Finch	-21.81

Among the commonly occurring species, we identified 11 for which there was clear evidence of high site fidelity. We classified these species as sedentary on the following basis: individuals were regularly encountered and (a) demonstrated fidelity to a site as indicated by a recapture rate >10% and (b) a maximum mean time between recaptures that was >240 days (8 months) or longer than a migratory cycle. Of the 11 species that we classified as sedentary, all except three were listed as a 'core' Mulga species by Cody (1994); this author listed the Redthroat as a peripheral species, Grey-crowned Babbler *Pomatostomus temporalis* as a casual species and did not list the Western Bowerbird *Ptilonorynchus guttata*. Below we discuss these three species first and then some of the other species that were classified as sedentary.

Although Cody (1994) listed the Grey-crowned Babbler as a casual Mulga species, he notes that babblers as a group rank as 'core' to Mulga, with the babbler species present differing

Table 5

Frequency of occurrence (expressed as the percentage of banding events) of species at different banding sites and over the entire study area.

Species	Frequency of occurrence (%)					
	Cummings (n = 8)	Ryans (n = 9)	Hugh (n = 9)	Desert Park E (n = 37)	Desert Park W (n = 20)	% of all sites and all trips
Splendid Fairy-wren	75.0	66.7	33.3	75.0	75.0	69.4
Singing Honeyeater	62.5	75.0	77.8	61.1	80.0	69.4
Zebra Finch	50.0	50.0	66.7	58.3	65.0	58.8
Rufous Whistler	37.5	83.3	77.8	52.8	50.0	57.7
Spiny-cheeked Honeyeater	50.0	33.3	55.6	63.9	50.0	54.1
Red-capped Robin	62.5	58.3	11.1	50.0	75.0	54.1
Inland Thornbill	37.5	58.3	44.4	27.8	55.0	40.0
Brown Honeyeater	25.0	25.0	11.1	50.0	15.0	31.8
Chestnut-rumped Thornbill	75.0	50.0	55.6	13.9	20.0	30.6
Diamond Dove	0.0	33.3	11.1	22.2	40.0	24.7
Yellow-rumped Thornbill	50.0	50.0	22.2	13.9	20.0	24.7
Hooded Robin	50.0	41.7	55.6	2.8	5.0	21.2
Willie Wagtail	37.5	8.3	22.2	16.7	15.0	17.7
Redthroat	0.0	33.3	0.0	11.1	30.0	16.5
Western Gerygone	0.0	25.0	11.1	11.1	25.0	15.3
White-browed Babbler	12.5	37.5	0.0	19.4	10.0	15.3
Western Bowerbird	25.0	0.0	0.0	27.8	0.0	14.2
Grey-headed Honeyeater	25.0	33.3	33.3	8.3	5.0	14.1
Mistletoebird	25.0	8.3	11.1	11.1	15.0	12.9
Southern Whiteface	12.5	41.7	0.0	2.8	10.0	10.6
Grey-crowned Babbler	12.5	16.7	33.3	11.1	0.0	10.6
White-plumed Honeyeater	0.0	0.0	11.1	19.4	0.0	9.4
Yellow-throated Miner	37.5	8.3	44.4	0.0	0.0	9.4
White-winged Triller	0.0	0.0	11.1	11.1	15.0	9.4
Pied Honeyeater	0.0	0.0	0.0	11.1	10.0	7.1
Crimson Chat	0.0	0.0	0.0	2.8	25.0	7.1
Budgerigar	0.0	0.0	11.1	2.8	5.0	3.5

with location. Both White-browed *Pomatostomus superciliosus* and Grey-crowned Babblers were encountered at most sites throughout the year in our study, but were only present in approximately 15% (White-browed) and 10% (Grey-crowned) of banding events, which may indicate they are less common residents of Mulga or that they are not easily trapped in mist nets. Our recapture data (numbers of recaptures and time between recaptures) indicate moderate site fidelity for these species. This is consistent with Higgins and Peter (2002) who describe both species as sedentary.

The absence of the Western Bowerbird in Cody's (1994) lists of *Acacia* shrubland birds may be partly explained by the limited distribution of this species in relation to his sites. The Western Bowerbird was considered a resident species of *Acacia* woodlands in the Finke bioregion by Pavey and Nano (2009). There are no ABBBS data on recapture rates for this species because of the limited number of banding studies in central Australia. Our recapture data suggest moderate site fidelity for this species.

Redthroats were not caught at every site and were only caught in small numbers. However, they exhibited the highest recapture rate of any species in our study, with over 50% of individuals banded being recaptured. They were caught in most months of the year at three out of five sites. This information suggests that they may have more specialised habitat requirements and live in larger territories compared to, for example, the Splendid Fairy-wren (which was commonly encountered at all sites in large numbers). The low numbers of Redthroats captured may also be the result of territorial instead of colonial habits. Higgins and Peter (2002) indicate a 20% recovery rate of banded individuals of this species; it is thought to be sedentary, with recoveries mainly occurring within 10km of the banding site, and this is supported by our data. The Redthroat's social organisation is poorly known, but it is thought to live in pairs or small family groups (Higgins and Peter 2002). The shy, cryptic nature of this species may limit sightings in observational surveys and probably accounts for it being described as peripheral to *Acacia* shrubland habitat by Cody (1994), and also why it was not recorded during the Finke Bioregion study (Pavey and Nano 2009). Based on our results, and contrary to Cody (1994), we suggest that the Redthroat is a 'core' species of some Mulga habitats; it was not found at every banding site, but where it occurred it was recaptured regularly.

Table 6

Classifications (sedentary vs. mobile) of species based on our mark-recapture results for species with >10 individuals banded compared with classifications of species from previous studies in arid Acacia habitat. A summary of the main variables from which our assessments were made is provided, along with recapture data from ABBBS (Higgins *et al.* 2001) for comparison.

Species	Our Classification	% Occurence (n = 83 banding events)	Mean days between recaptures	% Rate of recapture	% Rate of recapture (ABBBS)	Cody (1994)	Pavey and Nano (2009)
Splendid Fairy-wren	Sedentary	69.4	290	31.8	29.9	Core	Resident
Singing Honeyeater	Sedentary	69.4	268	16.8	21.6	Core	Resident
Zebra Finch	Mobile	58.8	74	3.5	23.8	Casual	Resident
Rufous Whistler	Sedentary	57.6	319	14.9	17.1	Core	Resident
Spiny-cheeked Honeyeater	Sedentary	54.1	369	15.4	6.4	Core	Resident
Red-capped Robin	Sedentary	54.1	247	11.5	11.7	Core	Resident
Inland Thornbill	Sedentary	40.0	331	15.6	24.8	Core	Resident
Brown Honeyeater	Mobile	31.8	78	4.1	9.7	Peripheral	n/a
Chestnut-rumped Thornbill	Sedentary	30.6	379	30.3	13.0	Core	Resident
Diamond Dove	Mobile	24.7	11	2.1	3.9	Core	Nomadic
Yellow-rumped Thornbill	Insufficient data	24.7	1	2.5	10.8	Core	Resident
Hooded Robin	Insufficient data	21.2	230	6.6	19.3	Peripheral	Resident
Willie Wagtail	Insufficient data	17.7	4	3.8	7.0	Core	Resident
Redthroat	Sedentary	16.5	334	70.5	19.4	Peripheral	n/a
Western Gerygone	Insufficient data	15.3	0	0.0	6.5	Core	Resident
White-browed Babbler	Sedentary	15.3	277	28.9	35.7	Core	Resident
Western Bowerbird	Sedentary	14.1	324	12.5	n/a	n/a	Resident
Grey-headed Honeyeater	Mobile	14.1	0	0.0	7.7	Casual	Resident
Mistletoebird	Insufficient data	12.9	0	0.0	8.3	Peripheral	Resident
Southern Whiteface	Insufficient data	10.6	155	18.7	13.0	Core	Resident
Grey-crowned Babbler	Sedentary	10.6	320	18.4	16.6	Casual	Resident
White-winged Triller	Mobile	9.4	0	0.0	0.9	Casual	Nomadic
White-plumed Honeyeater	Insufficient data	9.4	86	19.0	20.2	Casual	Resident
Yellow-throated Miner	Insufficient data	9.4	371	8.3	15.7	Peripheral	Resident
Pied Honeyeater	Mobile	7.1	0	0.0	0.9	n/a	Nomadic
Crimson Chat	Mobile	7.1	0	0.0	5.6	Casual	Nomadic
Budgerigar	Mobile	3.5	0	0.0	4.2	Peripheral	Nomadic

The Splendid Fairy-wren was encountered in 69% of banding events in our study. For this species, 23.6% of all captures were recaptures, with a mean time elapsed between encounters of 290 days and a total recapture rate of 31.8%. Individuals were caught at all study sites throughout the year. Splendid Fairy-wrens are social birds that live in family groups in relatively small territories. The high capture rate for this species occurred even though it is likely to be under-represented in our study because its terrestrial foraging habits may often take individuals underneath mist nets or, in common with other small passerines, they may bounce out of nets and avoid capture. Data in Higgins *et al*. (2001) and from the ABBBS indicate a 30% recapture rate within 10km of point of capture for this species and recaptures in the area of original capture up to 11 years after banding. Our study supports existing evidence that this species displays high site fidelity and may be regarded as sedentary. Other authors have listed this species as ‘core’ to *Acacia* habitat (Cody 1994; Pavey and Nano 2009).

Yellow-rumped Thornbills were caught in moderate numbers, but their recapture rate (2.5%) was much lower than those of two other co-existing species, the Inland *Acanthiza apicalis* (15.6%) and Chestnut-rumped Thornbills (30.3%). Yellow-rumped Thornbills are more terrestrial in their foraging behaviour than the other central Australian thornbills, and so may be more likely to move beneath mist nets, which may limit the chance of capture. It is noted in ABBBS data that recapture rates for this species are substantially lower than for other thornbills, although individuals have been recaptured up to thirteen years after original capture. Higgins and Peter (2002) documented a 14% recapture rate for Yellow-rumped Thornbills in other parts of their range, measurably lower than that in other thornbill species with higher degrees of site fidelity. This species, as well as the Inland and Chestnut-rumped Thornbill, was listed as ‘core’ to *Acacia* shrubland habitat by Cody (1994) and as resident by Pavey and Nano (2009). It may be, therefore, that whilst the species frequently resides in Mulga, it does not display the same degree of site fidelity as other thornbill species or may occupy larger home ranges. We did not have sufficient information to definitively rank this species as sedentary or mobile. The other central Australian thornbill species are also probably under-represented in our study, mainly due to their tendency to bounce out of mist nets in even a light breeze. Nevertheless, Higgins and Peter (2002) classify both Inland (30% recapture rate) and Chestnut–rumped Thornbills

(18%) as sedentary, a conclusion supported by our results. The Slaty-backed Thornbill *A. robutirostris*, also present at our sites (Appendix 1), was not among the species that we trapped more than 10 times. When observed, it seemed to be foraging mainly in the upper strata of the shrubland above the mist nets, which probably accounts for our low capture rates.

Red-capped Robins *Petroica rutenovii* were caught at all sites in every month of the year. They exhibited a recapture rate >10% and individuals were caught at their original capture site up to 600 days after being banded, indicating a degree of site fidelity. Higgins and Peter (2002) describe Red-capped Robin movements as unclear; they are designated as sedentary in some parts of their range, but migratory or nomadic in others. In arid Australia, they are thought to be sedentary, with a 22% recapture rate (Higgins and Peter 2002), which is consistent with our classification. Hooded Robins *Melanodryas cuculatta* were encountered in similar numbers as Red-capped Robins in our study and several individuals were recaptured after a year, suggesting a level of site fidelity; however, we did not have enough information on the species to definitively categorise it as sedentary. Red-capped Robins were found at all sites and captures were dispersed over the months of the year, which is consistent with Pavey and Nano's classification of the species as resident in *Acacia* woodland. They were also described as sedentary by Higgins and Peter (2002); however, observations have suggested some movement in central Australia.

The Rufous Whistler *Pachycephala rufiventris* was one of the more commonly encountered species in our study. Individuals were caught at all sites in all months of the year, and 13% of banded individuals were recaptured at the site of initial capture, some up to three years after they were originally banded. The overall recapture rate was 14.9%. Their movements are poorly understood. They are thought to be resident in the inland and possibly seasonal migrants near the coast (Higgins and Peter 2002), and have a national recapture rate of 24%. Of the eighty-seven individuals caught and banded during our study, fifty-five had adult plumage on initial capture; of these, 11 were recaptured, sometimes some years after the initial encounter. Of the birds with sub-adult or juvenile plumage which made up approximately 30% of the sample, only one was recaptured, nine days after it was initially banded. This turnover of juvenile birds would be expected to some extent in all species in the study and has been documented in other studies (e.g. Debus 2006).

Spiny-cheeked and Singing Honeyeaters were caught at all banding sites in all months of the year. More than 10% of individuals of each species captured were recaptured, and they were among the species most commonly recaptured, when scaled for the initial number banded. Elapsed time between recaptures for both species indicates that some members of the populations displayed a high degree of site fidelity, remaining at a site for over five years. These medium-sized honeyeaters are readily caught in mist nets, as they fly low down and at speed through the shrubs. Higgins *et al.* (2001) documented these species as sedentary in some parts of their range, but more mobile in others. The documented recapture rate nationally for Spiny-cheeked Honeyeaters is 6.4% (substantially lower than in our study) and for Singing Honeyeaters 21% (higher than our study). There is clear evidence that both species were sedentary at our sites.

Small numbers of White-plumed Honeyeaters were caught throughout the year at two sites closest to their preferred riverine environments. A small number of recaptures was recorded, with the longest time between recaptures being 122 days. Higgins and Peter (2002) consider this species to be sedentary (20% recapture rate) and our limited data tentatively support this categorization, although we have insufficient information to draw definitive conclusions.

Species not displaying site fidelity

In contrast to the species discussed above, there were other commonly-encountered species that were rarely recaptured, and we suggest that this is clear evidence against long-term site fidelity. In addition to the honeyeaters already discussed, we banded more than ten Grey-headed Honeyeaters *Lichenostomus keartlandi*, Brown Honeyeaters and Pied Honeyeaters *Certhionyx variegatus*. These species were caught at all sites and captures were spread throughout the year, but there were few recaptures. Hence, we have classified these species as mobile, which is consistent with honeyeaters often being generally regarded as nomadic or locally nomadic in response to flowering. However, this contrasts with the high degree of site fidelity that was apparent in Singing and Spiny-cheeked Honeyeaters, which may be mobile only within smaller home ranges.

Diamond Doves were caught in most months of the year and were present at four out of five sites. However, there were just a few recaptures, within two weeks of initial banding, indicating low site fidelity for this species. Although this species is clearly regularly present in *Acacia* shrubland and can be considered 'core' to this habitat (Cody 1994), it appears to be highly mobile. Our data are consistent with previous knowledge of the species; ABBBS data also indicate a low rate of recapture for Diamond Doves and Pavey and Nano (2009) list them as nomadic. Like many granivores, Diamond Doves may need to move frequently to track seed resources stimulated by local rain. Most of the Diamond Doves captured in this study were caught over two days in May 2010 after a substantial rainfall event in the preceding three months. Resource-based movements of this species have previously been documented (Higgins and Davies 1996) and are the most likely explanation for low recapture rates in our study.

Budgerigars *Melopsittacus undulatus* are well-known to be nomadic (Wyndham 1982). Small numbers of individuals were caught on a few occasions in our study, but there were no recaptures. In other banding studies, local recaptures have occurred only in the days soon after initial banding. The species is described as nomadic and irruptive (Higgins 1999). Other parrot species found in central Australia are relatively large birds that are dispersed in pairs or small groups across the landscape. They do not commonly congregate in large flocks like Budgerigars. Whilst they spend time foraging in the lower strata and on the ground, their size makes them unlikely to be caught in mist nets, and if they fly into nets they often do not become tangled and hence find their own way out. Thus, the Budgerigar was the only parrot that we banded in sufficient numbers to assess levels of site fidelity.

The Zebra Finch was one of the most commonly encountered species in this study, with an encounter rate of close to 60%

across all sites in all months of the year. Zebra finches had a low recapture rate of 3%, with few longer-term recaptures; hence we have classified them as mobile. In other studies, Zebra Finch recaptures have been up to 23% (Higgins *et al*. 2006) and investigations based on visual observations have labelled them as resident (Pavey and Nano 2009). However, this species is known to be highly mobile within its extensive home range, with movements being strongly influenced by food and water availability (Zann *et al*. 1995). Our study was not conducted in grassland habitats favoured by Zebra Finches and was not near water. Nets set close to sources of available water would probably produce higher rates of recapture if finches return repeatedly to the same water source.

Species with insufficient data for categorization and the limitations of mist-netting

There are some species for which we had insufficient data to be able to make meaningful inferences about whether they remain resident at a local site for long periods, some of which have been mentioned above. Information on these species was often limited due to the small numbers captured and banded, which is partly due to the limitations of mist netting for capturing some species.

For example, Western Gerygones *Gerygone fusca* were not regularly caught in our study, even though they were observed at four out of five sites. Mist netting, as applied in our study, appears to be ineffective for sampling this species. Western Gerygones are upper strata foliage gleaners and tend to fly over the top of mist nets (Higgins and Peter 2002). Due to their small size, they may also tend to bounce out of mist nets. This species shows no sign of regular movements in central Australia (i.e. it seems to be sedentary), although there are thought to be seasonal movement in south-western Western Australia (Higgins and Peter 2002). Similarly, some species (e.g. Southern Whiteface *Aphelocephala leucopsis*) did not meet our criteria to be classified as having high site fidelity, but showed some clear evidence of sedentary behaviour. Thus, it is important to note that the exclusion of a species from being classified as sedentary based on our research does not imply mobility.

Banding studies offer the opportunity to gain information on bird communities that is difficult to obtain, or unobtainable, through other survey methods (Dunn and Ralph 2004); for example, through the capture of cryptic, non-singing species. However, mist-netting has its own set of challenges. Variation in the capture efficiency of mist nets is brought about by mesh size, vegetation height, weather (including wind velocity), net visibility (due to cloud cover and other influences) and body-size of the species, as well as aspects of the flight and territorial behaviour of each species (Lukas and Leuenberger 1996; Lovei *et al*. 2001). Weather conditions can play a role in biasing mist net capture, with small birds such as thornbills bouncing off or seeing and avoiding the net, especially if the nets have been open for long periods (Saffer 2001; Faaborg *et al*. 2004).

Pardiek and Wade (1992) found that small individuals (<20 g) escaped more frequently than large individuals from 36mm nets, with only approximately 50% being retained, and Lukas and Leuenberger (1996) felt that wind added a 7-16% probability of escape to this effect. Saffer (2001) stated that the retaining efficiency of 25mm mesh nets for sparrow-sized passerines was 63%. On several occasions individuals of both small (<15 g) and large (>100 g) species were observed escaping from our 31mm nets. Furthermore, foraging height must also be considered. Mist nets appear to be most effective in catching fast-flying, medium-sized birds (15-50g) that forage in low to medium strata. Hence, the proportion of the community sampled may decrease as canopy height increases. In summary, mist netting over-represents some species in the community and under-represents others (Hardy and Farrell 1990; Faaborg *et al*. 2004; Mallory *et al*. 2004). Just as care needs to be taken in drawing conclusions about population size and demography based on mist netting data alone (Ballard *et al*. 2004), conclusions drawn from our mist netting study about site fidelity need to take into account the limitations of the method. Whereas large numbers of recaptures and long intervals between recapture of individuals is irrefutable evidence for high levels of site fidelity, results for species which did not apparently demonstrate high site fidelity and for species captured in low numbers need to be treated more cautiously.

Differences among species in the rate of decline of recaptures with elapsed time from initial banding may reflect differences in mobility, but could also result from disparities in longevity, mortality or dispersal patterns. Data from ABBBS indicate that many birds in our study are long-lived, surviving more than ten years (Baker *et al*. 1999). Mortality rates in populations of small Australian passerines have been estimated at between 32% and 58% (Debus 2006) and the reproductive potential of most species in our study, and their ability to produce multiple clutches over an extended breeding season, suggest that high mortality rates may be a factor contributing to low recapture rates. Our interpretations of the data have attempted to take these considerations into account.

Comparisons with banding studies in other regions

Similar general patterns of site fidelity to those that we have reported have been found in other long-term banding studies in a variety of Australian locations and habitats, from tropical rainforests (Frith and Frith 2005) to sclerophyll woodlands and forests (Tidemann *et al*. 1988; Leishman 2000). Irrespective of habitat, there seems to be a group of small, primarily insectivorous species of the mid- to lower vegetation strata that are sedentary. The number of sedentary species found in North Queensland rainforest (Frith and Frith 2005) and high-altitude *Eucalyptus* forest in the Australian alpine region (Tidemann *et al*. 1998) was almost double the number identified in our study and may be correlated with higher rainfall and therefore productivity at these sites. In contrast, Leishman (2000) found evidence of a similar number of sedentary species in *Eucalyptus* forest in eastern Australia as in our *Acacia* sites. It appears that species such as fairy-wrens, scrubwrens, thornbills, robins and whistlers may be resident for long periods of time across these different habitats (Tidemann *et al*. 1988; Leishman 2000; Frith and Frith 2005). In each of these banding studies, newly-banded immature birds were recaptured less often than adults, suggesting that the sedentary individuals are older, territorial birds. Estimates of the number of sedentary species from all banding studies are necessarily conservative, as more species than suggested by mark-recapture may be sedentary: uncertainty exists due to factors such as ‘shyness’ of mist nets, inconsistent ease of trapping, use by the birds of habitat strata out of mist net range, or spatial movements within home ranges that are larger than the areas sampled by nets (Leishman 2000; Ballard *et al*. 2004; Frith and Frith 2005).

Conclusions

Our results are broadly consistent with Cody's (1994) classification of the birds of arid *Acacia* shrublands and Pavey and Nano's (2009) classification based on surveys in the Finke bioregion. Together, these studies indicate that a predictable suite of bird species occurs in arid *Acacia* shrubland habitats over different months of the year and among different years. By following individual birds through time, our study enabled additional conclusions to be drawn about the sedentary versus mobile behaviour of these species. It also raised some interesting points of difference with previous studies that have relied on purely visual methods. For example, our very high recapture rates for Redthroats across several sites suggest that the species is probably a sedentary resident, at least in our study region, although it was previously described as peripheral to *Acacia* shrublands (Cody 1994) or simply not recorded (Pavey and Nano 2009). Redthroats are cryptic when not calling and their presence in the community is easily underestimated in visual surveys. Our results demonstrate that mark-recapture studies conducted over a long time-span can provide important insights into bird communities that are not easily obtained through observational techniques.

Overall, a significant proportion of small passerines encountered in our study displayed sedentary behaviour, resembling that found among suites of birds in coastal areas (Marchant 1982; Frith and Frith 2005). Despite the high variability of rainfall-driven resources in space and time in central Australia, the degree of site fidelity found amongst the suite of species present in *Acacia* shrubland suggests that many of them can persist in a single location over long time periods and be sustained by the resources available in the local area even during periods of low rainfall.

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Appendix 1

Species for which fewer than ten individuals were banded, showing comparative capture rates. Species are ordered by the rate at which they were captured across all banding events, from highest to lowest.

Species		No. banded	No. sites captured (n = 5)	Capture rate (% of all banding events)
Crested Bellbird	*Oreoica gutturalis*	9	4	10.6
Slaty-backed Thornbill	*Acanthiza robutirostris*	7	3	7.1
Little Button Quail	*Turnix velox*	6	2	4.7
Variegated Fairy-wren	*Malurus lamberti*	4	2	4.7
Grey Shrike-thrush	*Colluricincla harmonica*	5	2	4.7
Rufous Songlark	*Cinclorhamphus mathewsi*	9	2	4.7
Mulga Parrot	*Psephotus varius*	4	2	3.5
Red-browed Pardalote	*Pardalotus rubricatus*	4	2	3.5
Black-faced Woodswallow	*Artamus cinereus*	5	2	3.5
Grey Butcherbird	*Cracticus torquatus*	3	2	3.5
Horsfield's Bronze Cuckoo	*Chalcites basalis*	2	2	2.4
White-fronted Honeyeater	*Pumella albifrons*	5	1	2.4
Pied Butcherbird	*Cracticus nigrogularis*	5	2	2.4
Common Bronzewing	*Phaps chalcoptera*	1	1	1.2
Crested Pigeon	*Ochyphaps lophotes*	3	2	1.2
Bourke's Parrot	*Neosephotus bourkii*	1	1	1.2
Weebill	*Smicromis brevirostris*	3	1	1.2
Striated Pardalote	*Pardalotus striatus*	1	1	1.2
Black Honeyeater	*Sugomel nigrum*	1	1	1.2
Varied Sittella	*Daphoenositta chrysoptera*	3	1	1.2
Magpie Lark	*Grallina cyanoleuca*	1	1	1.2
Painted Finch	*Emblema pictum*	1	1	1.2

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Faecal analysis reveals the insectivorous diet of the Black-breasted Button-quail *Turnix melanogaster*

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The threatened Black- breasted Button-quail *Turnix melanogaster* is thought to have an omnivorous diet comprising seeds and invertebrates; however, very little study has been undertaken to confirm or refute this claim. A thorough understanding of a species' diet is required for its effective conservation management. To determine the species' diet, *T. melanogaster* faeces were collected from within or near platelets found on Fraser Island and in Yarraman State Forest, two different habitats, and analysed microscopically. Analysis showed that *T. melanogaster* has a diet comprised almost entirely of invertebrates and that it preferentially preys upon Dermaptera, Pseudoscorpionida and Coleoptera.

INTRODUCTION

The Black-breasted Button-quail *Turnix melanogaster* is a poorly known bird endemic to the east coast of Australia. It is listed as Vulnerable both nationally (Department of the Environment 2016) and in Queensland (Department of Environment and Heritage Protection 2013). In New South Wales, where it has become increasingly rare and records are few, it is listed as Critically Endangered under the Threatened Species Conservation Act 1995 (Major 2009). It is listed as a Critical species for the Australian Government Department of Environment and Heritage protection, Back on Track Species Prioritisation Framework (Department of Environment and Heritage Protection 2015).

T. melanogaster has been little researched and the exact composition of its diet is unknown. It is thought to be omnivorous, consuming both seeds and invertebrates (Hughes and Hughes 1991; Marchant and Higgins 1995; McConnell and Hobson 1995), the diet of captive individuals includes various arthropods and seeds (Phipps 1976; Mills 1985; Roulston 1992). Smyth and Pavey (2001) noted that the diet of *T. melanogaster* included crustaceans; however, it was not documented how this was determined. A dietary study by McConnell and Hobson (1995) examined the contents of 12 *T. melanogaster* faecal samples collected in May 1993 at Redwood Park, Toowoomba, southeast Queensland. Food items found during the faecal analysis included members of the Araneae, Formicidae, Chilopoda, Diplopoda, Coleoptera and Gastropoda. The dominant components were parts of Formicidae and Coleoptera, remnants of Chilopoda, Diplopoda and Gastropoda being scarce. Prior to the current investigation, McConnell and Hobson's (1995) research was the only study of the diet of *T. melanogaster*. The present paper reports the results of analysis of *T. melanogaster* faeces collected at two locations in Queensland.

METHODS

Study areas

The study was conducted at two locations, Fraser Island and Yarraman State Forest; these populations are 165 km apart. On Fraser Island (25.2398º S, 1534.1325º E) *T. melanogaster* is recorded in littoral forest along the east coast, which receives 1,572 mm of rainfall annually (Australian Bureau of Meteorology 2017). Yarraman State Forest (26.8531º S, 151.9053º E) supports dry rainforest in the form of Araucarian microphyll vine forest and has an annual rainfall of 816 mm (Australian Bureau of Meteorology 2017). These locations were selected because they comprise two different habitat types used by *T. melanogaster*.

T. melanogaster faeces were collected in both study locations from or near platelets, the scrapes made in the substrate by foraging button-quail. The Painted Button-quail *T. varius* has also been recorded at both locations and therefore certain criteria had to be met to ensure that the faeces collected could reliably be attributed to *T. melanogaster.* These criteria were that: (1) faeces were only collected from habitat suitable for *T. melanogaster* and this was either dry rainforest or littoral forest, (2) the presence of *T. melanogaster* was confirmed at each faecal collection location either visually or by the use of remote camera traps, and (3) the faeces included in the analysis had to be the correct size and shape, as previously described for the species (McConnell and Hobson 1995). A study by Lees and Smith (1998) indicated that faeces of *T. melanogaster* were not distinguishable from those *T. varia*. However, the birds in their study were from a captive population fed on an artificial diet and consequently their results cannot be reliably translated to a wild situation. Each faecal sample was stored in a labelled 5 mL plastic, screw-cap, specimen container and frozen as soon as possible after collection. Before analysis, the faeces were softened and broken apart by adding 1 mL of water to each container, which was placed in boiling water for 10 minutes, cooled and shaken vigorously, and the material was preserved by adding 3 mL of methylated spirits.

Samples were inspected using a SZ40 Olympus stereo microscope to identify plant and animal material. Invertebrates were identified by examining key fragments which were diagnostic for the different invertebrate groups (i.e. taxa and less well defined categories, such as insect larvae). The number of invertebrate groups in each sample was counted and recorded.

A reference collection was assembled which encompassed the diversity of Insecta, Arachnida, Entognatha, Diplopoda, Chilopoda and Crustacea found at the study sites. This reference collection was collected from both study sites using pitfall traps and Tullgren funnels. Pitfall traps comprised 250 mL plastic containers filled with 50 mL of 40% ethylene glycol. They were left open *in situ* for seven days. At Yarraman, 105 pitfall traps were used and at Fraser Island 50 were employed. The pitfall traps were placed in areas where platelets were evident and faeces had been collected. Leaf litter was collected from each study location and processed in Tullgren funnels. The leaf litter was collected from 105 individual sites in Yarraman State forest and 50 on Fraser Island. At each individual site, 6 L of leaf litter was collected, again in areas where platelets were evident and faeces had been collected. A 60-watt reflector globe was used to heat the Tullgren Funnel, which was operated for seven days. The findings of previous studies using insect fragments to determine avian diet were also used as a reference (Ralph *et al*. 1985; Michalski *et al*. 2011).Reference texts were used to assist in the identification of fragments, including those published by CSIRO (1970), Shattuck (1999), Beccaloni (2009), Bonato *et al*. (2010), Hangay and Zborowski (2010), Lawrence and Ślipiński (2013), Maruzzo and Bonato (2014) and Rentz (2014).

The prey preference of *T. melanogaster* at each study location was calculated using Pearre's Selection Index (V) (Pearre 1982). The index, V, returns a value ranging from -1 (strong negative selection) to +1 (strong positive selection), a selection index of zero indicating that there was neutral selection of prey. Pearre's Selection Index was calculated as:

$$Va = \frac{(a_d * b_e) - (a_e * b_d)}{\sqrt{a * b * d * e}}$$

where *Va* is the Pearre's Selection Index for prey selection of the prey species *a*, a_d is the relative abundance of species *a* in the diet, b_e is the relative abundance of all species other than *a* in the environment, a_e is the relative abundance of species *a* in the environment, b_d is the relative abundance of all species other than *a* in the diet, $a = a_d + a_e$, $b = b_d + b_e$, $d = a_d + b_d$, $e = a_e + b_e$.

Pearre's Selection Index was tested for statistical significance using a chi-squared test:

$$\chi^2 = \frac{(a_d * b_e - a_e * b_d)^2}{(a * b * d * e)}$$

where $n = a_d + a_e + b_d + b_e$. Alpha was set at 0.05.

Pearson's correlation coefficients (*r*) were calculated to determine the strength of the associations between the invertebrates present in the environment and those found in the faecal samples.

RESULTS

Sixty-four faecal samples were collected and examined, and 13 invertebrate groups were identified. The 38 faecal samples from Yarraman State Forest contained 13 invertebrate groups, the mean per sample being 3.6 groups, with a range of 1-8. The 26 faecal samples from Fraser Island contained 11 groups, the mean per sample being 2.8, with a range of 0-6.

Faecal analysis focused on identifying key fragments known to be diagnostic for the different invertebrate groups. Some of the fragments found in the faeces of *T. melanogaster* are shown in Figures 1, 2 and 3. A list of the key fragments with associated notes is given in Table 1. Most key fragments were mandibles, legs, head capsules and other chitinous pieces that are resistant to digestion. Softer fragments, such as wings and abdominal segments, were scarce; however, the integument of Dipteran larvae was frequently recorded. The size of the original prey items was estimated from some fragments. Coleoptera and Hymenoptera prey sizes were estimated using formulae presented by Calver and Wooller (1982) based on the relationship between the head width of the prey item and its total length. The original sizes of Pseudoscorpione specimens were estimated by comparing fragments of chelae in the faeces with those of complete specimens trapped at the same site. A complete snail shell found in faeces was measured, and its metrics are given in Table 2. The size of some prey items recorded in the faecal samples indicated that most of the diet may comprise small invertebrates of <10 mm.

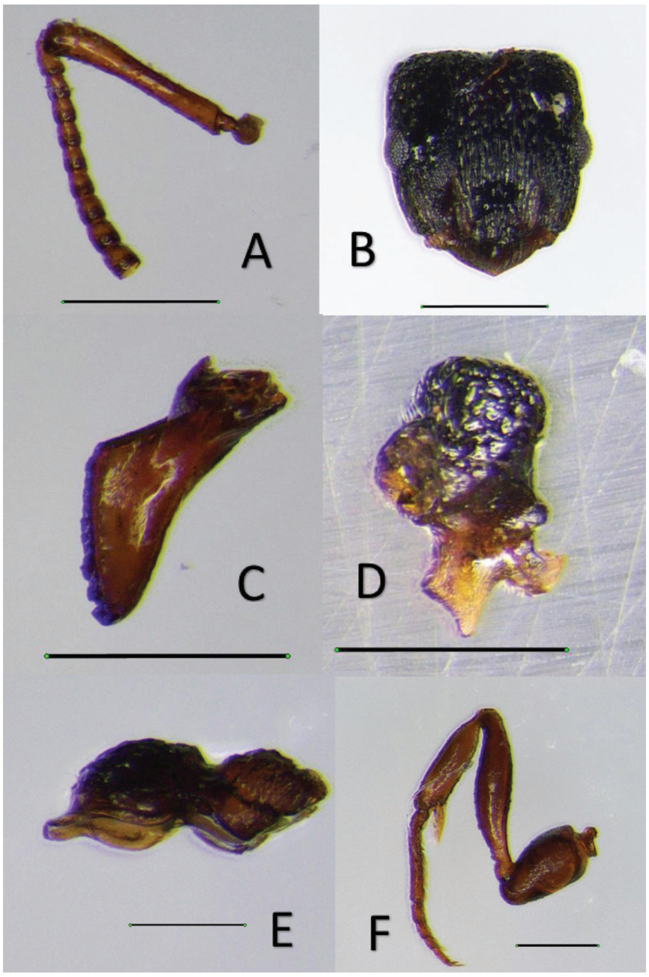

Figure 1. *Formicidae fragments found in the faeces of T. melanogaster, the horizontal line below the item represents 500 µm. A) antennae; B) head capsule; C) mandible; D) petiole; E) mesoma; F) leg.*

Fraser Island

In faecal samples from Fraser Island, Coleoptera (88.5%) was the most frequently observed invertebrate group, Dermaptera (53.8%) and Araneae (42.3%) were also frequently observed (Figure 4), whilst insect larvae (3.8%), Blattodea (3.8%) and Gastropoda (3.8%) were only occasionally found.

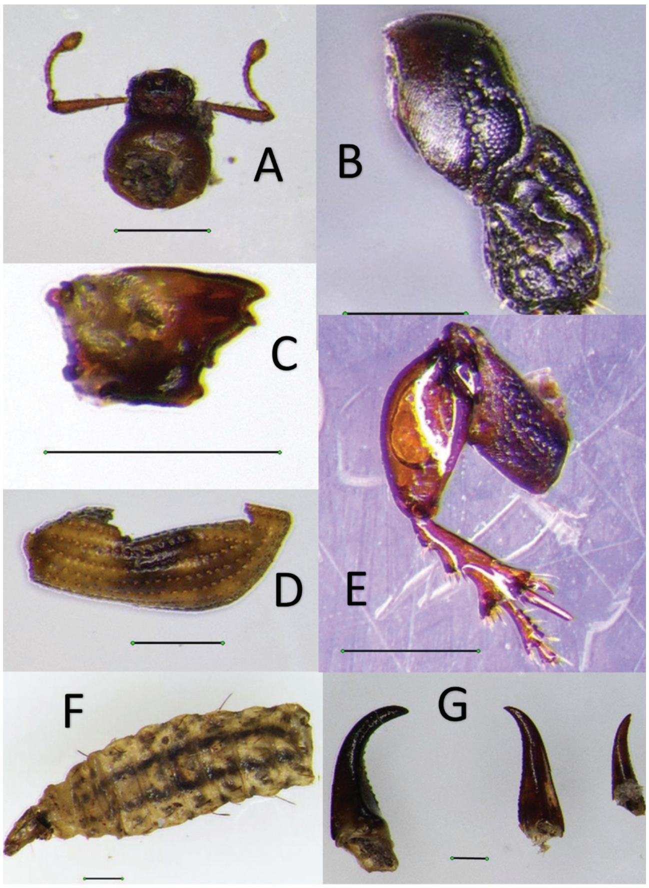

Figure 2. *Insect fragments (other than Formicidae) found in the faeces of T. melanogaster; the horizontal line represents 500 µm. A) head; (Coleoptera: Curculionidae); B) Head (Coleoptera: Curculioniodea); C) mandible, (Isoptera); D) elytron, (Coleoptera); E) leg (Coleoptera); F) larva, (Diptera); G) cerci (Dermaptera).*

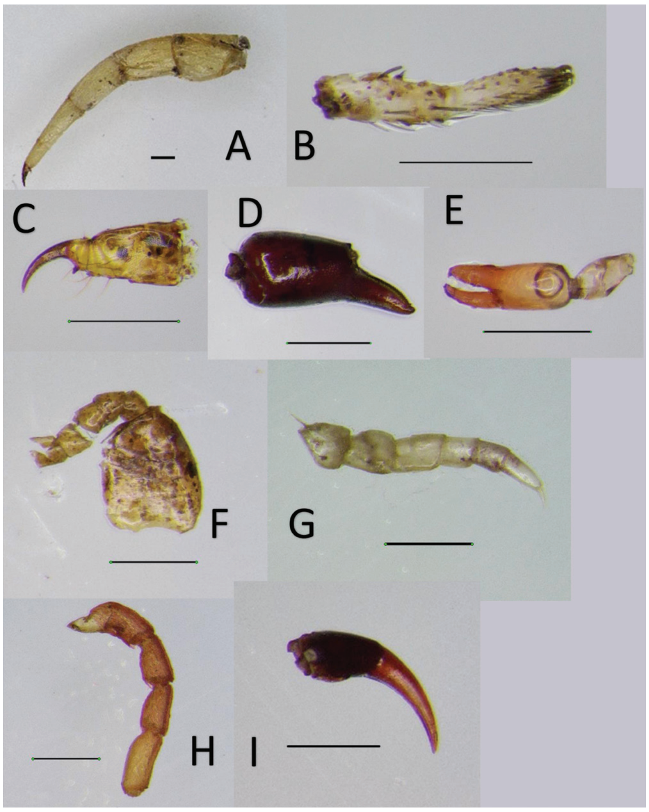

Figure 3. *Figure 3. Arthropod fragments (other than Insecta) found in the faeces of T. melanogaster; the horizontal line represents 500 µm. A) leg (Chilopoda); B) terminal portion of leg (Araneae); C) forcipule (Chilopoda); D) chela with moveable piece separated (Pseudoscorpione); E) chelae (Pseudoscorpione); F) head with one antenna attached (Chilopoda); G) leg (Diplopoda); H) leg (Acari: Trombidiidae); I) fang (Araneae).*

Some Coleopteran fragments were identified as belonging to the family Curculionidae. The invertebrate groups detected in the faeces of *T. melanogaster* on Fraser Island are shown in Figure 4. The samples were dominated by invertebrate remains, which comprised >99% of 13 samples. All faeces contained sand, vegetation (in the form of leaves, roots and other fibrous material) comprised 5-20% of nine samples, and unidentified seeds were present in four and feathers in seven samples.

The abundance of the various invertebrate prey in the environment where faecal sampling took place was reflected in the faeces of *T. melanogaster* (Figure 4). The correlation between the large invertebrates (≥ 2.5 mm) recorded from Fraser Island in the pitfall traps and Tullgren funnels combined and the invertebrates present in the faeces was significant ($r = + 0.55$, $n = 21$, $P < 0.01$). The invertebrates found in the faecal samples represented 55% of the large (≥ 2.5 mm) invertebrate diversity recorded on Fraser Island from the pitfall traps and Tullgren funnels.

Coleoptera (present in 88.5% of faecal samples) and Dermaptera (present in 53.8%) were the only two invertebrate groups significantly positively selected by *T. melanogaster* at Fraser Island ($P < 0.05$). The Pearre's Selection Indeces for Coleoptera ($V = 0.208$, $\chi^2 = 5.449$, $P < 0.05$) and Dermaptera ($V = 0.301$, $\chi^2 = 11.445$, $P < 0.01$) were significant (Table 3). Nine groupswere found to be significantly rejected or avoided ($P < 0.05$), namely Diptera, Hemiptera, Hymenoptera (other than Formicidae), Formicidae, Lepidoptera, Orthoptera, unidentified insect larvae, Acari and Isopoda (Table 3). None of these invertebrate groups were present in more than 35% of faecal samples.

Yarraman State Forest

Formicidae (97.4%) were a major component of *T. melanogaster* faeces collected from Yarraman State Forest, being absent from only one faecal sample. Coleoptera (84.2%) and insect larvae (50.0%) were also frequently found in the faeces and Isoptera (5.3%), Blattodea (7.9%) and Acari (7.9%) were occasionally recorded (Figure 5). Insect larvae were recorded in 20 of the 38 faecal samples; of these, 15 were Dipteran larvae belonging to the family Stratiomyidae (Soldier fly) and the remainder were possibly Coleoptera larvae, based on mandible and leg morphology. A leg belonging to an Acari species was identified to the family Trombidiidae (Red velvet mite). Several Coleoptera fragments were identified as being ascribable to the family Curculionidae (weevil). Plant material was infrequent in the Yarraman State Forest faecal samples, being present in only one sample of which it comprised < 2%. The remaining 37 faecal samples contained >99% of the undigested invertebrate material. Feathers were present in 37.5% of faecal samples.

Table 1

Key fragments of invertebrates found in the faeces of T. melanogaster that were used in identification.

Invertebrate group	Structure	Notes
Coleoptera	Elytra	Found as fragments, distinctive microsculpture of stria and strial punctures giving a pitted appearance.
	Legs	Strongly chitinized, variable but usually identifiable structure. Enlarged femur and tibia outer edge often toothed. Basal tarsomes often with tarsal pads, often with two claws.
Coleoptera: Curculionoidae	Head	Frontoclypeal region extended, forming a slender rostrum.
	Antennae	Elbowed antennae - subgeniculate, not to be confused with Formicidae antennae.
Hymenoptera: Formicidae	Head	Distinctive shape, eyes usually present on lateral edges of head. Antennae sockets and frontal carina distinctive, mandibles often absent.
	Mesoma	Variable in shape, sutures between pronotum, mesonotum and propodeum often visible. Leg attachments visible on ventral surface.
	Petiole	Upper surface protruding upwards (node) from attachment to gaster and propodeum. Subpetiolar process may be present.
	Leg	Comprises five segments: coxa, trochanter, femur, tibia and tarsus. Femur and tibia elongated. Tibial spur often present between junction of tibia and tarsus. Tarsus consists of five segments ending in claws.
	Antennae	Elbowed antennae, consisting of longer section - scape, and many shorter sections - funiculus.
	Mandibles	Highly variable, but typically consists of outer margin (smooth), masticatory margin (serrated edge created by teeth and denticels), basal angle and basal margin.
Diptera: Stratiomyidae	Larva	Elongated, flattened with obvious protruding head, and shagreen integument.
Chilopoda	Legs	Only five distal segments of leg recorded; trochanter, femur, tibia, tarsus and pretarsus. Entire structure was faint orange in coloration.
	Forcipules	Modified leg with distinctive shape. Tarsungulum curved and ending in sharp point and usually darker than other structures. Denticle present, folds between tarsungulum, tibia, femur and trochanter-prefemur evident.
Diplopoda	Leg	Segments of leg mostly of similar length though decreasing in width towards the terminal segment. Eight distinct section; coxa, trochanter, prefemur, femur, postfemur, tibia, tarsus and claw.
	Tergite	Usually broken and incomplete, however complete segments consisting of dorsal and ventral tergites were found forming a distinctive ring structure.
Isoptera	Mandible	Always found detached from head. Strongly sclerotised distinctive shape and arrangement of teeth.
Araneae	Legs	Always found in fragments. Surface is covered in fine and thick bristle-like hairs. Most distinctive were two claws at the terminal portion of the tarsus. Leg segments were straight-sided and not tapered at joints as in other arthropods.
	Fang	Found separated from remainder of chelicera. Curved structure leading to sharp point.
Acari: Trombidiidae	Leg	Covered in fine red setae. Legs with seven segments; coxa, trochanter, femur, genu, tibia and tarsus. Tip of tarsus (ambulacrum) rounded.
Blattodea	Head	Usually a triangular shape. Deep antenna sockets rostral to compound eyes. 'Y'-shaped ecdysial lines between eyes terminating in ocelliform spot.
Dermaptera	Cerci (forceps)	Smooth outer (convex) edge and serrated inner (concave) edge. Distinctive articulative groove on dorsal surface where cercus attaches to abdomen, triangular cross-section pointing dorsally.
Pseudoscorpiones	Chelae	Found entire or with moveable finger separated. Inside margin of fingers with many minute teeth. Specimens in this study were an orange or red colour.
Snail	Shell	Small fragment of shell. Distinctive shape and concentric spiralling structure.

Table 2

The size (total length (mm)) of various prey items found in the faeces of T. melanogaster.

Prey Item	Total length (mm)
Coleoptera	7.5
Curculionidae	9.1, 10
Formicidae	2.2, 2.7
Pseudoscorpiones	3, 6.2
Gastropoda	0.68

The abundance of invertebrate prey items collected in the environment where faecal sampling took place was again reflected in the faeces of *T. melanogaster* (Figure 5). The correlation between the large invertebrates ($\geq$2.5 mm) collected at Yarraman State Forest and the invertebrates present in the faeces was significant (r = + 0.77, n = 24, P < 0.001). The invertebrate groups identified in the faeces represented 52% of the large invertebrate ($\geq$2.5 mm) diversity recorded at the site from pitfall traps and Tullgren funnels.

Dermaptera (present in 28.9% of faecal samples) and Pseudoscorpiones (in 13.2%) were the only invertebrate groups that were significantly positively selected (P < 0.01) by *T. melanogaster* at Yarraman State Forest. Pearre's selection

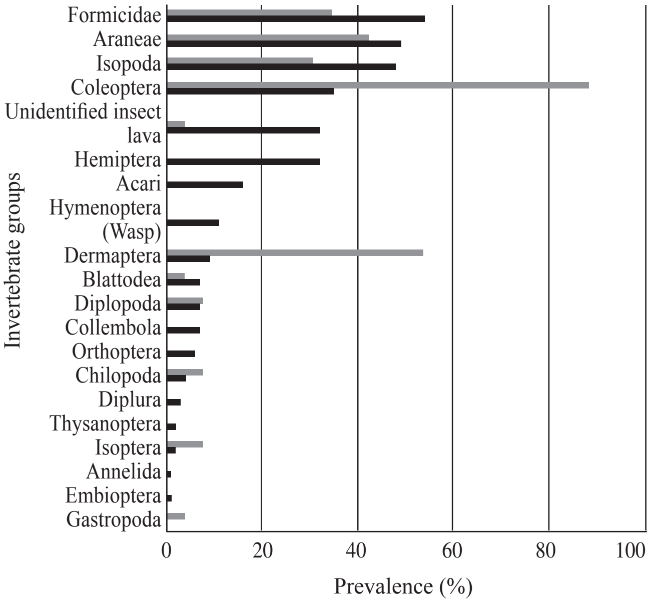

Figure 4. *The prevalence of invertebrates (%) (dark) collected on Fraser Island compared with that found in the faeces of T. melanogaster (light) at the same location.*

Table 3

Pearre's index for prey selection of T. melanogaster on Fraser Island, where the highlighting indicates statistical significance at P < 0.05.

Invertebrate Groups	Pearre's Index (V)	Chi Square (χ2)	P
Blattodea	-0.077	0.742	0.39
Coleoptera	0.208	5.449	0.02
Collembola	-0.195	4.801	0.03
Dermaptera	0.301	11.45	<0.01
Diplura	-0.129	2.113	0.15
Diptera	-0.228	6.545	0.01
Embioptera	-0.076	0.720	0.40
Hemiptera	-0.379	18.12	<0.01
Hymenoptera (other than Formicidae)	-0.238	7.128	0.01
Hymenoptera (Formicidae)	-0.205	5.295	0.02
Isoptera	0.120	1.812	0.18
Lepidoptera	-0.228	6.545	0.01
Orthoptera	-0.194	4.725	0.03
Thysanoptera	-0.106	1.424	0.23
Unidentified insect larvae	-0.402	20.33	<0.01
Unidentified insects	-0.076	0.720	0.40
Acari	-0.282	10.02	<0.01
Araneae	-0.067	0.557	0.46
Chilopoda	0.066	0.544	0.46
Diplopoda	0.005	0.003	0.96
Isopoda	-0.179	4.049	0.04

indeces for Dermaptera ($V = 0.194$, $\chi^2 = 7.472$, $P < 0.01$) and Pseudoscorpiones ($V = 0.179$, $\chi^2 = 6.487$, $P < 0.01$) were both significant. (Table 4). Nine invertebrate groups were significantly rejected or avoided ($P < 0.05$), namely Blattodea, Collembola, Diplura, Diptera, Hemiptera, Hymenoptera (other than Formicidae), Lepidoptera, Orthoptera and Araneae (Table 4).

Table 4

The Pearre's index for prey selection by T. melanogaster at Yarraman State Forest determined from faecal samples. Highlighted values were statistically significant (P < 0.05).

Invertebrate Groups	Pearre's Index (V)	Chi Square (χ2)	P
Archaeognatha	-0.075	1.242	0.27
Blattodea	-0.216	10.61	<0.01
Coleoptera	0.111	1.268	0.26
Collembola	-0.386	33.06	<0.01
Dermaptera	0.194	7.472	0.01
Diplura	-0.148	4.839	0.03
Diptera	-0.359	28.64	<0.01
Embioptera	-0.105	2.455	0.12
Hemiptera	-0.310	21.36	<0.01
Hymenoptera (other than Formicidae)	-0.203	9.166	<0.01
Hymenoptera (Formicidae)	0.035	0.305	0.58
Isoptera	-0.044	0.502	0.48
Lepidoptera	-0.320	22.77	<0.01
Orthoptera	-0.147	4.796	0.03
Psocoptera	-0.105	2.455	0.12
Thysanoptera	-0.091	1.852	0.17
Unidentified insect larva	-0.043	0.579	0.45
Unidentified insect	-0.117	3.051	0.08
Acari	-0.023	0.170	0.68
Araneae	-0.223	11.39	<0.01
Pseudoscorpiones	0.179	6.487	0.01
Scorpiones	-0.075	1.242	0.27
Chilopoda	0.105	2.031	0.15
Diplopoda	0.101	1.731	0.19
Isopoda	-0.122	3.510	0.06

DISCUSSION

Thirteen invertebrate groups were identified in *T. melanogaster* faeces at Yarraman State Forest and Fraser Island. Previously, wild *T. melanogaster* have been documented as preying upon Aranae, Formicidae, Chilopoda, Diplopoda, Coleoptera and Gastropoda (McConnell and Hobson 1995). Captive colonies are frequently fed live invertebrates, including Coleoptera, Dermaptera, Orthoptera and Isopoda (Roulston 1992). The current study extends the known diet of *T. melanogaster* to comprise the following invertebrate groups: Acari, Araneae, Blattodea, Chilopoda, Coleoptera, Dermaptera, Diplopoda, Diptera (larvae), Formicidae, Gastropoda, Isopoda, Isoptera and Pseudoscorpiones.

The size of the original prey items was estimated from some of the fragments found in the faeces. Coleoptera were the largest prey detected, with a specimen estimated to be 10 mm long. Large Pseudoscorpiones up to 6.2 mm were also found, but there was evidence of small invertebrate prey items in the diet. A single Formicidae fragment was judged to be equivalent to a 2.2 mm invertebrate and we also found a Gastropod shell as small as 0.68 mm. The size of some prey items in the faecal samples indicated that most of the diet may comprise small invertebrates of <10 mm.

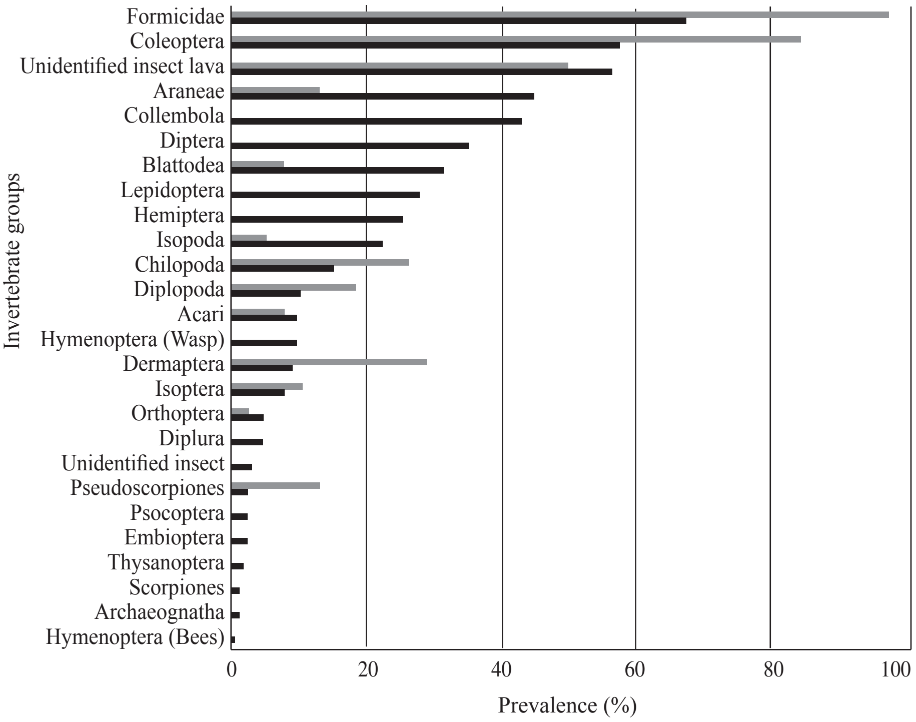

Figure 5. *The prevalence of invertebrates (%) (dark) collected at Yarraman State Forest compared with that found in the faeces of T. melanogaster (light) at the same location.*

Coleoptera, Formicidae and Dermaptera were consistently recorded in the faeces of *T. melanogaster* at both study locations, whilst other arthropods, such as Araneae and unidentified insect larvae, were moderately common. It is evident from this study that *T. melanogaster* are, or at least appear to be, generalist insectivores and are not discriminatory in their diet selection. This would suggest that they are not restricted by any one food resource. The species does, however, appear to be a specialist in its foraging style; the creation of platelets restricts it to invertebrate prey which can be found in the leaf litter or at the soil surface. Apparently, dietary preference does not limit the distribution of *T. melanogaster,* but prey availability might. As the invertebrate prey items were found in leaf litter, it is reasonable to suggest that the presence and type of leaf litter is a vital habitat requirement of *T. melanogaster*.

At both locations surveyed, the invertebrates recorded in the environment were reflected in those found in the faeces in terms of diversity and relative abundance. At Fraser Island 55% of the large invertebrate (≥2.5 mm) diversity recorded in the environment was also recorded in *T. melanogaster* faeces, and at Yarraman State Forest the corresponding figure was 52%. The abundance of invertebrate groups in the faeces was significantly correlated with that in the environment, suggesting that *T. melanogaster* utilise a large proportion of the invertebrate food resources in their environment.

Pearre's Selection Index indicated that *T. melanogaster* were preferentially preying upon certain invertebrate groups and rejecting others. At both locations, there was positive selection for Dermaptera, whilst at Yarraman State Forest *T. melanogaster* positively selected Pseudoscorpiones and at Fraser Island there was positive selection for Coleoptera. At both locations, there was significant rejection or avoidance of both adult Lepidoptera and Diptera, although Dipteran larvae were recorded in the faeces. Both Lepidoptera and Diptera are known to be attracted to the ethylene glycol preservative used in the pitfall traps (Robacker and Czokajlo 2006; Ni *et al*. 2008); this provides an explanation for the abundance of these insects in the pitfall samples, which contrasts with their absence from the faecal samples. Other invertebrate groups are potentially similarly attracted to the preservative, creating a bias in the pitfall method of assessing invertebrate diversity and abundance in the environment. This would alter Pearre's Selection Index, as the invertebrates trapped would appear more available to *T. melanogaster* than they normally are in the leaf litter.

The analysis of *T. melanogaster* faeces provides conclusive evidence of their predation on invertebrates: very little was observed to suggest that plant material constitutes a significant part of their diet as suggested by Marchant and Higgins (1995). However, some seed remains were recorded in the faeces, indicating that at times the diet is omnivorous, although the volume of such remains and/or other plant material in the diet appeared minimal. Faeces collected from Yarraman State Forest overwhelmingly comprised invertebrate material; only one faecal sample contained (a minimal amount of) plant material. The absence of plant material in these samples indicates that *T. melanogaster* in this region were insectivorous. However, more plant material was found in the faecal samples from Fraser Island; 34% contained 5-20% plant material in the form of rootlets and leaf fragments, and there was evidence of seeds in 15% of the samples. Plant material could potentially have been ingested while capturing invertebrates, or it may have been picked up with the faeces by the researchers upon collection, as it was noted during the collection of faeces that small pieces of dirt and plant material from the substrate were attached to the outside of damp faeces. This was seen more frequently at Fraser

Island, as the leaf litter layer was deeper and therefore the faeces were on a layer of decaying vegetation; this contrasted with faecal samples at Yarraman State forest which were on bare soil. The feather barbs present in about half of the faeces from both sites were probably the result of the bird ingesting fragments of feather during preening.

Limitations

There are limitations in this research. In describing a bird's diet from faecal analysis, it should be noted that there will be a bias toward prey items which are resistant to digestion (Calver and Wooller 1982; Jenni *et al*. 1990), such as Coleoptera. This may lead to an over-representation of such prey items and an under-representation of others, such as Isoptera, which have a soft integument and are therefore easily digested. This study was also performed in the some of the warmer months of the year (September-November) when rainfall was prevalent. Thus there is a possibility that the study occurred during a seasonal increase in invertebrate activity, as rainfall is a factor in the increase in abundance and diversity of invertebrate species (Gullan *et al*. 2010). The diet of *T. melanogaster* may be different in the cooler months of the year when insect activity is lower, and consequently seasonal patterns of invertebrate activity would be worth investigating to assess whether the *T. melanogaster's* diet varies during the year.

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Unravelling the mysteries of the Buff-breasted Button-quail *Turnix olivii*: a possible booming call revealed

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No alleged recorded calls of Buff-breasted Button-quail *Turnix olivii* have been directly linked to observations of an individual vocalising. Recorded calls have proven as elusive as a photograph of a live bird. The best descriptions of calls date back to the 1920s. Using spectrograms, we analysed the call structure of 'booming' calls recorded on automated recording units from the vicinity of Buff-breasted Button-quail sightings at Mt Mulligan, north-Queensland. These 'mystery calls' differed from spectrograms of other booming advertisement calls recorded elsewhere of other button-quail species with which the Buff-breasted Button-quail shares its habitat. The 'mystery calls' also differed from those of the Tawny Frogmouth *Podargus strigoides*, Papuan Frogmouth *P. papuensis*, and Common Bronze-wing Pigeon *Phaps chalcoptera*. The structure of the booming, advertisement calls recorded at Mt Mulligan was consistent with earlier descriptions by McLennan (1923) and White (1922) of booming calls of Buff-breasted Button-quail near Coen, north-Queensland. McLennan could imitate the call and successfully attract individuals of the species. We used playback of the 'mystery call' recorded on the automated recorders at Mt Mulligan to similarly entice a Buff-breasted Button-quail female, accompanied by a male, toward our playback location in February 2016, further suggesting that the 'mystery call' could be a recording of the focal species.

INTRODUCTION

A Mystery with History – The buff-breasted button-quail by Rogers (1995) paints a picture of a species of uncertain type locality, with few collected scientific specimens, and with poorly produced illustrations in several bird handbooks due to mistaken identity in some museum collections. During the 1930s, the Buff-breasted Button-quail *Turnix olivii* was lumped as a sub-species of the Chestnut-backed Button-quail *T. castanota*. Rogers (1995) argues that a lack of reported sightings of the species occurred between the 1920s and 1970s, possibly because of these issues. More recently, reported sightings have remained few, due in part to the cryptic and shy behaviour of Buff-breasted Button-quail, but also possibly because of the insufficient attention that bird observers, with greater interest in the more charismatic wet tropics species and environments, have paid to the dry habitat that it occupies (Rogers 1995; Squire 1990; L. Nielsen *pers. comm.*; AWC 2016, 2018; Mathieson and Smith 2017).

Additionally, the Buff-breasted Button-quail appears to be quite rare, although exactly how rare we do not really know. Its density and population size are likely to be low (Rogers 1995) and currently it is listed as endangered under Queensland and Commonwealth legislation. The species is, in reality, still poorly known (Mathieson and Smith 2009), with definitive photographs of a living bird and sound recordings of the species still lacking. Indeed, few people have heard the various calls it has been reported to make (McLennan 1923; Rogers 1995).

McLennan (1923) described five different calls of the Buff-breasted Button-quail, but his first encounter with its vocalisations was with the 'booming call,' which he imitated successfully. With respect to the booming calls, McLennan's diary entry (21 November 1921) reads: 'heard a deep booming call Oomm-oomm-oomm repeated rapidly for about 20 seconds, it begins very low & gradually gets louder & of a higher tone, last notes about 5 tones higher than first. Imitate call & bird answers a couple of times, in a few minutes I see it coming towards me through the short grass, get in a shot at 28 yds. & secure it.' He later adds that 'the *Turnix* dissection proved it to be a nesting female.' White's (1922) account of McLennan's observations from the same date adds that 'the first few notes were very low, and appeared to come from a great distance, the succeeding notes gradually higher in tone, louder, shorter, and were more rapidly uttered', and that 'the call takes about 30 seconds of time'.

McLennan (1923) mimicked the Buff-breasted Button-quail call (presumably the 'oom' call) on at least nine occasions, attracting single or multiple birds, or eliciting call responses. 'Oom' notes emitted by various *Turnix* species are considered advertising calls given by females, generally occur during the breeding season and can induce an aggressive response in other females (M. Mathieson, G. C. Smith *pers. obs.*; Rogers 1995). It is these 'booming' calls that Rogers (1995) suggests will prove most useful for bird watching purposes. Rogers (1995) cautioned that it will be necessary to distinguish the booming notes from the very similar notes of some other button-quail species, as well as from the Tawny Frogmouth *Podargus strigoides*, Papuan Frogmouth *P. papuensis* and Common Bronze-wing Pigeon *Phaps chalcoptera*, and that this should be achieved through an analysis of the call structures.

Rogers (1995) was frustrated by an inexplicable lack of calling at sites on the west of the Atherton Tablelands, but acknowledged that recordings of calls (which he added 'have never been tape-recorded') will be key to finding and identifying birds. Recorded calls will indeed provide a much-needed tool for making further observations, possibly aiding photography of the species and in developing knowledge of its distribution and population size through using playback. They will also facilitate future monitoring opportunities by permitting identification of calls recorded on automated recording devices deployed in suitable habitat.

Here, we present sonographic analysis of the structure of 'mystery calls' recorded near the vicinity of a pair of Buff-breasted Button-quail observed on the ground at Mt Mulligan, north-Queensland (Mathieson and Smith 2017). Buff-breasted Button-quail were not actually observed making these calls, but we present evidence to suggest that these vocalisations were the booming calls of the species.

METHODS

All times-of-day given in this paper are in Australian Eastern Standard Time. The observations described here occurred at Mt Mulligan Station, to the west of Mareeba on the Atherton Tableland, where two Buff-breasted Button-quail were initially flushed on the 17 January 2016 at 10:00 hours (Mathieson and Smith 2017). Excellent views were obtained of the birds on the ground and subsequently as they flew in different directions. Soft 'oom' notes were later heard coming from the area where one bird was thought to have landed.

A Bioacoustic Recorder (BAR – Frontier Labs™) was deployed near to where we flushed our first pair of birds and set to automatically record continuously for three hours prior to sunset and six hours after sunrise. We left the site at approximately 12:30 hours and visited intermittently over the next two days, sighting birds on a further two occasions during this time. The BAR was set to record from 15:51 hours on 17 January to 11:04 hours on 19 January, providing us with 24 hours of ambient sound to analyse.

To identify calls that could be considered as possible button-quail calls, we listened to the recordings through headphones and displayed spectrograms of the ambient noises recorded using Raven Lite™. Button-quail and frogmouth species call within a frequency range less than 500 Hz (BOCA 2001; *Xeno Canto* 2018), so we concentrated our effort on the lower frequencies, manipulating parameters of brightness, contrast and the Fast Fourier Transform (FFT) window size in Raven Lite™, so that calls within this range could be clearly distinguished.

Each of our 'mystery calls' was made up of a series of 'oom' syllables, which equated to the 'notes' or individual 'ooms' of McLennan (1923) and White (1922), whose descriptions originated from Coen, some 375kms to the north of the Mt Mulligan site. Spectrograms for each call sequence that we found on our recordings were measured as follows: mid-frequency of start 'oom'; mid-frequency of end 'oom'; the number of 'ooms' per second; duration of a mid-range 'oom'; 'oom' shape; number of 'ooms' to a full call and duration of the entire call from the beginning of the first identifiable 'oom' to the end of the last identifiable 'oom'. Mid-frequency measurements of 'ooms' were made at the point of maximum amplitude, using the waveform graph in Raven Lite™ where possible or the colour intensity output available in the spectrogram. Measurements of these parameters from the 'mystery' recordings were compared with measures for Painted Button-quail *T. varia*, Red-backed Button-quail *T. maculosa*, Little Button-quail *T. velox*, Tawny Frogmouth, Papuan Frogmouth and Common Bronze-wing obtained from recordings available in BOCA (2001) and *Xeno Canto* (2018). No calls were available from these sources for Red-chested Button-quail *T. pyrrhothorax*; the call previously thought to be that of a Red-chested Button-quail in BOCA (2001) was later reallocated to Red-backed Button-quail (D. Stewart *in litt.*).

Booming calls isolated as possible Buff-breasted Button-quail calls were snipped from the longer recordings and uploaded to a device for later playback in the field. Playback using the snipped call, tentatively identified as a Buff-breasted Button-quail vocalisation, was conducted during a second field trip (25 February to 2 March 2016) to the Mt Mulligan field site. The call was played through a single powered speaker at low volume several times on one occasion at this site.

RESULTS

Call analyses

Thirty-two vocal sequences were identified for further consideration as Buff-breasted Button-quail booming calls from the 24 hours of recording made in January 2016. However, many of the call sequences were not analysed for several reasons; some birds were too far from the recording unit and their calls were therefore indistinct, some calls were truncated at the beginning or end of the call sequence, and some calls seemed out of the plausible frequency range of the species. Measurements were consequently made of 25 call sequences. A summary of measurements obtained from the Mt Mulligan calls and the reference calls of other species (i.e. other button-quail, Tawny and Papuan Frogmouths and Common Bronze-wings) is provided in Table 1.

Two types of booming call were identified for the Buff-breasted Button-quail (Figure 1). One call began at low frequency in the 200-230 Hz range and then rose to a frequency around 270 Hz. The other call began in the frequency range below 210 Hz and either stayed at a low frequency or sometimes drifted lower to frequencies less than 200 Hz and down to c. 190 Hz. Combined measurements for these two call types are summarised in Table 1. All calls began with less distinct and less powerful 'ooms', but became more powerful as the train of 'ooms' proceeded. We could not detect that each 'oom' became shorter as each call sequence progressed.

Painted Button-quail calls from BOCA (2001) and *Xeno Canto* (2018) overlapped the frequency ranges of those of Buff-breasted Button-quail, but they tended to start and end at a higher frequency (Table 1). 'Ooms' were also somewhat different in shape and slightly longer in duration, but there was still possibility for confusion. Like the Buff-breasted Button-quail, the Painted Button-quail also make calls at a constant frequency, but this occurs at higher frequencies than the non-rising calls of Buff-breasted Button-quail.

In unambiguous contrast to Buff-breasted Button-quail, the rising calls of Red-backed Button-quail and Little Button-quail all began at higher frequency ranges and rose to a higher pitch (Table 1). Additionally, Little Button-quail called at higher frequencies and at a much slower rate than all the other button-quail. Furthermore, they can produce a double note to each 'oom' element of their call, which is not apparent among the other button-quail.

Table 1

Measurements (range, mean, standard deviation (s.d.) and sample size (n)) of calls of button-quail species, Tawny and Papuan Frogmouths and Common Bronze-wing Pigeon. Only complete calls were used where possible to provide figures for the number of 'ooms' to a full call, and duration of entire call comprised a train of 'ooms'. Complete calls were distinguished by noting significant time gaps between calls. Sources include: [1] Bird Observers Club of Australia (2001) published recording, [2] *Xeno Canto* (2018), and [3] www.graemechapman.com.au

Call ID	Main/mid-frequency (Hz) of start 'oom': range, mean ± s.d. (n)	Main/mid-frequency (Hz) of end 'oom': range, mean ± s.d. (n)	'Ooms' per second: range, mean ± s.d. (n)	Duration of mid-range 'oom' (secs): range, mean ± s.d. (n)	Description of 'ooms'	No. of 'ooms' to a full call: range, mean ± s.d. (n)	Duration of call of 'ooms' (secs): range, mean ± s.d. (n)	Source of call
Proposed Buff-breasted Button-quail from Mt Mulligan	195-230, 215 ± 9 (25)	192-280, 228 ± 36 (25)	1-1.1, 1.0±0.03 (25)	0.4-0.7, 0.6±0.1 (25)	Each 'oom' initially falls then rises in frequency. Individual 'ooms' shaped like upward horseshoe	16-34, 24±4 (25)	16-35, 23±4 (25)	G.C. Smith, M.T. Mathieson
Painted Button-quail	212-233, 222±9 (6)	260-293, 282±12 (7)	1.0-1.2, 1.1±0.1 (7)	0.5-1.0, 0.6±0.2 (7)	Slight upward inflection in each 'oom'	23-33, 28±4 (6)	22-28, 24±2 (6)	BOCA[1]; S. Connop[2], M. Anderson[2], G. McLachlan[2]; G. Chapman[3]
Red-backed Button-quail	299-318, 308±13 (2)	352-388, 370±25 (2)	0.9-0.95, 0.9±0.04 (2)	0.8-1.0, 0.9±0.1 (2)	Each 'oom' rises in frequency	21-25, 23±3 (2)	22-26, 24±2 (2)	BOCA[1]
Little Button-quail	390-440, 407±29 (3)	430-458, 440±16 (3)	0.3-0.4, 0.3±0.1 (3)	1-1.2, 1.1±0.1 (3)	Individual 'oom' rises in frequency, or some 'ooms' comprise a double note given in either high to low or low to high sequence.	9-10, 9±1 (3)	20-36, 27±8 (3)	BOCA[1]; M. Anderson[2]
Tawny Frogmouth	205-293, 237±33 (13)	237-296, 257±23 (13)	1.7-2.4, 2.1±0.3 (13)	0.3-0.6, 0.4±0.1 (13)	Each 'oom' rises in frequency. Across the call train, 'ooms' are rapid at first but then become more constant in timing.	21-48, 35±9 (13)	11-24, 17±4 (13)	BOCA[1]; M. Anderson[2], J. Hegge[2], N. Jackett[2]
Papuan Frogmouth	183-322, 264±40 (20)	192-370, 294±55 (20)	0.8-1.2, 1.0±0.1 (20)	0.5-0.9, 0.6±0.1 (20)	Across the call train, 'ooms' of one sex rise to a peak then fall. Sex differences apparent in calling frequency.	5-16, 11±3 (20)	5-16, 11±3 (20)	BOCA[1]; H. Mateve[2], G. Wagner[2], J.V. Moore[2], F. Lambert[2], J. Dumbacher[2]
Common Bronze-wing	239-301, 273±20 (7)	242-303, 275±20 (7)	0.3-0.5, 0.4±0.1 (7)	0.7-1.1, 0.8±0.2 (7)	Downward inflection in frequency to each 'oom'.	8-29, 18±8 (6)	20-68, 43±20 (6)	BOCA[1]; M. Harper[2], M. Anderson[2], N. Jackett[2], G. McLachlan[2], S. Bushell[2]

The booming calls of the Tawny Frogmouth, whilst in the same frequency range as those of Buff-breasted Button-quail, were twice the speed of those of Buff-breasted Button-quail and were therefore distinctive on that basis alone (Table 1). Papuan Frogmouths began and finished their calls at frequencies that spanned those of Buff-breasted Button-quail. Unlike the Tawny Frogmouth, the Papuan Frogmouth called at similar speed and 'oom' duration to Buff-breasted Button-quail; however, its calls always contained fewer 'ooms' and were shorter. The Papuan Frogmouth calls analysed from *Xeno Canto* (2018) appeared complete, with periods of silence between them, but it was unclear whether the BOCA recordings were complete. The BOCA recordings of calls of Papuan Frogmouths in Australia were also lower in frequency than all those recorded in New Guinea. Other low, soft calls of the Papuan Frogmouth were also recorded in New Guinea and were given in response to the higher call, presumably of the mate (Marchant and Higgins 1993). The low frequency calls recorded in Australia and New Guinea changed little in frequency from the beginning 'oom' to the end 'oom' of the call, whilst the higher frequency calls increased in pitch.

In comparison to the Common Bronze-wing calls, the 'mystery' calls obtained from the Mt Mulligan area were much faster, began at a lower frequency and tended to rise in frequency, whereas the frequency of 'ooms' in the Common Bronze-wing call did not rise or fall throughout the call.

Call Playback

On the 25 February 2016, we returned to Mt Mulligan Station where Buff-breasted Button-quail had been observed in January 2016. Between 08:15 and 11:30 hours, we checked a

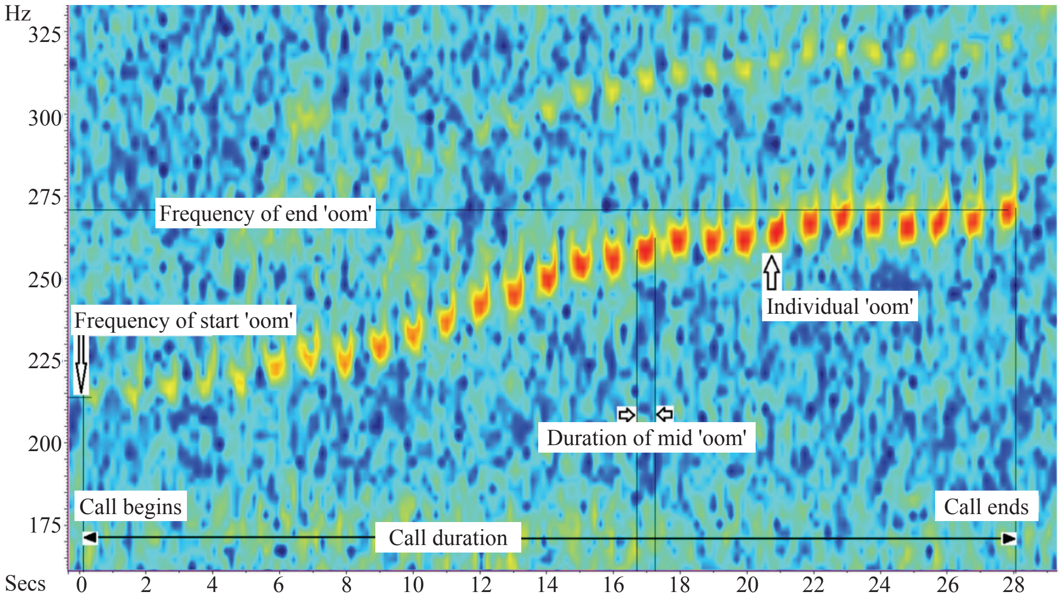

Figure 1. *Spectrogram of a 'mystery' booming call from Mt Mulligan, showing the characteristic rising call described by McLennan (1923) and White (1922). In addition to the fundamental note of the call, harmonics are also displayed. Vertical axis is in Hz and horizontal axis in seconds.*

large part of the 12ha area previously visited. Throughout our January fieldtrip we had encountered no other button-quail species during our visits to this site. However, on the morning of the 25 February 2016 we flushed a Red-chested Button-quail. Whilst we did not see Painted Button-quail that morning, this species was encountered the following day.

Despite the possibility that now existed for confusion, on the morning of the 25 February we heard the deep booming of a button-quail that was compatible with those we had heard on the January 2016 recordings and which we had available for an opportunity to perform playback. We promptly played the call and presently a female Buff-breasted Button-quail appeared. At approximately 8m from the playback speaker the bird stopped and, having evidently seen one or both of us, turned around and disappeared through the grass. After a brief period of continued playback and waiting, no bird returned and we were sufficiently confident that the bird had been 'spooked' by our presence. We packed up and walked in the direction that the female had retreated. After a short traverse of some 20m we again encountered the female (and an accompanying male) Buff-breasted Button-quail, getting good identifying views before they flew off a considerable distance.

DISCUSSION

Although we have not obtained calls directly from observed vocalising birds, we are confident that the 'mystery calls' recorded on the automated recording devices deployed at Mt Mulligan are those of Buff-breasted Button-quail. The evidence is three-fold. Firstly, the calls are mostly different to calls issued by similar booming species that also inhabit the range of the Buff-breasted Button-quail. Secondly, these recordings fit the descriptions given by McLennan (1923) and White (1922). Thirdly, the behavioural response of Buff-breasted Button-quail to playback of the call was interpreted as a reaction to a perceived conspecific.

The calls recorded at Mt Mulligan appear to differ sufficiently from the reference calls that we have obtained from various sources for co-occurring species, with which Rogers (1995) expressed concern about misidentification. In summary, Painted Button-quail (the button-quail species with the most similar call) tended to call at higher frequencies than those of the calls from Mt Mulligan, Tawny Frogmouths called at a faster rate, whilst Papuan Frogmouths called for shorter times with fewer 'ooms' in each call. In addition, Papuan Frogmouth calls sound different to the human ear, which is also reflected in the spectrograms possessing a slight upward inflection to each 'oom' of the call. The Common Bronze-wing calls at a slower rate, at a higher frequency and its call neither ascends nor descends in frequency across its duration.

McLennan (1923) reported the booming call as a deep 'oomm-oomm-oomm,' repeated rapidly for about 20 seconds (or 30 seconds, White 1922). The calls recorded from Mt Mulligan ranged in duration from 21.6 to 27.9 seconds, giving 23 to 28 'booms' per entire call duration, which appears to match the McLennan (1923) observations. This author and White (1922) made two further remarks: firstly, the 'oom' call began with very low notes, appearing to come from a great distance, and they gradually got louder and were of a higher tone by the end of the call, and secondly the last notes were about five tones higher than the first one. Observations at Mt Mulligan accord with the first point, in that the lowest frequencies of the recorded ascending calls (Figure 1, Table 1) were typically quieter and 'less forced' than the higher frequencies, giving an overall impression that they could have been uttered at a distance. Additionally, the calls got louder, as evidenced in the increasing intensity of colour in each 'oom' syllable, and of a higher pitch (or frequency) (Fig. 1). Addressing the second observation is more complicated and our findings are equivocal with those of McLennan and White. Whilst the pitch of each 'oom' cannot be converted directly to a tone (as a tone is an overall quality of pitch), the low notes recorded in our call sequences (*c.* 209 Hz

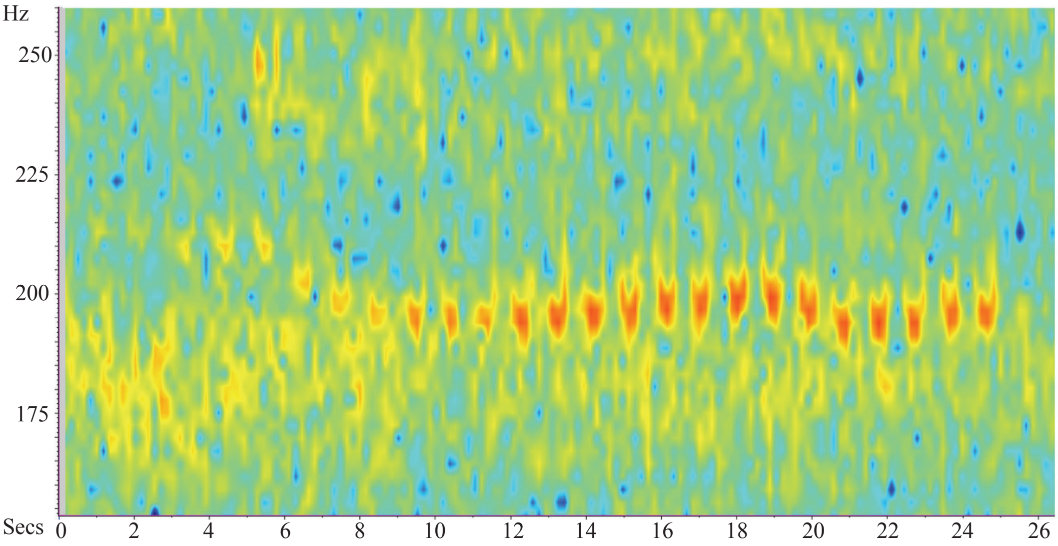

Figure 2. *Spectrogram of a 'mystery' booming call from Mt Mulligan, showing a low, non-rising call. Vertical axis is in Hz and horizontal axis is in seconds.*

of the rising calls in Figure 1 and 192 Hz in the low meandering calls in Figure 2) corresponded to somewhere around a G note, whilst the high notes (*c*. 270 Hz) corresponded to a C or C# note. Thus, the rise in pitch of the Mt Mulligan calls could be interpreted as a rise of some five to six semi-tones from lowest to highest, not the 'five tones higher' as recorded by McLennan (1923) and White (1922), but more like five to six notes higher, which is possibly what McLennan was referring to, although this remains speculative.

The final piece of evidence to support our contention that the 'mystery calls' from Mt Mulligan are those of Buff-breasted Button-quail is that a female of this species (with an accompanying male) was attracted to playback of the call that we believe to be that of her own species. Rogers (1995) believed that the 'oom' calls given by button-quail are 'interesting in that they often provoke an aggressive response from females'. McLennan (1923) attracted several individuals by imitating booming calls, and it is likely that still better results could be achieved with modern play-back equipment. We suggest that the attraction of the female Buff-breasted Button-quail to a digitally recorded call of the same species at Mt Mulligan constituted the aggressive response that Rogers (1995) alluded to and that McLennan (1923) observed.

Whilst further research is needed to be wholly assured of the identity of the calls that we obtained, we are confident that obtaining calls of this species (such as the call that we have recorded) will greatly assist future searches for, and monitoring of, the species by allowing the use of playback and call recognition. If the distinctive low tones that we have seen on spectrograms are emitted by the Buff-breasted Button-quail rather than any other button-quail species, then a significant call 'signature' has possibly been found. This signature will be useful in developing an automatic call recognition algorithm for identifying Buff-breasted Button-quail from remote and automatic recorders deployed in the field. Recognition software and automatic recorders are one of the ways of the future for studying cryptic, shy and rare species, such as the Buff-breasted Button-quail.

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Effectiveness of transects, point counts and area searches for bird surveys in arid *Acacia* shrubland

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Several different survey techniques are commonly used to assess the richness and abundance of birds. These methods can vary with respect to the likelihood of detecting species with different habits or characteristics and their effectiveness in different vegetation structures. It is advisable, therefore, to test the effectiveness of different methods for specific vegetation types and the bird assemblages associated with them before deciding on the most appropriate technique. We tested the effectiveness of three of the most commonly used bird survey methods – interval point counts, strip transect counts and timed area searches – in a replicated study in arid *Acacia* shrubland in central Australia. Timed area searches produced the highest estimates of species richness and abundance, and point counts were the least effective method. Timed area counts are probably more effective in the relatively dense vegetation structure characteristic of *Acacia* shrublands because they allow the observer to examine thicker patches of vegetation more closely than with the other methods, thereby enabling the observer to locate more cryptic species. Timed area searches may increase survey effectiveness in sites with thicker vegetation.

INTRODUCTION

Developing effective methods to assess species richness and relative abundance of specific plant and animal groups is a fundamental aspect of biological surveying and monitoring. The choice of appropriate methods is an important starting point in designing surveys and monitoring programmes. For most groups of animals and plants, multiple survey methods are available, each with strengths and weaknesses. Understanding the limitations of alternative methods and choosing the method that best matches the questions being addressed by the study and the variables that are being measured will dictate the success, or otherwise, of the research programme.

Birds are a very commonly encountered and active class of vertebrates that are relatively easy to identify. Consequently, bird surveying is usually conducted visually, and a variety of techniques has been developed to assess avian species richness and relative abundance across space and time (Krebs 1999). A wide range of methods developed in the Northern Hemisphere has been applied, sometimes with modifications, to survey Austral avifaunas. Among the commonly used methods are transect counts, point counts, area mapping, area searches and mark-recapture studies (Pyke and Recher 1984). The most appropriate method for a particular study will depend not only on the project's objectives, but also on the suite of species comprising the avian community and the vegetation structure of the habitat (Martin *et al*. 2017). Given such variation, survey methodology should ideally be tested prior to the commencement of larger research projects (Totterman 2015) with the aim of determining which method will achieve the most complete survey (i.e. the highest number of species and most accurate measure of abundance) for the least effort (Watson 2003; Witmer 2005). Such methodological testing has not previously been undertaken in arid *Acacia* shrubland, despite this being one of the most widespread vegetation types in inland Australia (Nano *et al*. 2017).

Transects, point counts and area searches are among the most common methods used for bird surveying in Australia. These methods all give measures of relative abundance (birds observed per unit of time and area), rather than absolute densities. Transects involve an observer moving along a set route (usually a line) for a set distance at a measured pace, while recording all birds detected. Line transects may involve the observer estimating the distance from the line to each bird detected, thus enabling density estimates to be calculated (Buckland *et al*. 1993). An alternative is to use strip or fixed-width transects where boundaries of the search area are marked and the observer walks along the centre line of the strip, with only birds within the marked areas being included (Bell and Ferrier 1985). Transects are normally long and narrow, because few birds are detected more than 30m from the transect line and most detection has been reported to occur within 20m (Recher 1984). Point counts are undertaken by a stationary observer who records all birds detected from the location over a set period. As with line transects, point counts can involve an estimate of the distance to each individual observed, or can be made within a set radius. Interval point counts are a series of point counts made at set intervals, normally along a transect line. These intervals need to be far enough apart for each count to be independent, but close enough to ensure that the area covered is similar to that in other methods (Pyke and Recher 1984). Area searches differ from transect and point counts in that the observer can move freely about the designated locale, for a fixed amount of time. When this method was first initiated, 20-minute area searches were undertaken on unmarked areas of approximately three hectares; 2 ha has been used as the standard in most subsequent studies and marked areas are also sometimes used (Loyn 1986).

Comparisons have been carried out to ascertain the most efficient survey technique in different Australian conditions. Loyn (1986) found that estimates of density from transect counts were less than those arrived at from area mapping, a technique that relies on mapping nest locations or individual territories. He reported that area searches are more effective for cryptic species, but birds may be counted more than once if care is not taken by the observer when moving through the plot. Bell and Ferrier (1985) found that all transect procedures tended to underestimate the densities of birds on plots. Davies (1982) found that point counts gave higher estimates of density than transects. Hermes (1977) compared estimates of bird populations obtained by transect counts, interval point counts, area searches and mapping. He found that each method gave a different estimate for density, as did Arnold (1984), who found transects to be more effective than point counts at locating inconspicuous species. Recher (1984) reported that surveying conducted on transects was the only method among four (mapping, nest searches and mist netting being the others) that would adequately sample the complete avifauna of an area. Harden *et al*. (1986) found that estimates of birds in strip transects are affected by the rate of observer movement and strip width.

Some of the variation among the studies outlined above may have been caused by factors independent of the survey method, including observer bias and differences in how each method was applied. Kavanagh and Recher (1983) found that results could differ significantly even when several observers, each with extensive experience, used the same method on the same survey plot. As birds are highly mobile, the presence of the observer can affect their detectability (Pyke and Recher 1984), and movement by both birds and the observer can result in individuals being counted more than once, a likelihood that increases the longer an observer is in a plot. Weather, season and time of day will also affect survey results (Keast 1984). All these factors need to be considered in study design.

The aim of this study was to determine which method, out of strip transect counts, fixed radius interval point counts and timed area searches, would be the most cost-effective, delivering the highest estimates of species richness and abundance of birds in *Acacia* shrubland for the least effort.

METHODS

Study site

This study was undertaken in *Acacia* shrubland at the Alice Springs Desert Park (23.7066° S, 133.8326° E), a 1300ha reserve on the western boundary of Alice Springs, Northern Territory, Australia. The environment is dominated by Mulga *Acacia aneura* and Witchetty Bush *A. kempeana* and characterised by a generally open structure, with scattered shrubs and grasses interspersed with clumps of dense vegetation along small drainage lines. The shrub layer is one to two metres tall in open areas and up to six metres along drainage lines.

Study Design

To eliminate as many sources of bias as possible and by reference to the literature, the following survey guidelines were established:

1. Only one observer familiar with the central Australian avifauna carried out surveys (Kavanagh and Recher 1983).
2. Procedures were fully defined prior to undertaking surveys (Kavanagh and Recher 1983).
3. The various methods were trialled at the same sites to minimize differences resulting from location (Recher 1988).
4. Procedures were conducted during periods of maximum detectability (the first three hours after sunrise) and were not undertaken in high wind or rain (Keast 1984).
5. Survey plots were narrow to allow maximum visibility for differing methods, noting that few birds are detected more than 20m from the point of observation (Recher 1984).
6. Sites were surveyed on multiple occasions to maximise the chances of achieving a complete sample of avifauna present during the survey period (Dobkin and Rich 1998; Watson 2004).
7. Sites were surveyed only once per day to increase the probability of counting species that moved in and out of the plots (Field *et al*. 2002).
8. Surveys were limited to 30 or fewer minutes to allow for effective surveying whilst limiting the risk of double counting (Loyn 1986; Craig and Roberts 2001).

Three two-hectare sites were marked out as 400m x 50m transects using flagging tape. The centre line of each site was also marked. The sites were surveyed between December 2007 and February 2008. Each site was surveyed using each method six times. Weather permitting, sites were surveyed on consecutive days between 06:00 and 09:00 hours ACST (the hot weather in central Australia limits peak activity of birds to the early morning in summer). Only one site was surveyed per day, using all three methods.

Each site was surveyed using the three different methods consecutively (i.e. interval point count, strip transect and area search); the active sampling time for each method was 30 minutes, with a 10-minute interval between surveys to limit the impact of disturbance by the observer. The order in which survey methods were used was changed each day. All birds identified by sight or sound were recorded. Observations were made using Canon 8 x 40 binoculars.

When conducting transect counts, the centre line of the plot was walked at a measured pace, taking 30 minutes to cover the 400m without leaving the centre line. Interval point counts were conducted at eight points marked down the centre line of the plot. This number was chosen to maximize coverage of the whole plot within a viewing radius of about 50 m. The observer walked to each point, waited for five minutes to allow for effects of the disturbance to subside, and then recorded all birds seen by scanning the area for 3.75 minutes. For area searches, the observer moved through the plot without a fixed path and actively searched for birds without going over area already covered. Thicker patches of vegetation were studied closely.

Data Analysis was conducted using *Primer v7* (Clarke and Gorley 2015) and *Permanova+ for Primer* (Anderson *et al*. 2008). For each variable of interest, data were square-root transformed prior to analyses, and Bray-Curtis similarities were calculated between samples. We then used permutational analysis of variance to test whether estimates of bird species richness, total abundance or community composition differed among survey methods using a two-factor model with survey method as a fixed factor and site as a random factor. We used the total number of species detected and the mean abundance over the six surveys at a site as our response variable (i.e. there was no replication within sites). Non-metric multi-dimensional scaling plots (nMDS) were also generated from the Bray-Curtis similarities to enable visual representation of the species composition of each site as estimated by each survey method.

RESULTS

Four hundred and ninety-six bird sightings of twenty-two species were recorded during the surveys. The number of species detected differed significantly depending on the survey method used (Pseudo-F$_{(2, 8)}$ = 11.1, P = 0.035). Similar numbers of species were identified at each site using the transect and the area search methods, whereas consistently fewer species were detected using point counts (Table 1). There was a significant difference among sites in the number of species detected (Pseudo-F$_{(2, 8)}$ = 15.1, P = 0.022), with site 2 having the lowest number of species detected regardless of the survey method used (Table 1).

More species were located more rapidly using the area search method compared to the other two methods (Figure 1). The cumulative species richness for the area search method may have begun to plateau after six surveys, but additional surveys would be required to test this possibility. There was also a significant difference in the abundance of birds detected by the different methods (Pseudo-F$_{(2, 4)}$ = 14.84, P = 0.001). Abundance also varied across sites (Pseudo-F$_{(2, 4)}$ = 41.52, P = 0.034). Many more individual birds were seen at each site using the area search method compared to point counts or transects, and the fewest birds were detected using point counts (Table 2).

Indices of relative abundance for each species were calculated (separately for each survey method) as the mean number of individuals observed per survey (six surveys at each of three sites) (Table 3). The comparisons suggest that point counts gave the lowest or equal-lowest estimates of abundance for most species. Area searches and transects resulted in the highest estimates of abundance for the most species (12 of 22 species in each case). The estimates of abundance based on the area search method tended to be higher for smaller species (i.e. those with body mass ≤10g). Six of the seven species with a body mass <10g were recorded most often during surveys conducted with the area search method.

An nMDS plot and a PERMANOVA representing the relative similarity in species composition among sites as estimated by the different survey methods (Figure 2) revealed clumping by site rather than by survey method. Indeed, the composition of the bird assemblage differed significantly among sites (Pseudo-F$_{(2, 4)}$ = 7.42, P = 0.007), consistent with the detected differences in species richness and abundance among sites. However, no significant differences in assemblage composition were detected with different survey methods (Pseudo-F$_{(2, 4)}$ = 1.76, P = 0.053).

Table 1

The number of bird species recorded at three Acacia shrubland sites using three survey methods over six surveys at each site.

Site	Area search	Point count	Transect	Total
Site 1	11	7	11	14
Site 2	8	6	8	9
Site 3	14	9	10	16
Total	19	12	19	22

Table 2

Numbers of individuals of all species surveyed at three Acacia shrubland sites using three survey methods over six surveys at each site.

	Point count	Transect	Area search	Total
Site 1	55	68	98	221
Site 2	18	22	37	78
Site 3	43	61	93	197
Total	116	151	229	496

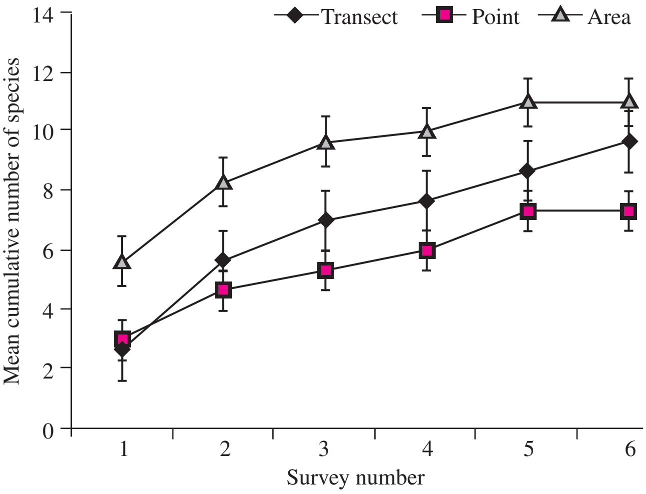

Figure 1. *Cumulative species richness of birds at three Acacia shrubland sites using three survey methods over six surveys at each site.*

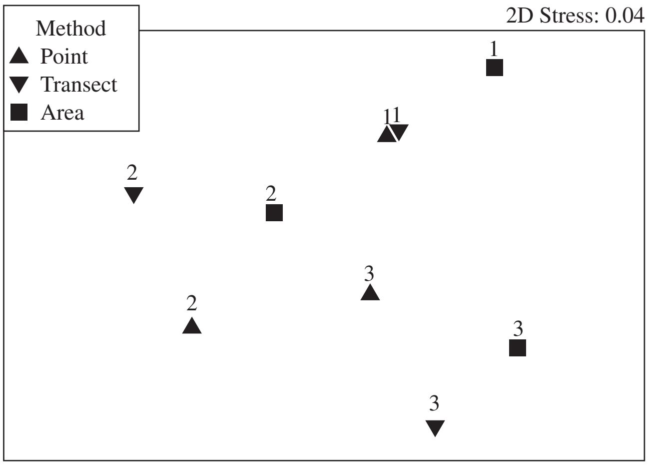

Figure 2. *Non-metric multi-dimensional scaling plot representing the relative similarity among avian communities at different sites as assessed by different survey methods. The nMDS was conducted using Bray-Curtis similarities between sites and methods, calculated from species composition and abundance data averaged over 6 survey periods.*

Table 3

Index of relative abundance (average individuals observed per survey) of bird species across all sites based on each method. Body mass taken from the Handbook of Australian New Zealand and Antarctic Birds (Marchant and Higgins, 1993; Higgins and Davies, 1996; Higgins, 1999; Higgins *et al.,* 2001; Higgins and Peter, 2002; Higgins *et al.*, 2006) Volumes 2-7. Species are arranged in descending order of body mass. The method/s that resulted in the highest or equal highest abundance estimates for each species are shown in bold.

			Relative abundance		
English name	Scientific name	Body mass (g)	Transect	Point count	Area search
Crested Pigeon	*Ocyphaps lophotes*	150-250	**0.16**	0.05	0.05
Australian Ringneck	*Barnardius zonarius*	150-175	**0.05**	0	0
Western Bowerbird	*Ptilonorhynchus guttatus*	140	**0.05**	0	0
Black-faced Cuckoo-shrike	*Coracina novaehollandiae*	115	0	0	**0.05**
Grey Shrike-thrush	*Colluricincla harmonica*	65	**0.11**	0	0
Spiny-cheeked Honeyeater	*Acanthagenys rufogularis*	50	2	2.17	**2.34**
Little Button-Quail	*Turnix velox*	35-50	**1.22**	0	0.5
White-browed Babbler	*Pomatostomus superciliosus*	40	**0.27**	0.11	0.17
Diamond Dove	*Geopelia cuneata*	33	**0.05**	0	**0.05**
Singing Honeyeater	*Lichenostomus virescens*	28	0.44	**0.55**	**0.55**
Rufous Whistler	*Pachycephala rufiventris*	25	**1.05**	0.2	1
Horsfield's Bronze-cuckoo	*Chalcites basalis*	23	0	0	**0.05**
Willie Wagtail	*Rhipidura leucophrys*	18	**0.17**	0.05	0.16
Zebra Finch	*Taeniopygia guttata*	12	0.11	0.11	**0.61**
Red-browed Pardalote	*Pardalotus rubricatus*	11	**0.16**	0	0.11
Splendid Fairy-wren	*Malurus splendens*	9	3.5	3.39	**5.66**
Mistletoebird	*Dicaeum hirundinaceum*	9	**0.33**	**0.33**	**0.33**
Yellow-rumped Thornbill	*Acanthiza chrysorrhoa*	9	0	0	**0.11**
Red-capped Robin	*Petroica goodenovii*	9	0.16	0.22	**0.67**
Variegated Fairy-wren	*Malurus lamberti*	8	**0.11**	**0.11**	0.05
Inland Thornbill	*Acanthiza apicalis*	7	0.28	0.28	**1.61**
Western Gerygone	*Gerygone fusca*	6	0.05	0	**0.11**

DISCUSSION

In this study, we compared estimates of species composition and relative abundance in an arid *Acacia* shrubland bird assemblage using three commonly used survey methods. Area search and transect methods yielded higher estimates of species richness than did interval point counts. Nearly twice as many individual birds were observed when using the area search method compared to the other methods. The high number of individuals detected partly explains why the number of species detected accumulated most rapidly when using area searches. Although we did not detect significant differences in overall species composition using different survey methods, area searches appeared to be more effective at detecting some species (Table 3), particularly the smaller ones. Nevertheless, no method was completely successful in sampling all the bird species in the area.

The species detected most often using the transect method included several large, conspicuous, mobile birds, such as the Western Bowerbird *Chlamydera guttata*, Australian Ringneck *Barnardius zonarius* and Grey Shrike-thrush *Colluricincla harmonica*. If these species were present at a site during an area search, a competent observer would be expected to locate them; therefore, it seems likely that these species were either absent from the sites during the area surveys or that disturbance by the observer caused them to leave. In contrast, of the seven smallest (< 10 g) species recorded, five were estimated as being most abundant based on area searches. The larger, but cryptic, Horsfield's Bronze-cuckoo *Chalcites basalis* was also only recorded during area searches, but on just one occasion. These findings are consistent with the conclusion of Hewish and Loyn (1989) that area search methods are more effective at locating smaller, more cryptic species. The area search method allows increased detection of more cryptic or non-calling species because of the observer's freedom to carry out closer examination of denser vegetation and to pursue identification of smaller species (Craig 2004). This is supported by our observations in the *Acacia* shrublands of central Australia, where close examination of dense clumps of Witchetty Bush and Mulga was often fruitful, and area searches provided a more complete representation of the bird assemblage than either point counts or transects.

Although there is an increased probability of counting birds more than once when using area searches, we do not think that this can fully account for the increased abundance of birds recorded during such searches. Higher abundances were recorded principally among a suite of small, relatively inconspicuous species, such as the Inland Thornbill *Acanthiza apicalis*, Splendid Fairy-wren *Malurus splendens* and Red-capped Robin *Petroica goodenovii*. For these species, up to twice as many individuals were found with the area search method than with each of the other two methods. Larger and more conspicuous species, such as Rufous Whistler *Pachycephala* *rufiventris* and Spiny-cheeked Honeyeater *Acanthagenys rufogularis*, were recorded more evenly across methods. This suggests that improved detection in large part accounts for the differences in abundance that we observed. Even if the likelihood of double counting was higher during area searches and abundance estimates consequently were slightly elevated, it is generally considered that this risk is outweighed by the tendency of other methods, such as transects, to underestimate relative abundance (Hermes1977; Arnold 1984; Bell and Ferrier 1985; Hewish and Loyn 1989). Craig (2004) stated that area searches produce higher density estimates than point counts and transects because they take longer to conduct. However, this was not true in this study, where the time spent actively surveying birds was identical for all methods; nor was it valid in a study in Wandoo woodland in south-west Western Australia, which also found that the highest density estimates were derived from area searches (Arnold 1984).

Our aim was to determine which of the three trialled survey methods would provide the highest species richness and abundance for the least effort. Based on our results, we conclude that timed area searches are the most suitable survey technique for arid *Acacia* shrublands, primarily due to the ability of the observer to search for the more cryptic species that make up a considerable proportion of the central Australian avifauna in denser, shrubby areas. Point counts were the least effective and efficient survey method in this vegetation type.

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SEABIRD ISLANDS

No. 39/1

Flinders Islet, Five Islands Group, New South Wales

Location: 34°27'16" S: 150°55'30" E: 2.6 km offshore from Port Kembla, New South Wales (NSW). It is part of the Five Islands Group, located 3.5 km north of Big Island No1.

Status: Nature Reserve administered by the NSW National Parks and Wildlife Service (NPWS), Office of Environment and Heritage. Entry permit required.

Other Names: Toothbrush, Tom Thumb Islands (including Bass Islet).

Description: Flinders Islet is part of the Five Islands Group, which also includes Bass Islet, Martin Islet and Big Island (comprising two main parts, known as No. 1 and No. 2). The total area of Flinders Islet is 2.6 ha, with 0.4 ha being vegetated. The geology of Flinders Islet resembles that of all islands in the Group and is as described for Big Island, comprising a Dapto-Saddleback Latite Member of the Permian Gerringong Volcanics[3].

Flinders Islet has a long, narrow shape and is aligned north-south, with its highest point at 13 m being on the plateau at the islet's south-western and widest end. The vegetated and elevated plateau is skirted by a cliff 260 m long that slopes down to the south-west to meet the rock platform. The extensive eastern rock platform includes shingle beds and shallow, fresh water pools. All approaches to the islet encounter a rocky shoreline (see Figure 1).

The plateau is dominated by the low-growing, exotic shrub Bitou Bush *Chrysanthemoides monilifera rotundata* and a single large Mirror Plant *Coprosma repens*, a New Zealand shrub. In the southwest, shallow soil areas support a mixture of Wandering Sailor *Commelina cyanea*, Kidney Weed *Dichondra repens* and Pigface *Carpobrotus glaucescens,* the latter being noted here in the 1970s[1]. All other plant species mentioned in that earlier survey are still extant on the island. The survey by Mills[4] in 2014 recorded 20 native and 16 exotic plant species.

Landing: Landing can be effected in moderate to light swell from a tender into the gutter on the northwest shoreline which terminates in a pebble beach. Alternatively, a landing can be made directly onto rocks to the north of the gutter where a deep-water approach allows a bow disembarkation (Figure 1).

Ornithological History: Battam[1] detailed the ornithological visits to Flinders Islet up until 1976. An additional visit by Iredale and Chisholm in November 1927 (to 'Bird Island') found Silver Gulls *Chroicocephalus novaehollandiae* and Crested Terns *Thalasseus bergii* in a mixed colony of 'thousands of birds'[5]. Neither of these species has since been recorded as breeding on Flinders Islet[1]. Since 1976, several banders and members of the Southern Ocean Seabird Study Association (SOSSA) have occasionally visited the islet to conduct banding (Australian Bird and Bat Banding Scheme [ABBBS], submitted data).

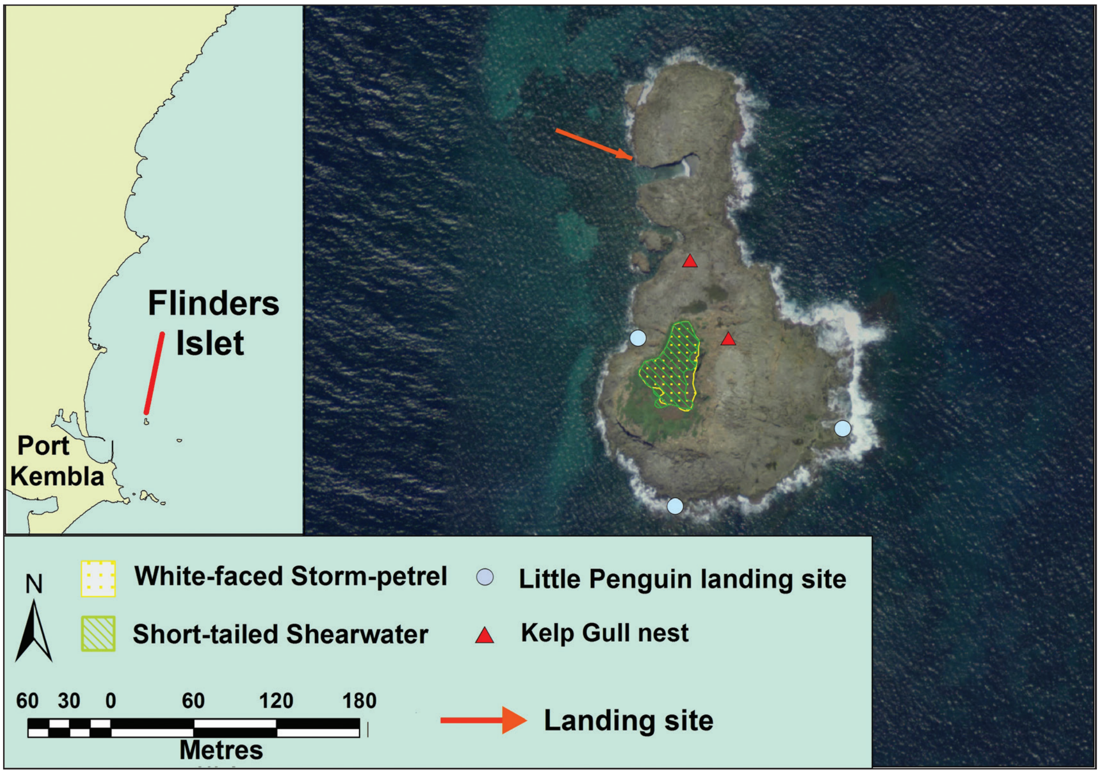

Figure 1. *Flinders Islet, Five Island Group, New South Wales*

C. Lloyd and C. Mower visited overnight on 20–21 September 2016 and C. Lloyd and N. Carlile overnight on 22–23 November 2016 to survey nesting seabirds. They paid a further day visit (with R. Morris) on 24 January 2017 to document shearwaters' distribution and burrow occupancy.

Breeding Seabirds and Status

Pelagodroma marina White-faced Storm-Petrel — Found on the plateau's northern half where soil depth is sufficient for burrowing and the height of exotic shrubs (< 800 mm) does not appear to hamper either the birds' access to the soil surface or to clear areas for take-off. In September 2016, up to 20 individuals were seen in the air during nocturnal observations. In November 2016, six 20 m-long transects were laid out east-west across the plateau and all burrows up to one metre either side of the transect were counted. After establishing the general presence or absence of petrel burrows in the area, the perimeter of the colony was walked using a hand-held GPS to gauge colony size. Despite great care being taken, one burrow that contained an adult incubating an egg was accidentally damaged. It was rebuilt with a stick-supported roof and the bird returned to the egg. The entrances to 35 burrows were fitted with stick palisades on the afternoon of 22 November 2016. These palisades were re-examined for disturbance on the following morning, with 10 having been dislodged. All these disturbed burrows were considered active nests. The total area on the plateau used for nesting was 1,622 m^2. Three of the original six transects were in storm-petrel habitat and collectively covered 7% of the suitable, available habitat. They had 11, 29 and 18 burrows, respectively, giving an overall mean nesting density of 0.12 ± 0.03 burrows per m^2. Combined with an estimated 29% burrow occupation rate, this density estimate suggests a minimum breeding population of approximately 56 ± 15 pairs. This is within the range recorded between the late 1960s and mid-1970s[1], but is considerably less than the 1999/2000[6] estimate of 300 breeding pairs.

Ardenna pacifica Wedge-tailed Shearwater — Originally recorded as nesting in an area now dominated by a large Mirror Plant[1], and probably with the deepest soils on the plateau. Despite several hours of nocturnal listening in September and November 2016, no calls of this species were heard. The checking of shearwater-size burrows as part of transect surveys (see below) also failed to detect the presence of this species. From the survey in the 1970s[1], 5 to 10 breeding pairs were estimated to be present on the island, but the species' presence was not detected by banding activities until 1994 (maximum of 28 birds recorded in one day out of a total of 106 birds in October 1995; ABBBS data). A larger population of 30 pairs was estimated in the late 1990s[6].

Ardenna tenuirostris Short-tailed Shearwater — Nests sparsely across the northern half of the plateau, where soil depth allows for scrapes below thick shrubs or nesting in shallow burrows. No calls of this species were heard during more than seven hours of listening in September and November 2016. In January 2017, the perimeter of the area of burrow occurrence was walked with a hand-held GPS before five (20 m long x 2 m wide) transects were laid out and surveyed (covering 8% of the available habitat). All 7 burrows identified were examined for occupants, with only a single chick (< 1 week of age) being encountered. The total area of available habitat was 1,500 m^2. The burrow density within the transects was 0.02 ± 0.01 per m^2, giving an estimated total of 30 burrows on the islet. If the average burrow occupation rate from nearby islands[2] of 50% is applied, we would estimate the breeding numbers on Flinders Islet to be about 15 ± 8 pairs. This species was not identified on the islet in the 1970s[1], but its presence was detected during banding activities in the 1970s-1990s (maxima of 33 individuals on one day in 1987 and 10 on one day in 1992; ABBBS data) and its population was estimated by the late 1990s[6] to be 30 pairs.

Eudyptula minor Little Penguin — Although it occasionally nests below the plateau in rock cavities and overhangs, most of this species' breeding takes place on the plateau in scrapes under shrubs. The landing sites for access to the islet were mapped during the overnight visit in September 2016 (Figure 1) and we attempted to count all penguins that came ashore. Counts began at dusk and continued until no penguins had arrived during two consecutive 15-min periods (until approximately 20:30 hours). In November 2016, Little Penguins on nests were identified during transect walks (which covered 7% of the total plateau area; see above) surveying Storm-Petrel density. From the September 2016 counts, 14 birds were observed ascending the plateau (-34.456745 S: 150.929299 E), two were seen moving to rock cavities and overhangs (-34.456056 S: 150.92969 E) and one to a rock crevice (-34.45608 S: 150.929349 E). On the following day, these latter two sites contained penguins incubating eggs. The rest of the penguins ascended the plateau up a gradual slope from the south where later three birds were found incubating eggs and two brooding chicks. From the ratio of nests with one adult incubating eggs to nests with one adult brooding chicks, combined with known breeding behaviour (i.e. three-day incubation shifts, meaning that 1/3 of incubating adults return each night, and nightly change-overs of brooding adults[7]), we estimate that each bird landing on the islet 'represented' 2.4 active nests, giving a total population of 34 breeding pairs. The November 2016 check (three nests with either incubating birds or chicks in six transects covering the entire plateau) yielded lower numbers at this later time in the penguins' breeding season, but the September estimate resembles previous published results[1,6].

Larus dominicanus Kelp Gull —Previously found to breed on the islet[8], and during our visits individuals were observed on both occasions and two empty nests were located. The evidence is thus that the species still breeds on the islet.

Haematopus fuliginosus Sooty Oystercatcher — The extensive area of rock platform and shingle beds favours this species. Lloyd and Mower recorded five active nests and six pairs in 2016 and similar numbers were recorded on the 2017 visit.

Factors Affecting Status

The population of the White-faced Storm-Petrel on the islet has probably remained stable since the 1970s. Due to available soil depth and seasonal drying out, the exotic Bitou Bush may now almost be at its limits of spread and canopy height. From observations on Flinders Islet, but without knowing soil depth, it appears that the Storm-Petrel readily nests under Bitou Bush when it is less than approximately 400 mm high; shrubs over 800 mm had no burrowing beneath them. Restoration of native vegetation by the removal of the dominant exotic shrubs has been recommended[4]. It would be prudent to have the White-faced Storm-Petrel re-established on Big Island before Bitou

Bush control was applied on Flinders Islet. Consideration should be given to drone delivery of herbicide[9] on this islet to avoid destruction of burrows by trampling.

In comparison with the 1970s surveys, the absence of Wedge-tailed Shearwaters has been 'counterbalanced' by the presence of similar numbers of Short-tailed Shearwaters. It appears that the limited habitat here ensures that no large burrowing species will occur on Flinders Islet in large numbers. The significant increase of both *Ardenna* species in the late 1980s to mid-1990s based on banding returns is inexplicable given the available habitat. The increase in available habitat on Big Island due to regeneration[2] may have caused the shearwaters to abandon the marginal habitat on Flinders Islet in recent times. The local extinction of Little Penguins on Martin Islet[10] was not replicated on Flinders Islet, which Australian Fur seals *Arctocephalus pusillus* have not yet (re)colonised.

Other Seabirds Recorded

Other seabirds observed during the current survey:

Arenaria interpres	Ruddy Turnstone
Thalasseus bergii	Crested Tern
Chroicocephalus novaehollandiae	Silver Gull

Other Vertebrates Recorded

A skink, *Eulamprus* sp*.*, previously identified by Battam[1], was identified as *Eulamprus tympanum* during these surveys. Solomon Buckman from the University of Wollongong photographed a Barn Owl, *Tyto javanica,*in August 2018 while undertaking geological survey work. This species is also known to visit Big Island.[1] The species responsible for a large abandoned nest found in a cliff cavity of the planteau's northern is yet to be identified.

Banding

Data for all banding records from December 1968 to 2010:

Pelagodroma marina – 276 adults and 30 nestlings, with 27 recoveries of adults on the islet.

Ardenna pacifica – 262 adults and 7 nestlings, with 47 recoveries of adults on the islet, 76 on nearby Big Island, one off Ulladulla, NSW and one on Tollgate Islands, Batemans Bay, NSW.

Ardenna tenuirostris – 54 adults, with 4 recoveries - two on the islet and one each on Big Island and Long Reef, Sydney.

Eudyptula minor – 141 adults and 29 nestlings, with 22 adults and 3 nestlings being re-trapped; 17 were recovered on the islet. Four (> 10 years of age) were recovered as far north as Terrigal (linear distance of 120 km) on the NSW central coast. Four were recovered as far south as Phillip Island (688 km) and The Twelve Apostles (839 km), Victoria. Additionally, three nestlings fledged on Big Island were recovered on Flinders Islet and another Little Penguin that fledged on Lipson Cove, 1,345 km south in South Australia, was also recovered on the islet.

Larus dominicanus – 7 nestlings, with no recoveries.

Haematopus fuliginosus – 1 adult and 23 nestlings, with 12 recoveries: eight recoveries made locally and others as far north as Long Reef, Sydney and as far south as Bermagui (238 km), NSW.

Acknowledgements

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Corella, 2019, 43: 39-41

SEABIRD ISLANDS No. 41/1

Martin Islet, Five Islands Group, New South Wales

Location: 34°29'40" S, 150°56'15" E: 1.3 km offshore from Hill 60, Port Kembla, New South Wales (NSW). It is part of the Five Islands Group, located 150 m east of Big Island No. 2.

Status: Nature Reserve administered by the NSW National Parks and Wildlife Service (NPWS), Office of Environment and Heritage (OEH). Entry permit required.

Other Names: Previously Five Islands No 3[1].

Description: Martin Islet is the smallest islet in the Five Islands Group[2], which also includes Bass Islet, Flinders Islet, and Big Island (comprising two main parts known as No. 1 and No. 2). Martin Islet is 2.33 ha in area, of which 0.26 ha is vegetated. Geologically, the islet resembles Big Island and Bass Islet in the Group, being derived principally from the Dapto-Saddleback Latite Member of the Gerringong Permian Volcanics[3].

Martin Islet is irregularly shaped, with the highest point at 20 m on the plateau at the western end. All approaches to the islet encounter a rocky shoreline. Extensive rock platforms cover the islet, with a large, eroded, basalt dyke almost bisecting it from southeast to northwest one third of the way across the islet from the eastern shore (see Figure 1).

The plateau is dominated by the introduced shrub Bitou Bush *Chrysanthemoides monilifera rotundata* and the New Zealand Mirror Plant *Coprosma repens,* with the slopes supporting native Prickly Couch *Zoysia macrantha*. Since it was last surveyed, the most notable losses of native plant species have been the Prickly Couch and Pigface *Carpobrotus glaucescens* communities on the plateau, as previously described by Battam[1]. These have been overcome by introduced shrubs and the establishment of an Australian Pelican *Pelecanus conspicillatus* population, which has hardened off and compacted the soil and generated considerable guano deposits. Other vegetation not mentioned in Battam[1] includes (*indicates exotic species):

Amaranthus viridis, Atriplex australasica, Cenchrus clandestinus*, Chenopodium album*, Chenopodium murale*, Commelina cyanea, Einadia trigonos, Eleusine indica*, Enchylaena tomentosa, Lycium ferocissimum*, Malva parviflora*, Portulaca pilosa, Sonchus oleraceus** and *Tetragonia tetragonoides.*

Landing: Landing can be effected from a tender on the northwest shoreline where a deep-water approach allows a bow disembarkation in low to moderate seas (Figure 1).

Ornithological History: Battam[1] detailed the ornithological visits to Martin Islet up until 1976. Over the next decade, four banders visited it a total of nine times (Australian Bird and Bat Banding Scheme [ABBBS], submitted data), but no further

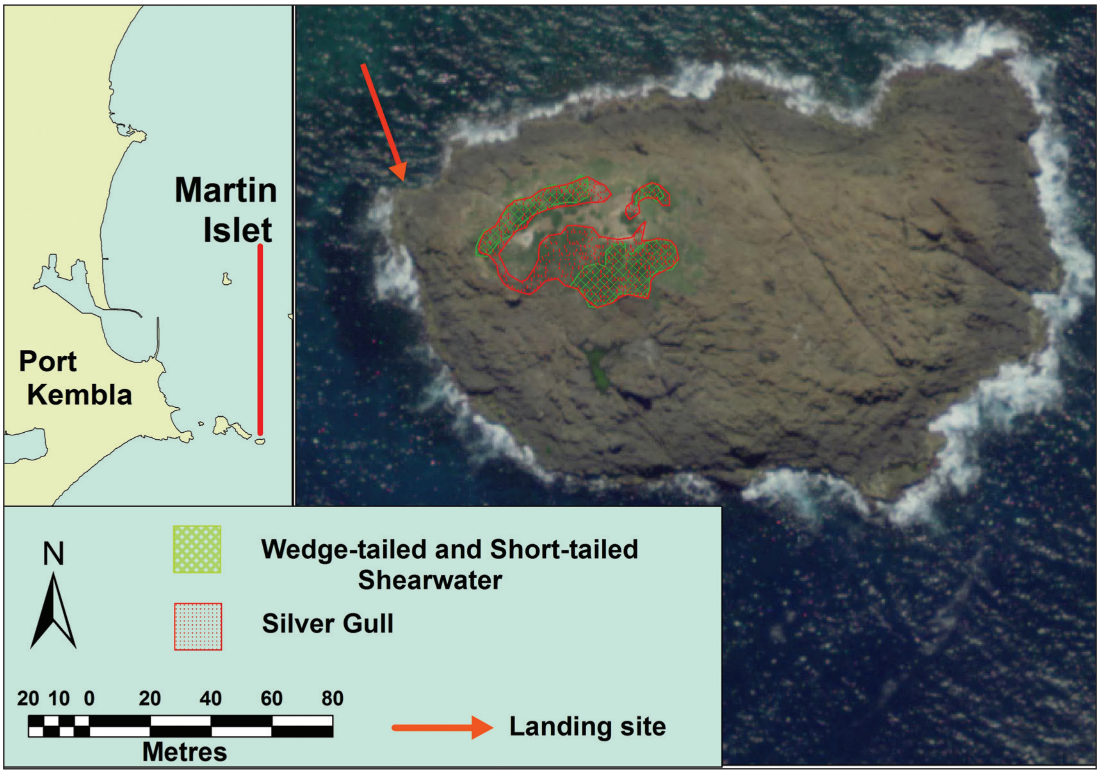

Figure 1. *Martin Islet, Five Island Group, New South Wales*

banding has been attempted since then. N. Carlile and N. Whitelaw visited overnight on 20–21 September 2016 to survey nesting seabirds and N. Carlile and R. Morris visited for an hour on 26 January 2017 to document shearwater distribution and burrow occupancy.

Breeding Seabirds and Status

Pelagodroma marina White-faced Storm-Petrel — Previously found on the plateau of the islet in an area now dominated by an Australian Pelican crèche. There was no evidence of this species in the air over the previous colony area or on the ground during an overnight visit in September 2016, despite sightings of it at the same time on nearby Flinders Islet[4]. No burrows were seen during a burrow search in January 2017 and the species is likely to be locally extinct.

Ardenna pacifica Wedge-tailed Shearwater — Nests on the edge of the plateau and on some slopes with sufficient soil depth for burrowing. This species was seen at night among burrows during September 2016. Population size was estimated by counting all known burrows across the available habitat in January 2017. On the north-western edge of the plateau, burrows were checked for the proportion occupied and ratio of species (Wedge-tailed to Short-tailed Shearwaters). Each burrow was hand-searched for the presence of birds and, if it was occupied, the occupant was either extracted or evidence of its presence collected (downy feathers). Burrows with unreachable occupants were considered to have the same ratio of species as those where the identity of birds was determined. In total, 88 burrows were counted. From the search of 42 burrows, 40% were occupied, all with young chicks. Of the 15 observed chicks, all but one was a Wedge-tailed Shearwater. The average expected breeding success (i.e. eggs that produce chicks) is 50%[5] for this species, suggesting that the islet supports approximately 28 breeding pairs. This resembles the "30 (+) breeding pairs" estimated in the 1970s[1], but is substantially more than estimated in the late 1990s[2] when search effort was not quantified.

Ardenna tenuirostris Short-tailed Shearwater — Nests are among those of Wedge-tailed Shearwaters. Whilst no calls of this species were documented during an overnight stay in September 2016, a single chick was found during a search of burrows in late January 2017. The population here is likely to comprise only a few pairs and much fewer than the estimated 40 (+) pairs in the mid 1970s[1] or 30 pairs in the late 1990s[2].

Eudyptula minor Little Penguin — Previously known to breed in an area south of the plateau that is currently dominated by Prickly Couch[1], but none were heard either swimming near the islet at dusk or onshore during an overnight visit in September 2016.

Thalasseus bergii Crested Tern — The breeding population recorded irregularly on Martin Islet in the 1970s[1] was not evident during the survey in September 2016, but birds did breed on the islet in 1999[2]. They were noted breeding on Big Island in 2016 (unpubl. data), which possibly explains their absence from Martin Islet during our visits.

Chroicocephalus novaehollandiae Silver Gull — This species now dominates the vegetated areas of Martin Islet that are not being used by Australian Pelicans or covered in shrubs. A direct count of nests in September 2016 indicated that 230 pairs were breeding on the islet. This is significantly fewer than the 1970s estimate of 1,000 breeding pairs[1] or the 500 pairs suggested in the late 1990s[2].

Larus dominicanus Kelp Gull —Has been observed both on the islet (2014, unpubl. data) or near it (this survey), but no nests were found for the species. Previously two pairs were known from this site[6].

Haematopus fuliginosus Sooty Oystercatcher — The extensive area of rock platform favours this species, but in September 2016 Carlile and Whitelaw recorded only a single pair defending territory which may have gone on to breed.

Pelecanus conspicillatus Australian Pelican — A small breeding population became established at the eastern end of No. 2 plateau on Big Island in 1983[5], very near to Martin Islet. As part of observations on the growth of the Big Island colony[5], it was noted that on Martin Islet by September 1991 there were two adults on nests and four 'loafing' nearby. In September 1995, up to 55 adults were noted on the islet and 50 breeding pairs were present in the late 1990s[2]; however, in 2005 there were only 33 adults. During the current survey period, 16 incubating adults and 33 crèche young were noted occupying the central section of the small plateau in September 2016.

Threskiornis molucca Australian White Ibis — This species first appeared breeding in the Five Islands Group on Big Island in the late 1990s[5]. As part of observations on the growth of the main colony[5], it was noted that up to 25 White Ibis were seen on Martin Islet by 2005. This expansion of breeding onto Martin Islet probably occurred after the establishment of Mirror Plant at this site. In September 2016, an estimated 80 birds were occupying the available habitat. A direct count of nests was not possible due to the unacceptable disturbance this would have caused to a crèche of juvenile Australian Pelicans.

Factors Affecting Status

The loss of White-faced Storm-Petrels on Martin Islet sometime between the 1970s[1] and late 1990s[2] probably occurred because substrate conditions deteriorated during the increase in nesting Australian Pelicans.

The Wedge-tailed Shearwater has managed to retain its breeding population size since the 1970s survey despite a significant decline in available habitat[1]. The Short-tailed Shearwater is in decline on Martin Islet for unknown reasons. On nearby Big Island the population has remained stable over the same period[5] and the species has established itself on Flinders Islet[4].

The local extinction of Little Penguins on Martin Islet is probably an outcome of the re-establishment of Australian Fur Seals *Arctocephalus pusillus* in the island group. From the location of the mapped colony in the 1970s[1], the current haul-out area of seals now dominates the rocks where penguin landings would previously have occurred. The presence of the seals would now probably be deterring any penguin arrivals, as has been seen previously on Montague Island off Narooma, NSW. On Montague Island, as seal numbers rise and their haul-out sites expand[7], the Little Penguin landing sites in the immediate vicinity appear to diminish or cease to be used (unpubl. data). It is almost certainly this impact rather than other land-based changes that have led to their disappearance from Martin Islet, as their former breeding location near the plateau appears to be little changed since the previous survey[1].

The reduction in the Silver Gull population since the 1970s survey[1] mirrors the decline now recorded for this species on Big Island[5]. At the higher elevations on Martin Islet, the dominance of the Australian Pelican rookery and the spread of exotic shrubs may also be restricting gulls from breeding. Certainly, the area previously known for Crested Tern breeding[1] is now dominated by shrubs and this may preclude terns reusing this islet in the future.

Australian Pelicans and Australian White Ibis are recent arrivals on Martin Islet. Whilst the pelicans appear to favour the skeletal soil areas on the plateau, the presence and uncontrolled expansion of introduced shrubs may eliminate the area available to them. This will be to the advantage of the Australian White Ibis. The removal of shrubs will reduce seed spread to other islands and assist recovery of native vegetation nearby[5].

Whilst not recorded on or over Martin Islet during the survey, the Swamp Harrier *Circus approximans,* White-bellied Sea-Eagle *Haliaeetus leucogaster* and Peregrine Falcon *Falco peregrinus* are known to frequent Big Island[5], and would probably impact colonial nesting populations on Martin Islet.

Other Seabirds Recorded

Other seabirds observed during the current survey:

Phalacrocorax carbo	Great Cormorant
Phalacrocorax sulcirostris	Little Black Cormorant

Other Vertebrates Recorded

The Eastern Water Skink *Eulamprus quoyii,* previously identified by Battam[1], was not recorded during these surveys. Australian Fur Seal numbers are likely to rise, as the count of 90 individuals during this survey has increased from 20 seen from Big Island in August 2012 and 34 counted during a circumnavigation of the islet in April 2014 (unpubl. data).

Banding

Data for all banding records from December 1969 to December 1986:

Ardenna pacifica	– 16 adults, with two recoveries: one nesting on nearby Big Island and the second as a beach-washed recovery 10 km to the south.
Ardenna tenuirostris	– 16 adults, with no recoveries.
Pelecanus conspicillatus	– 48 nestlings, with 8 recoveries away from the site: Lake Wooloweyah near Yamba on the NSW north coast is the greatest distance at 600 km.

Acknowledgements

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Reproductive effort of urban Little Ravens: nest site selection and brood defence

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Altricial birds' reproductive effort typically includes choosing an optimal nest site and protecting it in some manner against species constituting a threat to successful breeding. Pairs of urban Little Ravens *Corvus* mellori nested predominantly in tall eucalypts with a broader, denser canopy and fewer neighbouring trees of similar or greater height than control trees 100 m distant. Nest-trees also had fewer neighbouring trees of similar or greater height and 1.2 x greater estimated visibility over 100 m horizontally at nest height than nearby paired control trees of the same height. The main advantage of such distinctive nest sites may be providing superior surveillance for intruding nest predators and competing conspecifics. Nine identified bird species invaded Little Raven nest-trees during breeding, particularly honeyeaters and lorikeets; twenty-seven bird species intruded into 40 m zones around Little Raven nest-trees, the most frequent being the types of bird mentioned above and Common Mynas *Acridotheres tristis*. However, Little Ravens defended their nest site aggressively, and usually successfully, only against potential nest predators (currawongs and magpies) and competing conspecifics. Aggressive response rates to intrusions by these species, however, appeared to be rather low, but many possible factors affecting brood defence decisions were unknown in this study and may be influential. Literature indicates that the main species eliciting brood defence in other *Corvus* species are (1) raptors, including predators and nest usurpers of corvids, (2) other known predators of avian broods (e.g. kookaburras), (3) large (e.g. cockatoos) and smaller (e.g. pigeons and honeyeaters) birds seemingly posing little threat to nesting corvids, and (4) competing conspecifics. Reproductive effort expended on nest site selection by urban Little Ravens was probably limited, given the frequent re-use of nests. However, aggressive brood defence appeared costly, mainly because of the energetic behaviour and likely injury risk involved rather than the actual response rate.

INTRODUCTION

Reproductive effort (RE) is the percentage of an organism's current energy budget devoted to reproductive success. Life history theory predicts a trade-off between current and future reproduction; it is hypothesised that elevating RE increases current reproductive success, but decreases survivorship and/or future fecundity (Roff 1992). The trade-off is predicted as a large RE is usually costly because it is likely to require diversion of energy from growth and maintenance, and consequently impairment of other vital functions (e.g. immune competence; Hanssen *et al*. 2005). In altricial birds, RE is expended *inter alia* on parental care, including choosing an optimal nest site and protecting the nest, clutch and brood against species posing a threat to breeding success (hereinafter 'brood defence').

Nest sites' physical characteristics influence avian breeding success in several ways and choosing an optimal site is therefore critical and may require substantial time and energy allocations. Nest predation is a major cause of avian breeding failure, so in vulnerable species natural selection should favour individuals that choose nest sites with a low predation risk because of their inconspicuousness or inaccessibility (Fontaine and Martin 2006; Remes *et al*. 2012; LaManna *et al*. 2015). Both properties can also be important in reducing the risk of fitness losses through brood parasitism (Fiorini *et al*. 2009). Sheltered nest sites can be beneficial thermally through reducing heat loss by incubating and brooding parents, decreasing egg warming costs after nest recesses, and increasing nestlings' growth rate (Martin *et al*. 2017). Sites with low ectoparasite densities are likely to have lower nestling mortality attributable to blood-borne pathogens (Loye and Carroll 1998).

Another line of resistance against nest usurpation, nest predation, brood parasitism and extra-pair copulations is aggressive interception of intruders posing such threats. However, because this strategy is inherently costly and risky, there is likely to be a trade-off for the defending breeders between enhanced current reproductive success and possible injury or death and hence reduced residual reproductive value. Characteristics postulated to affect the brood defence cost: benefit ratio include parents' re-nesting potential, life expectancy, experience, sex and past parenting effort, and offspring age, stage of development, quality, vulnerability and brood size (Montgomerie and Weatherhead 1988). Although many of these postulated influences are difficult to test, some have been demonstrated convincingly (e.g. offspring age, number and quality, Curio 1987; offspring stage of development, Campobello 2008; parental sex and quality, Klvaňová *et al*. 2011 and Kryštofková *et al*. 2011).

The aims of this study were to determine:

(a) whether urban Little Ravens *Corvus mellori* select nest-trees non-randomly i.e. having distinctive characteristics. This was achieved by searching urban Melbourne for active nests, measuring their characteristics and comparing these metrics with those of systematically chosen control trees. I predicted that nest-trees would have characteristics distinguishing them from controls because Little Ravens in Melbourne are potentially at risk of clutch/brood predation, nest usurpation, brood parasitism and extra-pair copulations. Lill and Hales (2015) showed that in one season urban Little Ravens mainly nested in tall eucalypts, but did not analyse this trend further.

(b) which bird species entering the nest area do/do not elicit aggressive, defensive behaviour by nesting pairs of urban Little Ravens. It was predicted that many common species in suburbia would be ignored because they pose no obvious threat to nesting Little Ravens, but that potential nest predators, brood parasites and reproductive competitors would elicit brood defence.

(c) how this defensive spectrum compared with that of congeners. This was done by conducting a literature review, mainly of primary sources. The review was not exhaustive, but nor was it selective. The intention was simply to ascertain whether the targeting of brood defence in urban Little Ravens broadly resembled that in populations of exurban Little Ravens and urban and exurban congeners.

METHODS

Study species and area

Little Ravens are restricted to southeast Australia, from the Great Australian Bight to northeastern New South Wales. They occur in treed farmland, woodland, open forest and conurbations from the coast to alpine altitudes. The species is the numerically dominant *Corvus* species in Melbourne (Dooley 2012).

Nests were found by driving extensively around suburban Melbourne in three successive breeding seasons (June - December) searching for Little Ravens showing clear signs of nesting behaviour. The two closest nests studied were 225 m apart and the two most spatially distant ones were ~40 km apart.

Measurement of nest-tree and control tree characteristics

All nest-trees were identified to genus, but the genera *Eucalyptus* and *Corymbia* were lumped as 'eucalypts' (Wilson *et al*. 2005). Consequently, when presenting data on types of nest-tree used, the label 'groups' rather than genera is employed. I measured other characteristics of a subset of 88 nest-trees that were sufficiently accessible to permit such measurement. Distances were measured with a laser rangefinder and heights with a rangefinder and clinometer. The following measurements were made on this subset of nest-trees:

1 Height; height of the nest was also measured (both ± 0.1 m)

2 Maximum canopy diameter on North-South compass bearing (± 1 m).

3 Canopy cover, measured with *Canopy App* on a cell phone at 2 or 3 points below the canopy at my breast height and averaged. Higher values indicate greater canopy cover (i.e. a denser canopy).

4 Isolation index, the number of trees of similar height to the nest tree within 30 m of it.

5 Distance to nearest concealing cover (± 1 m), defined as a tree or built structure potentially offering nearly total concealment for potential nest predators. Pied Currawongs *Strepera graculina*, particularly, sometimes behaved cryptically around Little Raven nests.

6 Distance to nearest human food outlet (± 1 m); outlets were places where there was a potential for Little Ravens to access human food waste (e.g. cafes or large food stores with outdoor food waste bins etc.) (Yap *et al*. 2002; Lill and Hales 2015). This metric was obtained from *Google Earth* images.

A control tree was selected 100 m away from each nest-tree (100 m control) and the measurements detailed above were made on this tree for comparison. The rationale for this was that such a control was usually likely to be within the nesting pair's territory and in theory could equally have been chosen as the nest-tree. Ideally these controls would be chosen at random, but this was impracticable because many would have been inaccessible for measurement. Therefore, a systematic but unbiased selection process was used. On a Google satellite image of the nest site area, a 100 m control tree was selected by randomly choosing a main compass coordinate (N, S, E or W), drawing a straight line along that coordinate outwards from the nest-tree and selecting the tree intersected by the line at, or as close as possible to, 100 m. If there was no tree on or near the line about 100 m from the nest-tree, a second main compass coordinate was randomly chosen etc., until a control tree was obtained.

A second type of control tree was selected, a similar height control tree (SH control), namely the tree of similar height to each nest-tree within a 100-m radius of it that was closest to it. This was done for an unbiased sub-sample of 56 accessible nest-trees, although nine of them proved to have no suitable candidate SH control. Lill and Hales (2015) suggested that tall trees were preferentially chosen as nest sites by urban Little Ravens, so the rationale for these controls was to determine whether a tree of similar height in the chosen nesting area had other characteristics that made it less suitable for nesting. Again, the same set of measurements outlined above was made, but additionally I measured a coarse-grained Visibility Index for nest-trees and their paired SH control. This involved estimating whether there was a clear line of sight outwards horizontally for 100 m at nest height along the main compass coordinates (N, S, E and W). The index could thus range from 0 (no clear line of sight for 100 m on any co-ordinate) to 4 (unimpeded visibility over 100 m on all four coordinates).

Goodness-of-fit tests were used to examine disparity in: (a) taxonomic identity of nest-trees and their controls, and (b) response rates to intruders by nesting Little Ravens in the incubation versus the nestling stage. A series of paired samples *t* tests was employed to compare separately the characteristics of nest-trees with those of their individually paired 100 m and SH controls. Before conducting these tests, I determined that tree metrics were not inter-correlated. Data analysed by *t* test were checked for normality and homogeneity of variances; canopy cover was square root transformed. Sample sizes varied a little among tree metric comparisons, mainly due to varying accessibility for measurement.

Measurement of brood defence behaviour

Brood defence was studied mainly in one breeding season at a subset of all nests found that was chosen for visibility and to encompass a broad geographical spread within Melbourne. The closest two nests studied were 225 m apart and the two most widely separated nests ~21 km apart. Most brood defence observations (*BDOBS*) were made from a vehicle with tinted windows about 40 m from the nest-tree; the Little Ravens and intruders were clearly unaware of my presence. Observation sessions (58 to 185 minutes long, mean ~74 minutes) were conducted at various times of day from early morning to late afternoon, and overall at most nesting stages except nest building they were split evenly between morning and afternoon. No nest was observed more than once per day. The nesting birds could not be sexed or individually recognised.

I recorded intrusions by members of all bird species into a 40-m zone around the Little Ravens' nest-tree (or as much of it as was visible to me) and whether such intrusions entailed visiting the Little Ravens' nest-tree. The zone's radius was based on both visibility for the observer and my previous experience of Little Ravens' responses to birds near their nest-tree. I also recorded all aggressive interactions between the nesting ravens and these intruders and the outcome of these encounters. The one exception was that I did not record retaliatory aggression by intruding conspecifics, because this would have detracted from properly recording the nesting pair's defensive behaviour against them. Some intruders (mostly fast-flying, small birds) could not be identified to species and were designated 'unidentified'. The frequency of intrusions by birds did not necessarily reflect the actual number of individuals invading the nest zone, because some individuals continuously used the same space as the nesting Little Ravens and made repeated 'intrusions'.

Similar, limited observations of brood defence were also made at 4 nests observed primarily to record parental nest attendance (*PAOBS*) (Lill, in review). However, in these observations I only recorded intrusions into the nest zone and tree by, and responses of the breeding pair to, intruders to which the Little Ravens responded aggressively. There were 28 hours of such observations, 40.5% being pre-midday; they were spread across the incubation (44%), nestling (14%) and peri-fledging (42%) stages.

RESULTS

Nest site selection

Nest-trees (n=144) were found in public and residential gardens, streets, parkland, carparks, school grounds and golf courses. A bias towards streets and gardens was dictated partly by accessibility for the observer.

Tree groups used for nesting

Twelve tree groups were used for nesting by urban Little Ravens (Table 1); additionally, two nests were constructed on artificial structures (tall lamp posts). Eucalypts comprised 84% of nest-trees and no other tree group accounted for > 2.8%. In contrast, only 18.2% of the 100 m controls were eucalypts, and nest-trees and their 100 m paired controls (n= 88 pairs) were in different tree groups in 85.2% of cases (P < 0.0001, Binomial test). Among the 100 m controls, tree genera that were not used for nesting by urban Little Ravens included *Fraxinus*, *Grevillea*, *Kolreuteri, Melaleuca, Melia*, *Olea, Photinia*, *Pieris*, *Populus*, *Prunus, Pyrus, Quercus* and *Schinus.*

Table 1

Identity of Little Raven nest-trees and Similar Height control trees. Upper percentage for nest-trees is for total sample (n = 144), lower percentage in bold is just for nest-trees matched with an SH Control tree (n = 47).

Tree category	Percentage	
	Nest-tree	Similar height control tree
Eucalypt	84.0	
Eucalyptus/Corymbia	**83.0**	**74.5**
Norfolk Island Pine	0.7	
Auracaria		**2.1**
Cypress	2.8	
Cupressus	**2.1**	**4.3**
Cedar	0.7	
Cedrus	**2.1**	
Monterey Pine	0.7	
Pinus		
She-oak	2.8	
Casuarina/Allocasuarina	**8.5**	**2.1**
Plane	1.4	
Platanus	**2.1**	**8.5**
Elm	2.1	
Ulmus		
Fig	1.4	
Ficus	**2.1**	
Flame Tree	0.7	
Brachychiton		
Palm	0.7	
Phoenix		
Brush Box	0.7	
Lophostemon		
Oak		
Quercus		**4.3**
Silky Oak		
Grevillea		**2.1**
Poplar		
Populus		**2.1**

Mean distance between a nest-tree and its paired SH control was 31.3 ± 3.4 m, but 16.1% of nest-trees lacked an SH control within the specified area (Table 1). Nest-trees and their paired SH controls (n= 47 pairs) were in the same tree group in 74.5% of pairings (P = 0.001, Binomial test), mainly because eucalypts comprised ~75% of the SH controls. Although eight tree groups were represented in the control sample, only three of them (genera *Quercus*, *Grevillea* and *Populus*) failed to feature as nest-trees for urban Little Ravens.

Tree and nest height

The mean height of nest-trees was 23.3 ± 0.6 m (n = 83) and that of nests 18.0 ± 0.5 m (n = 79); the two metrics were positively correlated (Pearson $r_{(79)} = 0.877$, $P < 0.001$) (Fig 1). On average, nest-trees were about twice the height of their 100 m controls, whose mean height was 11.5 ± 0.7 m ($t_{(77)} = 13.621$, $P < 0.001$) (Fig 2a); they were numerically taller than them in 96% of nest-tree x 100 m control tree pairings, only 12.4% of which were eucalypt x eucalypt.

Tree canopy diameter and cover

Maximum canopy diameter and tree height were not correlated for nest-trees (Pearson $r_{(72)} = 0.210$, $P > 0.05$). On average, maximum canopy diameter was 1.7 x greater in nest-trees than in their 100 m controls (14.7 ± 0.8 versus 8.5 ± 0.5 m; $t_{(70)} = 9.065$, $P < 0.001$) (Fig 2b. 1). However, canopy diameter was similar in nest-trees and their paired SH controls, whose mean canopy diameter was 13.3 ± 0.8 m ($t_{(37)} = 0.945$, $P > 0.05$) (Fig 2b. 2).

Canopy cover was not correlated with maximum canopy diameter for nest-trees (Pearson $r_{(68)} = 0.027$, $P > 0.05$). Overall, mean canopy cover was 1.3 x greater in nest-trees than in their paired 100 m controls (41.1 ± 1.5 versus 32.1 ± 3.0%; $t_{(68)} = 4.226$, $P < 0.0001$) (Fig 2c. 1). However, canopy cover was similar in nest-trees and their paired SH controls, whose mean canopy cover was 43.1 ± 3.3% ($t_{(37)} = 2.012$, $P > 0.05$) (Fig 2c.2).

Tree isolation index

On average, nest-trees had fewer neighbouring trees of similar (or greater) height than did their 100 m controls (means: 1.2 ± 0.2 versus 5.2 ± 0.4 neighbours; $t_{(85)} = 11.331$, $P < 0.0001$) (Fig 2d. 1). Nest-trees also had fewer neighbouring trees of similar (or greater) height than did paired SH controls, whose mean was 2.0 ± 0.3 neighbours ($t_{(41)} = 3.315$, $P < 0.01$) (Fig 2d. 2).

Distance to concealing cover and nearest human food outlet

Mean distance to concealing cover was similar for nest-trees (18.1 ± 1.1 m) and their paired 100 m controls (19.6 ± 1.9 m) ($t_{(81)} = 0.694$, $P > 0.05$) (Fig 2e.1). Mean distance to the nearest human food outlet was also similar for nest-trees (395.4 ± 33.2 m) and their paired 100 m controls (367.6 ± 30.6 m) ($t_{(84)} = 0.335$, $P > 0.05$) (Fig 2f). Paired nest-trees and SH controls (mean 20.7 ± 2.1 m) were also a similar distance from concealing cover ($t_{(41)} = 0.485$, $P > 0.05$) (Fig 2e. 2). As most SH controls were found to be very close to their paired nest-tree, comparing their respective distances from the nearest human food outlet was redundant.

Tree visibility index

There was a 1.2 x greater mean estimated visibility over 100 m horizontally at nest height from nest-trees than from paired SH controls (2.7 ± 0.2 versus 2.2 ± 0.1; $t_{(41)} = 3.130$, $P < 0.01$) (Fig 2g). Estimated visibility was numerically greater from the nest-tree in 54% and from the paired SH control in just 8% of such pairings, 38% of pairings exhibiting no difference.

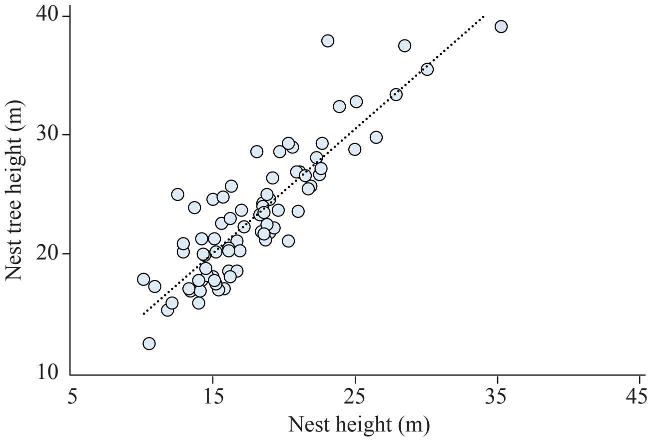


Figure 1. *Relationship between nest tree height and nest height for urban Little Ravens. Linear trend line is shown.*

Brood defence

Species entering Little Raven nest zones

Brood defence by urban Little Ravens against species invading their nest sites was monitored at 22 nests during ~113 hours of *BDOBS* covering all nesting stages. Additionally, it was documented on a more limited basis during 17 *PAOBS* sessions (Lill, in prep.) (see Methods).

In the *BDOBS* sessions, the mean rate of invading Little Raven nest-trees by birds (other than the nesting pair) was 6 intrusions/h; the mean rate of invading 40-m zones around nest-trees by birds and Domestic Cats *Felis catus* was 30 invasions/h. Nine identified bird species invaded Little Raven nest-trees, the most frequent being the Red Wattlebird *Anthochaera carunculata*, Noisy Miner *Manorina melanocepha,* Rainbow Lorikeet *Trichoglossus moluccanus* and Common Myna *Acridotheres tristis* (Table 2). Twenty-seven identified bird species invaded Little Raven nest zones and Domestic Cats entered two raven nest zones infrequently at ground level (Appendix 1, Table 2). No members of brood parasitic species entered Little Raven nest zones or trees.

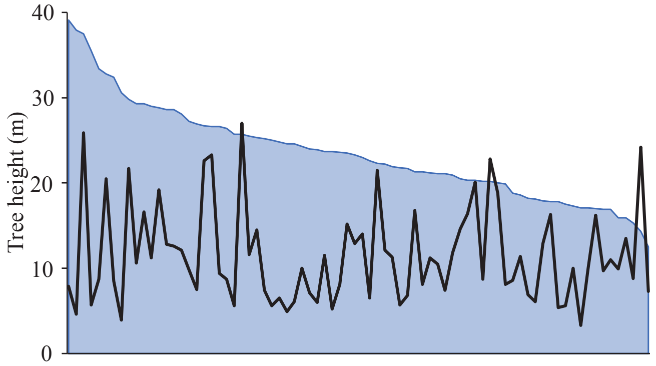
Species that elicited aggression in nesting Little Ravens

In *BDOBS* sessions, nesting Little Ravens responded aggressively to only four (44%) of the identified bird species that perched in, or flew through the canopy of their nest-trees, although at least one raven pair member was in the nest zone during 51% of the 568 nest-tree intrusions made collectively by these species (Table 2). Nesting Little Ravens only reacted aggressively to members of seven (26%) of the identified bird species that invaded their 40-m nest zones, although at least one pair member was present in the zone during 52% of the 2,552 zone intrusions made collectively by all intruding species (Table 2, Appendix 1).

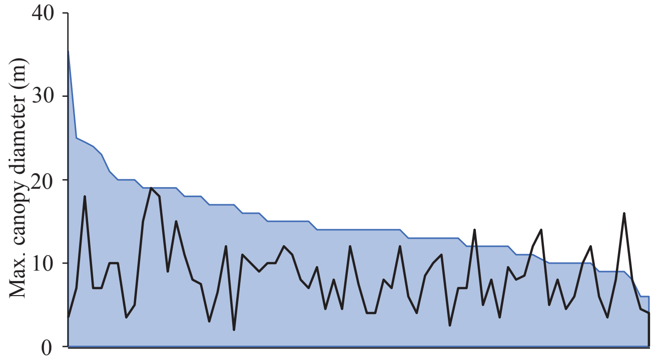
a. Conspecifics

At least one Little Raven pair member was at the nest site during 61% of intrusions by conspecifics. By far the greatest response rate by nesting ravens to any species was to these intruders, just over a third of whose intrusions elicited

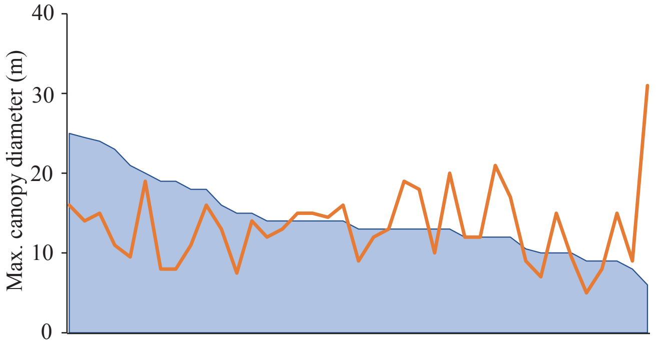
(a) Nest-trees x 100 m controls



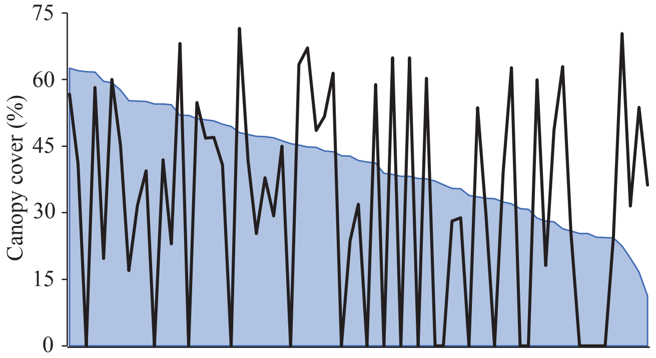
(b. 1) Nest-trees × 100 m controls



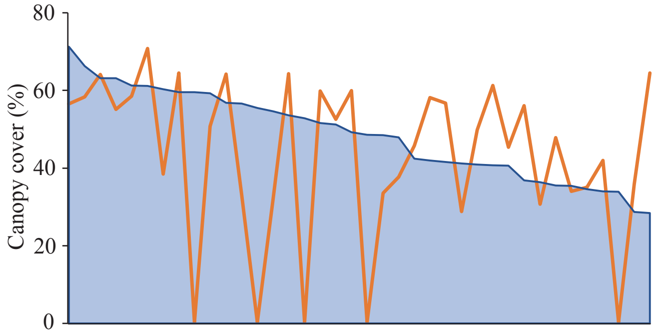
(b. 2) Nest-trees × Same Height controls



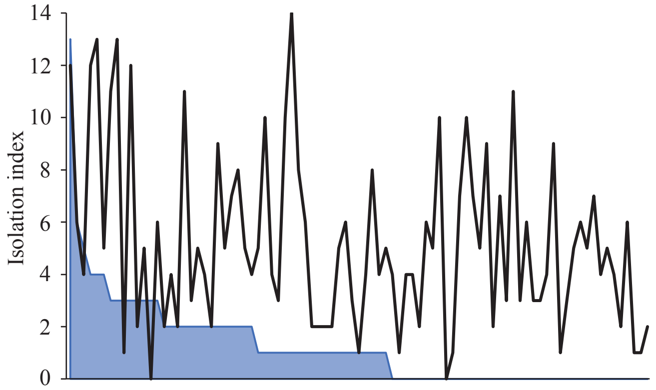
(c. 1) Nest-trees × 100 m controls



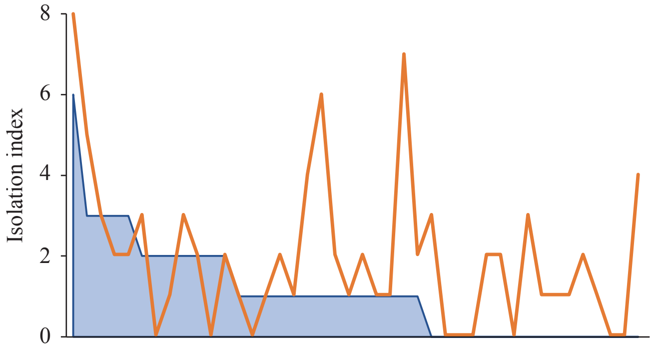
(c. 2) Nest-trees × Same Height controls



(d. 1) Nest-trees x 100 m controls



(d. 2) Nest-trees × Same Height controls



(e. 1) Nest-trees × 100 m controls

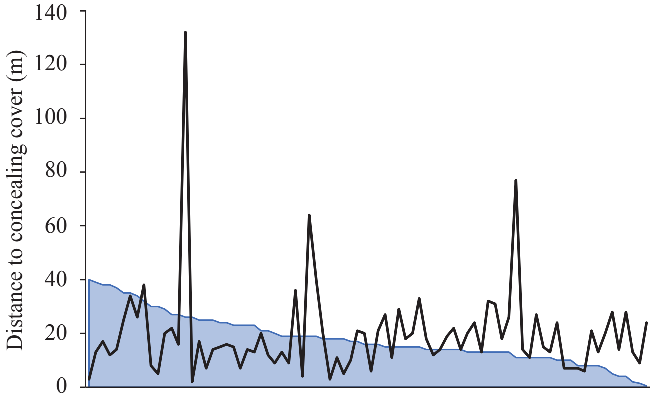
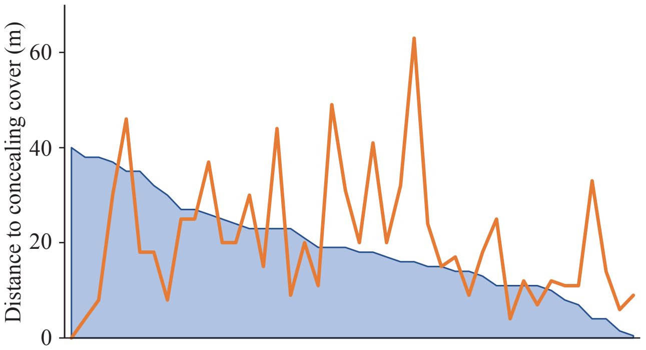
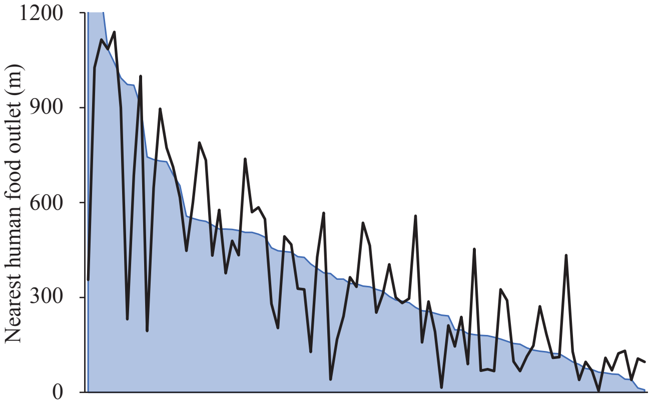


Figure 2. *Comparison of characteristics of urban Little Raven nest-trees and control trees. In all graphs, the nest-tree population is shaded in blue and ordered from the highest value for that variable on the left to the lowest on the right. The distributions of the paired controls are shown by a black line for 100 m controls and an orange line for the Same Height controls.*

(e. 2) Nest-trees × Same Height controls



(f) Nest-trees × 100 m controls



(g) Nest-trees x Same Height controls

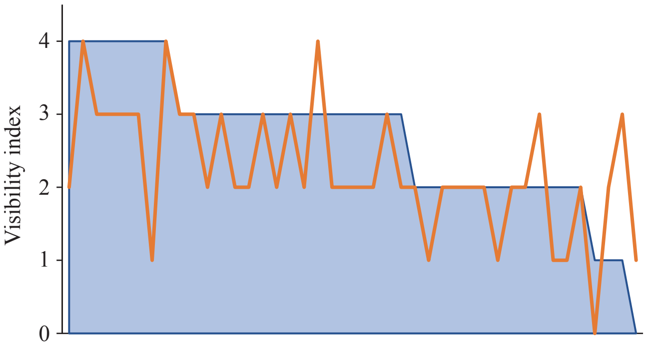


Figure 2 (continued). *Comparison of characteristics of urban Little Raven nest-trees and control trees. In all graphs, the nest-tree population is shaded in blue and ordered from the highest value for that variable on the left to the lowest on the right. The distributions of the paired controls are shown by a black line for 100 m controls and an orange line for the Same Height controls.*

aggression by at least one nesting pair member (Table 2). Nesting Little Ravens reacted aggressively to conspecific intruders at all breeding stages, but especially frequently during the nestling and peri-fledging stages, when around half of conspecifics' intrusions elicited nesting pair aggression. Often after aggressively chasing and expelling conspecifics from the nest zone, the breeding pair immediately returned to the nest-tree and performed wing-flicking calling displays (WFCD), possibly a sort of 'triumph display' in this context (Bigot *et al.* 1995). During *PAOBS* sessions, 46 conspecific intruders entered nest zones. At least one pair member was present on 98% of these occasions and 61% of the conspecific intruders were aggressively chased away by the nesting ravens.

Breeding pairs' responses to visible conspecifics well outside the nest zone were variable; sometimes they reacted overtly aggressively to them, sometimes they just performed WFCD in the nest zone, and often they showed no overt response to them, especially if they were clearly visible but more than ~100 m from the nest-tree. This response pattern was evident in both *BDOBS* and *PAOBS* sessions.

b. Currawongs

Pied Currawongs that entered Little Raven nest zones during *BDOBS* sessions elicited considerable breeding pair aggression. At least one nesting pair member was in the nest zone during nearly half of the currawong intrusions into ten nest zones and reacted aggressively on 23% of occasions (Table 2), always stimulating the intruder to flee. Similarly, during *PAOBS* sessions, when at least one Little Raven pair member was present during all 31 nest zone intrusions by currawongs, the ravens responded aggressively to only ~13% of these invasions. In contrast, although at least one raven pair member was also at the nest site during all 27 nest-tree intrusions by currawongs, the nesting bird(s) responded aggressively to 64.3% of them.

c. Magpies

During *BDOBS* sessions, at least one Little Raven pair member was present in the nest zone or nest-tree during nearly two thirds of the Australian Magpie *Gymnorhina tibicen* intrusions recorded, but reacted aggressively to only 11% of them (Table 2). The outcome of these encounters was less clear-cut, because magpies were also aggressive to the nesting raven(s) during some of their intrusions (Table 2). During *PAOBS* sessions, a further eight nest zone intrusions by magpies were recorded; although at least one nesting Little Raven was present on each occasion, no aggression towards the intruders was observed.

Collectively, for the three species to which nesting Little Ravens showed substantial aggression (conspecifics, currawongs and magpies), there was no difference in nesting birds' defensive response rates in their incubation and nestling periods (23.2% versus 31.6%, $\chi^2_{(1)} = 2.160$, $P > 0.05$).

d. Other intruders

During *BDOBS* sessions, a pair of nesting Little Ravens responded very aggressively to a Nankeen Kestrel *Falco cenchroides* that invaded their nest-tree, but without much obvious effect (Table 2). Nesting Little Ravens were in the nest-tree during nearly two thirds of Rainbow Lorikeets' entries and responded with low level aggression to 6% of them, although usually causing just local displacement. However, they did not respond aggressively during the lorikeets' nest zone intrusions which were 11.2 x more frequent, despite being in their nest zone during just over half of these intrusions (Table 2). Nesting Little Ravens also responded aggressively to intruding Noisy Miners, but to < 1% of their numerous intrusions. Red

Table 2

Agonistic interactions between breeding urban Little Ravens and birds invading the ravens' nest zone and nest-tree. Numbers in square brackets are the number of nest sites involved. Breeding stage indicated by NBO (nest building and oviposition), INC (incubation), NLG (nestling), P-F (peri-fledging) and UN (unknown). LR = Little Raven. Percentages of intrusions eliciting aggressive responses by nesting ravens italicized. Percentages of intrusions in which intruder was aggressive underlined. No percentages of intruders' aggressive responses given for Little Raven intruders (see Methods).

Intruding species	No. zone intrusions [no. nests]	% zone intrusions LR(s) present	% zone intrusions LR(s) aggressive	No. nest-tree intrusions [no. nests]	% nest-tree intrusions LR(s) present	% nest-tree intrusions LR(s) aggressive	% ALL intrusions when intruder aggressive
Nankeen Kestrel *Falco cenchroides*	**NLG: 1 [1]**	**100**	***100***	**0**			**0**
Galah *Eolophus roseicapilla*	INC: 14 [4]	100	0				0
	NLG: 8 [3]	37.5	*12.5*				0
	UN: 8 [1]	100	0				0
	TOTAL: 30 [6]	**83.3**	***3.3***				**0**
Rainbow Lorikeet *Trichoglossus moluccanus*	NBO: 41 [8]	34.2	0	19 [4]	68.4	*10.5*	0
	INC: 164 [11]	82.1	0	10 [1]	100	*10*	0
	NLG: 501 [12]	43.6	0	32 [6]	46.9	*3.1*	0
	P-F: 43 [5]	65.1	0	2 [1]	100	0	0
	UN: 49 [5]	16.3	0	5 [2]	0	0	0
	TOTAL: 762 [21]	**53.2**	**0**	**68 [8]**	**60.3**	***5.9***	**0**
Noisy Miner *Manorina melanocephala*	NBO: 73 [2]	41.1	*1.4*	40 [2]	27.5	0	12.4
	INC: 619 [6]	94.2	*0.2*	30 [5]	86.7	0	2
	NLG: 542 [7]	41.3	0	71 [5]	46.5	0	6
	P-F: 73 [3]	50.7	0	33 [2]	21.2	0	14.2
	TOTAL: 1307 [12]	**67.6**	***0.2***	**174 [9]**	**44.3**	**0**	**5.6**
Red Wattlebird *Anthochaera carunculata*	NBO: 50 [9]	14	0	37 [5]	43.2	*2.7*	0
	INC: 187 [9]	48.4	0	95 [9]	57.9	0	0
	NLG: 480 [12]	63.1	0	313 [11]	39.9	0	2.2
	P-F: 67 [4]	53.7	0	39 [4]	46.2	0	0
	UN: 69 [4]	21.7	0	12 [3]	50	0	0
	TOTAL: 988 [18]	**51.3**	**0**	**496 [15]**	**48.5**	***0.2***	**1.4**
Pied Currawong *Strepera graculina*	INC: 6 [2]	66.7	0	0			0
	NLG: 17 [5]	58.8	*29.4*	1 [1]	0		0
	P-F: 5 [3]	0	0	0			0
	UN: 7 [1]	28.6	*14.3*	0			0
	TOTAL: 35 [10]	**45.7**	***22.9***	**1 [1]**	**0**		**0**
Australian Magpie *Gymnorhina tibicen*	NBO: 8 [4]	37.5	0	1 [1]	100	*100*	11.1
	INC: 20 [5]	85	*10*	0			5
	NLG: 57 [12]	57.9	*7*	2 [2]	100	*50*	3.4
	P-F: 10 [2]	60	*20*	0			30
	UN: 35 [2]	62.9	*14.3*	0			0
	62.9	14.3	0				
	TOTAL: 130 [19]	**62.3**	***10***	**3 [3]**	**100**	***66.7***	**5.3**
Little Raven *Corvus mellori*	NBO: 25 [5]	68	*12*	0			
	INC: 73 [6]	83.3	*28.8*	0			
	NLG: 57 [11]	59.7	*49.1*	1 [1]	100	*100*	
	P-F: 28 [4]	96.4	53.6	0			
	UN: 4 [2]	100	*100*	0			
	TOTAL: 187 [17]	**76.3**	***38***	**1 [1]**	**100**	***100***	
Common Myna *Acridotheres tristis*	NBO: 73 [7]	43.8	0	4 [2]	75	0	0
	INC: 171 [8]	86.5	*1.2*	4 [1]	100	0	0
	NLG: 257 [11]	59.6	*0.4*	0			0
	P-F: 38 [4]	23.7	0	1 [1]	0	0	0
	UN: 56 [5]	44.6	0	0			0
	TOTAL: 595 [19]	**61.7**	***0.5***	**9 [3]**	**77.8**	**0**	**0**

Wattlebirds elicited Little Raven aggression during just one of their many intrusions into nest sites (Table 2), although during a *PAOBS* session I also observed a nesting raven displace a Red Wattlebird. Common Mynas stimulated brood defence by nesting Little Ravens in < 1% of their nearly 600 nest zone intrusions, and in none of their few nest-tree invasions. A Galah *Eolophus roseicapilla* elicited Little Raven aggression in one of the species' zone intrusions, the target bird fleeing in response to the threat (Table 2).

Actively incubating or brooding Little Ravens mostly did not overtly respond during *BDOBS* sessions to intruders of species to which they often reacted aggressively when off the nest. Only six instances of an aggressive response by an incubating or brooding raven were recorded in these sessions, five directed at intruding conspecifics and one at a magpie. Some of these intruders were in the nest-tree when the Little Raven pair-member vacated the nest to chase them. However, during *PAOBS* sessions currawongs entered the Fitzwilliam St nest-tree 27 times and the incubating female left the nest to aggressively chase them on 41% of these occasions.

Brood defence by other Corvus species

Information in the literature about the responses of nesting members of other Little Raven populations and other *Corvus* species to nest site incursions by vertebrates possibly constituting a threat to their breeding attempt is summarised in Table 3. Few authors list the species to which nesting ravens and crows do *not* respond.

The species that elicited aggressive defence by nesting members of other *Corvus* species are in 4 main categories: (a) raptors, including known predators of adult crows and ravens and their nest contents, and the main heterospecific usurpers of their nests, (b) other known nest predators (e.g. kookaburras, Australian Magpies and Domestic Cats), (c) large (e.g. cockatoos) and smaller (e.g. pigeons and honeyeaters) birds that seemingly pose little threat to nesting crows and ravens, and (d) conspecifics. The species that elicited defensive aggression in nesting rural Little Ravens were mostly in categories (a) and (d) (Rowley 1973), but in urban Albert Park in Melbourne they were in all four categories (Talmage 2011).

Aggression towards nesting Little Ravens by intruders

There was occasionally a little retaliatory aggression towards nesting pair members by intruding conspecifics being evicted from a Little Raven nest site. However, members of three other intruding bird species displayed more spontaneous aggression towards nesting Little Ravens, although the frequency was only substantial in Noisy Miners and Australian Magpies (Table 2). Miners and magpies were aggressive to raven pair members during ~6% and 5% of their intrusions, respectively. Red Wattlebirds were also aggressive to nesting Little Ravens, but during < 2% of their nest site intrusions in *BDOBS* sessions (Table 2). In *PAOBS* sessions, two further threats towards members of a Little Raven nesting pair by Red Wattlebirds were observed. Although no aggression towards nesting Little Ravens by intruding currawongs was witnessed in *BDOBS* sessions, one incidence was recorded during raven nest building in a *PAOBS* session, although it had little apparent effect.

SYNTHESIS AND DISCUSSION

Nest site selection

Urban Little Ravens predominantly built their nests in tall eucalypts that had few trees of similar (or greater) height nearby. Nest-trees had a broader and denser canopy than 100 m, but not SH, control trees. Visibility of the surrounding area at nest height was estimated to be better from nest-trees than from SH controls.

The observed predominance of eucalypts as Little Raven nest-trees in Melbourne replicated Lill and Hales' (2015) finding, suggesting that it was a stable trend over at least several years. That it involved choice rather than just being frequency-dependent was suggested by the high level of identity disparity between nest-trees and their paired 100 m controls and the diversity of tree groups among those controls. Little Ravens usually constructed their nests in the upper canopy of these eucalypts which, on average, were much taller than paired 100 m control trees. Nests that were not in tall eucalypts were usually in similarly tall trees belonging to other tree groups. Talmage (2011) found that Little Raven nests in urban Albert Park, Melbourne were mainly in Monterey Pines *Pinus radiata* and eucalypts, the most common tall trees at that location. However, pines constituted < 1% of nest-trees in my investigation.

The only likely nest predators potentially deterred by the substantial height of urban Little Ravens' nests would appear to be Domestic Cats. However, few cats were recorded in nest zones during (admittedly diurnal) observations and they did not elicit aggressive defence by nesting Little Ravens. The considerable height of most nests was conceivably most advantageous in enabling better surveillance from the nest for avian nest predators and competing conspecifics. This could have been augmented by the relative scarcity around the nest-tree of trees of similar (or greater) height that could restrict the view of the surrounding area from the nest. Due to the comparatively dense canopy of nest-trees, surveillance could also be conducted from the nest in relative concealment. However, given the alacrity with which absent parent Little Ravens sometimes returned to the nest site when potential nest predators invaded it, good visibility of the elevated nest area for parents foraging away from the nest site may be as important as outward visibility from the nest itself.

Boree *Acacia pendula* and Snow Gums *Eucalyptus niphophila* were the most frequent Little Raven nest-trees in Rowley's (1973) two rural study sites. He argued that rural Little Ravens probably did not use the nest as a 'lookout' because most nests in his study were only 3–9 m above ground level, whereas mean nest height in urban Melbourne was ~18 m in both the present investigation and that of Lill and Hales (2015). Mean nest height in Albert Park (15.5 m; Talmage 2011) was a little lower than that in the present study and that recorded by Lill and Hales (2015). Lee (2011) reported a mean nest height of 16.6 m for 21 urban Melbourne nests, again slightly lower than the mean height in the present study, but he also mentions some early records of much lower nests. Rowley (1973) deemed shading from sunlight unimportant in the placement of rural Little Ravens' nests, because they frequently built them in dead trees and on telephone poles. In contrast, only a few urban Little Ravens in my study built nests that were very exposed and

Table 3

Aspects of interspecific nest site defence by fifteen Corvus species derived from a search of largely original literature. Nest use relationship indicates that *Corvus* species uses old nests of the named species or vice versa. Grey shading indicates a lack of information.

Corvus species	Nest predators	Species involved in nest use relationship	Species against which nest site defended aggressively	Species tolerated at nest site without aggression	References
Pied Crow *albus*			Palm-nut Vulture (*Gypohierax angolensis*)		Lamm 1958
American Crow *brachyrynchos*	Raccoon (*Procyon lotor*) Great Horned Owl (*Bubo virginianus*) Grey Squirrel (*Sciurus carolinensis*)				McGowan 2001
		Black-crowned Night Heron (*N. nycticorax*) Coopers Hawk (*Accipiter cooperii*) Broad-winged Hawk (*Buteo platypterus*) Long-eared Owl (*Asio otus*) Great Horned Owl Mallard (*Anas platyrynchos*) Squirrel			Good 1952
Black or Cape Crow *capensis*			Jackal Buzzard (*Buteo rufofuscus*)		Skead 1952
Common Raven *corax*		Great Horned Owl Golden Eagle (*Aquila chrysaetos*) Red-tailed Hawk (*Buteo jamaicensis*)			Stiehl 1979
Carrion Crow *corone*			Rook		Coombs 1960
Australian Raven *coronoides*	Wedge-tailed Eagle (*Aquila audax*)	Black Falcon (*Falco subniger*)	Wedge-tailed Eagle		Rowley 1973
			Black Falcon		Debus *et al.* 2017
Chihuahuan Raven *cryptoleucus*			Swainson's Hawk (*Buteo swainsonii*) Northern Harrier (*Circus cyaneus*) Coyote (*Canis latrans*)		D'Auria and Caccamise 2007
Rook *frugilegus*			Carrion Crow Jackdaw Heron Wood Pigeon (*Columba palumbus*) Herring Gull (*Larus argentatus)* Buzzard (*B. buteo*) Peregrine Falcon (*Falco peregrinus*) Kestrel (*F. tinnunculus*) Sparrowhawk (*Accipiter nisus*) Eurasian Hoopoe (*Upupa epops*)		Coombs 1960
White-necked Crow *leucognaphalus*			Red-tailed Hawk Ridgway's Hawk (*Buteo ridgwayi*) Sharp-shinned Hawk (*Accipiter striatus*) Turkey Vulture (*Cathartes aura*) Hispaniolan Parrot (*Amazona ventralis*) Scaly-naped Pigeon (*Patagioenas squamosa*) Plain Pigeon (*P. inornata*) White-crowned Pigeon (*P. leucocephala*)		Wiley 2006

Table 3 *(continued)*

Corvus species	Nest predators	Species involved in nest use relationship	Species against which nest site defended aggressively	Species tolerated at nest site without aggression	References
Thick- or Large-billed Crow *macrorhynchos*			Raptors	Koel (*Eudynamys scolopaceus*) Sparrows (*Passer*) Bulbuls (*Pycnonotus*) Flycatchers Sunbirds	Lamba 1976
Little Raven *mellori* (rural)	Wedge-tailed Eagle	Nankeen Kestrel (*Falco cenchroides*)	Brown Falcon *(Falco berigoria)* Brown Goshawk (*Accipiter fasciatus*) Whistling Kite (*Haliastur sphenurus*)		Rowley 1973
(urban; Albert Park)			Little Eagle (*Hieraaetus morphnoides*) White-bellied Sea-Eagle (*Haliaeetus leucogaster*) Kestrel (presumably Nankeen Kestrel) Sulphur-crested Cockatoo (*Cacatua galerita*) Australian Magpie (*Gymnorhina tibicen*) Pacific Gull (*Larus pacificus*) Brush-tailed Possum (*Trichosurus vulpecula*)		Talmage 2011
Jackdaw *monedula*			Carrion Crow		Roell and Bossema 1982
	Pine Marten (*M. martes*)	Black Woodpecker (*Dryocopus martius*)			Johnsson 1984
	Stone Marten (*Martens foina*) Domestic cat (*Felis catus*)				Kaminski *et al.* 2015
	Common Raven (*C. corax*) Tawny Owl (*Strix aluco*) Least Weasel (*Mustela nivalis*) Brown Rat *(Rattus norvegicus)*	Stock Dove (*Columba oenas*) Tawny Owl			Madge and Burn 1994
Torresian Crow *orru*			Laughing Kookaburra (*Dacelo novaeguineae*) Grey Goshawk (*Accipiter novaehollandiae*)		Secomb 2005a
Fish Crow *ossifragus*			Coopers Hawk Common Grackle (*Q. quiscalus*)		McNair 1974
House Crow *splendens*			Raptors Koel Monkeys Domestic cat Snakes		Lamba 1976
Tasmanian Forest Raven *t. tasmanicus*			Grey Goshawk (*Accipiter novaehollandiae*)		Lawrence 2009
Northern Forest Raven *t. boreus*			White-bellied Sea Eagle Pacific Baza (*Aviceda subcristata*) Whistling Kite Brahminy Kite (*Haliastur indus*) Little Eagle Torresian Crow (*orru*) Eastern Rosella (*Platycercus eximius*) Noisy Friarbird (*Philemon corniculatus*)		Secomb 2005b

only 1.4% of nests were in artificial structures. Moreover, there was an indication that shade may be important for urban Little Ravens in that parents at a moderately exposed nest appeared to brood nestlings more on very sunny days (Lill, in review).

Nest heights and preferred nest-tree groups of the other four Australian corvids are: Australian Raven *C. coronoides*, rural, 12.2–8.3 m, 70% in eucalypts (Rowley 1973), and urban, mostly 10-25 m, 85% in eucalypts in northern and 62% in *Pinus* and *Auracaria* in southern Perth suburbs (Stewart 1997); Torresian Crow *C. orru,* rural, 12.2–15.2 m, 63% in eucalypts (Rowley 1973); Little Crow *C. bennetti*, rural, 6.1–9.1 m, 95% in Leopard Wood *Flindersia maculosa* (Rowley 1973); Tasmanian Forest Raven *C. tasmanicus tasmanicus*, urban and rural, mean 23.7 m (Lawrence 2009) and Northern Forest Raven *C. t. boreus*, rural, 23–36 m+ in coastal eucalypts (Secomb 2005a) and 18–21 m in tableland eucalypts (Debus and Rose 2006).

Collectively, these data suggest that both urban and rural Australian Ravens probably nest at a similar height to that used by Little Ravens in Melbourne. However, rural Torresian Crows, and particularly Little Crows, tend to nest at considerably lower heights, and rural and urban Forest Ravens mostly at greater heights than urban Little Ravens. More broadly, and not unexpectedly, there is great variation in nest sites of *Corvus* species and choice of site is not a conserved feature of their breeding biology.

Brood defence

Species eliciting little or no brood defence by Little Ravens

During *BDOBS* sessions, on average 30 hetero- and conspecific individuals intruded into Little Raven nest zones per hour, but only about a third as many species and one fifth as many individuals entered raven nest-trees. Although at least one Little Raven nesting pair member was in the nest zone or tree during just over half of these intrusions, < 2% of them elicited aggression by the nesting birds. There were two aspects to this low response rate:

1. Eighteen species (and unidentified birds) collectively made 2,006 intrusions without eliciting any Little Raven aggression (Appendix 1). This is not surprising given that only two of them, the Grey Butcherbird *Cracticus torquatus* and the Magpie-lark *Grallina cyanoleuca*, have been documented preying upon birds' nest contents (Major and Gowing 1994; Guppy *et al*. 2017). In the present study, butcherbirds were rare visitors to Little Raven nest sites, although Magpie-larks made nearly 100 invasions of raven nest zones and even a few of their nest-trees. Omnivorous urban Little Ravens consume soil and ground cover invertebrates, carrion and human food waste (Lill and Hales 2015), and inspection of Appendix 1 suggests that it contains few species with a similar diet to that of Little Ravens and likely to be major food competitors with them.
2. Collectively, five of nine species whose intrusions *did* stimulate aggression by nesting Little Ravens only elicited such behaviour very rarely *i.e.* on just 0.2% of occasions. For three of these species (Noisy Miner, Red Wattlebird and Common Myna), this seems a little puzzling at first because they are known to prey on birds' nest contents (Major and Gowing 1994; Fulton 2006). Moreover, in a *PAOBS* session in the present study a Noisy Miner that perched 3 m from a Little Raven nest during the nestling stage stimulated rapid return by the absent nesting pair, which expelled the intruder very aggressively. However, Noisy Miners, Red Wattlebirds and Common Mynas tend to be nest predators on species much smaller than the Little Raven. The low raven response rate to the other two species is understandable, as Galahs and Rainbow Lorikeets primarily eat plant components (although the lorikeets consume supplementary meat at feeding tables, Gillanders *et al*. 2017). However, again in a *PAOBS* session, a Rainbow Lorikeet that approached a Little Raven nest very closely was aggressively chased away by the incubating bird that left its nest briefly to do so.

Species eliciting substantial brood defence by Little Ravens

a. Currawongs

Breeding Pied Currawongs prey on eggs and nestlings of many bird species in urban and exurban environments (e.g. Priddel *et al.* 1995; Major *et al*. 1996; Prawiradilaga 1996; Bayly and Blumstein 2001; Fulton and Ford 2001; Guppy *et al*. 2017). They have colonised urban Melbourne progressively over the last approximately 30 years and thus now potentially pose a significant predatory threat to nesting Little Ravens in the city. During *BDOBS* sessions, currawongs entered Little Raven nest sites solitarily, and rarely invaded the nest-tree. Their intrusions were limited to only 45% of the monitored nest sites, at an overall rate of just 0.3 intrusions/h, although they intruded in all nesting stages except nest building.

Nesting Little Ravens responded aggressively to ~23% of currawong intrusions. Given that one or both raven pair members were at the nest site during nearly half of these intrusions, this means that they responded aggressively to only 47% of intrusions of which they must have been aware ('known intrusions'). This seems a rather low response rate, especially given that they were usually successful in displacing currawongs when they responded aggressively. However, no predation of Little Ravens' nest contents by a currawong was observed, although it was strongly suspected at the Fitzwilliam St nest observed during *PAOBS* sessions. This breeding attempt failed during incubation a day after multiple, simultaneous currawong invasions of the nest-tree that stimulated strong defence by both nesting ravens.

One factor contributing to Little Ravens' relatively low aggressive response rates to currawongs (and possibly magpies) could have been 'reluctance' of actively incubating and brooding individuals to leave eggs or young nestlings exposed, unless an intruder approached the nest very closely. Little Ravens had high incubation and early brooding attentiveness and typically left the nest unattended for only a few minutes during an unprovoked recess (Lill in review). During *BDOBS* sessions, incubating females left their nest to evict an avian intruder on just 3 occasions, once each for a currawong, a magpie and a conspecific that entered the nest-tree. Although high attentiveness is primarily important for maintaining optimal temperatures of embryos and ectothermic young nestlings (Deeming 2002), 'sitting tight' may also draw less attention by predators to incubating and brooding ravens than would vacating the nest to respond aggressively to them (Lawrence 2017), and consequently be particularly adaptive when the mate is absent. However, it was apparent in *PAOBS* sessions at the Fitzwilliam St nest that if currawongs approached a nest very closely, and especially if there was more than one of them present simultaneously, the incubating female would respond by leaving the nest, often several times in a few minutes, to try to aggressively evict them from the nest-tree.

b. Magpies

Australian Magpies prey on avian nest contents (e.g. Fulton 2006; Guppy *et al*. 2017), although the magnitude of their predatory impact may be less than that of currawongs and requires further clarification (Morgan *et al*. 2006). They are abundant in urban Melbourne (White *et al*. 2005) and during *BDOBS* sessions invaded Little Raven nest sites in all nesting stages, either solitarily or in small groups. They intruded much more extensively than did currawongs, being observed at 86% of nest sites monitored for brood defence and having an overall intrusion rate (1.2/h) 4 x that of currawongs. However, they too also mainly invaded nest zones rather than nest-trees. Nesting Little Ravens responded aggressively to 12% of magpie intrusions. Given that one or both raven pair members were present during 63% of these intrusions, this means that they responded aggressively to only 18.5% of the ‘known intrusions’. This seems a very low response rate if magpies constitute a significant threat to Little Ravens’ eggs and/or nestlings. Moreover, magpies may to some extent also be ecological competitors with Little Ravens, because they nest in quite similar situations (albeit often at a lower height), obtain much of their natural invertebrate food from the soil and ground cover, and consume supplementary food provided by humans (Jones 2018).

c. Conspecifics

Conspecific intruders visited Little Ravens’ nest sites at a rate of 1.7/h, respectively 1.4 x and 5.7 x more frequently than did magpies and currawongs. Nesting Little Ravens responded aggressively to ~38% of these intrusions. As at least one raven pair member was at the nest site during 76% of these intrusions, this means that they responded to just half of the ‘known intrusions’. Although this rate too seems rather low, it is a comparable response rate to that for ‘known intrusions’ by currawongs, but 2.7 x that for magpies. However, when considering Little Ravens’ low response rates to ‘known intrusions’ into their nesting territories by conspecifics, currawongs and magpies, it must be remembered that the magnitude of the parental and offspring factors thought to influence the cost-benefit equation underpinning brood defence decisions (Montgomerie and Weatherhead 1988) was mostly unknown in this study. The magnitude of these factors could conceivably help to explain the apparently low response rates of nesting ravens, and warrants detailed examination.

There are three main, plausible reasons for nesting Little Ravens responding aggressively to intruding conspecifics: (a) like many other *Corvus* species (e.g. Erikstad *et al*. 1982; Shields and Parnell 1986; Gaston and Elliot 1996; Carle *et al*. 2017), Little Ravens commonly prey on other bird species’ eggs and nestlings (Berry 2002; Ekanayake *et al*. 2015 a,b) and could conceivably prey on conspecifics’ nest contents (Davis and Dunn 1976), (b) intruding conspecifics may pose a threat in terms of extra-pair copulations, and (c) nesting ravens’ higher aggressive response rate to conspecifics than to currawongs and magpies may indicate that their intraspecific territoriality is primarily concerned with defence of limited optimal nest sites (and the food resources in the surrounding area required to sustain breeding). All three hypotheses are plausible. Intraspecific nest predation is believed to occur in Rooks *C. frugilegus*, Carrion Crows *C. corone* and some other *Corvus* species in Great Britain (Holyoak 1967; Coleman 1972; Tompa 1975) and extra-pair copulations have been documented in Rooks, American Crows *C. brachyrynchos*, Hawaiian Crows *C. hawaiiensis* and Common Ravens *C. corax* (Coombs 1960; Boarman and Heinrich 1999; HCWCS 2005; Townsend *et al*. 2010). As demonstrated above, Little Ravens select nest-trees with distinct characteristics and conceivably these trees are in limited supply and a source of intra-specific competition.

Hypothetically, nesting adults in altricial species should respond defensively more readily or intensely to intruders posing a threat to their breeding success during the nestling than the incubation stage; this is predicted because dependent offspring become more valuable in gene replication terms as they age (Montgomerie and Weatherhead 1988). However, such a disparity was not observed in Little Ravens’ responses to the intruder species to which they exhibited substantial aggressive behaviour.

Responses to raptors

Only two invasions of Little Raven nest sites by raptors were observed, one of which was around the nest-tree and elicited an aggressive response by a nesting pair member. This response was in one sense predictable because predation of Australian birds’ nest contents by raptors, such as goshawks, sparrowhawks and eagles, is well documented (Guppy *et al*. 2014), although to the best of my knowledge Nankeen Kestrels do not figure prominently among such records. They may constitute more of a threat of nest take-over than nest predation for Little Ravens, as they have been observed using old Little Raven nests (Rowley 1973; Table 3). Falcons, including small species such as the Australian Hobby *Falco longipennis*, are known nest usurpers of corvids and aggressive competition for nests and nest sites between Australian Ravens and raptors is well documented (Debus *et al*. 2017; Bauer and M^{c}Donald 2018; Morley in press).

Brood defence in other Corvus species

The major contrast between the species eliciting brood defence in most other studies of crows and ravens (mainly conducted in exurban environments) and those in Melbourne was that raptors featured minimally in my urban observations (Tables 2 and 3). Urban Albert Park, especially pre-modification to accommodate the Formula 1 Grand Prix, appears to be an exception to this disparity (Talmage 2011), possibly because it comprises 225 ha of parkland (including a lake) that may be more suitable for raptors than Melbourne’s residential suburbs. However, it is not entirely clear why birds-of-prey were so scarce in my observations, because many bird-hunting raptors have recently colonised and now thrive in urban environments worldwide (Kettle *et al*. 2017; Boal 2018; Kopij 2018). The absence of Pied Currawongs from Talmage’s (2011) inventory of species stimulating Little Raven brood defence in Albert Park is interesting, as they certainly occur in Melbourne’s southern suburbs.

Aggression towards Little Ravens by nest-site intruders

The two species that exhibited substantial aggression towards nesting Little Ravens, namely Noisy Miners and Australian Magpies, are well known for being very aggressive to other bird species (Jones 2002; Piper and Catterall 2003), although the reasons for this are not entirely understood. Some of the Noisy Miners involved were nesting within the ravens' nest site area, which would probably have enhanced their inherent, broadly-directed, aggressive tendencies because, as noted earlier, Little Ravens are nest predators. Red Wattlebirds are also quite aggressive to other bird species (Higgins *et al*. 2006), but were less aggressive towards nesting Little Ravens than miners and magpies. The most frequent type of aggressive behaviour towards nesting Little Ravens exhibited by heterospecific nest site intruders was threatening (including 'buzzing' – close aerial approach without physical contact); physical attack was rare, occurring 14 x less often than threatening. In most instances, nesting Little Ravens showed no overt response to such aggression; fleeing from the aggressor was very rare, occurring almost 30 x less often than a lack of an overt response. Thus, aggression by heterospecific nest site intruders had little effect on nesting Little Ravens, except for occasional minor disturbance.

Reproductive Effort

Nest sites had distinct characteristics, and although identifying an optimal site may not involve a huge time and energy expenditure by urban Little Ravens, it is likely to be crucial to breeding success. The substantial re-use of old nests would, of course, reduce the average RE expended on nest site selection. In contrast, defence of the nest and brood, especially against potential nest predators and competing conspecifics, appeared to be a substantial component of RE that is likely to have both significant benefits and costs for urban Little Ravens.

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Appendix 1

Bird species (and Domestic Cats) entering twenty-two 40 m Little Raven nest zones in urban Melbourne that did not elicit aggressive responses from the nesting birds. Numbers after each species in order are: number of intrusions [number of nest zones entered] and percentage of intrusions in which one or both breeding ravens were present in the nest, nest-tree or nest zone. The only species that visited the actual nest-tree were the Spotted Dove, Magpie-lark and some unidentified bird species. Species in taxonomic order by rows.

Silver Gull *Chroicocephalus novaehollandiae*	59 [6], 40%	Australian White Ibis *Threskiornis molucca*	12 [5], 0%
Little Corella *Cacatua sanguinea*	14 [5], 21.4%	Sulphur-crested Cockatoo *Cacatua galerita*	31 [1], 87.1%
Musk Lorikeet *Glossopsitta concinna*	4 [1], 100%	Eastern Rosella *Platycercus eximius*	5 [3], 80%
Rock Dove *Columbia livia*	451 [13], 45%	Spotted Dove *Spilopelia chinensis*	364 [17], 60.3%
Crested Pigeon *Ocyphaps lophotes*	6 [2], 66.6%	Welcome Swallow *Hirundo neoxena*	19 [6], 42.1%
Brown Thornbill *Acanthiza pusilla*	3 [1], 33.3%	White-plumed Honeyeater *Ptilotula penicillata*	4 [3], 100%
Little Wattlebird *Anthochaera chrysoptera*	1 [1], 0%	Black-faced Cuckoo-shrike *Coracina novaehollandiae*	2 [2], 50%
Grey Butcherbird *Cracticus torquatus*	2 [2], 50%	Magpie-lark *Grallina cyanoleuca*	96 [10], 57.3%
Common Blackbird *Turdus merula*	39 [9], 66.6%	Common Starling *Sturnus vulgaris*	262 [12], 65.7%
Unidentified raptor	2 [1], 100%	Other unidentified bird species	624 [22], 47.8%
Domestic Cat *Felis catus*	6 [2], 100%		

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A method for investigating Rufous Scrub-birds using automated recording and rapid, semi-automated data analysis

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Calls made in a Rufous Scrub-bird *Atrichornis rufescens* territory were recorded for periods of about seven days using an automated recording unit. We developed a method using *Raven Pro* to scan these recordings for scrub-bird chipping calls for rapid analysis. We present a preliminary analysis of field data showing that the use of this analytical tool will facilitate investigations into how the singing behaviour of Rufous Scrub-birds varies daily and seasonally, knowledge that is important when designing population monitoring programs. Our study also suggests that an automated recording unit in combination with the *Raven Pro* identifier will provide a viable alternative to standard techniques for surveying sites for the presence of scrub-birds.

INTRODUCTION

The Rufous Scrub-bird *Atrichornis rufescens* is classified as endangered under the Commonwealth *Environment Protection and Biodiversity Conservation Act 1999* (EPBC Act) and in the IUCN Red List, and as vulnerable under the New South Wales *Biodiversity Conservation Act 2017*. It occurs in five isolated, remnant populations in New South Wales and southern Queensland (Newman *et al.* 2014). The populations of both the northern (*A. r. rufescens*) and southern (*A. r. ferrieri*) subspecies are suspected to be in decline (Garnett *et al.* 2011).

It is difficult to see Rufous Scrub-birds, which mostly forage within and below the dense ground level vegetation in their territories (Ferrier 1984). Typically, the species' presence is confirmed by hearing a singing male. Females make a soft call which can only be heard if the listener is very close (Ferrier 1984). This makes it difficult to study the species and assess its status. All five Rufous Scrub-bird locations are designated as Key Biodiversity Areas (KBAs), with the scrub-bird in each case being the trigger species for the nomination (Dutson *et al.* 2009; BirdLife Australia 2017). Monitoring the status of trigger species is a requirement of the KBA process (Dutson *et al.* 2009) and there are active monitoring programs in all the scrub-bird KBAs (Newman *et al.* 2014; Andren 2016; Stuart and Newman 2018; F. Hill, R. Jordan, S. Dixon and P. Redpath pers. comm.), which currently involve listening for singing males (Ferrier 1984; Newman and Stuart 2011; Newman *et al.* 2014; Andren 2016; Stuart and Newman 2018).

The Rufous Scrub-bird's vocal repertoire includes a variety of calls and mimicry (Gole and Newman 2010). The most distinctive call is known as a "chipping" song, involving 2–10+ single syllables delivered in rapid succession (Stuart *et al.* 2012). Other calls have been described by observers as "whistles", "seeps" and "thrips," and there is also a contact call (Ferrier 1984; Stuart *et al.* 2012). In principle, all the scrub-bird's calls can be used to detect its presence. However, in monitoring programs for Rufous Scrub-bird populations using teams of volunteers, only documentations of chipping calls are accepted as confirmed records (Newman *et al.* 2014; Stuart and Newman 2018). This is so because inexperienced surveyors sometimes struggle to differentiate the other scrub-bird calls from those of other species.

The design of effective monitoring programs for Rufous Scrub-birds using the chipping call thus requires an understanding of how often the birds utter this vocalization and how this varies during the day and throughout the year. For example, when visiting a known or former territory to establish its occupancy status, a key question is how long to wait before it can be confidently concluded that a territory is no longer occupied? Similarly, when searching for new territories it is important to know how much time should be spent in the target area. To make these determinations, information about the singing behaviour of individual scrub-birds is required. As their behaviour can be affected by the presence of people near their territory (Ferrier 1984; Stuart *et al.* 2012), a potential role for automated recording units (ARUs) is apparent. A preliminary investigation of ARUs in this context, involving manual post-field analysis of the recordings, appeared promising for Rufous Scrub-bird monitoring (Stuart *et al.* 2012).

The use of ARUs in bird monitoring programs is growing (*e.g.* see Zwart *et al.* 2014; Sidie-Slettedahl *et al.* 2015; Bluff 2016; Joshi *et al.* 2017). The advantages of using ARUs include removal of observer bias, more natural bird behaviour (when there is no human presence), reduced time and effort in data collection, and the enabling of prolonged monitoring programs at sites which are remote or otherwise difficult to access. However, analysis of the recordings made with an ARU is problematic. An option is to manually scan sonograms and detect the target species by ear, or by sight if the sonogram pattern of their song is sufficiently distinct. This is a time-consuming option, but all the above advantages of using an ARU are retained. An alternative is automated data analysis using various algorithms that in effect act as an electronic "recogniser" of the calls of the target species (Joshi *et al.* 2017 and references therein). However, generation of a reliable recogniser can be challenging, especially if the call or song has a high degree of variability. Most electronic recognisers have suffered from high error rates, as the result of a combination of false positives (misidentification of the target species) and false negatives (failure to detect the target species when it is present) (Joshi *et al.* 2017). A recent review concluded that computer recognition of bird species from their calls was mostly inadequate for practical application, but commented that species-specific methods will generally be more successful (Priyadarshani *et al.* 2018).

The chipping call of a Rufous Scrub-bird is readily recognisable as a sequence of evenly spaced signals when a sonagram is scanned visually (see Fig. 1 for an example). Thus, it seemed a good candidate for an approach involving species-specific computer recognition. The focus of the present study was therefore on optimising the detection of chipping calls in recordings made in a scrub-bird territory using an automatic recogniser, with the aim of facilitating long-term monitoring of known or suspected Rufous Scrub-bird territories.

METHODS

We made recordings in a known Rufous Scrub-bird territory at 1,305 m altitude in the Gloucester Tops, New South Wales (Stuart and Newman 2018). The exact location is confidential; it was within a study area of approximately 5 km radius, centred at 32º04'S, 151º34'E.

The ARU comprised a Wildlife Acoustics Inc. Song Meter™ model SM3 with two omnidirectional microphones. We placed it ~0.3 m above ground in a steel-mesh framed stand in the scrub-bird territory and programmed it to record in one-hour files from 30 minutes before dawn until 30 minutes after dusk. It had previously been established that scrub-birds in the Gloucester Tops did not call at night (Stuart *et al.* 2012). Usually we collected 7–8 days (80–90+ hours) of recordings per field trip; battery lifetime governed the amount of recording that could be accomplished on each trip.

We recorded the data on SD cards, and later transferred them to a computer and analysed them using *Raven Pro 1.5* software. We developed detection conditions for the chipping call as per *Raven* software protocols. The conditions identified for the Band Limited Energy Detector were: minimum frequency 3000 Hz, maximum frequency 6,400 Hz, minimum duration 1 sec, maximum duration 6 secs, minimum separation 1 sec, minimum occupancy 20%, SNR threshold 2 dB, block size 8 secs and hop size 2 secs. We found these conditions to be the optimal ones for rapid, semi-automated analysis of recordings.

False positive results, usually associated with overlapping calls of other species, could quickly be eliminated by manual vetting of the results from the initial electronic analysis. Vetting was facilitated by the characteristic appearance of Rufous Scrub-bird chipping calls (Fig. 1). To estimate the proportion of false negatives, we analysed three hours of recordings manually and compared the results from the manual and automated analyses. We selected the period for this analysis at random, except that it was chosen from a time when the scrub-bird was making many calls. We found that the scrub-bird made 460 chipping calls in that 3-hour period, of which 446 were detected by the software (3% false negatives). In the results presented below, no correction has been made to address the occurrence of 3% false negatives.

We analysed the recordings by noting the number of singing events per 20-minute period. We chose this length of period because, when walking at a rate of 1 km/h through a Rufous Scrub-bird territory (the recommended standard survey method *e.g.* see Newman *et al.* 2014), a surveyor has an approximately 20-minute window of opportunity to hear a scrub-bird, given that calls can be heard from 150 m away under favourable conditions (Ferrier 1984).

We exported the results into *Excel* for further processing. We logged each chipping call as a single singing event under the automated search protocol, regardless of how many syllables it had. To assess if rainfall affected the scrub-bird's singing behaviour, we obtained data for the Careys Peak weather station (Station 61413) from the Bureau of Meteorology website (www.bom.gov.au). This station is located at 1,430 m altitude in the Gloucester Tops and is approximately 10 km from the Rufous Scrub-bird territory under investigation.

RESULTS

Recordings

We investigated recordings from six 7-day periods for this study (Table 1). Each 7-day period involved 83–95 h of recording, and generated total file sizes of *c.* 30 Gigabytes. Two of the time periods (29 September to 5 October 2015 and 23 to 29 September 2016) were during what is believed to be the onset of the breeding season for Rufous Scrub-birds; the other periods were outside the breeding season.

In Tables 2–7, we show data for each of the six 7-day periods. In each table, we firstly indicate the duration of each day's recording and the number of 20-minute periods into which that recording period could be divided. We then present the number of 20-minute periods in which we detected any singing activity. Comparing the number of active (*i.e.* with singing) 20-minute periods to the total possible number of 20-minute periods is a simple, first-pass indicator of the detectability of the scrub-bird on a given day. For example, on 29 September 2015 (Table 2), the scrub-bird called in 34 of the 39 possible 20-minute pre-dawn to post-dusk periods. In contrast, on 22 February 2017 (Table 4), we only detected the bird singing in two of the 42 possible 20-minute periods. Using these two examples of singing

Table 1

Rufous Scrub-bird recordings used in this study.

Session	Start Date	Finish Date	Total hours recorded (h)	Total file size (GB)
1	29 Sep 2015	5 Oct 2015	95	30.1
2	23 Sep 2016	29 Sep 2016	89	31.7
3	16 Feb 2017	22 Feb 2017	83	26.7
4	17 Aug 2017	23 Aug 2017	87	27.1
5	16 April 2018	22 April 2018	92	29.4
6	24 June 2018	30 June 2018	91	29.5

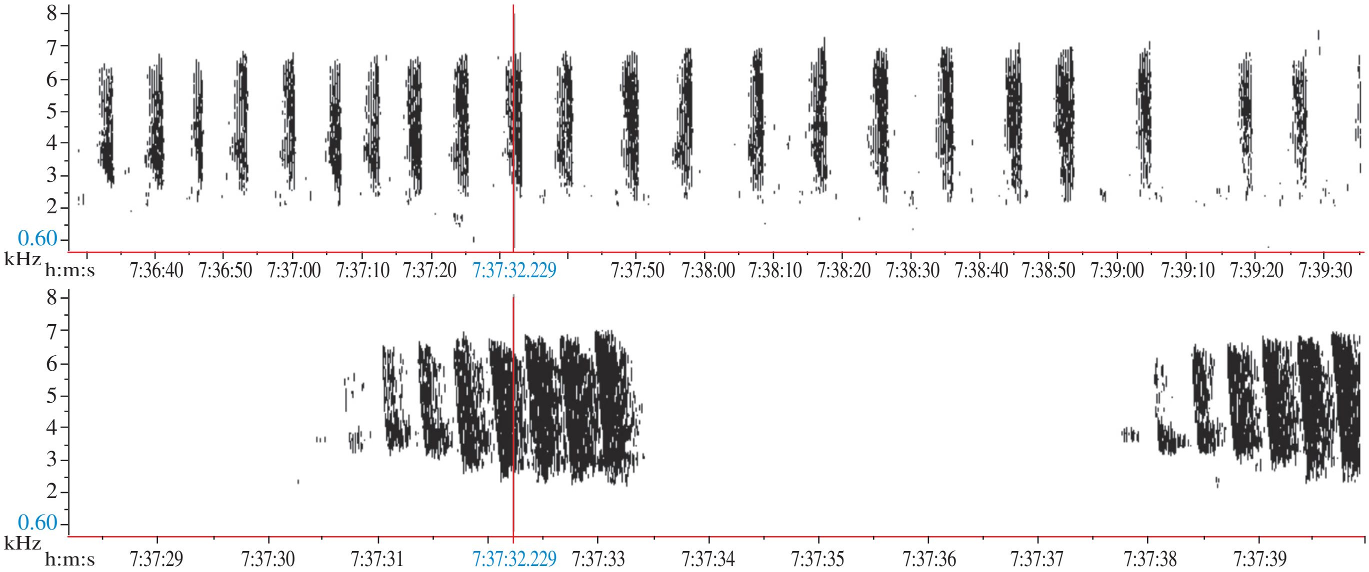


Figure 1. *Sonogram excerpt showing an example of a Rufous Scrub-bird's chipping song. Upper chart: a series of multiple chip calls. Lower chart: an expanded view showing two of the multiple chip calls.*

Table 2

Rufous Scrub-bird chipping call singing events 29 September to 5 October 2015.

	29 Sep	30 Sep	1 Oct	2 Oct	3 Oct	4 Oct	5 Oct
Length of recording (h)	13.3	13.3	13.3	13.4	13.4	13.4	13.5
No. of possible 20 min periods	39	40	40	40	40	40	40
No. of 20 min periods with activity	34	34	36	37	37	36	39
Total calls/day	1604	1643	1893	1669	1930	1568	1719
Maximum no. of calls in 20 min period	88	86	86	84	87	73	74
Minimum no. of calls in active 20 min periods	8	3	11	3	7	3	7
Median no. of calls in active 20 min periods	50	50	55	45	57	44	47
Careys Peak rainfall (mm)	0.2	0	2.6	0	0	0	0

Table 3

Rufous Scrub-bird chipping call singing events 23-29 September 2016.

	23 Sep	24 Sep	25 Sep	26 Sep	27 Sep	28 Sep	29 Sep#
Length of recording (h)	13.1	13.1	13.2	13.2	13.2	13.3	9.2
No. of possible 20 min periods	39	39	39	39	39	39	27
No. of 20 min periods with activity	34	38	34	37	32	37	23
Total calls/day	1481	1804	1170	1851	922	1887	796
Maximum no. of calls in 20 min period	74	92	80	82	81	96	81
Minimum no. of calls in active 20 min periods	1	2	1	5	1	5	2
Median no. of calls in active 20 min periods	51	50	31	46	29	53	33
Careys Peak rainfall (mm)	0.2	0.2	6.2	0.4	0	0	0

#recording stopped at 14:12 hrs

behaviour, the likelihood of establishing the bird's presence in a known territory would have been low in February 2017, but the detection probability in September 2015 would have been much higher. Similar analyses across all six of the tables suggest that the breeding season is the most reliable period for detecting a scrub-bird. In the other time periods investigated, there were sometimes days when the scrub-bird called often, but other days when it did not. For example, in April 2018 (Table 6) there were two dates, the 16th and 19th, when the scrub-bird called in 28 or 29 of the 39 possible 20-minute periods, but on all the other days in April 2018 it was silent most of the time.

Tables 2-7 also show the total number of chipping calls produced by the scrub-bird each day, the maximum number of calls it made in any 20-minute period and the median and minimum number of calls in 20-minute periods when the

Table 4

Rufous Scrub-bird chipping call singing events 16-22 February 2017.

	16 Feb	17 Feb	18 Feb	19 Feb	20 Feb	21 Feb	22 Feb
Length of recording (h)	14.2	14.1	Data missing	11.0	14.0	14.0	14.0
No. of possible 20 min periods	42	42		33	42	42	42
No. of 20 min periods with activity	9	12		2	8	4	2
Total calls/day	71	114		21	44	42	23
Maximum no. of calls in 20 min period	34	25		20	19	21	13
Minimum no. of calls in active 20 min periods	1	1		1	1	1	10
Median no. of calls in active 20 min periods	3	5		11	3	10	12
Careys Peak rainfall (mm)	0	0	4.0	1.0	0.6	0	0

Table 5

Rufous Scrub-bird chipping call singing events 17-23 August 2017.

	17 Aug	18 Aug	19 Aug	20 Aug	21 Aug	22 Aug	23 Aug
Length of recording (h)	12.0	12.0	12.0	12.1	12.1	12.1	12.2
No. of possible 20 min periods	36	36	36	36	36	36	36
No. of 20 min periods with activity	15	5	9	7	2	15	10
Total calls/day	270	37	76	61	11	291	168
Maximum no. of calls in 20 min period	60	20	22	22	10	52	65
Minimum no. of calls in active 20 min periods	2	1	1	1	1	2	2
Median no. of calls in active 20 min periods	12	6	8	3	6	11	12
Careys Peak rainfall (mm)	0	0	0	0	0	0	0

Table 6

Rufous Scrub-bird chipping call singing events 16-22 April 2018.

	16 Apr	17 Apr	18 Apr	19 Apr	20 Apr	21 Apr	22 Apr
Length of recording (h)	13.1	13.1	13.1	13.1	13.1	13.1	13.1
No. of possible 20 min periods	39	39	39	39	39	39	39
No. of 20 min periods with activity	29	2	10	28	11	9	10
Total calls/day	1170	473	157	879	137	176	197
Maximum no. of calls in 20 min period	82	46	33	74	47	34	63
Minimum no. of calls in active 20 min periods	13	2	2	1	1	3	2
Median no. of calls in active 20 min periods	39	19	14	33	8	19	12
Careys Peak rainfall (mm)	0	0	2.8	0.2	17.8	2.0	4.6

Table 7

Rufous Scrub-bird chipping call singing events 24-30 June 2018.

	24 June	25 June	26 June	27 June	28 June	29 June	30 June
Length of recording (h)	13.1	13.1	13.1	13.1	13.1	13.1	13.1
No. of possible 20 min periods	39	39	39	39	39	39	39
No. of 20 min periods with activity	8	3	18	27	10	15	12
Total calls/day	142	127	304	756	394	251	387
Maximum no. of calls in 20 min period	20	8	51	51	48	41	42
Minimum no. of calls in active 20 min periods	5	3	1	3	2	1	1
Median no. of calls in active 20 min periods	15	5	21	28	21	16	13
Careys Peak rainfall (mm)	0	0	0	0	0.6	2.0	0

Table 8

Proposed Rufous Scrub-bird detectability parameters.

Detectability rating	% of active periods	No. of calls/day	Median no. of calls in active periods
High	>70%	>1500	>40
Moderate	30-70%	500-1500	10-40
Low	<30%	<500	<10

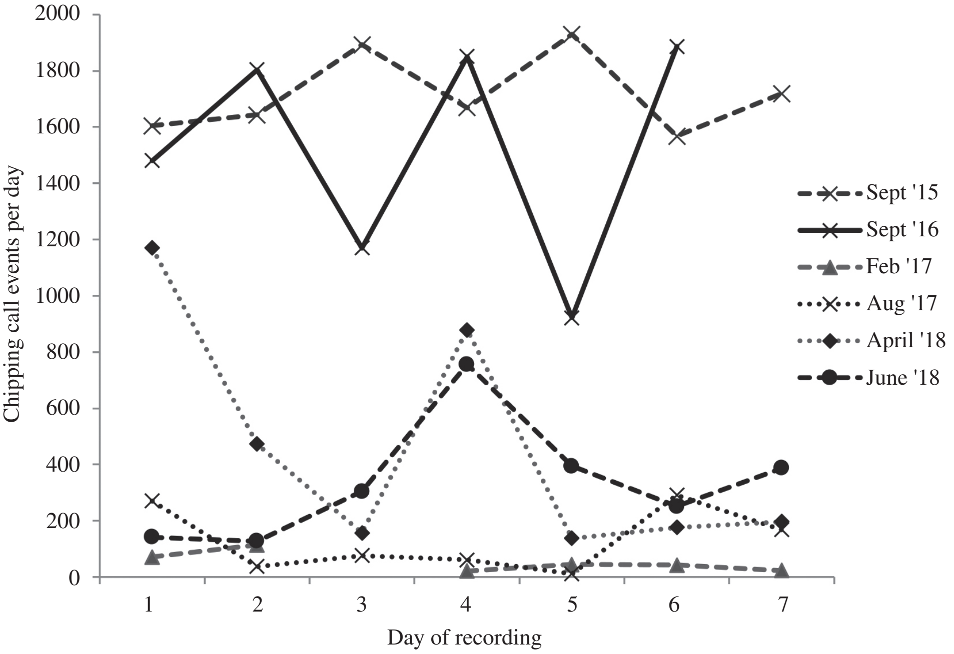


Figure 2. *The number of Rufous Scrub-bird chipping call events per day during six recording sessions.*

bird was actively singing. All these parameters are additional indicators of the detectability of the scrub-bird on any given day. For example, in the 2015 and 2016 breeding seasons (Tables 2 and 3), the scrub-bird usually produced more than 1,000 chipping calls each day, with medians of 40-50 calls per 20-minute period on most days. In periods of low singing activity, it usually still called at least a few times. Conversely, in February 2017 (Table 4) the scrub-bird mostly made fewer than 100 calls per day, with medians of just 3–12 calls per 20-minute period when active. The median numbers of calls per 20-minute active period were also low in August 2017 (Table 5), but more substantial in April and June 2018 (Tables 6 and 7).

In Tables 2-7 we also show the daily rainfall totals at the Careys Peak weather station. There was only one day of heavy rain in the six 7-day periods, on 20 April 2018 when 17.8 mm fell (Table 6). There was light rain (2-6 mm) on three other days in April 2018 (Table 6) and on 18 February 2017 (Table 4) and 29 June 2018 (Table 7). On all other dates on which we collected scrub-bird singing data there was either no rain or only light drizzle.

Number of chipping call events per day

The daily total numbers of chipping call events ("calls") are presented in Figure 2 (and in Tables 2-7). During the onset of the breeding season, the scrub-bird mostly uttered 1,500-2,000 calls per day. In September-October 2015 there was little daily variability, but greater variability was evident in the analogous period in the following year (23-29 September). Although four of the full days of recording in September 2016 each yielded more than 1,500 calls, two days (25 and 27 September) had fewer than 1,200 calls. The scrub-bird called less often in all the other periods investigated (Fig. 2); usually it produced fewer than 300 calls daily. In February 2017, the median was 43 calls per day, but in April and June 2018 the bird sometimes called more frequently, including producing 1,170 calls on 16 April (Table 6).

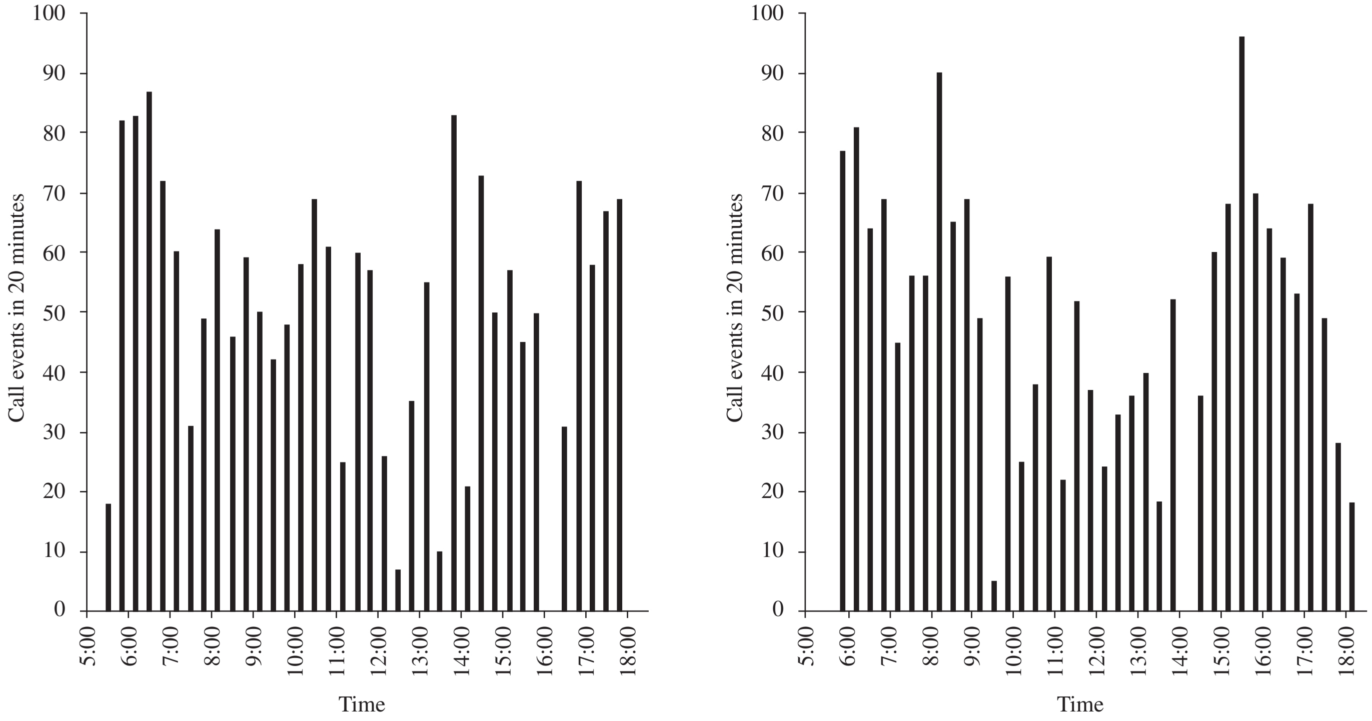
Daily and seasonal variability in chipping call events

Figure 3 shows four examples of single-day singing behaviour by the scrub-bird, presented in 20-minute segments. During the onset of the 2015 and 2016 breeding seasons, the bird sang throughout the day, with occasional breaks of 20-40 minutes (Figures 3a and 3b). The maximum number of calls in any 20-minute period ranged between 73 and 96 calls, with daily medians of 44–55 calls in 2015 (Table 2) and 29–53 calls in 2016 (Table 3). At the other times of the year investigated, the scrub-bird called far less frequently and with many long breaks. Details are summarised in Tables 4-7, whilst Figures 3c and 3d provide examples that illustrate the daily variability. Across all dates, there was considerable variability in the times of the day at which the bird called and in the maximum and median numbers of singing events each day. Also, on most days there were a considerable number of 20-minute periods when the bird did not produce any chipping calls. Often, less than 25% of the 20-minute periods in a day had any calling activity.

DISCUSSION

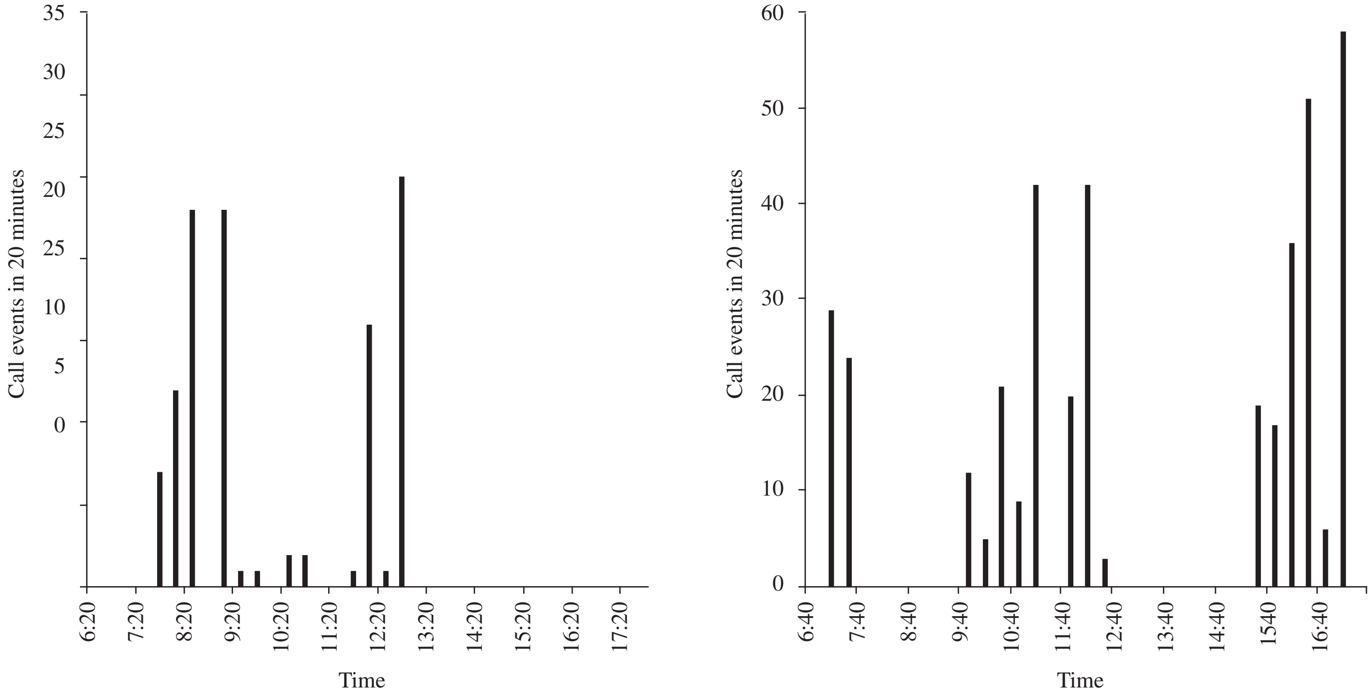
Daily and seasonal variability of calling

There are no breeding records for Rufous Scrub-birds in the Gloucester Tops, but individuals in more northerly populations had nests with eggs or young from late October onwards (Jackson 1911,1921; Chisholm 1951). This suggests that breeding activity in the northern populations, including territorial advertising by males, would have commenced in earnest at least one month earlier. Extrapolation to the Gloucester Tops suggests that the September-October recordings in 2015 and 2016 were probably made during the onset of the breeding season. There was a clear difference in singing behaviour by the Rufous Scrub-bird in September-October from other times of year. At those other times, it usually called infrequently and unpredictably, but in the breeding season it called very frequently and with only occasional short breaks.



a) 3 October 2015 (breeding season)

b) 28 September 2016 (breeding season)



c) 17 February 2017

d) 28 June 2018

Figure 3. *Examples of daily singing behaviour of a male Rufous Scrub-bird at its territory in the Gloucester Tops. Plots a) and b) are for what is believed to be the breeding season, plots c) and d) are in the non-breeding season.*

Daily variability appeared sometimes to be associated with weather conditions. For example, in April 2018 the scrub-bird called often on three days which had zero or very low rainfall (16-17 and 19 April) and far less often on the other four days when there was 2.0-17.8 mm daily rainfall (Table 6). Similarly, the scrub-bird made ~35% fewer calls on 25 September 2016 when 6.2 mm of rain fell than on the days immediately before and after that date (Table 3). However, its calling behaviour was unaffected on 1 October 2015 when 2.6 mm fell (Table 2). In spring 2016, the least number of calls in a day was on 27 September, a dry day (Table 3). However, these conclusions are tentative, as a much broader sample would be required to test statistically and convincingly for a possible weather effect.

Diurnal rhythmicity of calling

The ARU was programmed to record from 30 minutes before dawn until 30 minutes after dusk, as it had previously been established that scrub-birds in the Gloucester Tops did not call at night (Stuart *et al.* 2012). Results from the current study support those conclusions. There were never any scrub-bird chipping calls in the first 20-minute recording period of the day; calling usually began around dawn (or later). However, sometimes in spring there were a few calls in the final 20-minute recording period *i.e.* just after dusk.

Detectability of the Rufous Scrub-bird

Of the parameters that we investigated, three seem to have the greatest potential as indicators of seasonal and daily variability in Rufous Scrub-bird singing behaviour, namely the number of active 20-minute periods per day (as a ratio of the number of possible 20-minute periods), the total number of calls per day, and the median number of calls per active 20-minute period. When values for all these three parameters are high, a scrub-bird should be detected easily by a surveyor walking through its territory; when all three are low it most likely would escape detection. In Table 8 we suggest possible ranges for the three parameters as Rufous Scrub-bird singing indicators; in future studies, we plan to assess this proposal further.

Recordings from the 2015 and 2016 breeding seasons suggest a high probability that a surveyor would detect the scrub-bird while traversing its territory. In September-October 2015, there were very few 20-minute periods without any calling activity (Table 2) and none were consecutive. The scrub-bird's detectability in September 2016 would have been similarly high. Although there were sometimes fewer calls over the whole day then than in the 2015 season, there were very few 20-minute periods without any calling activity (Table 3), although two of the days had periods of *c.* 40 minutes without calling activity. Recordings obtained outside of the breeding season suggest that the detectability of the scrub-bird would be much reduced. There were many periods of inactivity, and when active the bird usually produced fewer calls per 20 minutes than it did in the breeding season (Tables 4–7).

Potential of the recording and analysis method as a tool to support monitoring

Analysis of automated recordings detected 97% of Rufous Scrub-bird chipping calls. Although these were results for a single territory, they suggest that using an ARU at a known or suspected Rufous Scrub-bird territory, with semi-automated analysis of the recordings, might quickly reveal whether the territory is occupied. A full day of recordings can be processed in less than 30 minutes, including manual vetting to eliminate false positives. Similarly, it may become possible to locate new scrub-bird territories by placing an ARU in areas of promising habitat. The effectiveness of this approach will depend on how far from the core of a territory the ARU can be placed. In the present study, the bounds of the core territory were known from prior studies (Stuart 2018) and the ARU was placed well inside the territory.

Future research directions

The results presented here are for a single scrub-bird territory. To optimise the design of Rufous Scrub-bird monitoring programs in the Gloucester Tops, it will be necessary to collect and analyse data from this territory for all seasons and to assess annual variability, and then compare these findings with results from several other territories.

Understanding the effectiveness of automated or semi-automated data analysis for recording of Rufous Scrub-birds from other parts of their population distribution is also required. There are known to be differences in the calls of the northern and southern subspecies (Ferrier 1984), so it may be necessary to develop a new electronic recogniser for some populations outside the Gloucester Tops.

The focus here has been on developing a tool that will help us to determine how often a Rufous Scrub-bird makes its characteristic chipping call, because that knowledge will underpin monitoring programs being used for the various populations. Eventually, the frequency of other call types should also be investigated, as that would further enhance the potential for ARUs/automated data analysis to be used in Rufous Scrub-bird population monitoring.

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Reproductive effort of urban Little Ravens: the nest attendance regime

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Parental care is a major component of reproductive effort in altricial birds, but the time allocated to it is patchily documented for *Corvus* species, including Little Ravens *Corvus mellori*. Nest attendance by Little Ravens was documented in urban Melbourne to: (a) assess its extent and potential to entail costs sufficient to significantly reduce its obvious fitness benefits, and (b) compare it with that of congeners, as reported in the literature. Both sexes built the nest and, on average, six 2-minute nest visits/hour were made during intensive nest building. Incubation was probably conducted exclusively or largely by the female, which was fed at the nest once an hour by her mate, whose visits lasted ~1 minute. Mean diurnal incubation attentiveness was 83% and there was a mean of 1.8 incubation bouts and 1.2 incubation recesses/hour. Both sexes brooded and fed the nestlings, although one sex (probably the female) appeared to do much more of the brooding after the first two weeks of nestling life. Mean diurnal brooding attentiveness considered over the nestling period *in toto* averaged ~20%, but it was as high as 75-90% early in development, before declining to close to zero. Provisioning of the brooding individual and/or nestlings occurred ~5.5 times/hour. When both nestlings and fledglings were present at the nest site around fledging time, they received an average of 7 provisioning visits/hour from parents. Nest attendance broadly resembled that of congeners, and overall was probably at a sufficiently high level to potentially have short- and long-term costs (as well as benefits) for parents.

INTRODUCTION

Reproductive effort (RE) is the proportion of an organism's total energy budget devoted to reproductive success. Life history theory predicts a trade-off between current and future reproduction; current reproductive success should increase and future reproductive success decrease as a function of increasing current RE (Stearns 1992). The trade-off is predicted because a high RE typically has a cost in terms of reduced adult survival or future fecundity (Hanssen *et al*. 2005), as it is likely to involve diversion of energy from growth and maintenance. Beneficially adjusting RE hinges on adult animals' ability to 'predict' the relative quality of a given breeding season for promoting growth and survivorship of young. Reproductive effort is expended in many ways, but in altricial birds is reflected strongly in the extent of parental care, as expressed in nest construction, incubation, brooding, and provisioning of nestlings and incubating and brooding adults. Quantitatively documenting this aspect of RE is one necessary step towards thoroughly understanding the hypothesised life history trade-off between current and future reproductive output in any altricial bird species.

Many aspects of breeding biology in the genus *Corvus* have been studied extensively (e.g. phenology, clutch and egg size, fledging success), but surprisingly, quantitative documentation of nest attendance is limited and patchy. Rowley's (1973) valuable pioneering study of four of the five native Australian *Corvus* species, Talmage's (2011) long-term study of Little Ravens *Corvus mellori* in a Melbourne park and investigations of native Forest Ravens *C. tasmanicus* by Secomb (2005a) and Lawrence (2009) have established the basic breeding biology of the Australian members of the genus, but there are still knowledge gaps and weaknesses, notably with respect to parental nest attendance. *Corvus* species' breeding biology is particularly interesting because it encompasses features of considerable theoretical significance. For example, incubation in most species is performed solely or largely by the female, who is provisioned by her mate. Whether the selection pressure influencing the male's rate of provisioning the female in such species is nest predation intensity, microclimate or food availability has attracted the attention of researchers trying to understand the selection pressures driving avian life history evolution (e.g. Martin and Ghalambor 1999; Conway and Martin 2000).

Our limited knowledge of Little Ravens' RE is based mainly on the work of Rowley (1973) for two rural New South Wales locations, Talmage's (2011) longitudinal data for a single urban park, and scattered information for other locations (Higgins *et al*. 2006). Although exploiting the abundant human food waste in cities (Lill and Hales 2015) may conceivably reduce the effort required to successfully rear young in urban environments, Little Ravens have a protracted pre-fledging development over ~59 days (Rowley 1973), so one would expect that the adults' total nest attendance levels would be high. This could have a negative effect on adult survival and future reproductive success unless other compensatory strategies occur (e.g. single broodedness within a season; Rowley 1973).

The aims of the present study were to:

(1) strengthen and broaden our knowledge of RE in Little Ravens, especially in the urban environment, by quantitatively documenting the nest attendance of breeding pairs widely dispersed in suburban Melbourne. I predicted that overall nest attendance levels would be high, given the protracted development of offspring.

(2) conduct an original literature search to facilitate comparison of nest attendance by urban Little Ravens with that of congeners in Australia and elsewhere. Avian nest attendance regimes vary geographically and between coexisting species with differing rates of nest predation risk, and they also exhibit intraspecific phenotypic plasticity in response to ambient nest predation risk (Martin and Briskie 2009; Chalfoun and Martin 2010). Given that the genus *Corvus* has a very broad geographical distribution, an underlying rationale for the literature search was to assess the extent to which this aspect of RE appears to be evolutionarily conserved or phenotypically plastic in the genus.

METHODS

Study species and area

Little Ravens are restricted to southeast Australia, from the Great Australian Bight to northeastern New South Wales. They inhabit treed farmland, woodland, open forest and conurbations from the coast to alpine altitudes. Rowley (1973) reported the duration of the incubation and nestling stages in rural New South Wales as 19–21 days and 37–38 days, respectively, and Talmage (2011) gives a mean nestling stage duration of 38 days (range 33–41 days) for Albert Park, Melbourne. The Little Raven is the numerically dominant *Corvus* species in Melbourne (Lee 2011; Dooley 2012).

Nests were found mostly by systematically driving around suburban Melbourne in three successive breeding seasons (June–December) searching for individuals showing clear signs of nesting. The closest two nests studied were 225 m apart and the two most spatially separated nests were about 21 km apart. Nests were mainly in suburban streets and residential gardens.

Nest attendance monitoring

Three points are pertinent with respect to the observation strategy:

(1) it mostly entailed watching several widely-dispersed nests at each nesting stage, mainly for just a few, relatively short sessions each, to provide a representative picture of nest attendance by Little Ravens in the city. The trade-off was that this strategy somewhat masked some trends (e.g. a developmental decrease in brooding attentiveness) that more long-term observation on particularly visible nests can document, although such observations were possible at a few nests.

(2) as I often could not clearly see the fine details of the behaviour that was occurring at the nest because of its height and the obscuring foliage (e.g. was a provisioning bird feeding just the brooding bird, the brooding bird and the nestlings, or just the nestlings?), the emphasis here is mainly on overall nest attendance patterns.

(3) because nests were too high up to permit inspection of contents, I often did not know how many young were present except at fledging. However, the number of nests studied at each nesting stage should be sufficient to encompass the natural variation in clutch and brood sizes.

Observations were made mostly from a vehicle with tinted windows about 40 m from the nest tree; the nesting ravens were clearly unaware of my presence. Sessions lasted 58–198 minutes (mean 74 minutes) and the ravens' activities were timed throughout a session. Observations were made from early morning to late afternoon, but were somewhat biased towards the morning and afternoon in the nest building and nestling stages, respectively. The sexually monomorphic ravens could not be sexed or individually recognised, but from observation and by analogy with Rowley (1973) some reasonable assumptions were made about some aspects of the sexual division of labour. Nesting stages had to be inferred from the birds' behaviour; any observations that could not be confidently ascribed to a stage were treated as 'unknown' in the analysis.

The following variables were measured, most frequencies being on a per hour (h) basis and durations in minutes (min):

[1] Nest building:

(a) frequency and duration of building visits and duration of intervals between consecutive visits during intensive construction.

(b) proportion of building visits that were by a single adult or the nesting pair.

Sessions that were known to be in the nest building stage, but in which no building behaviour occurred, were excluded from analysis.

[2] Incubation:

(a) diurnal incubation attentiveness (i.e. percentage of an observation session during which the presumed female incubated the eggs).

(b) number of complete and incomplete (i.e. wholly within and extending beyond an observation session, respectively) incubation bouts and recesses/h.

(c) duration of recesses occurring entirely within an observation session.

(d) frequency and duration of provisioning visits to the nest by the presumed male.

[3] Nestling:

(a) frequency and duration of provisioning visits to the nest by parents, and duration of intervals between consecutive visits.

(b) percentage of provisioning visits that were by just one parent (when little brooding occurred in a session).

(c) diurnal brooding attentiveness (i.e. percentage of a session during which nestlings were brooded) and the duration of brooding bouts.

(d) frequency of 'adventitious' nest building visits (see Results).

[4] Peri-fledging:

This period was defined as the time at which there were nestling(s) in the nest and sibling fledgling(s) in the nest tree or nearby or, less often, just fledglings in the nest tree and adjacent trees. Metrics recorded were:

(a) frequency and duration of provisioning visits to nestlings and fledglings, and duration of intervals between consecutive nestling provisioning visits.

Table 1

Nest building behaviour of Little Ravens at nine nests in urban Melbourne. Months abbreviated as Ju (June), Jly (July), Aug (August). Location of nests shown in top row: W St = Warra Street West, T H = Tramways Hotel, C St = Church Street, K Rd = Kooyong Rd, E Av = Elster Avenue, F St = Foch Street, G St = Goe Street, M St = Michael St and Wa Rd = Wallen Rd. Numbers in round brackets are standard errors and numbers in square brackets are sample sizes (nests or values). Summary column gives the means for all nests; no SEs are given because data are a mixture of 1 or 2 values and means for larger samples for nests. Number of sessions not indicated for nests individually for 'Mean no. nest building visits/h' because they are the same as in 'Minutes of observation'.

	W St	T H	C St	K Rd	E Av	F St	G St	M St	Wa Rd	Summary
Month(s)	Ju, Jly	Ju, Jly, Aug	Ju, Jly	Ju	Ju	Aug	Jly	Ju	Ju, Jly	**Ju, Jly, Aug**
Minutes of observation [no. sessions]	183 [3]	180 [3]	247 [4]	186 [2]	246 [3]	60 [1]	60 [1]	73 [1]	313 [5]	**1,548** **[23 sessions]**
Percent observation pre -12:00 hrs	100	33	49	100	100	100	0	100	100	**76.3**
Mean no. nest building visits /h	8.3	4.7	1.7	3.7	5.7	6	5	3.3	11	**5.5** **[9 nests; 23 sessions]**
Mean duration of nest building visits (min)	1.8 (0.2) [19]	3.0 (0.6) [11]	2.0 (0.3) [15]	2.2 (0.6) [9]	2.6 (0.3) [14]	1 [2]	1 (0.4) [4]	2 (0.6) [4]	2.7 (0.2) [54]	**2.0** **[9 nests; 131 visits]**
Mean interval between successive nest building visits (min)	9.4 (3.7) [15]		13 (2.9) [6]	15.7 (4.0) [6]	16.8 (4.5) [7]		18.7 (3.8) [3]	2 [2]	3.6 (0.6) [31]	**11.3** **[7 nests; 70 intervals]**

(b) frequency and duration of 'adventitious' nest building visits (see Results).

Where one or more nests contributed only one or two values for a measured variable, the grand mean for all nests and the mean of all the individual values for all nests for that variable were usually in close agreement, so only the former is presented. Variation among nesting pairs in the duration of nest visits and the interval between consecutive visits were analysed where possible (sufficient pairs with n ≥6) with single factor analysis of variance (ANOVA) after checking for data normality and homogeneity of variances.

The review of original, comparative data from the literature is not exhaustive, but neither is it selective. Many of the samples are small or narrowly-based, but collectively they provide a useful comparative framework. Studies in which helpers were involved in nest attendance have been omitted, as urban Little Ravens in my investigation did not exhibit this phenomenon.

RESULTS

Nest attendance

Nest building stage

Nest building was documented from early June to late September at nine nests in observations made predominantly before midday, as more building occurred in the morning (Table 1). The sample included new nests under construction and old nests being refurbished; these processes usually lasted two or more weeks. At this stage, the members of some pairs spent much of the day very close together, but members of other pairs were more independent in their movements. Both sexes built the nest. In the early stages, nest building ravens carried single twigs to the nest (including London Plane *Plantanus acerifolia, Eucalyptus* spp. and Queensland Brush Box *Lophostemon confertus*) gathered both close to (≤10 m) and well away from (>40 m) the nest tree. Sampling, by manipulation with the beak, to select an appropriate twig could sometimes take up to 5 min. Living twigs were detached from the tree with the beak and dead twigs were picked up from the ground, including ones that had been dropped during earlier construction. Little Ravens also transported moss, dry leaves and fine *Melaleuca* bark to their nest for the nest bowl and its lining. At some stages of building, twig and lining loads were interspersed both between and within the contributions of pair members. On some nest visits at this stage no material appeared to be transported to the nest.

Collectively, on average, during nest building the adults made ~6 nest visits/h; the sessional frequency ranged from 1.7 to 11 visits/h, reflecting the fact that building was sometimes performed in intensive bouts and sometimes more perfunctorily (Table 1). On average, building visits were short (~2 min), their duration being invariant among nesting pairs ($F_{5,116} = 1.871$, $P = 0.105$), and consecutive visits were at ~8 min intervals. Visits to the nest site for building (n = 122) were variously: [a] solo (one pair member visited the nest on its own (57.4%), [b] overlapping (pair members arrived at the nest asynchronously, but nonetheless both were then present at the nest simultaneously) (19.7%), [c] synchronised (pair members arrived at the nest together) (13.1%), and [d] 'partially synchronised' (pair members arrived synchronously at the nest and nest tree, respectively, and one or both visited the nest, but if both did so it was asynchronously) (9.8%). The Kooyong Rd pair were seen performing courtship feeding once below the nest tree at this stage.

Oviposition stage

The egg-laying stage could only be observed with certainty at one nest. Observations (140 min) were made at this nest in two afternoon sessions in June and July. Copulation was observed twice in this pair, on a telephone pole and in a tree, both about 20 m from the nest tree. The pair made 3.2 visits/h to the nest, each lasting 2 min on average, and consecutive visits were about 13

Table 2

Parental nest attendance at twelve Little Raven nests in urban Melbourne in the incubation stage. Location of nests shown in top row; abbreviations as in Table 1, with addition of Con St = Constance Street, Oak Cr = Oakleigh Crescent, Cha Quad = Chatsworth Quadrant, St G Sth = St Georges Road South, Orr Rd = Orrong Road, Fitz St = Fitzwilliam St and LTU Bund = La Trobe University Bundoora Campus. Months abbreviated as in Table 2. Temporal spread of observations is the period (in days) from the first to the last observation. In data rows, numbers in round brackets are standard errors and those in square brackets are sample sizes (sessions or values analysed). Summary column for data rows gives mean for all nests; no SEs are given because data are a mixture of 1 or 2 values and means of larger samples for nests. * indicates two breeding attempts involved.

	Con St	K Rd	Oak Cr	Cha Quad	St G Sth	C St	E Ave	F St	Orr Rd	T H	Fitz St	LTU Bund	Summary
Month(s)	Sep, Oct	Ju, Jly	Aug	Sep, Oct	Aug	Jly, Aug	Ju, Jly	Aug	Oct	Aug	Sep	Sep, Oct, Nov	Ju to Nov
Observation mins [no. sessions] and temporal spread of observations (in days)	426 [8] 18	399 [7] 40	125 [2] 15	240 [4] 12	120 [2] 1	240 [4] 26	123 [2] 22	120 [1] 1	62 [1] 1	60 [1] 1	660 [6] 9	764 [10] 21*	Total 3,866 [52 sessions] 1–40 days
Percent observation pre-12:00 hrs	37.5	82.5	50	50	0	75	100	0	0	0	86.4	40.6	Mean 51.5
Mean incubation attentiveness (%)	74.9 (11.1) [8]	84.8 (5.3) [7]	72.6 [2]	97.1 [2]	89.2 [2]	81.7 [2]	100 [1]	91.7 [1]	66.9 [1]	57.5 [1]	95.8 (1.2) [6]	85.7 (4.3) [10]	83.2 [12 nests; 43 sessions]
Mean number of (complete and incomplete) incubation bouts/h	2.5 (0.3) [8]	1.9 (0.4) [7]	2.4 [2]	1.0 [2]	1.5 [2]	2.3 (0.3) [3]	1.9 [2]	1.0 [1]	1.0 [1]	2.0 [1]	1.7 (0.2) [6]	2.2 (0.2) [10]	1.8 [12 nests; 45 sessions]
Mean number of (complete and incomplete) recesses/h	1.7 (0.4) [8]	1.5 (0.4) [7]	1.6 [2]	0.5 [2]	1.0 [1]	1.0 [2]	0 [1]	1.0 [1]	1.0 [1]	2 [1]	0.8 (0.3) [6]	1.7 (0.3) [10]	1.2 [12 nests; 42 sessions]
Mean duration of complete recesses (min)	4.9 (1.0) [13]	6.9 (2.0) [8]	3.5 [2]	1.0 [2]		3.5 [2]		5.0 [1]		5.5 [1]	1.6 (0.3) [8]	5.7 (1.6) [18]	4.2 [9 nests; 56 recesses]
Grand mean provisioning nest visits/h	0 [8]	1.6 (0.5) [7]	0 [2]	1.3 (0.5) [4]	3.5 [2]	3.5 (1.3) [4]	1.9 [2]	2.5 [1]	1.0 [1]	1.0 [1]	1.3 (0.4) [7]	0.7 (0.3) [10]	1.2 [12 nests; 43 sessions]
Mean duration provisioning visits (min)		0.8 (0.1) [9]		0.7 (0.3) [5]	1.8 (0.5) [7]	1.2 (0.9) [13]	1.0 [1]	0.5 [1]		0.5 [1]	0.7 (0.1) [17]	0.5 (0) [5]	0.9 [9 nests; 59 visits]

min apart. Mean incubation attentiveness was very low (4.4%), reflecting the incompleteness of the incubation regime at this stage (e.g. Rowley 1973; Wang and Beissinger 2011).

Incubation stage

Incubation was documented at twelve nests from June to October in ~64 hours of observation (Table 2). By analogy with Rowley (1973), it was assumed that probably only females incubated, because no incubation change-overs were seen at nests where visibility was good.

Mean diurnal incubation attentiveness was 83%, and 72% of the individual sessional values were ≥80% (Table 2). On average, there were 1.8 complete (i.e. wholly within an observation session) and incomplete (i.e. extending beyond the observation session) incubation bouts/h and 1.2 complete and incomplete incubation recesses/h. Complete bouts lasted 24.9 ± 3 S.E. min (n = 43). However, the longest recorded complete bout (during a 3.1-hour observation session) lasted 109 min and 44.4% of incomplete bouts (n = 63) also lasted at least 25 min or considerably longer. The mean duration of complete (i.e. entirely within an observation session) incubation recesses was short (~4 min), but nine of 15 incomplete ones (i.e. extending beyond the observation session) exceeded this duration. The incubating bird was provisioned on the nest by her presumed mate 1.2 times/h on average, the mean duration of these visits being ~1 min.

Some incubating females exhibited ‘shaking’ behaviour, involving much rapid shaking of the wing and tail feathers. Its extent varied substantially among females, e.g. at the LTU Bundoora nest over 10 observation sessions (765 min), the incubating female ‘shook’ a mean of 0.9 ± 0.2 S.E. times/10 min of incubation, whereas the Fitzwilliam St female ‘shook’ a mean of 2.5 ± 0.7 times/10 min of incubating (7 sessions; 732

min). Some incubating females also frequently changed their orientation in the nest by at least 23° and up to 180°, sometimes in association with 'shaking'. The extent of this behaviour also varied considerably among females. Thus, the LTU Bundoora female made a mean of 0.8 ± 0.2 such orientation changes/10 min of incubation (10 observation sessions), whereas the Fitzwilliam St female only changed orientation a mean of 0.3 ± 0.3 times/10 min of incubation, and in five of seven observation sessions did not change orientation at all. Incubating females also occasionally spontaneously (i.e. in the absence of obvious disturbance) vacated the nest, perched briefly alongside it and then resumed incubating.

It was quite common in what appeared to be 'guarding' behaviour for the presumed male to spend a considerable amount of time perching prominently in the nest tree or nearby and sometimes performing wing-flicking calling displays (WFCD) while the presumed female incubated. Examples included:

(a) Kooyong Rd male – often perching prominently at the top of a bare tree 50 m from the nest tree for extended periods while the female was incubating, one such period lasting 9 min.

(b) Elster Avenue male – after provisioning the incubating female, once perched in the nest tree for 21 min, occasionally calling.

(c) Fitzwilliam St male – executed guarding bouts in the nest tree of 13 and 24 min duration on separate days, the latter bout including some 'perfunctory' arboreal foraging.

(d) LTU Bundoora male – habitually spent much time perching on a building 40 m from the nest tree while the female was incubating. One such bout lasted 12 min and another in a tree adjacent to the nest tree lasted 14 min.

Nestling stage

Parents' nest attendance during the nestling stage was documented at 15 nests in 75 hours of observation (Table 3a).

Provisioning visits:

Both parents fed the nestlings and, on average, there were 5.4 provisioning visits/h (range in nest means 1.9–8.2/h). On average, visits lasted just over 1 min and did not vary in mean duration among nesting pairs (with n ≥6) ($F_{11, 233}$ = 1.293, P = 0.229). Consecutive visits were a mean of 10 min apart, but the average interval between them varied 4.7-fold among nesting pairs (with an n ≥6) from 4.2 to 19.7 min ($F_{10, 155}$ = 2.599, P = 0.008). During this developmental stage in observation sessions when no brooding occurred, provisioning visits to the nest by parents (n = 100) were variously: [a] solo (81%), [b] synchronised (parents arrived at nest together) (10%), [c] overlapping (parents arrived asynchronously, but each visited the nest while the other was there) (8%), and [d] 'partially synchronised' (parents arrived synchronously at the nest and nest tree, respectively, but only one visited the nest) (1%). Feeding of one breeder by the other away from (~40 m) the nest was observed twice at the LTU Bundoora nest site during the nestling stage and was elicited by begging behaviour by the recipient. The recipient did not immediately fly to the nest, so it was unclear if this food was eventually given to, or shared with, the nestlings. This provisioning of the mate away from the nest could possibly be common in urban Little Ravens, but breeding adults were mostly out of my sight when not at the nest. Allopreening between the breeding pair away from the nest was observed twice during the nestling stage.

At the Kooyong Rd nest site parents approached the nest early in the nestling period through a series of short flights from branch to branch starting low in the nest tree, but later they nearly always flew directly to the nest. However, this was not a universal pattern, because the percentage of nest approaches that were directly to the nest at the LTU Bundoora nest was: day12, 80%; day 14, 100%; day 15, 40%; day 17, 43%; day 19, 37.5%; day 21, 25%; day 22, 80%; day 24, 75% and day 26, 75%. Over this period, 58% of nest approaches were directly to the nest (n = 45 approaches).

Brooding:

The mean duration of complete (i.e. wholly within an observation session) brooding bouts was ~14 min (range 2–60 min), but many incomplete bouts (i.e. extending beyond the observation session) were 15–60 min long. Diurnal brooding attentiveness averaged 19.6% over all observation sessions conducted at the nestling stage (Table 3a), but the average was slightly higher (23.1%) if only those sessions in which brooding was ongoing were considered. However, it must be emphasised that these data are averages for the entire nestling period. Observations at the particularly visible LTU Bundoora nest indicated that diurnal brooding attentiveness was 76–91% over the first six days of the nestling period, but declined to 15% by day 12 (Fig. 1). Thereafter it oscillated in a possibly weather-dependent manner (perhaps affected by ambient temperature and wind velocity) between 10% and 47% between days 13 and 21, before dropping to close to zero on day 23.

Over the first 17 days of the nestling period at the LTU Bundoora nest, both sexes brooded the nestlings. The percentage of brooding bouts that commenced with an identifiable change-over of birds was 40% on day 1, 14% on day 4, 25% on day 10 and 33% on day 17. On the intervening days and after day 17, no change-overs were observed. Change-overs could only be detected when one adult relieved its brooding partner and commenced a new brooding bout, as the sexes were indistinguishable. When an adult returned to brood when the nest was unoccupied (except for the nestlings), it was impossible to determine whether it was the same individual that had executed the previous bout of brooding. Both adults were present at the start of a brooding bout in only 32% of instances during that part of the nestling period in which change-overs were recorded. Identifiable change-overs occurred at the commencement of only 21% of brooding bouts in the 17-day initial nestling developmental period. Moreover, in two or three of the brooding bouts occurring after a change-over, the sitting bird seemed to be just covering the nestlings rather than actively brooding them. Therefore, it is at least conceivable that one sex (probably the female by analogy with Rowley, 1973) did most of the brooding overall.

Provisioning visits that took place when brooding was ongoing took various forms, including:

a) Visitor fed nestlings directly in presence of brooder.

b) Visitor just fed brooder.

c) Brooder departed when visitor arrived and visitor then fed nestlings directly.

Table 3a

Parental nest attendance at fifteen Little Raven nests in urban Melbourne during the nestling stage. Nest sites are shown in top row; abbreviations are as in Tables 1 and 2, with the addition of: Bke Rd N = Burke Rd North, Bel Rd = Belmore Rd, Koo Kt = Kooyongkoot Rd, Viv Ave = Vivianne Avenue, Sac St = Sackville St. Complete brooding bouts are those occurring entirely within an observation session. Numbers in round brackets are standard errors; numbers in square brackets are sample sizes (observation sessions or number of values analysed). Summary column for data rows gives mean for all nests. * observations spread over two breeding attempts by a pair.

Variable	Cha Quad	K Rd	Bke Rd N	E Ave	Orr Rd	Bel Rd	F St	Koo Kt	C St	War/ Pow	Oak Cr	Viv Ave	Sac St	St G Sth	LTU Bund	Summary
Month(s)	Oct/ Nov	Jly, Aug, Sep	Aug, Sep	Jly, Aug	Jly, Aug, Sep, Oct	Aug, Sep	Sep, Oct	Sep	Aug, Sep	Sep	Aug	Aug	Sep	Aug	Sep, Oct, Nov	Jly to Nov
Observation min	993	457	300	250	248	183	181	180	147	137	120	60	60	60	1,257	Total 4,513
[no. sessions] and	[10]	[6]	[4]	[4]	[5]	[3]	[3]	[3]	[2]	[2]	[1]	[1]	[1]	[1]	[16]	62 sessions
below temporal spread of observations (days)	26	35	25	32	24*	34	28	11	15	14	1	1	1	1	27	1- 35
Percent observations pre-12:00	6.1	47.5	73.3	100	51.6	67.2	33.1	100	57.8	100	100	100	100	83.3	19.0	Mean 38.3
Mean no. provisioning visits/h	1.9	6.1	5	6.9	6.5	8.2	6.6	3.3	5.5	5.9	5.0	5.0	8.0	3.0	4.0	5.4
	(0.1)	(0.4)	(0.4)	(1.1)	(1.2)	(0.9)	(0.4)	(0.7)							(0.3)	
	[10]	[7]	[5]	[4]	[4]	[3]	[3]	[3]	[2]	[2]	[1]	[1]	[1]	[1]	[16]	15 nests 63 sessions
Mean duration provisioning visits (min)	1.8	1.3	1.4	1.6	1.6	1.0	1.4	1.0	1.3	1.8	0.7	1.0	1.6	2.5	1.1	1.4
	(0.7)	(0.0)	(0.7)	(0.1)	(0.0)	(0.2)	(0.1)	(0.1)	(0.1)	(0.1)	(0.1)	(0.2)	(0.1)	(0.7)	(0.2)	(0.1)
	[20]	[35]	[20]	[22]	[23]	[19]	[14]	[6]	[12]	[16]	[7]	[5]	[5]	[3]	[54]	15 nests 62 sessions 261 visits
Mean interval between successive provisioning visits (min)	19.7	10.6	6.7	8.8	5.7	4.2	8.9	17	10.9	9	10.6	2.1	2.0	19	14.0	10.0
	(1.9)	(0.4)	(0.4)	(1.0)	(0.7)	(0.5)	(1.0)	(1.5)	(0.8)	(1.4)	(1.0)	(0.4)			(1.6)	
	[8]	[21]	[13]	[9]	[17]	[6]	[9]	[4]	[7]	[6]	[6]	[4]	[1]	[2]	[59]	15 nests 53 sessions 172 intervals
Mean percent provisioning visits solo when <5% brooding attentiveness	0	46.1	71.5	100	61.5	100	62.5	69	66.7	100	100				50	63.9
		(9.8)			(18.0)											
	[2]	[4]	[2]	[1]	[3]	[1]	[2]	[1]	[1]	[1]	[1]				[1]	12 nests 20 sessions
Mean brooding attentiveness (%)	50.6	3.7	25.7	32.5	7.2	9.9	20.9	21.7	0	28	0		10		44.3	19.6
	(3.6)	(0.9)	(6.4)	(13.0)	(1.1)	(4.0)		(3.8)							(7.4)	
	[9]	[6]	[5]	[4]	[5]	[3]	[2]	[3]	[1]	[2]	[1]		[1]		[16]	13 nests 58 sessions
Mean duration of complete brooding bouts (min)	19.7	6.8	13.4	12.1		11.8		19.5		20.5		20	6		13.4	14.3
	(5.3)		(5.7)	(3.4)											(1.6)	
	[8]	[2]	[5]	[4]		[2]		[2]		[2]		[1]	[1]		[35]	10 nests 62 bouts
Maximum duration of brooding bouts (min)	>59.5	7.5	36	>26.5	>13	14.6	25	20	>14	34		20			36	>59.5

d) Brooder sometimes departed nest with visitor when the latter had fed the young.

e) Brooder joined visitor in giving the food that the visitor had brought to the nestlings.

At the LTU Bundoora nest, parents starting brooding bouts in the absence of their mate fed the nestlings before commencing brooding on 82.4% of occasions.

The 'shaking' and changes of orientation observed during incubation also occurred during brooding. At the LTU Bundoora nest over the first 26 days of the nestling period, brooding birds 'shook' a mean of 1.1 ± 0.3 times/10 min of brooding (14 observation sessions; 539 min of brooding) and they changed orientation a mean of 0.5 ± 0.2 times/10 min of brooding (15 sessions; 539 min brooding). 'Shaking' occurred when feeding nestlings and at intervals during a brooding bout, and as during incubation was sometimes concurrent with orientation changes.

Other aspects of nest attendance during the nestling period:

At the LTU Bundoora nest faecal sacs were transported up to 40 m from the nest by parents until day 30 of nestling development. Occasionally, nest building was conducted by a

Table 3b

Parental nest attendance in the peri-fledging stage at nine Little Raven nests in urban Melbourne. Months abbreviated as Sep (September), Oct (October) and Nov (November). Nest identities shown in top row; abbreviated versions as in Tables 1, 2 and 3a. Numbers in round brackets are standard errors; numbers in square brackets are sample sizes (sessions or values analysed). Values in data rows in summary column are means for all nests.

Variable	Glenferrie Rd	E Ave	Glen Huntly Rd	Oak Cr	Sac St	Viv Ave	War/Pow Sts	Willis St	St. G Sth	Summary
Month	Sep	Sep	Nov	Sep	Sep	Sep	Sep	Oct	Sep	Sep, Oct, Nov
Observation mins (no. sessions)	99 [1]	60 [1]	444 [4]	60 [1]	60 [1]	65 [1]	60 [1]	64 [1]	70 [1]	Total 1,046 12 sessions
Percent observation min pre-12:00 hrs	0	100	66.2	100	100	0	100	0	100	Mean 54.7
No. nestling provisioning visits/h	4.9 [1]		2.3 (0.6) [5]	6 [1]	7 [1]	4.6 [1]	2.0 [1]	0.9 [1]	1 [1]	3.6 8 nests 12 sessions
Mean duration nestling provisioning visits (min)	2.0 (0.6) [5]		0.9 (0.3) [6]	1.5 [1]	0.5 (0) [3]	3.8 (2.6) [3]	6.5 [1]		3.5 [1]	2.7 7 nests 20 visits
Mean interval between nestling provisioning visits (min)	8.4 (2.3) [4]		11 (4.3) [6]	7 [2]	5.5 [1]	14.7 (4.2) [3]	13 [1]			9.9 6 nests 17 intervals
Mean no. fledgling provisioning visits/h		5 [1]		1.8 (2.2) [4]		3.8 (4.5) [3]	2 [1]	0.9 [1]		2.7 5 nests 10 sessions
Status of young during peri-fledging observation	One nestling and one fledgling 2m from nest	Two fledglings in nest tree and adjacent tree	Two nestlings in and out of nest; later, both fledglings perching in nest tree and nearby	One nestling and one fledgling in neighbourhood	One nestling and one fledgling in nest tree and adjacent tree	One nestling and one fledgling in nest tree	One nestling and one fledgling in nest tree		One nestling and one fledgling in nest tree vicinity	

breeding pair late in the nestling period (e.g. two nest-building visits in 60 min at the Orrong Rd nest at the late nestling stage). Late in the nestling stage, nestlings at most nests were active, clambering around the nest, perching on the rim and sometimes climbing out of the nest to perch nearby.

Peri-fledging stage

The peri-fledging stage was documented from September to November at nine nests during 17.4 h of observation divided evenly between morning and afternoon (Table 3b). Among these nests and over time at individual nests there were combinations of young ranging from one nestling in the nest plus one fledgling in the nest tree or nearby trees to 2 to 3 fledglings out of the nest and perching in the nest tree or adjacent trees. Provisioning visits to the nest by the parents at this stage averaged 4/h, all being brief (mean ~3 min). The mean interval between consecutive provisioning visits to the nest was approximately 10 min, although many intervals that apparently extended beyond the end of an observation session were substantially longer. The number of provisioning visits to fledglings (young out of the nest) at this stage averaged 2.7/h. When both nestlings and fledglings were present at the nest site, the number of provisioning visits to all the young collectively averaged 7/h.

At three nests, parents also performed substantial nest building at this stage, usually at the nest still in use or just vacated, but in one case in a nearby nest probably used by the pair in a previous season. Collectively, parents at two of these nests executed a mean of 4 nest building visits/h at this stage, interspersed with feeding nestlings and fledglings. These visits lasted 2.5 min, on average.

Brood overlap, re-nesting and out-of-season nest visits

There was one exception to the almost universal provisioning of incubating (presumed) females by their mates. In 7.1 hours of observation spread over 18 days, the incubating Constance St female was *never* provisioned by her mate. However, an adult, usually accompanied by a juvenile, was often present in the vicinity, the nest tree and adjacent trees. It often perched in an adjacent tree a few metres from the nest for considerable periods and sometimes performed WFCD there. It was observed several times defending the area against intruding conspecifics, and sometimes the incubating female joined it in this defence. She also occasionally joined the presumed male (and juvenile) in foraging near the nest tree. This appeared to be a clear example of brood overlap, but the presumed second breeding attempt failed late in the incubation stage due to an unknown cause. A second possible, but less certain, instance of brood overlap occurred at another nest.

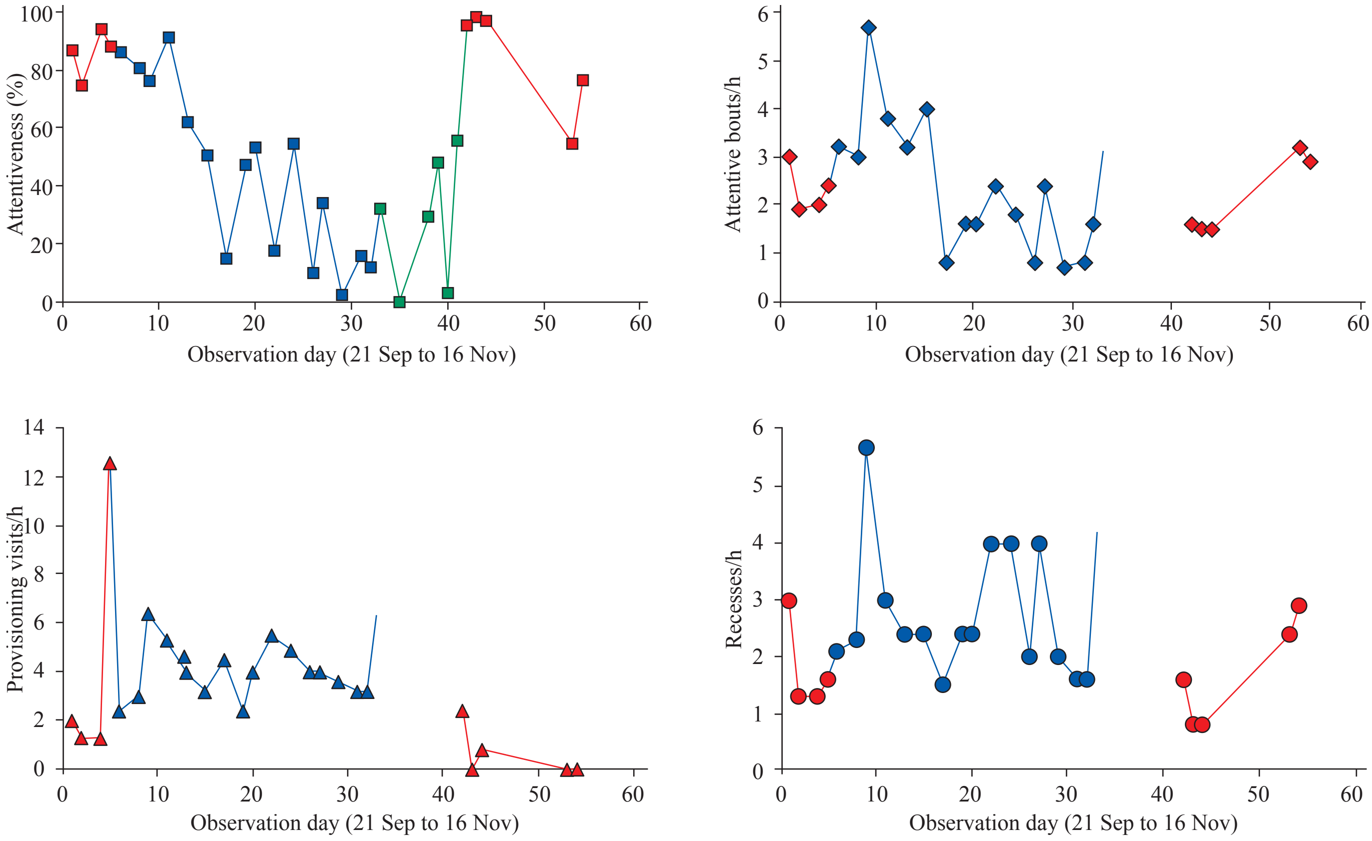

Figure 1. *Percentage attentiveness, provisioning visits/h, attentiveness bouts/h and recesses/h at the LTU Bundoora nest during a longitudinal sequence from incubation to brooding and then incubation again after breeding failure. Marker and line colours indicate: red, incubation stages; blue, nestling stage; green, "transition" from nestling to incubation stage. The green data points in the top graph were excluded from the summaries in Tables 2 and 3 because of their uncertain status, and are omitted from the other graphs in this figure for the same reason. The horizontal axis shows days since the inception of observation in the late incubation stage of the first breeding attempt. The only pronounced temporal trend was the decrease in percentage attentiveness during the brooding phase.*

Breeding pairs commonly re-used a nest that they had built (or probably built) in a previous season. However, when the Orrong Rd pair's first breeding attempt of the season appeared to fail soon after the peri-fledging stage, the pair was seen re-nesting 37 days later in a *different* nest in the same tree as the original nest, probably their own from a previous breeding season. The LTU Bundoora pair used the same nest twice during one season after their first breeding attempt failed at the nestling stage (Fig. 1). The second breeding attempt was initiated very soon after failure of the first, but it was impossible to accurately determine the exact interval between failure and re-laying. The second attempt failed at the incubation stage.

Adults visited nests in the non-breeding season. Some visits occurred within two months of fledging and included juveniles, but nest visiting by adults much further into the non-breeding season was occasionally seen too.

SYNTHESIS, COMPARISONS AND DISCUSSION

Nest attendance has not been widely documented for Little Ravens, but Rowley (1973) and Talmage (2011) provided valuable information for two rural and one urban location, respectively. Published information is more extensive for some of the other *Corvus* species in Australia and elsewhere (e.g. Butler *et al*. 1967; Rowley 1973; RØskaft *et al*. 1983; Secomb 2005a, b; Lawrence 2009) (Table 4). Nest attendance regimes vary among geographical regions and coexisting species with differing rates of nest predation risk (Badayaev and Ghalambor 2001), as well as intra-specifically in response to ambient nest predation risk (Martin and Briskie 2009; Chalfoun and Martin 2010). However, the nest attendance regime of urban Little Ravens broadly resembled that of both their rural counterparts (despite the probably greater food abundance in the city; Rebele 1994), and many other *Corvus* species globally. However, I saw no evidence of helpers-at-the-nest that have been described for a minority of *Corvus* species and populations (Verbeek and Butler 1981; Kilham 1984; Caffrey 1999).

Nest-building and egg-laying

The observation of nest-building being performed by both sexes of urban Little Ravens conforms with the pattern documented for rural populations (Rowley 1973), the Albert Park population in Melbourne (Talmage 2011), most other Australian *Corvus* species (Rowley 1973; Secomb 2005a, b; Lawrence 2009) and most congeners elsewhere (e.g. Lamm 1958; Stiehl 1985; Reaume 1987) (Table 4). Based on observation of colour-banded birds, Rowley (1973) stated that later in the building

Table 4

Comparative data on nest attendance for some *Corvus* taxa. A few values are expressed in the literature as per day rather than per hour and are so marked (/d). Durations are in minutes (min). Data are means, ranges or maxima. Values for certain times in a stage are indicated in square brackets. No data were found for the cells shaded grey. Sample sizes are given only for *C. mellori*. Albert Park and Langwarrin are in Melbourne, Victoria.

NESTING STAGE

Nest building:	Both sexes build	Female does most building later	Building visits/h	Duration of building visits (min)	Interval between successive building visits (min)	References
Pied Crow *albus*	✓		4.6 (but up to 12 in some obs. sessions)			Lamm 1958
Little Crow *bennetti*	✓	✓				Rowley 1973
American Crow *brachyrynchos*	✓		15–17	1.6 0.7-2.4	12	Reaume 1987
Black or Cape Crow *capensis*	✓					Skead 1952
Common Raven *corax*	✓	✓				Stiehl 1985
Australian Raven *coronoides*	✓		7 [early]			Rowley 1973
Rook *frugilegus*	✓	✓				RØskaft *et al.* 1983
Hawaiian Crow *hawaiiensis*	✓			7–12	2	HCWCS 2005 Tomich 1971
Mariana Crow *kubaryi*	✓	✓				Tomback 1986 Michael 1987 USFWS 2005
White-necked Crow *leucognaphalus*	✓			0.5		Wiley 2006
Large- or Thick-billed Crow *macrorhynchus*	✓					Madge and Burn 1994
Little Raven *mellori* (rural NSW)	✓	✓				Rowley 1973
(urban; Albert Park)	✓	✓				Talmage 2011
Torresian Crow *orru*	✓		8 [lining stage]			Rowley 1973
Fish Crow *ossifragus*	✓		9.2	1.9		McNair 1984
Forest Raven *t. tasmanicus & t. boreus*	✓		17–18	2.4–2.6		Secomb 2005a Lawrence 2009
House Crow *splendens*	✓	✓				Lamba 1976

process of rural Little Ravens the female does most of the actual building and the male just brings material to the nest, and similar divisions of labour have been noted in the Albert Park population and other *Corvus* species (e.g. RØskaft *et al*. 1983; Stiehl 1985; Talmage 2011). I could not determine whether this was true of urban birds generally, because I could not distinguish the sexes or often observe the fine details of behaviour at the nest. Sharing of nest building effort is probably important in permitting females to subsequently perform all the incubation. However, despite the shared nature of nest building, more than half of the building visits were by a single parent, as also reported for American Crows *C. brachyrynchos* (Reaume 1987).

Collectively, pair members made about six short building visits to the nest/h during intensive nest construction (Table 3). Comparable rates occur during early construction in Australian Ravens *C. coronoides,* at the lining stage in Torresian Crows *C. orru* and more generally in Pied Crows *C. alba* (Lamm 1958; Rowley 1973) (Table 4). However, much higher rates have been reported respectively for the Forest Raven *C. t. tasmanicus* (17–18/h; Lawrence 2009) and American Crow *C. brachyrynchos* (15–17/h; Reaume 1987). A visiting rate as high as these was only observed at one nest in one observation session in my investigation. However, the mean duration of nest building visits was similar (<2.6 min) in urban Little Ravens and all four species for which values are reported in Table 4. Rowley (1973) documented an equal sexual division of labour in Australian Ravens in the early stages and Torresian Crows in the later stages of nest building, but as noted above I could not distinguish the sexes in the Little Raven.

Forest Ravens sometimes add a few sticks to the nest wall around hatching time (Lawrence 2009) and I occasionally observed addition of nesting material during the incubation stage in urban Little Ravens. The substantial nest building observed in the late nestling and peri-fledging stages at a few Little Raven nests in my study and by Talmage (2011) at Albert Park has also been recorded for a pair of Australian Ravens (S. Debus pers. comm.). There are several plausible explanations for this intriguing behaviour in Little Ravens:

(a) urban Little Ravens often re-nest after a breeding failure (e.g. the Orrong Rd and LTU Bundoora pairs) (Talmage 2011), so this ‘adventitious’ nest building could be insurance against breeding failure soon after fledging. According to Rowley (1973), *Corvus* nests used for re-nesting after breeding failure are built (or re-furbished) much more rapidly than the original nest, underlining the urgency to commence a second breeding attempt.

Table 4 (continued)

Incubation:	By female only or mainly – fed by male	By both sexes	Provisioning visits/h	Interval between provisioning visits (min)	Duration of provisioning visits (min)	Incubation attentiveness (%)	Bout duration (min)	Recess duration (min)	Recesses/h	References
albus	✓					89 (Female: 77 Male: 12)	Female: 8-68; usually 10-25 Male: 2-6			Lamm 1958
bennetti	✓									Rowley 1973
brachyrynchos	✓							1-40		Good 1952
						46 [early] – 81 [late]		2-12	1-4	Kilham 1984
capensis		✓								Skead 1952
Northwestern Crow *caurinus*	✓		1.4			87		5.6		Butler *et al.* 1984
corax	✓		7/d					c. 10	0.2 [early] – 0.6 [late]	Stiehl 1979 Ratcliffe 1997
coronoides	✓		2				10-20			Rowley 1973
Chihuahuan Raven *cryptoleucus*	✓									D'Auria and Caccamise 2007
frugilegus	✓		1.3-1.6							RØskaft *et al.* 1983
			1.6-3.1	3-68						Coombs 1960
hawaiiensis	✓									HCWCS 2005
		✓				91	24.5	2.7	1.4	Tomich 1971
Taumalipas Crow *imparatus*	✓									Madge and Burn 1994
kubaryi	✓	Male gives minor assistance								Tomback 1986 Michael 1987 USFWS 2005
leucognaphalus	✓					96		5-15		Wiley 2006
macrorhynchus	✓									Kurosawa and Matsuda 2003 Lamba 1976
mellori (Albert Pk) (n = 2 sessions at different nests)	✓		2.6	22		96		3	0.3	Talmage 2011
Langwarrin (peri-urban) (n = 1 all-day session)			1.9	20		92		3	1.6	Thoday (cited in Talmage 2011)
NSW (rural) (n unknown)	✓									Rowley 1973
Jackdaw *monedula*	✓									Lockie 1955
			6.5							Henderson and Hart 1993
orru	✓									Rowley 1973
ossifragus	✓				0.6		31.5	3.8		McNair 1984
ruficollis	✓									Madge and Burn 1994
splendens	✓	(Male does ~ 33.3%)				89	126 (30-288)	18 (1-48) Male: 82 Female: 160		Lamba 1976
	✓	Male guards nest								Ranjan and Kushawa 2013

Table 4 (continued)

Nestling:	Brooding mainly by female	Both sexes brood	Brooding attentiveness (%)	Brooding bout duration (min)	No. brooding recesses/h	Brooding recess duration (min)	Provisionings of nestlings/h	Interval between provisioning visits (min)	References
albus	✓						2.9 [early] – 3.5 [mid] – 1.7 [late]		Lamm 1958
brachyrynchos	✓						3.8	15	Good 1952
									Caffrey 1999
caurinus	✓		93 [early] -18 [day 16-18]				2.7 [early] – 2 [late] Male: 1.8-0.8 Female: 0.9-1.2		Butler *et al.* 1984
corax	✓						45/d 102/d [mid] – 36/d [late]		Stiehl 1979
Hooded Crow *cornix*	✓		70 [early] – 25 [mid] – 0 [late]		10-20/d	1-5			Loman 1980
coronoides	✓		89 [early] – 33 [late]	39 [first 28 days]		8.3 [first 28 days]	1.1 [early] – 3.9 [late]		Rowley 1973
cryptoleucus		✓					9.4/h		D'Auria and Caccamise 2007
frugilegus	✓						1.4-3.3		Coleman 1972 RØskaft *et al.* 1983
hawaiiensis	✓								HCWCS 2005
leucognaphalus			84 [early] – 0 [mid-late]				5.1		Wiley 2006
macrorhynchos	✓								Kurosawa and Matsuda 2003
							13-16 [peak] to 2-5 [late]		Lamba 1976
mellori (Albert Pk) (n = 5 sessions at 4 nests)	✓		90 [early] – 0 [late]				3 [early] – 6 [late]		Talmage 2011
Langwarrin (periurban) (n = 1 all-day session)			54 [early-mid]				9 [early-mid] Male: 6 Female: 3	Male 10 Female 20	Thoday (cited in Talmage 2011)
NSW (rural)	✓								Rowley (1973)
monedula	✓								Lockie 1955
							6.5 [early/mid] – 13.5 [late]		Henderson and Hart 1993
orru	✓						3		Rowley 1973 Secomb 2005b
ossifragus	✓			*25*		*6*			*McNair 1984*
t. tasmanicus		✓							Lawrence 2009
t. boreus	✓		72-0 and 88-2	6-30			2-2.2		Secomb 2005a
splendens							16 [peak] – 6 [late]		Lamba 1976

(b) Forest Ravens sometimes build extra nests which are only used at night, possibly by roosting juveniles; however, unlike the situation in my study, such nests are built at the same time as the main nest (Lawrence 2009).

(c) Rowley (1973) states that the nest is sometimes used for nocturnal roosting by fledglings for a time after they depart from it. Conceivably the nest that is likely to be used by roosting juveniles sometimes requires running repairs to fulfil this function adequately, whether it is the one just used or an older one nearby.

Among Australian and many other *Corvus* species (and many other passerines), the eggs comprising a clutch are laid on successive days, except that one 2-day interval occurs somewhere in the laying sequence. Incubation is usually partial until several eggs have been laid (e.g. Emlen 1942; Skead 1952; Holyoak 1967; Rowley 1973). My observations at one urban Little Raven nest during egg-laying also suggested that the incubation regime was incomplete at this stage. Partial incubation is common in birds and may be functional in various ways, some of which do not require embryonic development to be initiated (e.g. preventing egg loss to predation, nest-site takeover or brood parasitism) and some which do (e.g. shortening the incubation period once the clutch is complete) (Wang and Beissinger 2011). Nest predation, and especially nest-site take-over by conspecifics, may well be threats to breeding urban Little Ravens (Lill, 2019). Partial incubation can also lead to asynchronous hatching in birds, which sometimes facilitates adaptive brood reduction in poor brood-rearing conditions (Stenning 2008).

Incubation

The female exclusively or mainly incubates the eggs and is fed by the male while she does so in most *Corvus* species studied, including rural and probably the Albert Park Little Ravens (*e.g.* Rowley 1973; Butler *et al*. 1984; Stiehl 1985; Lawrence 2009; Talmage 2011) (Table 4). However, in House Crows *C. splendens*, Thick-or Large-billed Crows *C. macrorhynchos*, Black or Cape Crows *C. capensis* and Hawaiian Crows *C. hawaiiensis* the male takes a minor role in incubation (Skead 1952; Tomich 1971; Lamba 1976). I assumed that exclusively female incubation happened in my study population because no incubation change-overs were observed during extensive observation at twelve nests, including two at which the details of activities at the nest were clearly visible.

Some incubating females frequently adjusted their orientation. These pronounced changes in orientation were not obviously concerned with egg turning and have been seen in congeners (e.g. Tomich 1971; McNair 1984). Lawrence (2009) has suggested for Tasmanian Forest Ravens that they may increase the efficiency of surveillance for predators and intruders, and this seems plausible for urban Little Ravens too. Female urban Little Ravens also 'shook' quite regularly, often without changing orientation. Although the bird's focus seemed to be on the eggs during 'shaking', it was unlikely that they were turned each time that this behaviour occurred and conceivably some of these movements were concerned more with adequate heat transference to the entire clutch. However, it is unclear how shaking the wing and tail feathers would enhance such transference and the function of the behaviour requires further investigation, probably with fixed cameras.

Incubation attentiveness is an evolved trait, albeit with some phenotypic flexibility in relation to available food supply and nest predation intensity (Chalfoun and Martin 2007). Diurnal attentiveness in urban Little Ravens was high in my study and Talmage (2011) reports a comparably high level based on a small sample for Albert Park. The level of attentiveness was comparable with that of many north temperate passerines (Chalfoun and Martin 2007) and many other *Corvus* species, irrespective of their breeding latitude (Table 4). For Little Ravens in urban Melbourne, a high attentiveness is probably critical in maintaining an optimal embryonic temperature and growth rate (Deeming 2002) at prevailing low winter/spring ambient temperatures. Mean maximum and minimum monthly ambient temperatures during the three months in which incubation mainly occurred are 13.5–17.3^{o}C and 6–8^{o}C, respectively (Australian Bureau of Meteorology). Even the ambient temperature maxima are well below the commonly accepted physiological zero temperature for avian embryonic development (25–27°C) (Conway and Martin 2000a). High attentiveness may also be important in minimising the eggs' visibility and exposure to nest predators and make their defence more efficient if the incubating bird is capable of repelling intruding predators, as in Little Ravens (Kleindorfer and Hoi 1987; Conway and Martin 2000b; Chalfoun and Martin 2007).

Incubation bouts wholly within an observation session typically lasted ~25 min., although some recorded during longer observation sessions and some that extended beyond the observation session were much longer. Rowley (1973) reports 10–120 min. durations for other Australian *Corvus* species and Lamm (1958) 8–68 min. durations for tropical Pied Crows (Table 4). Incubation recesses taken within an observation session were short (~4 min.) and comparable in duration with the mean values reported for Northwestern Crows *C. caurinus* and Forest Ravens (Butler *et al*. 1984; Lawrence 2009) (Table 4). However, some recesses taken by female urban Little Ravens that extended beyond the observation session were longer.

This kind of incubation regime, with high female attentiveness and (mostly) brief recesses, is facilitated by the male provisioning his incubating mate. This interpretation is supported by evidence that incubation attentiveness increases in uniparental incubator passerines as a function of the provisioning rate of the female by the male, at least up to an asymptotic rate of ~5 feeds/h (Martin and Ghalambor 1999). This relationship is thought to be influenced by nest predation intensity, because a high male provisioning rate is less likely to increase nest conspicuousness in a low than a high nest predation environment. On average, incubating female urban Little Ravens were provisioned by the male 1.2 times/h and similar rates have been reported for other Australian *Corvus* species, Northwestern Crows and Rooks *C. frugilegus* (Coombs 1960; Rowley 1973; Røskaft *et al*. 1983; Butler *et al*. 1984) (Table 4).

In some uniparental incubator species, the female is fed away from the nest by the male to some extent, which may adaptively reduce the nest predation risk by reducing nest conspicuousness (Lawrence 2017). Talmage (2011) observed such behaviour once at Albert Park. I did not observe it during the incubation stage in urban Little Ravens, but both sexes were out of my sight during many incubation recesses at most nests studied. If this behaviour is uncommon in *Corvus* species, their comparatively low male provisioning rates during incubation seem incompatible with the proposition that the nesting environment has a low nest predation intensity, as proposed for cavity-nesting passerines in Arizona, USA by Martin and Ghalambor (1999). Clearly, further targeted research is needed to decipher the major influences on the incubation regime in the genus *Corvus*.

'Guarding' behaviour was observed at several nest sites during incubation and was reported for Albert Park by Talmage (2011). It has also been recorded in Pied Crows, Common Ravens *C. corax*, Fish Crows *C. ossifragus* and Rooks (Lamm 1958; Coombs 1960; McNair 1984; Stiehl 1985) and seems likely to constitute surveillance for nest predators and/or conspecific competitors (Lill, 2019).

Brooding and provisioning nestlings

Altricial nestlings require brooding until they achieve endothermy, which is often substantially into the nestling period. Consequently, therefore, brooding attentiveness is high initially but declines during development. *Corvus* species exhibit this pattern, but in most of them the female alone broods the nestlings during their early development and is fed by the male while she does so (Table 4), although males do some brooding in some species (*e.g.* Forest Raven; Lawrence 2009). Rowley (1973) described brooding as being solely undertaken by the female in rural Little Ravens, but this was not the case in my study because I observed 6 change-overs at one particularly visible nest. However, male involvement in brooding may be fairly limited in urban Little Ravens, because these were the only change-overs observed in many hours of observation at 15 nests, including three at which the details of ongoing activity were clearly visible.

In urban Little Ravens, diurnal brooding attentiveness was ~20% over the entire nestling period. This figure is realistic, given that brooding attentiveness is initially very high but declines to a low level or zero in the second half of the (~38-day) nestling period, as documented for the LTU Bundoora nest in this study, Little Ravens at Albert Park, Australian and Forest Ravens and several *Corvus* species elsewhere (Lamm 1958; Rowley 1973; Loman 1980; Butler *et al*. 1984; Stiehl 1985; Secomb 2005a; Talmage 2011) (Table 4). The mean duration of brooding bouts that were completed within an observation session was 14 min., but many that started before or ended after an observation session were clearly much longer. Rowley (1973) reports a mean brooding bout duration of 39 min for the first 75% of Australian Raven nestling development and Secomb (2005a) bouts of up to 30 min. in Northern Forest Ravens *C. tasmanicus boreus* (Table 4). As with incubation, the high level of brooding attentiveness observed in *Corvus* species early in nestling development is probably facilitated by provisioning of the brooding bird by its mate. As happened during incubation, brooding Little Ravens exhibited 'shaking' and orientation changes. The function of 'shaking' during brooding and incubation is enigmatic, but the orientation changes during brooding may facilitate more efficient surveillance for predators and conspecific competitors. Certainly, brooding individuals indulged in much obvious visual surveillance of their surroundings.

Both urban Little Raven parents fed the nestlings, a pattern typical of virtually all *Corvus* species studied (Madge and Burn 1994), although feeding by the male is often done via the brooding female early in development in some species, including the Little Raven (Rowley 1973; Wiley 2006; Talmage 2011). Collectively over the entire nestling period, urban Little Raven parents fed their nestlings (and brooding mate) about 5–6 times/h, on average. Talmage's (2011) limited data for Albert Park equate to an overall rate of ~4 times/h. Frequencies of provisioning nestlings in some other *Corvus* species mostly appear to be a little lower than that in my investigation, although Pied Crows and White-necked Crows *C. leucognapthalus* may be exceptions (Table 4). Sixty to 70% of provisioning visits when brooding was not ongoing were solo visits. It has been suggested that synchronizing provisioning visits can be adaptive in reducing nest conspicuity to predators either by reducing 'traffic' at the nest site or calling by nestlings (Hall and Magrath 2011; Mariette and Griffiths 2012), but this was apparently either unimportant or not feasible in urban Little Ravens. Although Little Ravens cache food (Lill and Hales 2015), I did not observe any use of cached food in provisioning the nestlings, as reported for the species at Albert Park (Talmage 2011) and Northern Forest Ravens (Secomb 2005c), but it could have occurred out of my sight.

Urban Little Raven nestlings were very active towards the end of the nestling period, clambering onto the nest rim and even perching outside the nest, behaviour also noted in other *Corvus* species (e.g. Skead 1952; Lamba 1976; Wiley 2006; Lawrence 2009). Both Little Raven parents fed the young that were in and out of the nest through the few days of the peri-fledging stage. When a combination of nestlings and fledglings was present, the nestling(s) were fed collectively about 1.5 fewer 'meals'/h than the mean for the entire nestling period, but fledglings were also being fed a mean of 2.7 meals/h. Consequently, the overall rate of feeding young appeared to be slightly greater than that for the entire nestling stage. Of course, the parents' total workload at the three nests where 'adventitious' nest building also occurred at this stage was a bit greater again, although the nest building rate was 33.3% lower than in the true nest building phase.

Magnitude and costs of nest attendance

This study established that *in toto* urban Little Ravens exhibit a high level of nest attendance and parental care. On the average time-budgets documented, and allowing for the changing day-length during breeding and the differing time periods at which the breeding stages occurred, the following time expenditures can be approximately estimated:

a. Nest-building: would require a very substantial time (and energy) commitment by both sexes, but this is hard to quantify because of its discontinuous nature.

b. Incubation attentiveness: (calculated as mean incubation attentiveness × mean day or night length during main months when incubation occurred × incubation stage duration) – a female incubating throughout a complete incubation stage would spend an estimated 189 hours in diurnal and 291 hours in nocturnal incubation.

c. Provisioning of incubating female: (mean provisioning rate by male × mean day length in months when most incubation occurred × incubation stage duration) – during a complete incubation stage, a female would be fed by her mate an estimated 227 times (more if any substantial provisioning occurs away from the nest).

d. Brooding: (mean brooding attentiveness × mean day or night length in months when brooding mostly occurred × nestling stage duration) – parents that conducted a full brooding regime would brood the nestlings for an estimated 88 hours diurnally and 461 hours nocturnally. The latter number assumes that nestlings are brooded nocturnally right through until fledging, which was not definitely determined.

e. Provisioning of nestlings: (mean provisioning rate × mean day length during months of main nestling care × nestling stage duration) – a pair that provisioned each other (during brooding) and their nestlings throughout a complete nestling stage would collectively make an estimated 2,434 provisioning visits to the nest. It is not clear whether provisioning of one pair member by the other away from the nest adds to, or is incorporated in, this effort. There is a time commitment to faecal sac removal, but it is small.

f. Provisioning fledglings: parents feed the young for several weeks after they leave the nest (Rowley 1973).

Although it was beyond the scope of this inquiry, the energetic cost of egg-laying in Little Ravens must also be considerable because the most common clutch size of rural Little Ravens is four (Rowley 1973) and the mean egg dimensions of 44.4 × 29.9 mm translate into an egg volume of ~20 cm^3 (Hoyt 1979).

Incubation is critical, but involves a significant energy expenditure (Moreno *et al*. 1991; Tinbergen and Williams 2002) that can be reflected in immediate short-term costs to parents (e.g. reduced fledging success, Reid *et al*. 2002; reduced adult female mass, Hanssen *et al*. 2005). It may also be reflected in delayed costs, such as poorer survival to subsequent breeding seasons or lower future fecundity of the incubating birds (Visser and Lessells 2001; Hanssen *et al*. 2005). These costs are thought to occur because incubation's energetic cost must logically often be met by reallocating energy from other vital functions (e.g. immune competence; Hanssen *et al*. 2005). Brooding and provisioning nestlings are also energetically demanding activities; although these behaviours can strongly positively influence nestling growth rate (Henderson and Hart 1993), they can also have both immediate costs for the carers (e.g. reduced body condition; Dijkstra *et al*. 1990) and, as with incubation, longer-term fitness costs accrued through negative effects on their survival and future fecundity (Young 1996; Golet *et al*. 1998; Wernham and Bryant 1998). Such fecundity effects have been demonstrated experimentally in Rooks (Røskaft 1985). Thus, the high level of RE expressed in parental care, while increasing current reproductive success, may well have significant future fitness-reducing costs in urban Little Ravens.

Brood overlap and re-laying

Brood (or clutch) overlap occurs in a variety of bird species (Gru¨ebler and Naef-Daenzer 2010). It can potentially increase reproductive output when the breeding season is long relative to the developmental period of the young, the degree of cooperation between the breeders is high, and breeding associations are sufficiently stable and long-lasting for members to become experienced and efficient at breeding (Burley 1980). Although crows and ravens have high longevity and breeding pair membership is often stable over several breeding seasons, development is protracted (Marzluff and Angel 2005), which may be why brood overlap is uncommon (Rowley 1973). Unfortunately, the second breeding attempt of the Constance St pair failed late in incubation, so it was impossible to see how the female would cope with rearing a second brood after undertaking incubation in the first attempt without any provisioning by her mate. Talmage (2011) observed brood overlap at Albert Park, but all the second breeding attempts failed. This aspect of urban Little Ravens' breeding biology requires further investigation because it would be puzzling in such a long-lived bird if brood overlap is reasonably common but the second breeding attempts rarely succeed.

Re-laying within the same breeding season after breeding failure is well known for some *Corvus* species (e.g. Coleman 1972; Loman 1980; Stiehl 1985). However, Rowley (1973) found that it was uncommon in rural Little Ravens, but had been recorded up to 10 weeks after laying of the first clutch. Talmage (2011) reported that 80% of Albert Park pairs whose first breeding attempt of the season failed re-nested, and even 41% whose first attempt was successful re-nested. Judging from her behaviour, the Orrong Rd female appeared to re-lay about 9 weeks after her first clutch was laid and 37 days after the fledglings from this clutch disappeared. Interestingly, this female laid her second clutch in a different nest, but it was in the same tree as her first nest. If the first clutch was lost to predation, an adaptive shift in nest site might have been expected (Kearns and Rodewald 2013). Although it is very unlikely, I cannot entirely exclude the possibility that a different, late-nesting pair took over this nest tree. However, the LTU Bundoora female certainly laid a second clutch in the *same* nest that she used for her first breeding attempt of the season very soon after losing her brood to an unknown cause, although this clutch failed during incubation.

Future research

Knowledge of urban Little Ravens parents' nest attendance behaviour that requires further examination includes attendance during oviposition, attendance during the developmental decline in diurnal brooding attentiveness and the relative roles of the sexes in major attendance behaviours. Working out the last-named feature would require capture, genetic and/or morphological sexing and colour-banding of many individuals.

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Assessment of band recoveries for four Australian falcon species

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Available band recoveries from 1958 to 2015 were analysed for the Nankeen Kestrel *Falco cenchroides* (*n* = 97, recovery rate 3%), Brown Falcon *F. berigora* (*n* = 78, recovery rate 6%), Australian Hobby *F. longipennis* (*n* = 13, recovery rate 11%) and Peregrine Falcon *F. peregrinus* (*n* = 97, recovery rate 8%). Nankeen Kestrels banded as adults (including age 1+) were recovered up to 732 km (mean 42 km) from the banding site and up to 7 years (mean 1.6 y) after banding; those banded as pulli/juveniles were recovered up to 822 km (mean 63 km) away and up to 5 years (mean 0.8 y) later. Adult Brown Falcons were recovered up to 409 km (mean 27 km) away and up to 11.7 years (mean 2.4 y) later and juveniles up to 2,047 km (mean 68 km) away and up to 18 years (mean 3.1 y) later. Hobbies were recovered up to 322 km (mean 45 km) from the banding site and up to 6.7 years (mean 1 y) after banding. Peregrine Falcons banded as pulli/juveniles were recovered up to 333 km (mean 62 km) away and up to 15 years (mean 2.2 y) later: males were recovered up to 184 km (mean 32 km) away and up to 7 years (mean 1.4 y) later and females up to 293 km (mean 79 km) away and up to 15 years (mean 3.2 y) post-banding. Most recoveries (42–85%, depending on the species) were of birds either found dead (cause unknown) or sick/injured/exhausted; human-related mortalities, either deliberate (persecution) or accidental (e.g. collisions, interactions with infrastructure), largely formed the balance of the reported public recoveries of each species.

INTRODUCTION

Available banding recovery data for the Nankeen Kestrel *Falco cenchroides*, Brown Falcon *F. berigora*, Australian Hobby *F. longipennis* and Peregrine Falcon *F. peregrinus* as at the early1990s were summarised by Marchant and Higgins (1993). A 25-year update was therefore sought, to ascertain whether further band recoveries had been obtained for these falcon species, and thus whether their movements could be further elucidated. In the interim, reports of studies of banded Kestrels around Canberra, Australian Capital Territory (Baker *et al.* 1997), Brown Falcons in southern Victoria (M^{c}Donald 2003; M^{c}Donald *et al.* 2003, 2004) and Peregrine Falcons in Tasmania and Victoria (Mooney and Brothers 1993; Emison *et al.* 1998) were published, and a noteworthy recovery of a Hobby has also been reported (Goodwin 2017; Anon. 2018). The few band recoveries for the Black Falcon *F. subniger* were discussed by Debus and Olsen (2011), and band re-sightings/recoveries and satellite tracking of the Grey Falcon *F. hypoleucos* were reported by Sutton (2011) and Schoenjahn (2018). It is acknowledged that other datasets for the four focal falcon species around Canberra and for Peregrines in Victoria (the latter foreshadowed by Hurley 2013a, b), will be published separately elsewhere by the researchers involved.

The present paper collates publicly available band recoveries to date for the four most numerous Australian falcon species, derived from the banding efforts of 53 banders (including SD and JO; Appendix 1). As well as summarising data on dispersal distances, dispersal directions and longevity, this compilation elucidates mortality factors. Region-specific dispersal distances, site fidelity, life tables, survival and/or mortality have already been calculated for Peregrines from the present dataset (Mooney and Brothers 1993; Emison *et al.* 1998). Some relevant aspects of Peregrine Falcon sociobiology based on individually-marked birds have also been published (e.g. Olsen and Stevenson 1996; Olsen *et al.* 2006).

METHODS

Recovery data for the four species of falcon from 1958 to 2015 were provided by the Australian Bird and Bat Banding Scheme (ABBBS, courtesy of D. Drynan); they resulted from the banding activities of 53 registered banders whose data were not under embargo (Appendix 1). The usable data exclude short-term (<1 month) recoveries of rehabilitated birds where the attempt to return them to the wild clearly failed (i.e. birds returned to care). For dispersal distance and direction, only those recoveries at least 5 km from the banding site were mapped (the appropriate resolution for the mapping scale in Figures 1–3). Distances are simple linear displacements, with no implication being made about the routes taken or where the birds may have been in the interim; they are therefore minimum distances travelled from the banding site. Here, 'road-killed' means known (not assumed) to have collided with a moving vehicle, as in the ABBBS definition. Ageing is as defined by the ABBBS codes, e.g. 1+ = first year or older, 2 = second year and 2+ = second year or older etc.

There were 97 usable recoveries for the Nankeen Kestrel (1996–2009), 78 for the Brown Falcon (1963–2008), 13 for the Australian Hobby (1975–1996) and 96 for the Peregrine Falcon (1958–2015). For the Kestrel, all but three individuals were banded before 2000 (mostly in the 1970s to 1990s); for the Brown Falcon, all but one were banded before 2000 (mostly in the 1990s); for the Hobby, all were banded before 2005 (mostly in the 1990s), and for the Peregrine, all but six were banded before 2000 (mostly in the 1970s to 1990s).

For the Kestrel, almost half (*n* = 41) were aged at banding as a pullus/juvenile/first year bird (age 1), and of those about half were unsexed and the rest distributed quite evenly between the sexes. For the remainder (*n* = 56), the sexes were evenly split (with nine unsexed), and almost all were aged 1+ (two males 2+, one 3+; two females 2+).

For the Brown Falcon, almost half (*n* = 35) were aged at banding as a pullus/juvenile/first-year bird, and of those about one-third were unsexed and more were sexed as females (*n* = 15) than males (*n* = 9). Of the adults (*n* = 43), a few were aged 1+ but most were specifically aged as 2+ to 4+, with more females (*n* = 22) than males (*n* = 15) (and six unsexed).

For the Hobby, only three were aged at banding as a pullus/juvenile/first-year bird (two of these unsexed), and five males and five females were aged 1+ or older (one male 2+, two females 2+). Age and sex classes were therefore pooled for analysis.

For the Peregrine, almost all were banded as pulli (*n* = 78), juveniles (*n* = 3) or first-year birds (*n* = 7), with the sexes being quite evenly represented (and 16 unsexed). Eight were aged as 1+ or older: one male 1+, two females 1+ and two females 2+, and the other three birds were unsexed.

Almost all recovered falcons originated in south-eastern Australia (eastern and southern New South Wales, Victoria and south-east South Australia), Tasmania and south-western Australia, and most were also recovered within these regions. Stated causes of recovery, as per ABBBS status codes, are enumerated herein, other than retraps or resightings (band number read in the field or inferred from colour bands) by banders of their ‘own’ birds. For the Kestrel, Brown Falcon and Peregrine, stated reasons for recovery (as per ABBBS codes in the dataset) were, in a few cases (*n* = 1–4 per species), given as ‘captive bird (was from wild)’, and so are excluded from analysis of recovery, as the circumstances were unclear (e.g. possible misinterpretation by rehabilitators of method of encounter codes). For Peregrine pulli, there were three cases in which only the band was returned without accompanying data (in the 1960s to 1980s, i.e. during the persecution era); we assumed that these individuals had been killed by, for example, pigeon fanciers or duck hunters and the time elapsed and distance travelled since banding were assumed to be valid (two of these were short, <1 year, 4 km and 52 km, and the third unexceptional in both respects, 12 km and <5 years).

The term ‘migration’ is used here in the usually accepted sense of regular biannual return movements between breeding and wintering areas.

Data analysis

Small sample sizes and many zero values precluded meaningful comparisons of the recovery distances by analysis of variance. We therefore present summary data which we interpret conservatively, particularly as standard deviations were usually large. Means are given ± 1 standard deviation.

Table 1

Distance (linear displacement) and time elapsed (years) of three falcon species and their age/sex classes banded and recovered in Australia. Juvenile = banded at age 1 (includes pulli); adult = banded at age 2+ or assumed so (i.e. aged as 1+ or older by bander; see text). M = male, F = female; *n* in parentheses. For median distances, see text.

Species	Distance (km)		Time (y)	
	range	mean	range	mean
Nankeen Kestrel:				
All (97)	0–822	51	0–7	1.3
Juveniles (41)	0–822	63	0–5.1	0.8
Juv. M (9)	0–267	39	0.02–2.4	0.9
Juv. F (11)	0–822	89	0–5.1	1.7
Adults (56)	0–732	42	0–7	1.6
Ad. M (23)	0–732	75	0–7	1.9
Ad. F (24)	0–110	15	0.01–6	1.1
Brown Falcon:				
All (78)	0–2,047	45	0–18	2.7
Juveniles (35)	0–2,047	68	0.01–18	3.1
Juv. M (9)	0–2,047	231	0.1–8.7	2
Juv. F (15)	0–47	8.4	0.01–15	2.2
Adults (43)	0–409	27	0–11.7	2.4
Ad. M (15)	0–41	9.8	0–11.7	2.7
Ad. F (22)	0–409	40	0.01–10.9	2.3
Peregrine Falcon:				
Juveniles (88)	0–333	62	0–15.3	2.2
Juv. M (34)	0–184	32	0.02–7.2	1.4
Juv. F (38)	0–293	79	0.1–15.3	3.2

RESULTS

Nankeen Kestrel

The recovery rate was 99 birds out of 3,634 banded (3%). Overall, Kestrels (*n* = 97) were recovered up to 822 km (mean 50.6 ± 145.5 km) from the banding site and up to 7 years after banding (Table 1). Of individuals that were aged (*n* = 96), those banded as juveniles (*n* = 41) appeared to be recovered farther from the banding site than those banded as adults (*n* = 55) (means 62.6 ± 156.6 km vs 42.4 ± 139.0 km). Of those that were sexed, juvenile females (*n* = 11) appeared to be recovered farther from the banding site than juvenile males (*n* = 9) (means 118.9 ± 255.8 km vs 39.3 ± 86.9 km), but adult males (*n* = 23) appeared to be recovered farther from the banding site than adult females (*n* = 24) (means 74.6 ± 209.3 km vs 15.0 ± 31.1 km). Dispersal directions varied widely, but with a possible slight north–south bias in south-eastern Australia and a notable movement from King Island to the Victorian mainland (Figure 1).

The median distance of recovery for adults of both sexes was 2 km; the median for all juveniles (including unsexed individuals) and for juvenile males was 4 km, and that for juvenile females was 24 km. For adult males, 78% were recovered within 20 km and 65% within 2 km of the banding site (48% *at* the banding site). For adult females, 88% were recovered within 20 km and 54% within 2 km of the banding site (33% *at* the banding site). For juveniles, 88% were recovered within 100 km and 83% within 50 km of the banding site (53% at or within 5 km of site: males 67% within 5 km and females 36% within 5 km).

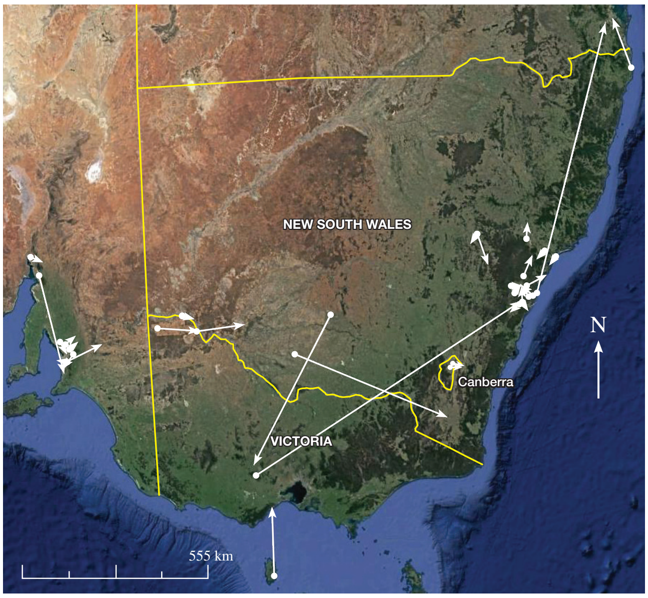

Figure 1: *Band recoveries for the Nankeen Kestrel in south-eastern Australia (>5 km,* n *= 42).*

Kestrels banded as adults had a greater average and maximum longevity than those banded as juveniles. However, juvenile females appeared to have a greater survival rate than juvenile males, whereas adult males appeared to have a greater survival rate than adult females (Table 1). From limited datasets, 73% of Kestrels banded as pulli or juveniles were recovered in their first year; this percentage declined to 10% in their second and third years and to 2% in their seventh year. Of Kestrels banded as adults, 54% were recovered within a year (48% of males and 67% of females), but this percentage declined to 4% by the seventh or eighth year.

Even allowing for some cases of 'found dead' being euphemistic for clandestine persecution, most Kestrel recoveries were of birds found sick/injured etc. or the result of accidental interactions with vehicles or human infrastructure (Table 2).

Brown Falcon

The recovery rate was 80 birds out of 1,425 banded (6%). Overall, Brown Falcons (*n* = 78) were recovered up to 2,047 km (mean 45.5 ± 235.7 km) from the banding site and up to 18 years (mean 2.7 ± 3.9 years) after banding (Table 1). Of those that were aged, individuals banded as juveniles (*n* = 35) seemed to be recovered farther from the banding site than those banded as adults (means 68.2 ± 344.7 km vs 28 ± 71.8 km). Of the Brown Falcons sexed, juvenile males (*n* = 9) appeared to be recovered farther from the banding site than juvenile females (*n* = 15) (means 231.4 ± 680.9 km vs 8.4 ± 14.2 km), but this difference is more dubious because it is inflated by one exceptional long-distance recovery. Adult females (*n* = 22) seemed to be recovered farther from the banding site than adult males (*n* = 15) (means 39.6 ± 94.6 km vs 9.8 ± 13.5 km). Excluding the outlier (a single movement from the arid zone to the tropics), for the temperate zone the mean recovery distances become 19.5 ± 53.8 km (all individuals), 9.7 ± 15.1 km (all juveniles) and 4.5 ± 12.7 km (juvenile males). Dispersal directions in southern Australia appear to be widely scattered, but with a north–south bias and including notable movements from north-east South Australia to the south-west Kimberley (a juvenile) and from southern Victoria to Tasmania (a female aged 2+ at banding) (Figure 2).

Table 2

Reasons for band recoveries of four Australian falcon species, excluding re-traps/re-sightings of their 'own' birds by researchers.

Reason	Kestrel	Br Falcon	Hobby	Peregrine
Found dead[A]	14 (26%)	12 (28%)	7 (54%)	34 (41%)
Sick/injured/exhausted	14 (26%)	6 (14%)	4 (31%)	11 (13%)
Vehicle collision	3 (6%)	8 (19%)		5 (6%)
Found on/near road[B]	3 (6%)	3 (7%)	1 (8%)	9 (11%)
Window collision	2 (4%)		1 (8%)	
Collision with solid object				1 (1%)
Collision with wire etc.		1 (2%)		6 (7%)
Inside man-made structure	8 (15%)	1 (2%)		
Protect domestic animals	1 (2%)	1 (2%)		
Prevent aircraft strike		1 (2%)		
Trapped				4 (5%)
Poisoned[C]	3 (6%)			
Shot	1 (2%)	1 (2%)		3 (4%)
Seized by law enforcement[D]				1 (1%)
Electrocuted		1 (2%)		
Found near powerlines[E]		1 (2%)		3 (4%)
Taken by animal	1 (2%)			
Found dead in fresh water	1 (2%)			1 (1%)
Band/col. marking read in field	2 (4%)	3 (7%)		
Band found on bird, no data		3 (7%)		2 (2%)
Band only found, no data				1 (1%)
Total	53	43	13	83

[A] Cause unknown
[B] Not certainly collided with vehicle
[C] Unknown if intentional
[D] Was dead
[E] Not certainly electrocuted/collided

The median distance of recovery of adult males was 6 km and of females 0 km; the median recovery distance for all juveniles including unsexed individuals was 4 km, but for juvenile males and females it was 0 km. For adult males, 87% were recovered within 20 km and 47% within 2 km (33% at the banding site). For adult females, 68% were recovered within 20 km and 59% within 2 km of the banding site (all the latter at the banding site). For juveniles, all except one (i.e. 97%) were recovered within 100 km and 94% within 50 km of the banding site (57% at or within 5 km of the banding site: males 78% within 5 km, females 60% within 5 km).

Longevity was similar across age and sex classes (Table 1), but was substantially influenced by re-sightings of colour-banded birds at one long-term study site. From the limited data, 40% of Brown Falcons banded as pulli or juveniles were recovered in their first year, declining to 23% in their second year, 11% in the third year and 3% by their eighteenth year. For those banded as adults, 44% were recovered within a year (40% of males and 41% of females), declining to 7% by the eleventh year.

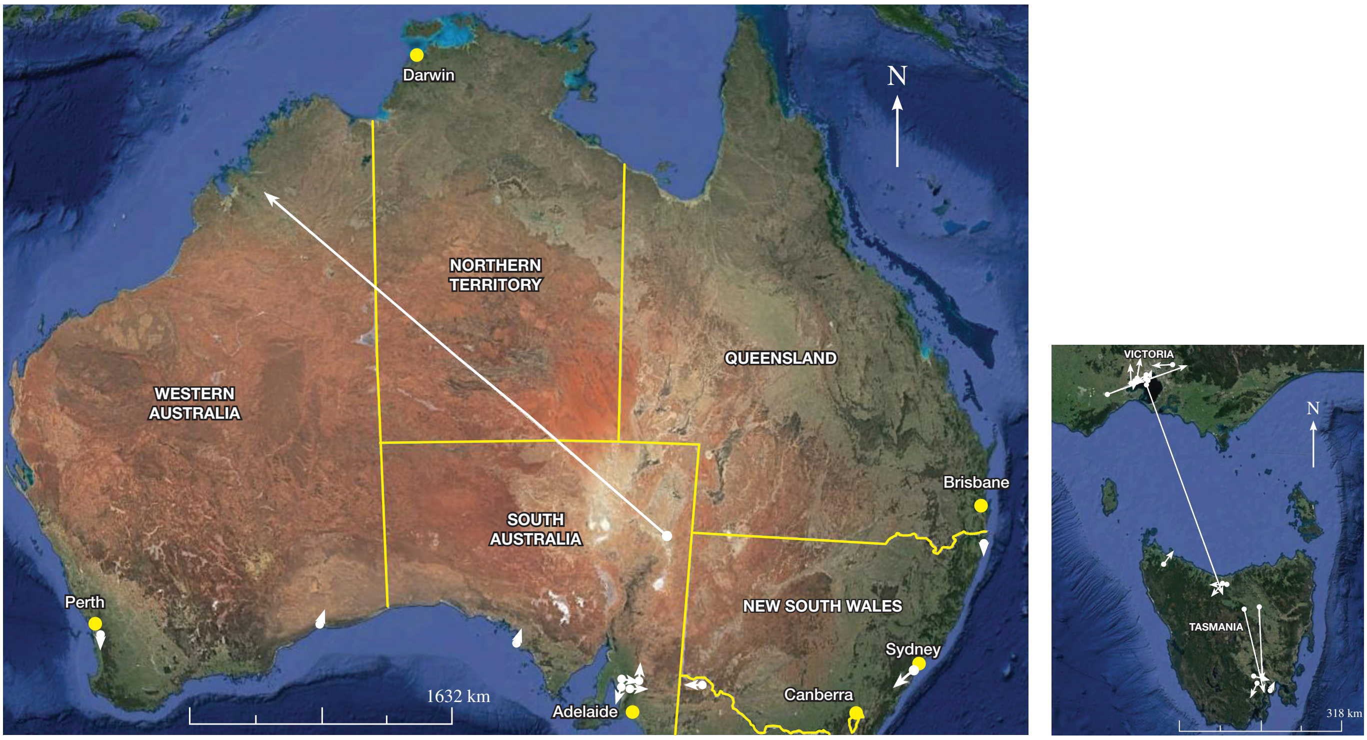

Figure 2: *Band recoveries for the Brown Falcon in Australia (>5 km, n = 35); Victoria and Tasmania.*

At least some instances of 'found dead' (with bands reported or returned with no accompanying data) may be euphemistic for clandestine persecution. Nevertheless, most recoveries were either of birds found sick/injured etc. or the result of accidental interactions with vehicles or human infrastructure, including several interactions with wires and powerlines (Table 2).

Australian Hobby

The recovery rate was 15 out of 143 birds banded (11%). Overall, Hobbies were recovered 0–322 km (mean 45 km) from the banding site and 0.02–6.7 years (mean 1 year) after banding (*n* = 13). Three banded as juveniles were recovered 0–71 km from the banding site up to 0.9 year later. Combining all ages, five males were recovered 0–61 km (mean 25 km) away from the banding site within a year of banding (mean 1.4 years), but with one record (age 1+ at banding) of 6.7 years. Six females were recovered 0–322 km (mean 60 km) away from the banding site 0.02–3.3 years (mean 0.8 year) after banding (the oldest female was aged 2+ at banding, i.e. > 5 years old at recovery). A male aged 2+ (61 km) and a female aged 2+ (322 km) were recovered farther away from the banding site than those aged 1 or 1+ at banding (≤41 km, *n* = 9), except for one pullus recovered 71 km away from the banding site. These records are eclipsed by a juvenile having moved 920 km (in a northerly direction) during its first month of independence (Marchant and Higgins 1993), and a later record of a juvenile recovered 10.2 years after banding and 18 km away from the banding site (Goodwin 2017; Anon. 2018). Dispersal directions appeared to be widely scattered, with a slight north–south bias in south-eastern Australia.

Recoveries were mostly of birds found dead or injured/sick/exhausted, with cases also of a probable road kill and a window strike (Table 2). The Hobby reported by Goodwin (2017) was also fatally road-injured (*contra* 'released alive with band' as misreported by Anon. (2018), perhaps a status error in the ABBBS database).

Peregrine Falcon

The recovery rate was 96 out of 1,215 birds banded (8%). Overall, Peregrines (*n* = 96) were recovered up to 333 km (mean 60.17 ± 74.08 km) from the banding site and up to 15.3 years (mean 2.25 ± 3.27 years) after banding (Table 1). These birds were mostly banded as pulli or juveniles (*n* = 88). Juvenile females (*n* = 38) appeared to be recovered farther from the banding site than juvenile males (*n* = 34) (means 78.7 ± 75.5 km vs 32.2 ± 44.1 km; medians 58 vs 15 km). Most juveniles (80%) were recovered within 100 km of, and 18% at or near (i.e. within 5 km), the banding site; 32% of males and 8% of females were recovered at or near the banding site. Of eight banded at 1+ or an older age, a male (1+) was recovered 2 km away, two females aged 1+ were recovered 109 and 113 km away, respectively, and two females aged 2+ were recovered 0 and 8 km away, respectively. Dispersal directions appeared to be widely scattered, but with notable movements from Flinders Island to Tasmania but no detected movements between Tasmania and the Australian mainland (Figure 3). These movements are eclipsed by one additional record of a recovery at 500 km from the banding site, i.e. Canberra to Melbourne (Olsen and Debus 2014).

Longevity records were 15.3 years for a female and 7.2 years for a male (both banded as pulli), with juvenile females apparently surviving longer than juvenile males (Table 1). Fifty-nine percent of the individuals banded as pulli or juveniles were recovered in their first year (68% of males, 50% of females).

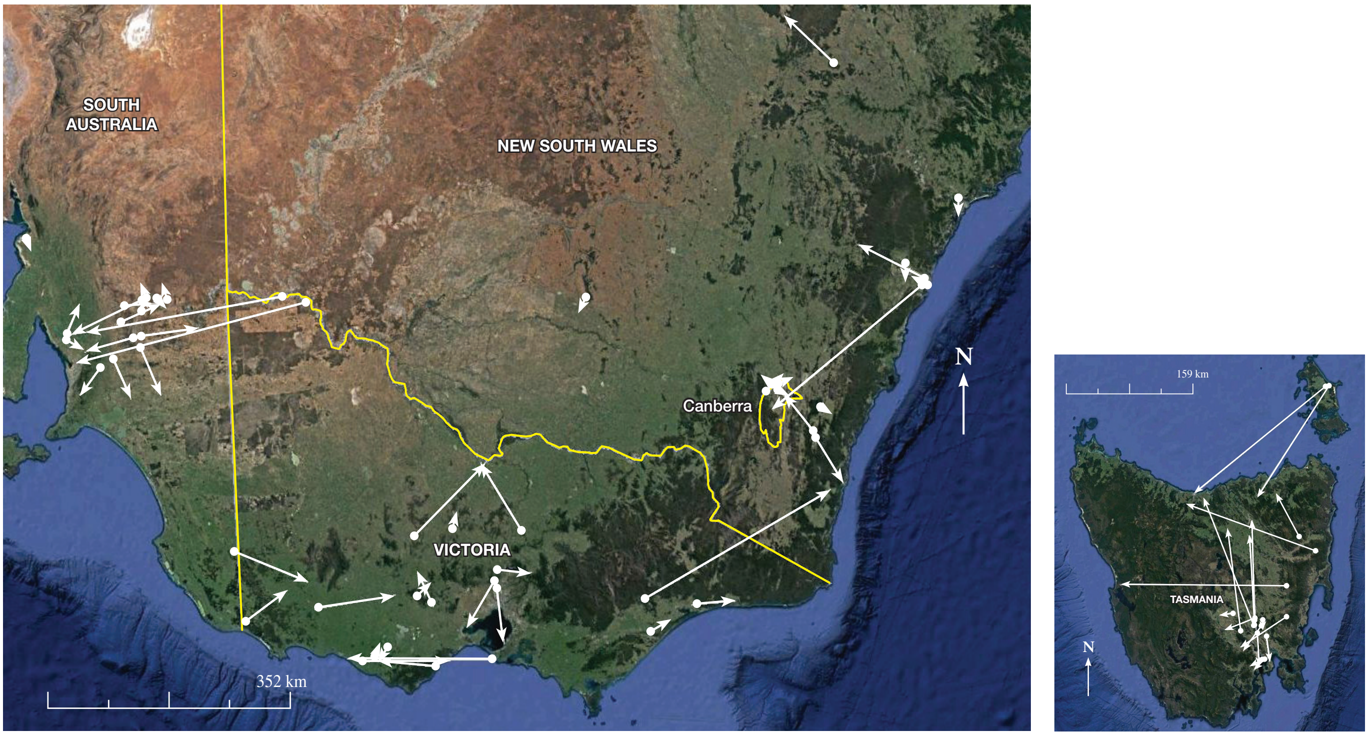

Figure 3: *Band recoveries for the Peregrine Falcon in south-eastern Australia (≥5 km, n = 78); Tasmania.*

It is highly likely that the substantial number of recoveries of birds 'found dead', together with band recoveries having no accompanying data, and the number trapped, shot and confiscated (Table 2), reflects persecution by, for example, pigeon fanciers. Birds found injured etc., together with collisions (or probable collisions) with vehicles, wires and powerlines, collectively also figure prominently.

DISCUSSION

Recoveries and their interpretation are affected by small initial sample sizes and various other limitations in the datasets. Notable among these deficiencies are low recovery rates and the substantial proportion of birds not aged (other than 1+), despite the distinctive juvenile (first-year) plumage being moulted to adult or adult-like plumage at the end of the first year in *Falco*. Further, many recovered birds were not sexed, despite the existence of adult sexual dichromatism in Nankeen Kestrels and to some extent Brown Falcons, and sexual size dimorphism that is evident by banding age, especially in the Peregrine Falcon (Marchant and Higgins 1993; M^{c}Donald 2003; Hurley *et al.* 2007). Interpretation of recoveries by age or sex class is thus affected by the possibility that some birds aged as 1+ (lumped as 'adult' here) were either still juvenile or were 'floaters' not yet settled on a territory. Thus, the movements of the different age classes may be obscured. Furthermore, recoveries are biased by the continental distribution of both banding effort and human population densities conducive to the finding of banded birds by the public, i.e. a heavy bias towards south-eastern and south-western Australia, with little chance of recoveries happening in the arid zone or tropics (Figures 1–3).

The band recoveries showed that all four species are capable of movements of hundreds of kilometres from the banding site and, in one case, across the continent (>2,000 km). A larger dataset, analysed for season of recovery, might demonstrate seasonal movements or migration. Conversely, the data for all four species seem to suggest female-biased dispersal and male-biased philopatry, which is consistent with the findings of previous studies on these species (Olsen and Olsen 1987; Mooney and Brothers 1993; Baker *et al.* 1997; Emison *et al.* 1998; McDonald *et al.* 2004; Hurley 2013a, b). Overall, the available recoveries up to 2015 do further elucidate the movements, longevity and mortality factors of these four species beyond what was summarised for the period up to *c.* 1990 by Marchant and Higgins (1993).

Nankeen Kestrel

The recovery data suggest that juvenile females probably disperse farther than juvenile males, that some adults apparently move almost as far as juveniles, and that some adult males appear to move (migrate?) farther than adult females. Conversely, many adults appear to remain on, or return to, their territories. These findings are consistent with (a) indications of seasonal movement or migration at a continental scale, including an 'Inland, Mid to Top North' pattern (Marchant and Higgins 1993; Griffioen and Clarke 2002; Barrett *et al.* 2003; Johnstone *et al.* 2013), (b) dispersal or altitudinal migration from high latitudes and altitudes (i.e. cold regions) of some of the population, including breeding adults, in winter (Olsen and Olsen 1987; Baker *et al.* 1997; Cooper *et al.* 2014), and (c) previous conclusions about the movements (or philopatry) of age and sex classes (Olsen and Olsen 1987). The recovery data suggest that there is high juvenile mortality in human-inhabited landscapes in the first year and rather high annual adult mortality (minimum adult survival being 57 or 58% in a colour-banded population: Baker *et al.* 1997).

Brown Falcon

The recovery data suggest that (a) juveniles probably move farther from the banding site than adults, (b) juvenile males probably move farther than juvenile females, and (c) adult females probably move farther from the banding site than adult males. However, the juvenile and adult samples are both skewed by gender, and the single long-distance recovery (arid zone to the tropics) tentatively suggests that Brown Falcons in the arid zone may move farther than those originating in the temperate humid and sub-humid zones. Exclusion of this outlier, and the use of median rather than mean distances, modify these conclusions somewhat and suggest that in the temperate zone juvenile females may disperse farther than juvenile males. These findings are generally consistent with (1) inferred continental-scale or regional-scale movement of juveniles and other age classes, including altitudinal movements at high elevations and an 'Inland, Mid to Top North' movement pattern, and (2) site fidelity (or philopatry) and local winter movements of breeding adults (Marchant and Higgins 1993; Griffioen and Clarke 2002; Barrett *et al*. 2003; McDonald *et al.* 2003, 2004; Johnstone *et al.* 2013; Cooper *et al.* 2014; Corbett *et al.* 2014). In productive temperate environments, breeding adults are sedentary on their home ranges (M^{c}Donald 2003). The recovery data suggest that high juvenile mortality occurs in human-inhabited landscapes in the first year and that there is rather high annual adult mortality (~40%).

Australian Hobby

The few available data suggest that some adults disperse or migrate and that females apparently disperse or move farther than males. There is little to add to previous inferences that Hobbies make continental-scale or regional-scale seasonal migrations, including altitudinal migration and a north–south movement (Marchant and Higgins 1993; Barrett *et al.* 2003; Johnstone *et al.* 2013; Cooper *et al.* 2014). However, Griffioen and Clarke (2002) found only suggestive evidence of local movements. Nevertheless, over three survey trips to Sumba in the austral winter (June–July) and summer (December–January), Hobbies resembling Australian birds (rather than the smaller *F. l. hanieli* resident on other Lesser Sunda Islands) were observed, apparently wintering, only in July (Olsen and Trost 2007).

Peregrine Falcon

The data show that juvenile females probably disperse farther than juvenile males, and suggest that other than two birds (aged 1+) which may have been 'floaters', adults tend to remain near the banding site. These findings, and the high mortality of juveniles (especially males), are consistent with findings in previous studies (Marchant and Higgins 1993; Mooney and Brothers 1993; Emison *et al.* 1998; Hurley 2013a).

One of the Peregrine recoveries was a re-sighting of a male, banded by JO as a pullus in a cliff nest, breeding in a stick nest in a tree ~20 km from its natal site. This record represented, at the time, the first published report of a banded Peregrine Falcon fledging from a cliff nest and breeding successfully in a tree-nest, i.e. changing its nesting 'tradition' (see further discussion by Olsen *et al.* 2006 and Hurley 2009). Olsen *et al.* (2006) postulated that cliff and tree nests were close together in their study area, so Peregrines fledged from cliffs could readily move to nests in trees; their study 'did not confirm Kirmse's (2004) claim that selection of tree-nest sites by breeding Peregrines is totally determined by imprinting to the natal nest-site' and that, because cliff sites are saturated in Australia, 'tree-nesting pairs remain sparsely distributed among cliff-nesting pairs and… the two types of nesters may mix more often than was once believed'. This conclusion was confirmed with a larger sample by Hurley (2013b), who recorded that 9% of natal dispersals were from a cliff to a stick nest, and that 'atypical' natal dispersals from one nest type to another accounted for 30% of dispersals ($n = 101$).

There is evidently some continental-scale movement by Australian Peregrines, apparently particularly of juveniles and floaters (Marchant and Higgins 1993; Barrett *et al.* 2003; Johnstone *et al.* 2013). However, Griffioen and Clarke (2002) found only suggestive evidence of a confused pattern of movements. The situation may be confounded by the occurrence in the austral summer of Northern Hemisphere migratory subspecies from northern Asia (notably *F. p. calidus* and possibly *japonensis*) in northern Australia mainly, but potentially anywhere in Australia, including the far southern mainland (Johnstone *et al.* 2013; Anon. 2014, 2015, 2017). These boreal migrants may be overlooked among Australian Peregrines, although they are recognisable by their narrow malar stripe, white auriculars and less chunky build (e.g. Menkhorst *et al.* 2017). Migratory *F. p. calidu*s certainly reach southern Africa (Meyburg *et al.* 2018), so the same thing may happen in Australia. It is worth noting that the high mobility of Australian Peregrines, among other evidence, argues against the recognition of alleged, but invalid, south-western Australian *F. p. submelanogeny*s (see Olsen and Debus 2014, *contra* White *et al.* 2013).

Conclusions

The different causes of mortality among the four falcon species are consistent with aspects of their ecology and foraging behaviour. For instance, the Nankeen Kestrel is a slow-flying, perch-hunting and hovering, roadside-frequenting generalist that commonly inhabits managed farmland (crops etc.) and thus may be susceptible to agricultural poisons (rodenticides, insecticides), and it frequents buildings. The similar, but larger Brown Falcon, with its larger wingspan, sometimes scavenges road-kill and may be more prone to collisions with or electrocutions on power poles or lines. The Australian Hobby and Peregrine Falcon are fast-flying bird-chasers, more prone to collisions with poorly visible human-created hazards (wires etc.) and vehicles, and they may be more vulnerable to injury because they take more prey that are more difficult to capture. The Peregrine is (or was) also prone to persecution (e.g. Marchant and Higgins 1993; Olsen and Stevenson 1996; Scuffins 2003; Olsen 2014), which was partly driven by pigeon-fanciers' myths concerning the supposed origin of killed Peregrines found to be wearing ABBBS bands (Mooney 2013).

It is apparent that there has been a general decline in research on Australian raptors, except for the charismatic and secure species such as the Peregrine Falcon and Wedge-tailed Eagle *Aquila audax*, precisely at a time when many other species, even those common in farmland, are declining (e.g. Barrett *et al.* 2003;

Cooper *et al.* 2014). This reduction in research is self-evident from the decade(s) in which members of the species examined here were banded, i.e. mostly pre-2000 (see 'Methods'). The decline in research somewhat reflects increased bureaucracy (mainly animal ethics and other permit requirements and fees), the consequent demise of the enthusiastic amateur, and perhaps other technologies replacing banding. For instance, traps with live lures cannot now be used in some States at least, but models and wind-up lures do not sufficiently attract the interest of, for example, Brown Falcons (N. Mooney pers. comm.). On the other hand, radio/GPS tracking is becoming popular and its use is attractive to funding bodies and students, although it is expensive.

To better understand the ecology and life history of the declining species, further banding/colour-banding research is required to obtain estimates of survival and mortality and life tables etc., and to further elucidate movements of age classes. For instance, with larger datasets incorporating the currently researcher-embargoed ones, it is already possible to 'animate' seasonal recovery maps of the more frequently banded/recovered species to reveal dispersal or migration patterns (Drynan 2014). Satellite telemetry, as well as helping in documenting home-range and habitat use at the local scale, can reveal hitherto unsuspected continental-scale movement by breeding adults (e.g. Little Eagle *Hieraaetus morphnoides*: Drynan 2017), which have since been confirmed as return migration to the breeding territory through the sighting of colour-bands and from transmitters (Dabb 2018; Olsen and Trost 2018). It is likely that similar return migration would be detected by satellite telemetry of some of the Australian falcons now that satellite transmitters are small enough to be fitted to kestrel-sized, adult raptors.

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Appendix 1

List of people who banded falcons in the dataset used in this study.

H. F. Archer
G. B. Baker
D. J. Baker-Gabb
C. Bennett
Bird Care and Conservation Society
E.F. Boehm
J. G. Brickhill
N. P. Brothers
G. R. and A. E. Cam
R. E. Chatto
G. P. Clancy
L. C. Currie
S. J. S. Debus
C. P. S. de Rebeira
J. N. Dymond
W. B. Emison
I. D. Falkenberg
J. R. Farrell
N. J. Favaloro
J. L. Gardner
D. J. Geering
J. W. Hardy
J. G. K. Harris
K. Henderson
M. C. Holdsworth
J. B. Hood
B. R. Hutchins
J. Klapste
W. L. Klau
N W. Kurtz
S. G. Lane
R.G. Lonnon
K. W. Lowe
I. McCallum
P. G. McDonald
E. J. McKenzie
N. Mooney
O. P. P. Mueller
M. T. Murn
J. Olsen
P. R. Pain
G. R. Park
D. C. Paton
M. R. Pople
D. I. Smedley
Taronga Zoo Rehab Program
M. T. Templeton
G. H. Underwood
M. H. Waterman OAM
R. M. Warneke
Wild Bird Rehabilitation Group
J. T. Willows
S. J. Wilson

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The potential for food resource partitioning among the predominant species in a Mountain Ash *(Eucalyptus regnans)* forest bird assemblage

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Food exploitation patterns in forest bird assemblages have: (1) management significance, with respect to maintaining the resources required to support these assemblages under various forest usage regimes, and (2) theoretical interest, regarding the roles of interspecific and intersexual competition in shaping such assemblages. The foraging behaviour of the bird assemblage of a vertically stratified Mountain Ash *Eucalyptus regnans* forest was studied over two years. Forty-seven bird species were recorded in the study area and assemblage members mainly consumed invertebrates. The predominant member species foraged disproportionately in the short tree stratum 3–12 m above ground level, and on foliage. The tall tree stratum was also used substantially for foraging, but relatively few of the more common member species foraged in the ground cover and herb strata. Gleaning and sally-snatching were the main foraging macro-behaviours, and 22 micro-variations of these behaviours were exhibited. Hawking and probing/prising were recorded for only a few of the common assemblage member species. Sexually dichromatic Golden Whistlers and White-throated Treecreepers exhibited only limited sex-specific foraging in just vegetation stratum use. There was considerable overlap in foraging variables among species with broadly similar foraging behaviour, which did not appear particularly consistent with a major role of interspecific competition in promoting foraging niche segregation. However, there probably was some food resource partitioning, because probing, hawking and trunk- and ground-gleaning most likely gave their few proponents access to invertebrates largely unexploited by the larger foliage-gleaning and sally-snatching guilds. Maintaining the integrity of the tall and short tree strata is likely to be very important in conserving avian diversity in this cool temperate rainforest habitat.

INTRODUCTION

Several investigations in temperate and tropical areas have greatly helped us to understand how bird species and guilds exploit food resources in Australian forests and woodlands (e.g. Frith 1984; Recher *et al*. 1985; Ford *et al*. 1986; Brooker *et al*. 1990; Cale 1994; Hannah *et al*. 2007; Antos *et al*. 2008). Understanding how birds exploit such resources is critical for designing effective management plans incorporating biodiversity conservation for forests used primarily for recreation or commercial timber production. It is also important from a fundamental, theoretical perspective with respect to the role of interspecific competition in determining the composition of forest bird assemblages.

McArthur's (1958) iconic study of co-habiting insectivorous warbler (Parulidae) species partitioning food resources in conifers by foraging in different microhabitats and in different ways stimulated many similar investigations and wide acceptance of the notion of species coexistence evolving through resource partitioning ('competitive exclusion') (*e.g.* Alatalo and Alatalo 1979; Holmes *et al*. 1979; Lara *et al*. 2015). This competition model has been extended to encompass the concept of coexistence of guilds of species with similar foraging behaviour within assemblages (Recher 2018). The evolution of sex differences in foraging ecology has also been attributed to selection for traits that reduce intersexual resource competition (Mand *et al*. 2013). Such sex differences occur in a diversity of bird species and are manifested in many ways, including foraging in disparate habitats or locations, at differing distances from the nest, at varying heights, on different substrates and using contrasting behaviours (Holmes 1986; Lewis *et al*. 2002; Noske 2003; Falconer *et al*. 2008; Hogstadt 2010; Buij *et al*. 2012; Widman *et al*. 2015). However, the resource partitioning model has been seriously questioned for bird assemblages by some authors, because it has been argued that: (a) the conditions necessary for competitive co-evolution to occur are likely to be rare, and (b) avian mobility is likely to limit opportunities for genetic differentiation driven by the selection pressure of interspecific competition (Mac Nally 1995). The role of resource partitioning through interspecific and intersexual competition in shaping avian assemblages is thus still somewhat contentious and warrants further investigation (Jankowski *et al*. 2012).

Mountain Ash *Eucalyptus regnans*, the dominant canopy tree species in some Victorian and Tasmanian tall wet forests, is the world's tallest flowering plant (Ashton 1975). Mountain Ash forest is valued for water and timber production, recreational and aesthetic attributes and its unique biodiversity (Lindenmayer 2009; Viggers *et al*. 2013). However, as a functioning ecosystem it is classified as critically endangered under the IUCN Ecosystem Assessment protocol, mainly due to the effects of wildfire and commercial logging (Burns *et al*. 2015). Mature Mountain Ash forests often have several distinct vertical vegetation strata, namely ground cover, herb, shrub, intermittent short and tall tree layers, and a canopy stratum. This structure creates a complex array of varying microhabitats that bird species can potentially exploit in diverse ways (Holmes and Recher 1986). There has been a substantial volume of research on the composition of avian assemblages in this habitat (e.g. Loyn 1985; Lindenmayer *et al*. 2015; Serong and Lill 2016), but more detailed work at more sites on the constituent species' foraging ecology and behaviour will help in fully determining the extent to which the potential alluded to by Holmes and Recher (1986) is exploited.

The main aims of this study were therefore to: (a) determine how the stratified vegetation of this forest is exploited for foraging by the various bird assemblage member species, (b) examine whether resource partitioning among species is likely to have been important in structuring the bird assemblage, and (c) investigate whether the sexes forage sufficiently differently to reduce intersexual food competition in two sexually dichromatic member species. To achieve these aims, regular observations were conducted over two successive years, and the vegetation strata, approximate heights, substrates and macro- and micro-behaviours used in foraging by assemblage members were documented and compared.

METHODS

Study area

The study was conducted in an ~200 ha segment of a tract of cool temperate rainforest in the East Victorian Central Highlands. The area's vegetation ranges from fern gullies dominated by tree-ferns and epiphytic ferns to tall open forest (Specht 1970) characterised by a high canopy dominated by Mountain Ash. An intermittent sub-canopy is formed by a mixture of short and tall trees (including the genera *Acacia*, *Bedfordia*, *Leptospermum* and *Pomaderris*), and there is a patchy shrub layer (including *Goodenia*, *Cassinia*, *Coprosma* and *Olearia*) and a ground cover of mesophytic herbs. Mean annual rainfall is over 1,000 mm and monthly mean maximum and minimum ambient temperatures range from 4–9ºC (winter) to 11–22ºC (summer).

Foraging observations

Forty-five observation sessions were conducted over the two-year study period. In Year 1 (Y1), 27 sessions were carried out at a frequency of two to four per month, using three transects approximately equally (transect sessions). Transects were necessarily mostly along established tracks, the longest being ~1.7 km. An additional 18 more opportunistic sessions were conducted over the two years; they were carried out on the same transects, but allowed greater observer flexibility to obtain observations on species encountered less often. The early to mid-morning observation sessions lasted 3.5–4 hours. For the transect sessions, the researcher walked a transect slowly, identifying and documenting the foraging behaviour of all birds seen. In both transect and opportunistic sessions, the observer used 10 × 50 power binoculars. Appendix 1 gives the scientific names of all bird species referred to in this paper. Despite the considerable number of sessions conducted, many uncommon species provided insufficient data for meaningful analysis of foraging behaviour.

Up to five records of foraging stratum, substrate and macro- and micro-behaviours were obtained per focal bird, but usually only one (the initial) estimated foraging height was recorded. The foraging variables recorded were:

(a) Stratum: the vertical vegetation stratum in which the focal bird was foraging, namely ground, herb (grasses, sedges, bracken, false bracken), shrub, short tree, tall tree and canopy tree crown.

(b) Height: the estimated categorical height (m) at which focal bird was foraging; 0 = ground, 1 = 0.1–3.1, 2 = 3.2–12.2, 3 = 12.3–24.4, 4 = 24.5–30.5, and 5 = > 30.5.

(c) Substrate: the surface from which food item was procured: air, leaf (including fronds), twig (up to ~1 cm diameter), branch (> ~1 cm in diameter), trunk, bud, inflorescence, ground (soil, ground litter), bark (including partly shed and detached bark) and 'other' (including cobweb, fungus, lichen, vine and gall).

(d) Macro- behaviour: the broad mode of behaviour employed: [i] glean (GL)- pick item off substrate with bill, [ii] sally-snatch (SS)- fly/jump from perch to take food item from *solid* substrate, such as leaf or twig, and fly/jump to original/ different perch, [iii] hawk (HWK)- fly from perch to capture invertebrate(s) *in air* and fly to original/ different perch to consume it, [iv] probe and prise (PP)- push bill below surface of substrate to acquire food item, sometimes after prising or tearing substrate open (*e.g.* decorticating bark), and [v] turn litter (TL) – performed with bill or feet, the invertebrates exposed underneath being consumed.

(e) Micro-behaviour: variants of basic GL, PP, SS and HWK *e.g.* GL while clinging upside down to vegetation, rather than perching upright; SS in which the food item is snatched from vegetation while hovering close to it (Table 5 footnote contains full list).

Crimson Rosellas' foraging behaviour was not recorded because Magrath and Lill (1983) had earlier documented the species' winter foraging ecology in this habitat in detail.

Data analysis

Foraging behaviour frequencies were pooled across sessions because totals were too small for meaningful analysis at the individual session level. Ideally, variation in the kind of data obtained here is analysed with statistical procedures such as log linear or generalised linear modelling. However, the foraging records were all obtained from the same relatively small area and often comprised several records per focal individual; they therefore included many within- and probably among-session repeat observations on the same, unmarked individuals that are not statistically independent. Consequently, rather than interrogating the data with significance testing of dubious validity, quantitative summaries of foraging behaviour are presented and interpreted conservatively. Pairwise percentage overlap indices between species for the various foraging variables were calculated with a formula commonly used in this context:

$$\mathrm{p}_{jk = [\,\sum\,(\mathrm{minimum}}\,\mathrm{p}_{ij}\,\mathrm{p}_{ik]100} \qquad \text{(Krebs 2014)}$$

where p_{ij} is proportion resource *i* is of total resources used by species *j* and p_{ik} is proportion resource *i* is of total resources used by species *k*, modified to examine each foraging variable separately.

RESULTS

All observation sessions combined yielded 3,629 sightings of members of 47 bird species. Transect sessions provided the most rigorous and comprehensive picture of the species composition of the bird assemblage. The relative representation in such sessions of the 16 species that each contributed at least 1% of the total sightings is given in Table 1. Six of all the species observed were recorded in 85–100% of the transect sessions (Crimson Rosella, Golden Whistler, Grey Fantail, White-browed Scrubwren, Silvereye and Brown Thornbill), three in 44–89% (Striated Thornbill, White-naped Honeyeater and Eastern Yellow Robin) and 38 in only 4–59% of transect sessions.

Diet

Foraging information for 19 species providing sufficient data for analysis (hereinafter termed analysable species) translated into the following *likely* dietary breakdown:

1. Exclusively invertebrates: 14 species (n = 20–893 foraging records per species).

2. Predominantly invertebrates, plus small volumes of fruit (0.4% and 7.7%, respectively): two species; Golden (n = 234 records) and Olive (n = 26) Whistlers.

3. Mainly invertebrates, but also small amounts of fruit *and* nectar: two species, White-naped Honeyeater (n = 132 records) – invertebrates (and possibly plant exudates) 95%, fruit and nectar 2% each; Silvereye (n =329) – invertebrates 74.8%, fruit 14.6% and nectar 10.6%.

4. Nectar and invertebrates: one species, Eastern Spinebill – nectar (55.6%) and invertebrates (44.4%), but n was small.

The ensuing sections analyse information on foraging behaviour from the more comprehensive data set obtained from transect sessions for species for which ≥ 50 foraging records were obtained. However, supporting data obtained from the opportunistic sessions are also summarised in the accompanying tables and figures.

Foraging strata and heights

Meaningful analysis (n = ≥ 50 records) was possible for 12 species for foraging strata use (Table 2):

[1] The short tree layer was preferred most by six of these analysable species; no other stratum was preferred most by more than one or two species.

[2] The tall tree layer was the second stratum preference of five bird species, with other strata having this rank for no more than one to three species.

[3] The least-used strata were the ground cover and 'herb' layers, each exploited substantially by only one or two species.

Only White-browed Scrubwrens (herb, shrub and ground) and Eastern Yellow Robins (ground and short trees) foraged predominantly in the lower vegetation strata, and only White-naped Honeyeaters, Satin Flycatchers and Striated Thornbills mainly in the higher strata *i.e.* tall and canopy trees (Table 2). Between these extremes, Large-billed Scrubwrens, Rufous Fantails and Silvereyes foraged mostly in the short tree and shrub layers, whilst White-throated Treecreepers, Golden Whistlers and Grey Fantails mainly used a combination of the short and tall tree strata.

Table 1

Relative abundance of species contributing at least one percent of the sightings of assemblage members over the entire study. Collectively these species accounted for 92.1% of all sightings. Raven sp. indicates either Australian or Little Raven.

Species	Relative abundance (% of sightings)
Crimson Rosella	22.5
Brown Thornbill	17.5
Grey Fantail	9.8
Silvereye	9.0
Golden Whistler	6.5
White-browed Scrubwren	6.0
Striated Thornbill	3.8
White-naped Honeyeater	3.5
Eastern Yellow Robin	3.4
White-throated Treecreeper	2.0
Rufous Fantail	1.7
Eastern Spinebill	1.5
Crested Shrike-tit	1.4
Rose Robin	1.3
Raven sp.	1.2
Grey Shrike-thrush	1.0

Eight pairwise species combinations (12% of all combinations) had overlap indices >80% for foraging strata use (Table 3). White-throated Treecreepers, Brown and Striated Thornbills, Golden Whistlers and Rufous and Grey Fantails overlapped greatly with other assemblage members in foraging strata use (each ≥ 50% overlap with six-eight species), all predominantly using the small and tall tree layers disproportionately. In contrast, three species had low levels of interspecific overlap in foraging strata use. These were the White-browed Scrubwren and Eastern Yellow Robin (≥ 50% overlap with no and one species, respectively), with their extensive use of the lower strata little exploited by other assemblage members, and the Satin Flycatcher (≥ 50% overlap with two species) with its extensive use of the tall and canopy tree strata (Table 2).

With respect to foraging height, nine species were analysable and the six height categories (C) were exploited unevenly by these species (Fig. 1):

C2 (3.2–12.2 m) and C3 (12.3–24.4) were each the preferred height category of three of the analysable species and the second preference of three and four species, respectively.

C1 (0.1–3.1) was the preferred height category of two species and the second preference of one species.

C0, C4 (24.5–30.5 m) and C5 (> 30.5 m) were used relatively infrequently, except that C5 was the preferred category of one species and C0 the second preference of one species.

Table 2

Percentage of foraging conducted in six forest strata by twelve bird species. Only species for which there were ≥ 50 records overall are included. For each species, upper row shows transect data (bold) and lower row shows opportunistic data (smaller font). The two highest values in each row are underlined. Gaps indicate zero values. N is number of records (number of birds contributing). N for all species combined was 2,890 (1,409 birds).

		Foraging strata					
Species	Ground	Herb	Shrub	Small tree	Tall tree	Canopy tree	N (birds)
White-throated Treecreeper		**0.8**	**5.3**	**53.4**	**28.5**	**12**	**133 (50)**
			9.1	39.4	33.3	18.2	33 (9)
White-browed Scrubwren	**21.7**	**42.3**	**31.8**	**4.2**			**189 (121)**
	33.9	55.9	10.2				59 (39)
Large-billed Scrubwren		**5.6**	**12.5**	**75**		**12.5**	**24 (11)**
			36.1	41.7	16.7		36 (18)
Brown Thornbill		**1.8**	**13.7**	**61.2**	**18.8**	**4.5**	**849 (368)**
				62.5	21.9	15.6	32 (18)
Striated Thornbill				**36.6**	**36.6**	**26.8**	**142 (79)**
				17.4	56.5	82.6	23 (20)
White-naped Honeyeater				**13**	**26.9**	**60.1**	**108 (61)**
				15.7	19.6	64.7	51 (36)
Golden Whistler		**1.9**	**6.1**	**43.2**	**32.4**	**16.4**	**213 (118)**
Rufous Fantail		**2.5**	**47.5**	**45**	**2.5**	**2.5**	**40 (34)**
	14.3	14.3	31.4	28.6	11.4		35 (18)
Grey Fantail	**1.2**	**1.0**	**9.2**	**43.5**	**31.6**	**13.5**	**490 (202)**
Satin Flycatcher					**54.6**	**45.4**	**22 (14)**
					40.0	60.0	50 (16)
Eastern Yellow Robin	**48.8**	**11.9**	**10.7**	**23.8**	**4.8**		**84 (55)**
Silvereye		**5.5**	**23.9**	**52.8**	**9.8**	**8.0**	**163 (81)**
		0.9	41.2	55.3	1.7	0.9	114 (41)

Table 3

Matrix of percentage overlap indices for foraging stratum use. Values > 50% highlighted in bold font on light blue background. Species' acronyms given in Appendix 1.

	WBSW	LBSW	BTH	STH	WNH	GWH	RFAN	GFAN	SFLY	YROB	SEYE
WTTC	10.3	**70.7**	**82.8**	**77.1**	**66.7**	**89.8**	**56.1**	**90.1**	30.5	34.7	**76.7**
	WBSW	16.7	19.7	4.2	4.2	12.2	38.5	14.6	0.0	37.6	33.1
		LBSW	**78.2**	49.1	25.5	**61.8**	**60.0**	**52.7**	12.5	34.5	**66.1**
			BTH	**59.9**	36.3	**74.4**	**65.5**	**77.0**	23.3	**54.3**	**82.6**
				STH	**66.7**	**85.4**	41.6	**81.7**	**55.3**	28.6	**54.4**
					WNH	**56.3**	18.0	**53.4**	**72.3**	17.8	30.8
						GWH	**56.2**	**95.4**	48.8	35.7	**100.0**
							RFAN	**60.2**	5.0	38.0	**76.4**
								GFAN	45.1	39.0	**58.5**
									SFLY	4.8	17.8
										YROB	40.3

Table 4

Matrix of percentage overlap indices among species in use of foraging height categories. Values > 50% highlighted in bold font on light blue background. Species' acronyms given in Appendix 1.

	WTTC						
WBSW	12.9	**WBSW**					
BTH	**52.3**	14.6	**BTH**				
STH	47.4	3.9	**63.8**	**STH**			
WNH	24.6	18.5	36.4	45.5	**WNH**		
GWH	48.9	15.5	**80.5**	**68.7**	44.4	**GWH**	
YROB	21.6	**80.9**	33.7	23.0	25.5	34.6	**YROB**
GFAN	**53.4**	13.8	**83.2**	**95.4**	40.8	**94.3**	32.9

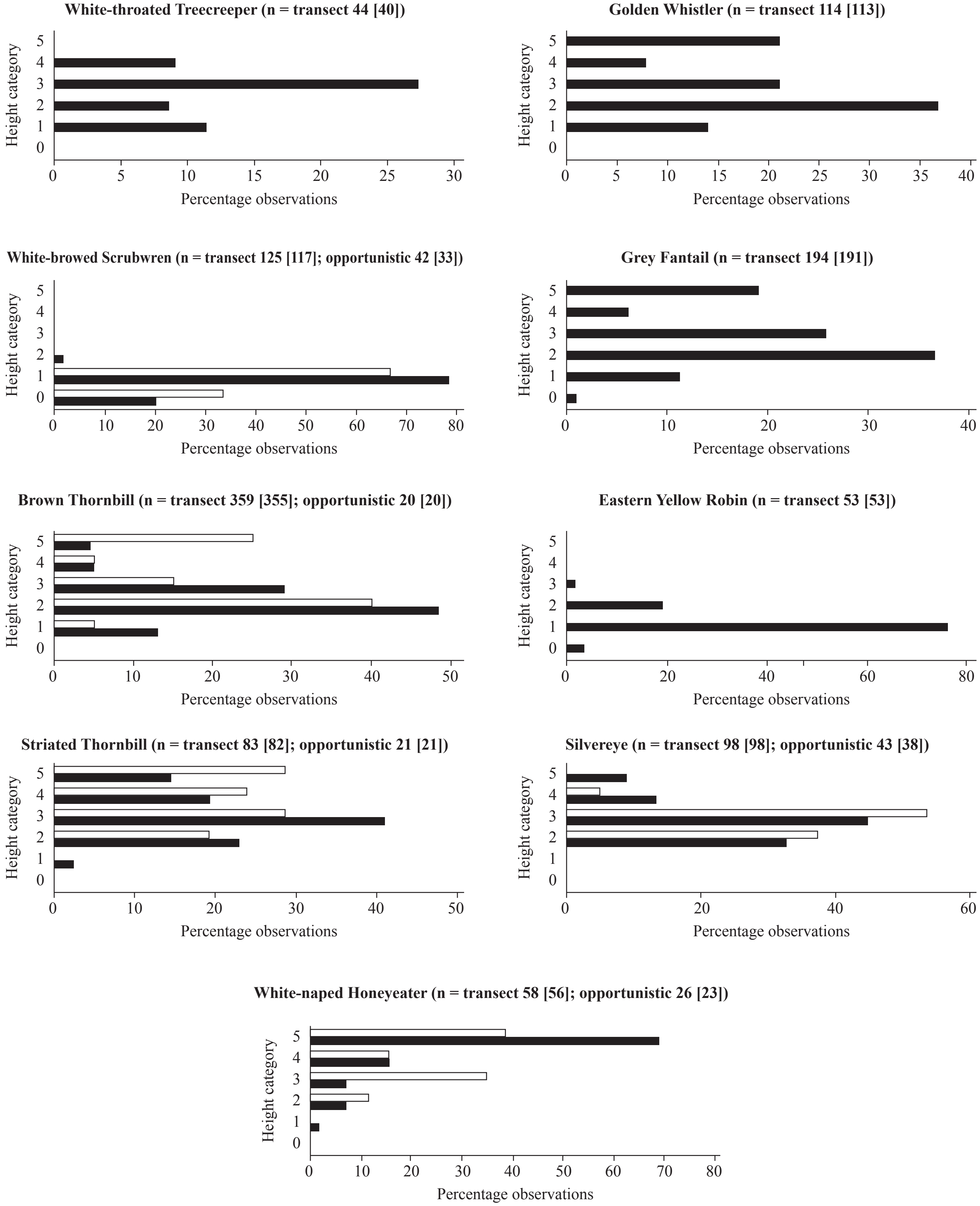

Figure 1: *Figure 1. Overall percentage of foraging conducted at various estimated heights by nine bird species. Only bird species for which there were ≥ 50 records are included. For each species, black bars are observations made on transects and (where present) light brown bars are opportunistic records. Height categories (m) are: 0 = ground, 1 = 0.1 – 3.1, 2 = 3.2 – 12.2, 3 = 12.3 – 24.4, 4 = 24.5 – 30.5 and 5 = > 30.5. n is number of observations (focal individuals). Note that focal individuals could contribute > 1 record per sequence, possibly in different height categories.*

Species' use of foraging strata and heights concurred. Thus White-browed Scrubwrens and Eastern Yellow Robins mainly foraged at lower heights (C0-C2), although less predictably Grey Fantails also foraged quite substantially in C0 and C1 (Fig. 1). White-naped Honeyeaters foraged mostly at greater heights (C5), Striated Thornbills and Golden Whistlers mainly in the intermediate to high categories and White-throated Treecreepers, Brown Thornbills and Silvereyes at intermediate heights (C2 and C3) (Fig. 1).

Five pairwise species combinations (18% of combinations) had overlap indices > 80% for foraging height (Table 4). Four species had overlap indices ≥ 50% with three or four other species. Brown Thornbills and Grey Fantails had the highest percentage overlap with other assemblage members (each ≥ 50% overlap with four species); they used a wide range of foraging heights, but especially C2, C3 and C5, which many other species also utilised.

Three species had limited percentage overlap with other assemblage members, exploiting either the comparatively little used lower height categories (C0–C2) or the moderately exploited highest category (C5).

Foraging substrates

Fourteen species were analysable for foraging substrate use. Foliage was the most frequently used substrate by nine of these species, but no other substrate was the most used substrate of more than one species (Table 5a). There was far less variation among species in their second most preferred foraging substrate. Tree branches occupied this rank for three species; all the other nine substrates were the second preference maximally of two species each (Table 5a).

White-browed Scrubwrens, both thornbill species, Rufous Fantails, Golden Whistlers, White-naped Honeyeaters, Rose Robins, Satin Flycatchers and Silvereyes used leaves and buds as their main, or a prominent, foraging substrate (Table 5a). Twigs and branches were used prominently by Golden Whistlers, Crested Shrike-Tits and Large-billed Scrubwrens. The latter two species, plus the White-throated Treecreeper, were the three bark-foraging species in the assemblage for which adequate data were obtained for analysis. The three species that hawked flying insects were the two fantails and the Satin Flycatcher. White-throated Treecreepers were the only common trunk-foraging specialists, and Eastern Yellow Robins and White-browed Scrubwrens the only significant ground-feeders (as alluded to under *Foraging strata*) (Table 5a).

Percentage overlap indices reflected these similarities and disparities in substrate use (Table 5b). A high degree of overlap (indices ≥ 50% with seven to nine other species) occurred among all the predominantly foliage-foraging species; however, only four pairwise species combinations (4% of combinations) had overlap indices > 80% for substrate use. A low degree of overlap (indices ≥ 50% with just one or two other species) characterised the few specialist foraging substrate users that predominantly exploited the air (Grey Fantail), ground cover (Eastern Yellow Robin), tree bark (Crested Shrike-Tit) and tree trunks (White-throated Treecreeper). Large-billed Scrubwrens, which obtained their food mostly from twigs and bark, were intermediate in overlap, having indices ≥ 50% with four species (Table 5b).

Foraging macro-behaviours

Fourteen species were analysable for foraging macro-behaviour use and the five identified macro-behaviours were used unevenly by these species. Gleaning and SS were the most common macro-behaviours of six and five of these species, respectively. The other three macro-behaviours were the most used methods maximally of one species (Table 6). Sally-snatching was also the second most frequently performed foraging behaviour of four species; the other macro-behaviours were the second most commonly employed methods of one to three species, respectively.

Gleaning was the most common foraging behaviour of White-throated Treecreepers, both scrubwren species, White-naped Honeyeaters and Silvereyes. It was also the second most common foraging behaviour of Striated Thornbills, Golden Whistlers, Crested Shrike-Tits and Rose and Eastern Yellow Robins (Table 6). Sally-snatching was the most common foraging behaviour of Golden Whistlers and both robin species, but was also used substantially by Brown Thornbills, White-naped Honeyeaters and Grey Fantails. Hawking was the principal foraging behaviour only of Grey Fantails, and the second most used macro-behaviour only of Rufous Fantails. Probing/prising was the principal foraging behaviour only of the Crested Shrike-Tit, but White-throated Treecreepers and Large-billed Scrubwrens also probed and prised substantially (Table 6).

Sixteen pairwise species combinations (18% of combinations) had overlap indices > 80% for foraging macro-behaviour use. Brown Thornbills exhibited a high degree of overlap (indices ≥ 50%) with nine species, reflecting their behavioural versatility; they employed both of the predominant foraging behaviours used in this assemblage (*i.e.* GL and SS) at high frequencies (Table 7). In contrast, Crested Shrike-Tits and Grey Fantails exhibited low interspecific overlap in foraging macro-behaviour, each specialising in a method infrequently used by most other assemblage members (PP and HWK, respectively). All other species exhibited moderate levels (indices ≥ 50% with five or six species) of macro-behavioural overlap with other assemblage members, because they predominantly used either GL or SS.

Foraging micro-behaviours

Foraging micro-behaviours were analysable for just five species:

[1] Eleven GL variations were recorded among these species (total n = 960). 'Perching upright' was the form used most by three of these species (White-browed Scrubwren, Brown Thornbill and Silvereye) and 'clinging' (White-naped Honeyeater) and 'ambulatory clinging' (White-throated Treecreeper) were used most by one species each (Table 8). This distribution was reflected in the percentage overlap indices (Table 9). Only one pairwise species combination (10% of combinations) had an index > 80% for micro-gleaning. Five (of 10) indices were > 50% and resulted mainly from multiple species using the two most common GL variations, 'perching upright' and 'clinging'.

[2] Three PP (n = 49) variations were observed in the Crested Shrike-Tit, the only analysable species for variants of this macro-behaviour. 'Clinging' was this species' most commonly used PP posture and, with 'perching upright', comprised 98% of the PP events it performed.

Table 5a

Overall percentage use of foraging substrates by fourteen common bird species. A = air, L = leaf, T = twig, Bch = branch, Tk = trunk, B = bud, F = Flower, G = ground, Bk = bark, O = other. *N* = number of records (focal individuals). Focal individuals could potentially use > 1 substrate in a foraging sequence. Upper row for each species contain transect data (*T*) in bold, lower row contain opportunistically (*O*) gathered data (smaller font). Highest two percentages in each data row underlined to facilitate visual assimilation of the patterns. Gaps indicate zero values. Only bird species for which overall ≥ 50 records were obtained are included. Overall N = 2,861 (1,012 birds).

Species		Foraging substrates										
		A	L	T	Bch	Tk	B	F	G	Bk	O	N
White-throated Treecreeper	***T***	**0.7**		**5.3**	**43.3**	**50.0**				**0.7**		**134 (41)**
	O			15.2	51.5	33.3						33 (11)
White-browed Scrubwren	***T***		**46.3**	**8.4**	**4.2**	**9.5**			**26.3**	**2.1**	**3.2**	**95 (57)**
	O		23.7	5.3	2.6	5.3			60.5	2.6		38 (13)
Large-billed Scrubwren	***T***		**7.1**	**28.6**	**16.7**	**14.3**				**26.1**	**7.2**	**42 (13)**
	O		48.5	15.2	3.0	3.0		3.0			12.1	33 (13)
Brown Thornbill	***T***	**2.4**	**74.7**	**9.1**	**2.8**	**2.5**	**0.3**	**4.9**		**2.8**	**0.5**	**889 (265)**
Striated Thornbill	***T***		**63.6**	**5.7**	**2.3**	**1.1**	**26.2**			**1.1**		**88 (33)**
White-naped Honeyeater	***T***	**3.2**	**43.6**	**16.0**	**22.3**	**1.1**	**1.1**			**12.7**		**94 (35)**
	O		20.6	35.3	14.7	2.9				26.5		34 (14)
Crested Shrike-Tit	***T***		**1.5**	**22.4**	**10.4**					**64.2**	**1.5**	**67 (32)**
Golden Whistler	***T***	**5.3**	**68.4**	**12.3**	**4.4**	**2.6**		**3.9**		**2.6**	**0.5**	**228 (91)**
Rufous Fantail	***T***	**29.7**	**51.6**	**4.7**		**1.6**		**7.8**		**2.6**		**64 (24)**
	O	45.5	39.4	9.1		3.0				3.0		33 (13)
Grey Fantail	***T***	**81.3**	**10.8**	**1.5**	**1.1**	**2.5**		**1.5**	**1.3**			**524 (166)**
Satin Flycatcher	***T***	**25.5**	**41.1**	**11.8**	**9.8**	**9.8**				**2.0**		**51 (16)**
Rose Robin	***T***	**11.1**	**37.8**	**15.6**	**20.0**	**11.1**		**4.4**		**8.8**		**45 (18)**
	O		8.8	67.7	2.9	2.9	5.9					34 (17)
Eastern Yellow Robin	***T***	**3.0**	**11.1**	**1.0**	**1.0**	**8.1**			**75.8**			**99 (56)**
Silvereye	***T***	**1.2**	**73.2**	**2.4**	**3.0**		**9.2**	**8.5**		**2.4**		**164 (62)**
	O		62.5				33.3	1.4		2.8		72 (22)

Table 5b

Matrix of percentage overlap indices for foraging substrate use. Indices > 50% highlighted in bold font on light blue background. Species' acronyms given in Appendix 1.).

	WBSW	**LBSW**	**BTH**	**STH**	**WNH**	**CST**	**GWH**	**RFAN**	**GFAN**	**SFLY**	**RROB**	**YROB**	**SEYE**
WTTC	**70.6**	**62.4**	12.0	9.4	30.1	17.1	13.7	7.7	5.7	26.3	37.8	10.8	6.8
WBSW		34.5	**62.6**	**56.5**	**59.4**	17.7	**64.1**	**54.7**	16.8	**65.2**	**62.0**	47.5	**53.8**
LBSW			26.2	17.3	**53.6**	**61.8**	29.5	9.0	12.1	40.2	**59.3**	17.2	14.9
BTH				**74.1**	**62.1**	16.7	**92.2**	**62.9**	18.2	**59.9**	**70.5**	18.6	**87.4**
STH					**54.9**	10.6	**76.4**	**56.1**	14.4	**51.3**	48.0	14.2	**78.6**
WNH						40.6	**67.2**	**55.2**	17.5	**68.9**	**77.6**	17.1	**53.7**
CST							21.3	8.8	4.1	25.1	35.5	3.5	9.3
GWH								**69.7**	22.7	**67.2**	**74.9**	18.7	**81.3**
RFAN									45.1	**74.9**	**62.2**	16.7	**65.4**
GFAN										41.4	28.5	19.6	16.1
SFLY											**81.5**	24.2	49.7
RROB												24.2	**51.2**
YROB													14.3

Table 6

Percentage use of five macro-foraging behaviours by 14 bird species. For each species, upper row shows transect data (in bold) and bottom row opportunistic data (smaller font). The two highest values in each row are underlined to facilitate assimilation of patterns. Gaps indicate zero values. N is number of records (number of contributing birds). Overall N = 2,628 (1,063 birds).

Species	Foraging macro-behaviours					
	Glean	Sally-snatch	Hawk	Probe	Litter-turn	N (birds)
White-throated Treecreeper	**86.9**	**0.8**		**12.3**		**122 (44)**
	74.3			25.7		35 (11)
White-browed Scrubwren	**86.0**	**2.2**		**12.3**	**11.8**	**93 (40)**
	75.7	2.7		2.7	18.9	37 (13)
Large-billed Scrubwren	**92.9**			**7.1**		**42 (13)**
	81.8	6.1		12.1		33 (14)
Brown Thornbill	**55.9**	**42.0**	**3.9**			**894 (270)**
Striated Thornbill	**28.4**	**70.5**		**1.1**		**88 (33)**
White-naped Honeyeater	**78.1**	**14.6**	**3.1**	**4.2**		**96 (38)**
	55.6	19.4		25.0		36 (17)
Crested Shrike-tit	**22.7**	**3**		**74.3**		**66 (21)**
Golden Whistler	**13.6**	**81.2**	**5.2**			**229 (113)**
Rufous Fantail	**12.5**	**57.8**	**29.7**			**64 (24)**
	15.2	36.4	48.5			33 (14)
Grey Fantail	**3.6**	**14.9**	**81.5**			**524 (166)**
Satin Flycatcher			**74.5**	**25.5**		**51 (17)**
Rose Robin	**6.7**	**82.2**	**11.1**			**45 (18)**
	2.9	88.2	8.8			34 (17)
Eastern Yellow Robin	**23.2**	**65.7**	**3.0**		**8.1**	**99 (48)**
Silvereye	**93.0**	**6.0**	**0.9**			**215 (81)**
	98.2	1.8				113 (41)

Table 7

Matrix of percentage overlap indices for foraging substrate use. Indices > 50% highlighted in bold font on light blue background. Species' acronyms given in Appendix 1.).

	WBSW	**LBSW**	**BTH**	**STH**	**WNH**	**CST**	**GWH**	**RFAN**	**GFAN**	**SFLY**	**RROB**	**YROB**	**SEYE**
WTTC	**90.9**	**94.0**	**63.9**	37.5	**90.3**	38.0	21.6	20.5	11.6	8.0	14.7	31.2	**93.0**
WBSW		**88.7**	**58.1**	31.7	**81.0**	27.5	15.8	14.7	5.8	2.2	8.9	31.2	**88.2**
LBSW			**55.9**	29.5	**82.3**	29.8	13.6	12.5	3.6	0.0	6.7	23.2	**92.9**
BTH				**70.4**	**72.6**	25.7	21.6	**56.6**	20.6	44.1	**50.8**	**67.3**	**62.9**
STH					44.1	26.8	**84.1**	**70.3**	18.5	**70.5**	**77.2**	**88.9**	34.5
WNH						41.5	31.3	30.2	21.3	17.7	24.4	40.8	**85.1**
CST							16.6	15.5	6.6	0.3	9.7	25.7	25.7
GWH								**75.5**	23.7	**79.7**	**93.1**	**82.3**	20.6
RFAN									48.2	**83.3**	**76.3**	**73.3**	19.5
GFAN										40.4	30.3	21.5	10.6
SFLY											**86.3**	**68.7**	7.0
RROB												**75.4**	13.7
YROB													30.2

Table 8

Percentage use of micro-foraging behaviours of ten bird species during transect surveys. Micro-behaviours are described below table. The two highest percentages for each species are underlined to facilitate easy assimilation of the patterns present. Gaps indicate zero values. Species' acronyms given in Appendix 1. Sample size = number of records of the macro-behaviour obtained for a species (number of focal individuals). Number of focal individuals was not recorded in three instances. Only species for which ≥ 49 records for the relevant macro-behaviour were obtained are included. var = variation.

Micro-behaviour	Micro-behaviour	Bird species				
		WTTC	WBSW	BTH	WNH	SEYE
GLEAN:	Perching upright	0.9	81.0	77.0	25.3	73.0
	Ambulation		19.0			1.0
	Cling	30.2		15.2	58.7	18.5
	Cling inverted	4.7		4.4	16.0	7.5
	Ambulatory cling	50.9		1.0		
	Ambulatory cling inverted	13.2				
	Jump up-jump back			1.4		
	Other Jump-up variants			1.0 (Four var)		0.5 (One var)
	Sample size:	**106 (57)**	**79 (38)**	**500 (214)**	**75 (31)**	**200 (80)**
		CST				
PROBE/PRISE:	Perching upright	34.7				
	Cling	63.3				
	Cling inverted	2.0				
	Sample size	**49 (23)**				
		BTH	STH	YROB	GWH	GFAN
SALLY-SNATCH:	Fly out-fly on to new perch	33.7	13.8	14.3	67.2	62.8
	Fly out-cling-fly on	9.1	50.0	1.6	3.3	3.9
	Fly out-hover-fly on	21.9	5.2		5.5	12.8
	Fly out-cling inverted-fly on	1.6	10.3			
	Fly out-flutter-fly on	2.1			0.6	1.3
	Fly out-cling-flutter-fly on	1.9	1.7	1.6	0.6	
	Fly out- hover-cling inverted-fly on	0.8				
	Fly out-hover-cling-fly on	0.8	5.2			
	Four other variants of fly out-move on to new perch	1.2				
	Fly out-fly back to same perch	11.8			14.2	7.7
	Fly out-cling-fly back	5.9	5.2	1.6	1.1	3.9
	Fly out-hover-fly back	7.0	3.5		4.9	5.1
	Fly out-flutter-fly back	1.1			2.7	1.3
	Fly out-cling-flutter-fly back	0.3	3.5			1.3
	Fly out-cling inverted-fly back	0.5	1.7			
	Three other variants of fly out-return to same perch	1.3				
	Fly down-fly up			81.0		
	Sample size	**375 (201)**	**57 (29)**	**60 (36)**	**183 (77)**	**78 (50)**
HAWK:	Fly out-fly on to new perch					37.7
	Fly out-hover-fly on					21.0
	Fly out-fly back to same perch					18.6
	Fly out-hover-fly back					22.6
	Sample size					**424 (105)**

Descriptions of micro-behavioural variants:

GLEANING –

Stationary perching upright: perching in upright standing posture.

Ambulation: gleaning during locomotion (other than flying).

Stationary cling: clinging to the vegetation from which food procured, not in upright posture.

Inverted stationary cling: clinging completely upside down to vegetation from which food procured.

Ambulatory cling: gleaning during locomotion involving clinging to substrate (e.g. WTTC feeding on tree trunk).

Inverted ambulatory cling: as in previous micro-behaviour, but moving downwards head first

Jump up-jump back: jump up to glean from surface above bird and then jump back down.

PROBING –

Three variants same as in gleaning, except that prey item obtained from beneath substrate.

SALLY-SNATCHING –

Fly out-fly on: fly out from perch, seize food item from vegetation and then fly to new perch.

Fly out-flutter-fly on: as in previous behaviour, but wings fluttered briefly while picking food off vegetation.

Fly out-cling-fly on: as in previous micro-behaviour, but clinging to vegetation to procure food item.

Fly out-cling inverted-fly on: as in previous micro-behaviour, but clinging upside down on target substrate.

Fly out-hover-fly on: hovering close to vegetation to pick item off it.

Fly out-cling-flutter-fly on: wings briefly fluttered while clinging to vegetation and picking food off it.

Fly out-hover-cling-fly on: hovering close to target vegetation before removing prey item while clinging to vegetation.

Fly out-hover-cling inverted-fly on: as in previous behaviour, but clinging upside down while removing prey item.

Fly out-fly back to same perch: fly out, snatch food item from vegetation and fly back to original perch.

Fly out-cling-fly back: as in previous behaviour, but clinging to target vegetation while removing prey item.

Fly out-hover-fly back: hovering near vegetation while removing food item from it.

Fly out-flutter-fly back: fluttering wings briefly while picking food item off vegetation.

Fly out-cling-flutter-fly back: clinging to vegetation while removing prey from it.

Fly out-cling inverted-fly back: as in previous behaviour, except clinging upside down while removing prey item.

Fly down-fly up: fly down from perch usually to ground, pounce on prey and fly back to original or a new perch.

HAWKING –

Four variants same as sallying equivalents, except that prey item snatched from the air.

[3] Twenty-four SS variations (n = 753 records) were recorded among the species analysed. The most common variations were 'fly out-fly on', 'fly out-cling-fly on', 'fly out-flutter-fly on', 'fly out-cling-flutter-fly on' and 'fly down-fly up'; the other variations occurred at very low frequencies (Table 8). Brown Thornbills, Golden Whistlers and Grey Fantails used 'fly out-fly on' most. Striated Thornbills and Eastern Yellow Robins respectively used 'fly out-cling-fly on' and 'fly down-fly up' most, whilst 'fly out-hover-fly on' was quite prominent in the SS repertoires of Brown Thornbills and Grey Fantails. Golden Whistlers used 'fly out-fly back' quite frequently (Table 8).

No pairwise species combinations had an overlap index > 80% for micro-SS. Brown Thornbills, Golden Whistlers and Grey Fantails each had high (≥ 50%) overlap indices with two other SS species, mainly because they frequently used the most common variation, 'fly out-fly on'. In contrast, neither Striated Thornbills nor Eastern Yellow Robins overlapped in their use of SS variations with any other species to this extent, principally because they mainly employed two less common variations, respectively 'fly out-cling-fly on' and 'fly down-fly up' (Table 9).

Foraging in two sexually dichromatic species

Sexual variation in foraging stratum use occurred in adult White-throated Treecreepers and Golden Whistlers. Male treecreepers appeared to use the tall tree stratum more, and shrub and canopy tree strata less, than females; male whistlers seemed to use the canopy tree stratum more and shrub layer less than females (Fig. 2). However, for all other foraging variables, adult males and females of each of these species seemed to forage very similarly.

SYNTHESIS AND DISCUSSION

Diet

Invertebrates (mainly insects) appeared to dominate the diet of the 18 analysable bird species, although small proportions of the diet of four of these species comprised fruit and nectar. A further 22 species in the study area provided insufficient records for meaningful, quantitative analysis. However, 13 of them are entirely or predominantly invertebrate consumers elsewhere, seven predominantly consume plant components supplemented with some insects, and one is largely granivorous (Higgins *et al.* 2006) (Table 10). Thus, overall the bird assemblage was quite strongly insectivorous; only six or seven constituent species consume more plant than invertebrate material and (adult) Red-browed Finches consume seeds and a very limited amount of invertebrate material. Recher *et al.* (1985) also found that in a bird assemblage in moist eucalypt forest in northern Victoria/southern New South Wales (NSW) insectivory predominated, nectarivory was exhibited by ~20% of species and granivory was rare.

Behaviour and forest attributes used in exploiting food resources

Only 9–14 bird species were analysable for the use of the various foraging variables, but the present synthesis also draws on qualitative information for other species in the study area obtained during this investigation and from the literature (Table 10).

Table 9

Matrices of percentage overlap indices in gleaning and sally-snatching micro-foraging behaviours. Indices ≥ 50% highlighted in bold and on light green background. Species' acronyms in Appendix 1.

GLEANING MICRO-VARIATIONS:

	WBSW	**BTH**	**WNH**	**SEYE**
WTTC	19.9	21.1	**64.3**	24.1
	WBSW	**77.0**	25.3	**74.0**
		BTH	44.5	**92.7**
			WNH	**51.3**

SALLY-SNATCHING MICRO-VARIATIONS:

	STH	**YROB**	**GWH**	**GFAN**
BTH	41.7	18.6	**52.0**	**68.4**
	STH	18.6	31.9	32.9
		YROB	18.1	17.5
			GWH	**79.2**

(1) Use of vegetation strata and foraging heights

The short and tall tree layers were the strata used most for foraging. These strata were exploited substantially by eight and six of the twelve analysable species, respectively. In marked contrast, the canopy and shrub strata were each used extensively by just three species, whilst only one or two species foraged substantially on the ground and in the 'herb' layer (Table 2). Qualitative information for the other 22 species at the site revealed a very similar pattern, except that the ground surface and cover were used by as many species as the intermittent tall and short tree strata (Table 10). In Recher *et al.*'s (1985) study, ~66% of foraging occurred equally in the shrub (0.2–≤ 4 m) and sub-canopy (4.1–10 m) layers, the remainder being split evenly between the ground and canopy (>10 m) strata. Serong and Lill (2016) noted that most foraging occurred in the shrub stratum in the oldest age-classes (60+ years) of wet temperate forest in the Victorian Central Highlands. Bell *et al.* (2010) demonstrated that 74% of species in eucalypt-dominated sites along an aridity gradient in south-western Australia favoured arboreal foraging. More broadly, Loyn (2002) showed that ecological segregation among co-habiting bird species in SE Australian forests and woodland often involves using different foraging strata.

(2) Use of substrates

Foliage, twigs, shed and attached bark and the air were the foraging substrates used by the most bird species (variously 4 to 11 of 12 analysable species); no other substrate was exploited by more than three analysable species (Table 5). Foliage and twigs were used for insectivory by a broad range of generalist insectivore and partial insectivore species, whereas bark and the air were mainly exploited by a few specialist foragers. Qualitative information indicates that foliage and the ground (including soil and leaf litter) are the foraging substrates most used by 22 other species recorded in the study site, but inflorescences, racemes and tree trunks and branches are also exploited substantially (Table 10).

Recher *et al.* (1985) similarly found that foliage was the main foraging substrate of birds inhabiting woodlots in moist *Eucalyptus* forest in NSW and Victoria. The ground acted as a food substrate only about half as often and ~ 11% of prey

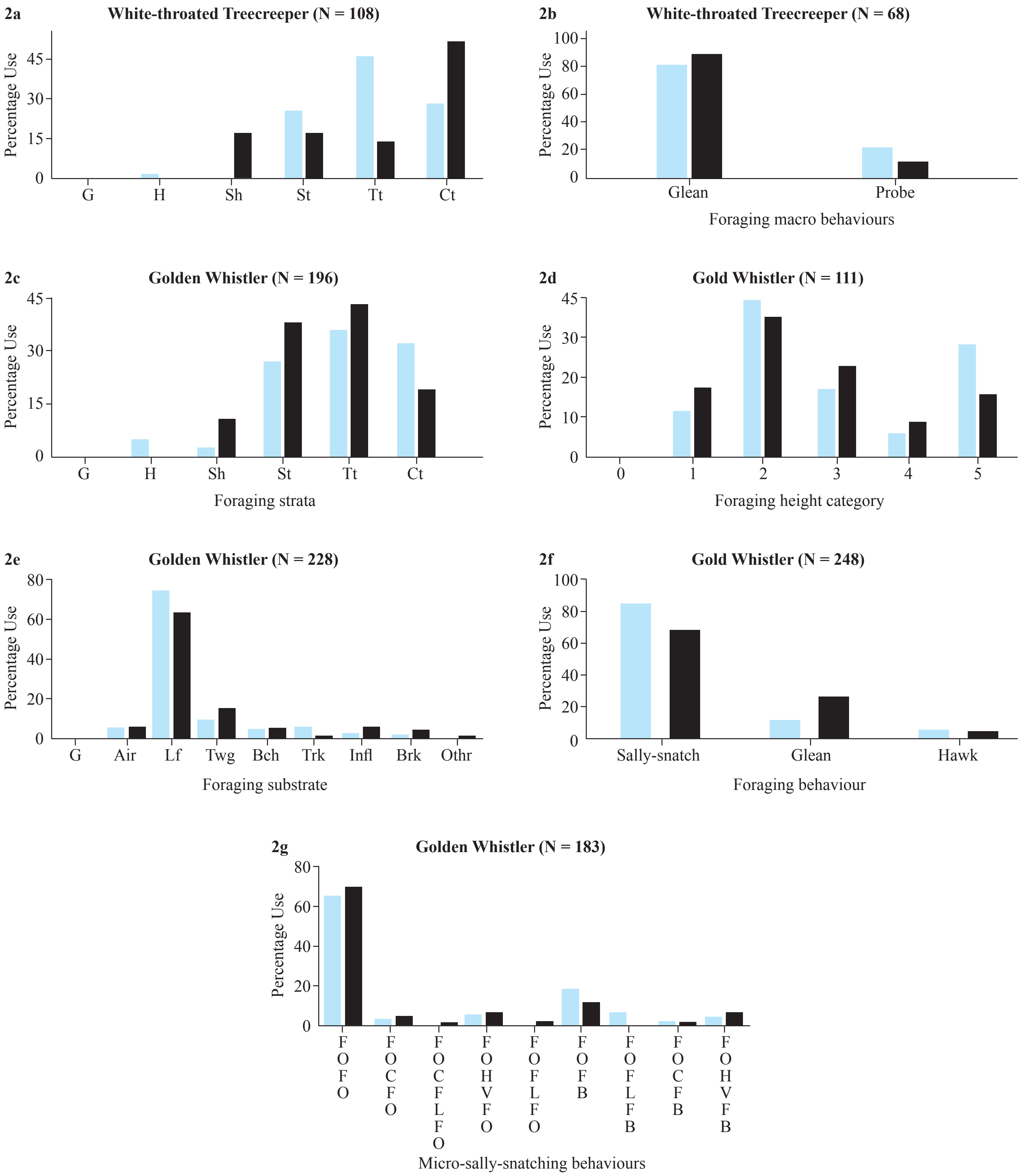

Figure 2: *Overall percentage use of various foraging variables by adult male and female-plumaged White-throated Treecreepers and Golden Whistlers. In all charts, black columns are males and light blue columns are female-plumaged birds. Strata are: G = ground, H = herb layer, Sh = shrub, St = small tree, Tt = tall tree and Ct = canopy tree. Foraging heights (m) are: 0 = ground, 1 = 0.1 – 3.1, 2 = 3.2 – 12.2, 3 = 12.3 – 24.4, 4 = 24.5 – 30.5 and 5 = > 30.5. Substrates are: G = ground, Air, Lf = leaf, Twg = twig, Bch = branch, Trk = trunk, Infl = inflorescence, Brk = bark and Other. Micro-sally-snatching behaviours are: FOFO fly out-fly on, FOCFO fly out-cling-fly on, FOCFLFO fly out-cling-flutter-fly on, FOHVFO fly out-hover-fly on, FOFLFO fly out-flutter-fly on, FOFB fly out-fly back to same parch, FOFLFB fly out-flutter-fly back, FOCFB fly out-cling-fly back and FOHVFB fly out-hover-fly back.*

captures were of flying insects. In contrast, Serong and Lill (2016) recorded that tree branches were the most used foraging substrate in wet temperate forest at various stages of secondary succession in the Victorian Central Highlands; foliage and inflorescences were exploited relatively infrequently. However, foliage was also the predominant foraging substrate in Indian mixed deciduous forest (Thivyanathan 2016), North American montane hardwood and subalpine forest (Sabo and Holmes 1983) and Malaysian mixed dipterocarp forest (Mansor and Sah 2012). Its prevalence as a food substrate for insectivorous forest birds probably reflects the fact that it attracts more insects than do other plant components because of its high content of photosynthetic products and nutrients (Kwok 2009).

(3) Use of macro- and micro-behaviours

Gleaning and SS were by far the most extensively used foraging macro-behaviours, each being the predominant foraging behaviour of six of the 14 analysable species. In contrast, HWK and PP were the predominant foraging behaviours of just one analysable species each. Qualitative information also indicated that GL is the major foraging behaviour of 15 of 22 other species recorded at the site, but SS and PP are also exhibited by four and five of these species, respectively (Table 10).

Serong and Lill (2016) also found that GL was by far the most common prey capture method in wet temperate forest in the Victorian Central Highlands. SS was also moderately common but, as in my investigation, PP and HWK were restricted to a few species. Recher *et al*. (1985) report a similar distribution of foraging behaviours in woodlots in eucalypt forest and woodland in NSW, except that HWK was slightly more common than in the present investigation and that of Serong and Lill (2016). Bell *et al*. (2010) reported that GL comprised 69% of foraging behaviour in bird assemblages in eight *Eucalyptus*-dominated sites in south-western Australia. It was also the most common foraging behaviour in bird assemblages in Indian tropical mixed dry deciduous forest (Thivyanathan 2016) and in North American montane hardwood and subalpine forests (Sabo and Holmes 1983). However, in marked contrast, sallying and hawking were the predominant foraging macro-behaviours in Malaysian mixed lowland dipterocarp forest (Mansor and Sah 2012) and southern Indian thorn forest (Golka 2001), respectively.

Foraging modes *inter alia* presumably maximize the net rate of energy gain per unit foraging time (Bautista *et al*. 2000). The main foraging macro-behaviours observed in the present study can realistically be ranked in terms of estimated energy expenditure (from greatest to least): HWK, SS, PP and GL. Gleaners tend to be small and hence have relatively high mass-specific energy requirements. However, they may be able to subsist on prey yielding a comparatively small individual energy reward provided that such items are abundant, precisely because GL is energetically a relatively low-cost behaviour. The co-existence of several foliage-gleaning species in the study assemblage suggested that insects were indeed abundant on this substrate. Bark PP, as displayed by Crested Shrike-Tits, is probably costlier than GL because it requires: (a) considerable force and (b) a substantial time expenditure per item acquired because many of the prey are concealed. Unlike GL and SS, it was the predominant foraging mode of only one species and so interspecific competition for bark insect prey was probably limited among the predominant species in this assemblage. Sally-snatching is likely to be more energetically costly than PP because it usually involves flight. However, its main benefit presumably lies in providing access to prey that are otherwise impossible or difficult to acquire, particularly by relatively heavy birds lacking agility. Hawking (especially hover-hawking) is presumably costlier energetically than SS because it consists entirely of flying (Dial *et al*. 1997), so one would predict that the individual prey of hawkers must provide a relatively high energy reward. However, this logic requires some qualification for the principal hawker in my study, the Grey Fantail, because many of its hawking manoeuvres involved apparent capture of multiple prey items, which was facilitated by its wide gape, a common trait in hawking flycatchers.

'Perching upright' was the predominant micro-behavioural GL posture. This is not surprising, as it is probably the least energetically expensive GL variation observed. 'Clinging' is limited by body size and was restricted to relatively small species (*e.g.* thornbills, treecreepers and small honeyeaters). 'Fly out-fly on' was the predominant SS variation (occurring in three of five species), with 'fly out-cling-fly on' and 'fly down-fly up' predominating in just Striated Thornbills and Eastern Yellow Robins, respectively. The main PP species, the Crested Shrike-Tit, commonly exploited insects found in hanging, decorticating bark, and so it probed while 'clinging' about twice as often as it probed while 'perching upright'.

Presumably the GL and SS variations observed are adaptive. Theoretically, for example, 'fly out-hover-fly on or back' could enable some SSs to obtain prey from foliage insufficiently robust and/or too flexible to snatch prey from in normal flight, or cling to or perch on. However, this cannot entirely explain hovering, because there were variations in which it was preceded or succeeded by clinging to the target foliage (Table 6). Conceivably it could sometimes allow a foraging bird to make a closer, more accurate assessment of the likely rewards and risks of landing on the target substrate to attack a prey item. Whatever the explanation for the hovering variant 'fly out-fly on or back', the benefits of using it must be substantial, because hovering is energetically costly. It requires the generation of much force and is therefore confined to small birds, because available power does not increase as a function of body size as rapidly as does the power required for flight. Species using hovering are also likely to be slow flyers, because it requires wings with a high aspect ratio (Dial *et al*. 1997). Relatively few studies have examined avian foraging micro-behaviours quantitatively, although Serong (2007) lists the bird species in a Victorian tall wet temperate forest that exhibited some of the GL and SS variations discussed here.

Sex-specific foraging

Major theories concerning the evolution of sex differences in avian foraging contend variously that they: (1) result from, and reduce, intersexual resource competition, (2) are the consequence of foraging constraints associated with reproductive or other sex-related activities, such as nest and song post locations, or (3) are a secondary consequence of sexual selection that results in sexual size dimorphism and hence differing nutritional requirements in males and females (Mand *et al*. 2013).

Table 10

Qualitative summary of foraging behaviour of twenty-two bird species recorded in the study site, for each of which < 50 foraging records were obtained. Not all descriptions are from studies conducted in temperate wet forests. beh = behaviour.

Species	Diet	Site(s)	Principal substrate(s)	Main beh (s)	Sources
Yellow-tailed Black-Cockatoo	seeds, insect larvae	tall and canopy trees	trunk, branch, cones, growing tips	excavate, manipulate, probe	1, 4, 22
Sulphur-crested Cockatoo	seeds, fruit, inflorescences, roots, insect larvae	ground, herb, short, tall and canopy tree	raceme, soil	glean, manipulate, dig	9, 10
Gang-Gang Cockatoo	seeds, fruit, nuts, insect larvae	tall and canopy tree	raceme, seed capsule	glean, manipulate, tear	11, 12
Crimson Rosella	seeds, buds, pith, sori, inverts	ground, shrubs, short, tall and canopy trees	ground, foliage, bark, branch	glean, manipulate	3, 23
Superb Lyrebird	inverts	ground	soil	dig	2
Fan-tailed Cuckoo	inverts, verts, fruit	ground,	ground, bark	sally-snatch, glean, hawk, pounce	21
Shining Bronze-Cuckoo	inverts	short and tall trees, shrubs	Foliage, bark, trunk	glean	22
Red-browed Treecreeper	insects, spiders	tall trees, shrub	bark on trunks and branches, ground	glean, probe, prise	1, 13, 14, 21, 23
Spotted Pardalote	inverts, exudates	tall trees	foliage	glean	5, 28
Crescent Honeyeater	nectar, fruit, insects, exudates	tall and canopy trees, shrubs	inflorescence, foliage, trunk, twig, branch	probe, glean, sally-snatch	6,18, 19, 22
Eastern Spinebill	nectar, inverts	herb, shrub, short tree	flower, foliage	probe, glean	1, 7, 22
Yellow-faced Honeyeater	nectar, pollen, fruit, seeds, exudates, inverts	shrub, short tree	flower, foliage, bark	glean, probe, sally-snatch	17, 21
White-eared Honeyeater	insects, nectar, fruit, exudates,	tall and canopy tree	bark on trunks and branches, foliage, inflorescences	probe, glean	14, 15, 16
Eastern Whipbird	inverts, verts	ground	leaf litter, fallen bark	litter turn, probe	8, 21, 28
Olive Whistler	inverts, fruit	shrub, herb		glean	1, 22, 28
Rufous Whistler	inverts, seeds, fruit	shrub, short and tall tree	Foliage, bark, air	sally-snatch, glean, hawk	1, 17, 21
Grey Shrike-Thrush	inverts, verts, eggs, carrion, fruit, seed	ground short and tall tree	ground, branch, trunk, foliage	glean	1, 17, 23
Raven sp.	inverts, verts, carrion, refuse, fruit, seeds, nectar	ground, short and tall tree	ground, foliage	glean, probe, manipulate, sweep	20, 26
Pink Robin	inverts	ground, shrub	ground, foliage	glean, sally-snatch	17, 22, 28
Common Blackbird	inverts, fruit, seeds	ground, short tree	ground, leaf litter	litter turn, glean	17
Bassian Thrush	inverts, fruit	herb, ground	ground, shrub	litter turn, probe	22, 23, 27
Red-browed Finch	seed, inverts	ground, herb	raceme, ground	glean	1, 24, 25

References: 1 this study, 2 Lill (1996), 3 Magrath and Lill (1983), 4 Mcinnes *et al*. (1978), 5 Woinarski (2008), 6 Thomas (1980), 7 Ford and Pursey (1991), 8 Rogers and Mulder (2004), 9 Emison and Nicholls (1992), 10 Noske (1980), 11 Osborne and Green (1992), 12 Recher and Holmes (1985), 13 Noske (1979), 14 Wykes (1985), 15 Paton (1980), 16 Loyn (1980), 17 Recher *et al*. (1985), 18 Routley (1980), 19 Paton and Ford (1977), 20 Lill and Hales (2015), 21 Holmes and Recher (1986), 22 Thomas (1980b), 23 Recher (2016), 24 Todd (1996), 25 Read (1994), 26 Stewart (1997), 27 Edlington (1983), 28 Thomas (1978).

Adult male and female Golden Whistlers are similarly-sized (Bell 1986) and generally foraged very similarly, as noted in other studies in mature wet temperate forest (Recher and Holmes 2000; Mac Nally 2000; Serong and Lill 2016). However, males appeared to forage in the canopy more, and possibly the shrub and short tree strata less, than females. This seemed to result, on average, in males foraging at greater heights than females, as recorded in several other temperate forest habitats (Bridges 1980; Paton 1981; Bell 1986; Wheeler and Culver 1996). This height disparity cannot be a product of sexual size dimorphism nor, as it was not restricted to the breeding season, of constraints imposed by reproduction, but it could potentially reduce intersexual food competition. However, it should be noted that Recher and Holmes (2000), Mac Nally (2000) and Serong and Lill (2016) found no sex difference in foraging heights in this species.

Male White-throated Treecreepers are slightly larger than females (Noske 1986) and appeared to forage in the tall tree layer more, and the canopy and shrub strata less, than did females. There was no sex-specificity in other foraging variables (Bell 1986; Recher and Holmes 2000). Noske (1986) documented sex differences in foraging substrates, but not heights, in this species in dry sclerophyll eucalypt forest, whereas Recher and Holmes (2000) reported sex differences in foraging height, substrate and behaviour in populations in regrowth and mature temperate eucalypt forest. The sex differences in foraging in the size-dimorphic treecreepers in the present investigation could potentially be an adaptive consequence of either sexual selection or intersexual competition. However, the disparity in foraging strata use was more complex than that in Golden Whistlers and it is less clear theoretically whether it could limit intersexual competition.

Species-specific foraging viewed from three perspectives:

(1) Overlap indices

Considering all five foraging variables *in toto*, 60% of the 306 pairwise species overlap indices calculated were ≥ 50%. However, no pairwise species combinations had overlap indices > 70% for all five, or even four, of the foraging variables, and only four species combinations had them for three foraging variables (Golden Whistler × Brown Thornbill, Striated Thornbill and Grey Fantail; Silvereye × Brown Thornbill). Only one species combination (White-browed Scrubwren × Grey Fantail) had very low overlap indices (< 30%) for four foraging variables, and three species combinations (White-browed Scrubwren × White-throated Treecreeper, White-naped Honeyeater and Golden Whistler) had them for three variables. Thus overall, the overlap indices indicated some interspecific overlap in foraging behaviour, particularly for the Golden Whistler, but the White-browed Scrubwren appeared to occupy a relatively exclusive foraging niche.

(2) Individual foraging variables

At the individual foraging variable level, stratum use and type of micro-GL behaviour employed varied *least* among analysable assemblage member species, both having overlap indices ≥ 50% among half of the member species. In contrast, foraging height and type of micro-SS behaviour used varied *most* among analysable assemblage member species, both having overlap indices of < 50% in ~70% of pairwise species comparisons. Foraging substrate use and macro-behaviours were intermediate in overlap among species, having indices < 50% in 57% and 63%, respectively, of species interactions. Thus, at this level of resolution, there were indications of both niche segregation and overlap.

Foraging substrates, heights and behaviours varied among species in insectivorous bird assemblages inhabiting *Eucalyptus* forest and woodland in NSW (Recher *et al*. 1985) and among honeyeaters in Western Australian *Eucalyptus* woodlands (Recher *et al*. 2016). Loyn (2002) concluded more generally that using different foraging strata and substrates was important in ecological segregation of co-habiting bird species in SE Australian temperate forests and woodlands. These variables are also important to varying degrees in niche segregation in bird assemblages in forest habitats elsewhere, including North America, South India, Europe, Malaysia and the West Indies (Sabo and Holmes 1983; Latta and Wunderle 1998; Styring and Zakaria 2004; Somasudaram and Vijayan 2008; Kornan *et al*. 2013).

(3) Foraging 'guilds'

Using a categorization based simply on type of foraging behaviour, two main 'guilds' were recognisable among the analysable species:

(a) the six primarily GL species showed substantial overlap in substrate use. Four of them were principally foliage gleaners (White-browed Scrubwren, White-naped Honeyeater, Silvereye and Brown Thornbill), but of these the scrubwren mostly exploited 'herb' and shrub foliage, whereas the other three species mainly exploited tree foliage. The White-naped Honeyeater was further distinguished by its tendency to exploit the highest tree layer (canopy) and to predominantly use the 'clinging' variation of GL, whereas Brown Thornbills and Silvereyes mostly used the lower tree layers and the 'perching upright' variation. The two GL species that did not significantly exploit foliage mainly used tree trunks and branches (White-throated Treecreeper) and bark and twigs (Large-billed Scrubwren), respectively, as their main foraging substrates. Thus, among GL 'guild' member species there was some foraging behaviour diversity that would probably translate into dietary differences.

(b) Five of the six primarily SS analysable species overlapped strongly because they foraged mainly in foliage. However, there was some variation among them in foraging strata use, because Rufous Fantails and Satin Flycatchers exhibited biases for the shrub and tall tree layers, respectively, whereas Striated Thornbills and Golden Whistlers both favoured the short tree layer, but predominantly used different SS variations ('fly out-fly on' and 'fly out-cling-fly on', respectively). The Grey Fantail was secondarily an SS species; its SS profile closely resembled that of Golden Whistlers, but it used the 'fly out-hover-fly on' variation more.

Additionally, two analysable species hawked insects in the air to a substantial extent; the Grey Fantail was primarily a hawker, whereas the Rufous Fantail was only secondarily a hawker. The latter species foraged mainly in the shrub and small tree layers, whereas the former only exploited the tree strata prominently. As observed elsewhere (Noske 2003), the Crested Shrike-Tit was a specialist bark forager, employing tearing and probing to access insects beneath attached and decorticating bark. No other analysable species exploited this niche substantially, but Eastern Whipbirds and Red-browed Treecreepers, which both occurred at the study site, are also bark foragers (Table 8).

Even if the insect fauna varied among foraging strata and substrates, there was probably considerable overlap in foraging ecology within and between the SS and GL 'guilds'. However, there was some very clear resource partitioning in the assemblage too, because probing, hawking and trunk-gleaning presumably gave their few proponents access to food resources largely unexploited by most GL and SS species.

Caveats

A limitation of the investigation was that the focus on one relatively small area of forest precluded valid statistical analysis of results. Some researchers reporting similar studies have simply ignored this problem, although admittedly it would be difficult to eliminate it. Further, although considerable effort was expended on observation over two years, insufficient data were obtained to quantitatively characterise the foraging behaviour of many less common species. Notwithstanding these limitations, the study provides some useful insights into the likely role of foraging niche segregation in shaping a Mountain Ash forest bird assemblage. From a management perspective, it highlights the importance of the short and tall tree strata in the food acquisition of assemblage member species.

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Appendix 1

Common and scientific names of the bird species recorded in the study. Acronyms are given for species occurring in Tables 1−10.

Brush Bronzewing *Phaps elegans*
Wedge-tailed Eagle *Aquila audax*
Yellow-tailed Black-Cockatoo *Calyptorhyncus funereus* (YTBC)
Gang-gang Cockatoo *Callocephalon fimbriatum*
Sulphur-crested Cockatoo *Cacatua galerita*
Australian King-Parrot *Alisterus capularis*
Crimson Rosella *Platycercus elegans* (CROS)
Eastern Rosella *P. eximius*
Fan-tailed Cuckoo *Cacomantis flabelliformis*
Shining Bronze-Cuckoo *Chalcites lucidus*
Southern Boobook *Ninox novaeseelandiae*
Laughing Kookaburra *Dacelo novaeguineae* (LK)
Superb Lyrebird *Menura novaehollandiae*
White-throated Treecreeper *Cormobates leucophaea* (WTTC)
Red-browed Treecreeper *Climacteris erythrops*
Superb Fairy-Wren *Malurus cyaneus*
White-browed Scrubwren *Sericornis frontalis* (WBSW)
Large-billed Scrubwren *S. magnirostra* (LBSW)
Brown Thornbill *Acanthiza pusilla* (BTH)
Striated Thornbill *A. lineata* (STH)
Spotted Pardalote *Pardalotus punctatus*
Crescent Honeyeater *Phylidonyris pyrrhopterus*
Eastern Spinebill *Acanthorynchus tenuirostris* (ESPB)
Yellow-faced Honeyeater *Lichenostomus chrysops*
White-eared Honeyeater *L. leucotis*
New Holland Honeyeater *Phylidonyris novaehollandiae*
White-naped Honeyeater *Melithreptus lunatus* (WNH)
Red Wattlebird *Anthochaera carunculata*
Eastern Whipbird *Psophodes olivaceus*
Varied Sitella *Daphoenositta chrysoptera*
Crested Shrike-Tit *Falcunculus frontalis* (CST)
Olive Whistler *Pachycephala olivacea*
Golden Whistler *P. pectoralis* (GWH)
Rufous Whistler *P. rufiventris*
Grey Shrike-Thrush *Colluricincla harmonica* (GST)
Olive-backed Oriole *Oriolus sagittatus*
Australian Raven *Corvus coronoides* (RSP)
Little Raven *C. mellori* (RSP)
Rufous Fantail *Rhipidura rufifrons* (RFAN)
Grey Fantail *R. albiscapa* (GFAN)
Satin Flycatcher *Myiagra cyanoleuca* (SFLY)
Rose Robin *Petroica rosea* (RROB)
Pink Robin *P. rodinogaster*
Eastern Yellow Robin *Eopsaltria australis* (YROB)
Silvereye *Zosterops lateralis* (SEYE)
Common Blackbird *Turdus merula*
Bassian Thrush *Zoothera lunulata*
Mistletoebird *Dicaeum hirundinaceum*
Red-browed Finch *Neochmia temporalis*

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Moult timing and morphometrics of Mangrove Gerygones: a comparison of monsoon-tropical and subtropical populations

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Mangrove Gerygones *Gerygone levigaster* were banded at six sites in the Greater Brisbane region, Queensland over 5.5 years, and at three sites in Darwin, Northern Territory, over 8-9 years. The species was highly sedentary in both regions, and no movements were recorded among sites at either location. In Darwin, males were larger than females in three out of five morphometrics, whilst in Brisbane they were larger in the remaining two, suggesting that different selection pressures may be operating on morphometrics in the two areas. Juvenile birds were present year-round in Brisbane, the highest numbers occurring from April to July and November to January, indicating that the breeding season, like that in Darwin, is biannual, but with a lag of 1-2 months. Months in which breeding activity occurred, indicated by the presence of cloacal protuberances or brood patches, and the occurrence of fledglings, also suggested that there were two egg-laying peaks. In Darwin, primary wing moult occurred mostly from October to December, after the second annual egg-laying pulse, whilst very few individuals (possibly in their first year) moulted after the first egg-laying pulse (March-April). In Brisbane, however, primary moult occurred from November to April, peaking in February and March, about four months after the peak in Darwin. Sites that were inundated only on king tides had a higher proportion of juveniles than those in riparian or intertidal areas, suggesting that the former may offer better breeding or foraging habitat for non-breeding birds. Body mass adjusted for structural size varied significantly among months in Brisbane, being highest in March and April, and lowest during May.

INTRODUCTION

Of the 14 or 15 species of mangrove-specialised birds in Australia (Noske 1996), the Mangrove Gerygone *Gerygone levigaster* has one of the broadest geographical ranges, stretching from the southwest Kimberley region of Western Australia to Port Hacking, New South Wales, and including the southern coast of New Guinea (Higgins and Peter 2002; Cooper *et al*. 2016). However, this range is discontinuous, and a gap on the east coast of Cape York Peninsula separates two recognised Australian subspecies, the nominate *levigaster*, which is confined to the tropics, and *cantator*, which occurs in eastern Australia from around Townsville southwards (Higgins and Peter 2002). Plumage differences between these two races are slight, but *cantator* is heavier and larger in most dimensions (Ford 1981; Higgins and Peter 2002). Throughout its range, the species is largely restricted to mangroves in estuaries and along tidal rivers, but in parts of the Kimberley it also occurs in adjacent paperbark thickets (Ford 1982; Johnstone 1990).

Although the reproductive ecology and morphometrics of the Mangrove Gerygone have been studied in detail in Darwin, Northern Territory (Noske 2001; Mulyani 2004), there has been no comparable published study covering southern Australia. In Darwin, the species was found to breed biannually, with egg-laying peaking in both March-April and September-October (Noske 2001; Mulyani 2004). In contrast, in New South Wales and south-eastern Queensland, egg-laying reputedly occurs from late August to late January, with a single peak in late October–early November (Ford 1981; see also Higgins and Peter 2002). If the apparent disparity in breeding seasons between north-western and south-eastern populations of the species is real, we might also expect differences in the timing of moult, as adult Australian passerines normally moult after breeding. A preliminary analysis of moult based on museum skins suggested that the moult of nominate (tropical) individuals often started just before the wet season, but sometimes not until after the wet season (Higgins and Peter 2002).

Since 2007, Mangrove Gerygones have been banded as part of a long-term study of the demography of mangrove-dwelling birds in the Brisbane region. This study provided an opportunity to compare the annual cycle of the population in this region with that of Darwin. In this paper, we compare the timing of moult and breeding, as well as the morphometrics of these two populations.

METHODS

Climate of study areas

Darwin's (12.4634° S, 130.8456° E) climate is monsoon-tropical, with year-round warm to hot temperatures, and a mean annual rainfall (MAR) of c.1,500 mm, of which roughly 90% falls in the wet season (November through April) and the remainder in an equally long dry season (May to October, Fig. 1a). In contrast, Brisbane (27.4698° S, 153.0251° E) is sub-tropical, with warm summers and drier, cooler winters, and a MAR of c.1,050 mm, with a short dry season (c.10% of MAR) from July through September (Fig 1b). About two-thirds of Brisbane's MAR falls during Darwin's wet season (Australian Bureau of Meteorology 2017).

Capture and measurement of gerygones

In Darwin, Mangrove Gerygones were captured and banded at three mangrove sites, the majority at Ludmilla Creek, between January 1986 and April 2009 (Table 1). At each of these sites, banding was conducted over 8-9 years; 149 sessions were conducted in total, but sampling was not systematic. Nevertheless, at each site sampling occurred in each calendar month in at least one of the study years. In Brisbane, Mangrove Gerygones were captured and banded at six sites between June 2007 and December 2012 (Table 1) as part of a constant-effort bird banding program. The majority were caught at Nudgee Road cycle track, Kedron Wetlands and Nudgee Beach Mangrove Boardwalk. Smaller numbers were captured infrequently at a further three sites (Osprey House, Eagleby Wetlands and Wynnum Mangrove Boardwalk). Each site was sampled each month for the duration of its use, giving a total of 261sampling sessions. The dominant mangrove species at all sites was the Grey Mangrove *Avicennia marina*.

In both Darwin and Brisbane, birds were captured in mist-nets (2.6 m high × 6-18 m long, mesh size 12 or 14 mm). In Brisbane, each net location at each site was marked using a GPS device, so that the same number of nets could be set in the same locations on every banding visit. The sites, number of visits and dates of visits are shown in Table 1. Mist-netting commenced at dawn and continued for 4– 6 h. After processing, captured birds were released at the capture site. All birds were banded with Australian Bird and Bat Banding Scheme (ABBBS) aluminium bands, but in Darwin they were also colour-banded for individual recognition during regular monitoring (Mulyani 2004). However, the smallest available coloured, celluloid bands could slip over the toes of gerygones, so aluminium bands were placed on each tarsus and a single coloured, celluloid band was placed above them. Anodized (coloured, metal) bands were used for nine birds, but because of the limited range of available colours and the difficulty of distinguishing them in the field, these bands were not used after 2000.

Each captured bird was scored for wing moult, using the methods described in Lowe (1989). Morphometrics obtained comprised flattened wing chord length and tail length (both ± 1 mm), total head length, tarsus length and bill length (all ± 0.1 mm) and body mass (± 0.1 g). In Brisbane, the sex of the bird was determined by examining the underparts for evidence of a well vascularised brood patch (females) or distinct cloacal protuberances (males); in Darwin, birds were sexed on whether a brood patch was present during the breeding season and this sexing was later checked by observation of colour-banded birds at the nest. Following Rebeira (2006), birds were aged according to the colour of the eyebrow. Those with yellow eyebrows were recorded as Age "1" (juveniles), those with buff tones to the eyebrow as Age "2-" (sub-adult) and those with pure white eyebrows as Age "2+" (adults). The yellowish tone to the eye brow in age code "1" birds is lost during the first post-juvenile moult when the bird attains adult plumage and small numbers of retained and worn juvenile feathers are the only means of distinguishing older juveniles (age code "2-") from adults. Unfortunately, post-juvenile moult in this species is not well documented and the time between fledging and the first post-juvenile moult is not known (Higgins and Peter 2002), although in most bird species this normally occurs within the first few weeks after fledging (Ginn and Melville 1983).

Morphometric data were analysed with StatsDirect v3.1.18. Samples were compared using independent t-tests and Analyses of Variance (ANOVA). Variation in the percentage of sub-adults over the six calendar years of the study in Brisbane was examined with simple linear regression analysis. Principal Components Analysis (PCA) was used to further analyse and describe size variation between male and female Mangrove Gerygones in the two study areas. To remove the influence of body size on the body mass measurement, an adjusted body mass index was calculated by dividing body mass by tarsus length (Coleman *et al*. 2002; Coleman *et al*. 2009).

RESULTS

Geographical and sexual variation in morphometrics

Table 2 compares the morphometrics of 112 adult or subadult Mangrove Gerygones banded at Darwin sites and 257 banded at Brisbane sites. Darwin birds were significantly smaller than Brisbane birds in wing, head-bill and tail lengths, and lower in body mass (Table 2). Sixty of the Mangrove Gerygones banded in Darwin were reliably sexed, 39 (65%) being male, whilst 33 (63%) of the 52 birds sexed in Brisbane were male. In Darwin, male Mangrove Gerygones were significantly larger than females in wing and tail length, and were also heavier (Table 3). However, tarsus and head-bill lengths did not differ significantly between the sexes. In Brisbane, males were significantly larger than females in tarsus and head-bill length, but not in wing or tail length or mass (Table 4).

Further analysis of size variation between males and females using PCA showed that the first PCA component only accounted for 45.8% and 44.2% of the variance in the Brisbane and Darwin data, respectively, with subsequent components being even weaker in their power to describe the variance observed. Scatter plots of PCA components 1 and 2 showed no separation of the data into discrete clusters, confirming that although some morphometric variation occurs between the sexes, there is significant overlap in size.

Moult and adjusted body mass

In Darwin, primary moult was evident in most birds captured from October through December, and in a minority of birds captured in February, April and May (Fig. 2a). The highest proportion of moulting birds caught was in October, when 84.6% were in active wing moult, followed by November with 72.7%. In Brisbane, primary moult was evident in captured birds from November through April, but the highest proportions showing active wing moult were in February (63.6%) and March (57.1%) (Fig. 2b). Of the 44 Brisbane birds caught while in active primary moult, 32 (72.7%) were aged as being adult (Age 2+), nine (20.5%) as immature (Age 2-) and three (6.8%) as juvenile (Age 1) (Fig. 1b).

Table 1

Study sites where Mangrove Gerygones were captured.

Site Name	Lat, long	Month of first visit	Month of final visit	Habitat	No. birds caught
Nudgee Road Cycle Track, Qld	27.36S, 153.1E	June 2007	December 2012	Rarely inundated mangroves	120
Kedron Wetlands, Qld	27.4S, 153.1E	November 2010	November 2012	Rarely inundated mangroves	104
Nudgee Beach, Qld	27.36S, 153.1E	October 2007	June 2012	Frequently inundated mangroves	66
Ludmilla Creek, NT	12.41S, 130.85E	April 2000	March 2009	Rarely inundated mangroves	66
Rapid Creek, NT	12.38S, 130.86E	April 2000	January 2008	Rarely inundated mangroves	33
Osprey House, Qld	27.28S, 153.0E	July 2011	November 2011	Riparian mangroves	12
Palmerston Sewage Ponds, NT	12.50S, 130.95E	January 1986	November 1994	Rarely inundated mangroves	11
Eagleby Wetlands, Qld	27.71S, 153.2E	November 2006	December 2012	Riparian mangroves	4
Wynnum Boardwalk, Qld	27.43S, 153.18E	October 2007	July 2008	Frequently inundated mangroves	3

Table 2

Morphometrics of all adult (2+, 1+) and subadult (2, 2-) Mangrove Gerygones caught in the Brisbane (1997–2012) and Darwin (1986-2009) regions. All lengths in mm.

Character	Mean, *SE, n* (Brisbane)	Range (Brisbane)	Mean *SE, n* (Darwin)	Range (Darwin)	t	p
Wing length	56.7 ± 0.1 (255)	50-64	52.8 ± 0.2 (102)	47-60	*-10.1*	<0.0001
Tail length	41.8 ± 0.2 (254)	33-51	39.8 ± 0.2 (97)	32-45	*-3.1*	0.02
Head-bill length	27.3 ± 0.04 (255)	25.2-30.8	26.7 ± 0.1 (74)	24.1-28.3	*-5.9*	<0.0001
Tarsus length	19.0 ± 0.1 (255)	15.9-21.0	19.2 ± 0.1 (74)	17.5-20.6	*-1.3*	0.18
Mass (g)	7.8 ± 0.03 (253)	6.0-9.5	6.7 ± 0.1 (102)	4.7-12.5	*-2.2*	0.02

Table 3

Morphometric comparison of adult male and female Mangrove Gerygones in Darwin region. All lengths in mm, mass in g.

Character	Male (mean, *SE, n*)	Female (mean, *SE, n*)	t	p
Mass	7.1 ± 0.2 (37)	6.4 ± 0.1 (21)	*-2.26*	0.04
Wing length	54.1 ± 0.4 (39)	51.5 ± 0.4 (15)	*-4.4*	0.0003
Tail length	40.8 ± 0.3 (37)	38.3 ± 0.5 (21)	*-3.46*	0.0028
Tarsus length	19.4 ± 0.1 (36)	18.8 ± 0.2 (17)	*-1.54*	0.142
Head-bill length	26.3 ± 0.5 (29)	26.5 ± 0.02 (10)	*-0.42*	0.6832

Table 4

Morphometric comparison of adult male and female Mangrove Gerygones in Brisbane region. All lengths in mm, mass in g.

Character	Male (mean, *SE, n*)	Female (mean, *SE, n*)	t	p
Mass	8.0 ± 0.1 (33)	8.0 ± 0.1 (19)	*-0.1*	0.919
Wing length	58.2 ± 0.4 (33)	56.6 ± 0.5 (19)	*-2.0*	0.06
Tail length	41.7 ± 0.4 (33)	41.3 ± 0.5 (19)	*-0.513*	0.61
Tarsus length	19.2 ± 0.1 (33)	18.7 ± 0.1 (19)	*-2.5*	0.02
Head-bill length	27.4 ± 0.1 (33)	27.0 ± 0.1 (19)	*-2.59*	0.01

In Brisbane, the more regular catching allowed adjusted body mass to be compared among age classes and months. However, as adjusted body mass did not vary among the three age classes used in the analysis (F=0.61, df=17,361, P=0.8), all age classes were combined for further analysis. Adjusted body mass varied significantly among years (F=3.1, df=5,372, P=0.008; Fig. 3), but this was primarily the result just of a noticeable decrease in recorded body mass index in 2009. When this year was removed from the analysis, there was no significant variation among the other years (F=0.76, df=4,316, P=0.551). Adjusted body mass also varied significantly among months (F=2.9, df=11,366, P=0.001); mean mass was highest during March and April, and lowest during May (Fig. 4).

Proportion of juveniles caught in Brisbane

Mangrove Gerygones banded over the study period in Brisbane comprised 195 sub-adults (fledglings, juveniles, and immature birds) and 114 adults. The percentage of sub-adults ranged from 61% to 79% over the six calendar years of the study (Fig. 5), but simple linear regression analysis showed no significant trend over the study period (r^2= 0.03, df =4, P=0.7). The population at Nudgee Road Cycle Track had a consistently higher annual percentage of juveniles (range 64.1–92.3%) than those at Nudgee Beach (range 37.5–62.5%) and Kedron Wetlands (range 50.0–66.6%) in each year of the study (Fig. 5). The differences between Nudgee Beach and Nudgee Cycle Track road were statistically significant (F=23.4, df=1,10, P<0.001). Juvenile birds (Age code 1) constituted more than 30% of all birds caught in each month except February and August, when the percentage dropped below 20% (Fig. 6). The relative abundance of juveniles was highest in April and May, when they constituted more than 50% of all birds caught.

In Brisbane, males with cloacal protuberances (indicating recent breeding activity) were caught in each month from September to March (n=4,7,7,3,4,2 and 6, respectively). Similarly, adult females with brood patches were caught in September (4), October (5), November (4), January (1), February (1), and March (4).

DISCUSSION

Morphometrics

Mangrove Gerygones were sexually dimorphic in both studied regions, males being larger than females in one or more characters, and this appears to be case in other parts of their range (Ford 1981; Johnstone 1990; Higgins and Peter 2002; Mulyani 2004). However, the degree of inter-sexual overlap in all characters makes morphometrics alone unsuitable for discriminating between the sexes. Breeding characters (the presence of brood patches or cloacal protuberances) were the only way to differentiate the sex of at least some individuals. Sexual dimorphism was much more pronounced in the monsoon-tropical population than in the sub-tropical population.

The physical characters in which sexual dimorphism was demonstrated differed between the two populations. Whilst males in Brisbane had longer head-bill and tarsus lengths, these characters did not differ between the sexes in the Darwin population. As Darwin males were larger than females in all other characters, the lack of head-bill length dimorphism suggests that females were relatively long-billed. In the Darwin region, Mangrove Gerygones are highly specialised in their foraging ecology, foraging mostly in Grey Mangroves, whereas coexisting Large-billed Gerygones *G. magnirostris* are more generalised in all foraging dimensions (Noske 1996; Mohd-Azlan *et al.* 2015). However, the latter species shows similar levels of morphological sexual dimorphism, suggesting that dimorphism is unrelated to foraging specialisation and rather may be the result of sexual selection. Moreover, members of Brisbane populations are probably just as specialised, as the Grey Mangrove is overwhelmingly the dominant tree species among the mangroves in the region. Thus, it seems likely that the greater degree of sexual dimorphism in the tropical than in the sub-tropical Mangrove Gerygone populations is related to higher levels of interspecific competition, especially with other gerygone species (absent in Brisbane), and possibly also to the greater diversity of mangrove species or mangrove-dwelling insects.

Ford (1981) collated measurements of Mangrove Gerygones from around Australia and concluded that eastern Australian birds *(cantator)* were larger than northern Australian birds (*levigaster*), which resembled one another. Measurements provided in Higgins and Peter (2002) also suggest that *cantator* averages 4-5 mm and 2-3 mm longer than *levigaster* in the wing and tail, respectively, and measurements of our study populations confirm the size differences described between these two subspecies.

Breeding seasons

The trade-off between fecundity and survival is well documented (e.g. Murray 1985; Johnston *et al.* 1997). Our studies suggest that the Mangrove Gerygone has a shorter lifespan than most Australian passerines studied to date (Coleman and Noske 2017), but the presence of juvenile birds year-round in Brisbane indicates a long breeding season with the potential for several broods. Nevertheless, the relative abundance of juveniles in Brisbane peaked in April–May, with a smaller peak during December–January. Although the phenology of egg-laying of Mangrove Gerygones in the Brisbane region is not known, birds in breeding condition were found from September to March, with the highest numbers for both sexes occurring in September through November, and in March, indicating two widely-separated peaks of breeding activity. The timing of these peaks in juvenile abundance and breeding in adults contradicts the statement of Ford (1981), who said that in south-eastern Queensland and New South Wales the species lays eggs from late August to late January, with a single peak in late October–early November.

The bimodal pattern of abundance of juveniles and breeding adults among Mangrove Gerygones in Brisbane parallels the breeding season in Darwin, Northern Territory (Noske 2001, 2003; Mulyani 2004), where the species breeds biannually, with two egg laying pulses of similar intensity, the first from March to May and the second, from August to October. Mangrove Gerygones are insectivorous, eating (in order of decreasing frequency) bugs, beetles, wasps, moths, spiders, flies and insect larvae (Johnstone 1990; Noske 2003). Egg-laying peaks of Mangrove Gerygones in Darwin were not correlated with rainfall or temperature, but were significantly related to the abundance of small flying insects, especially bugs (Hemiptera) and flies (Diptera) in mangroves around salt flats, the habitat of the species (Noske 2003; Mulyani 2004). Studies of pest insects show that mosquito diversity around Darwin is consistently high from late in the wet season (March) to mid-

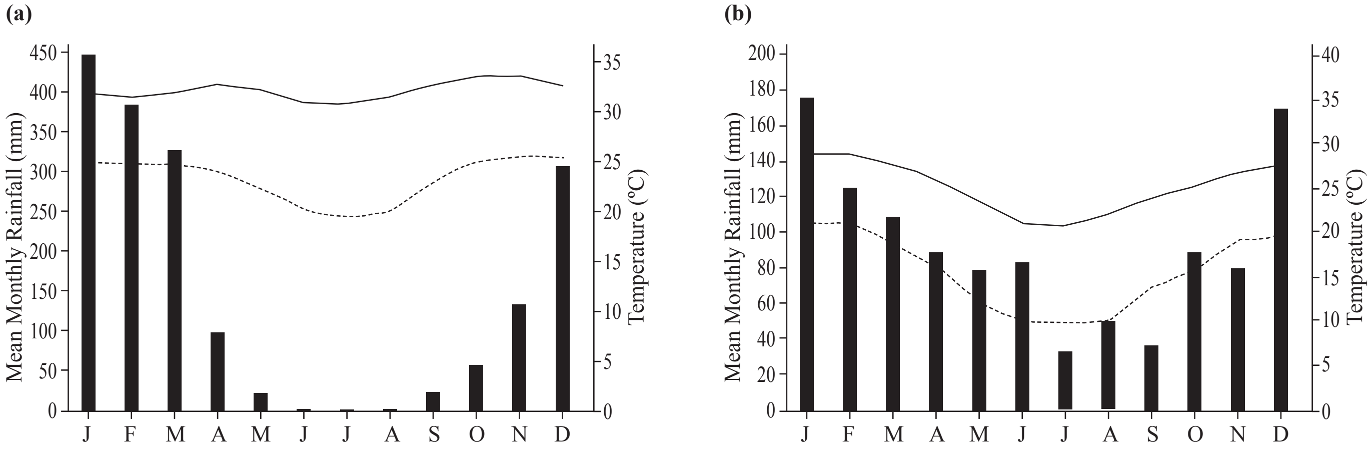

Figure 1. *Mean maximum (solid line) and minimum (dotted line) monthly temperature (°C) and rainfall (mm, bars) for (a) Darwin and (b) Moreton Bay over the respective study periods. Source of data, Bureau of Meteorology, December 2018.*

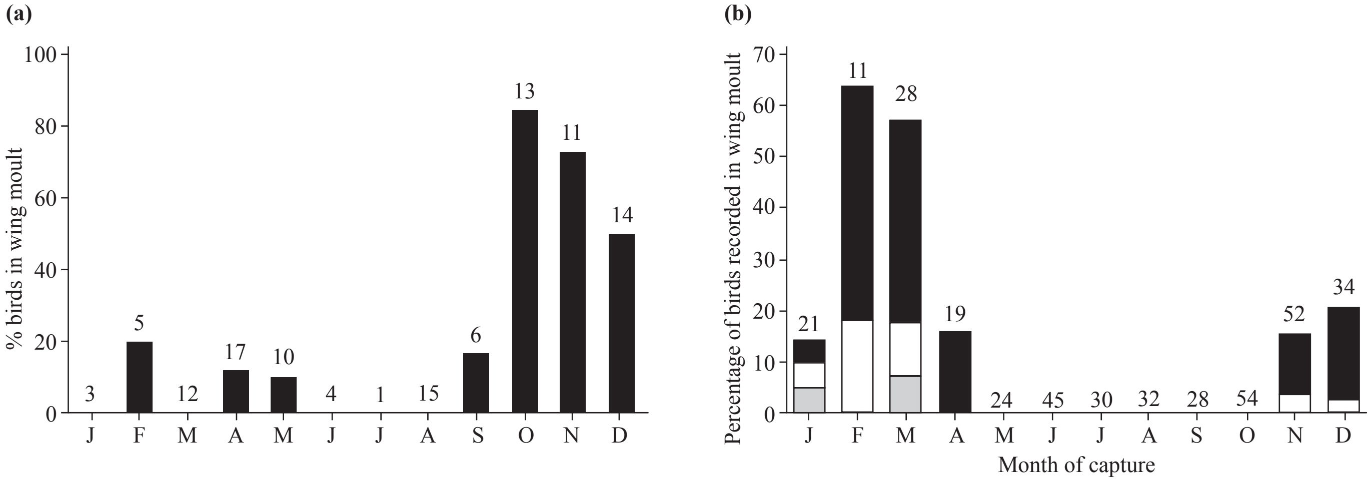

Figure 2. *Percentage of Mangrove Gerygones caught in each month that showed active wing moult in (a) Darwin (n=111) and (b) Brisbane (n= 378) regions. Adults and immature birds not distinguished in Darwin; for Brisbane: black, adults (2+); white, immatures (2-); grey, juveniles (1). Values above the histogram bars are monthly totals caught, including recaptures (n).*

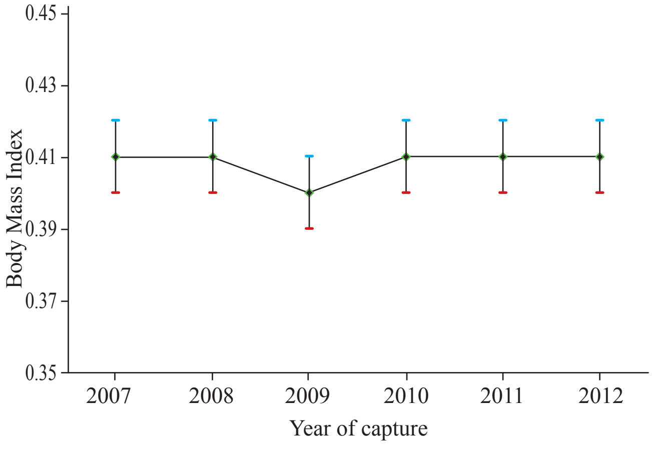

Figure 3. *Annual adjusted body mass index for Mangrove Gerygones caught between 2007 and 2012 in Brisbane. Data combined for all age and sex categories. Bars represent standard errors.*

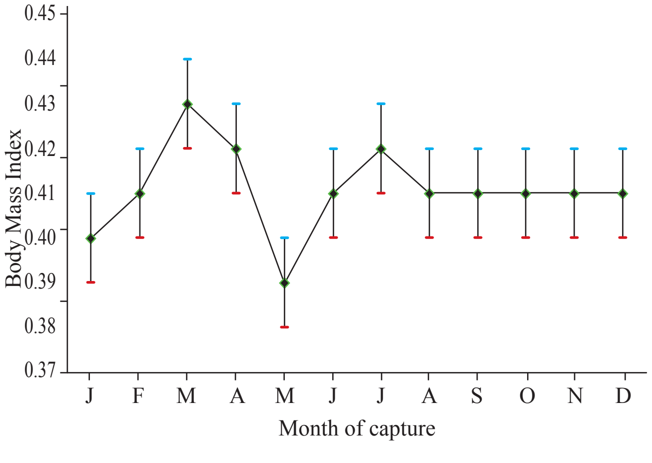

Figure 4. *Mean monthly adjusted body mass index for Mangrove Gerygones caught between 2007 and 2012. Data combined for all age and sex categories. Bars represent standard errors.*

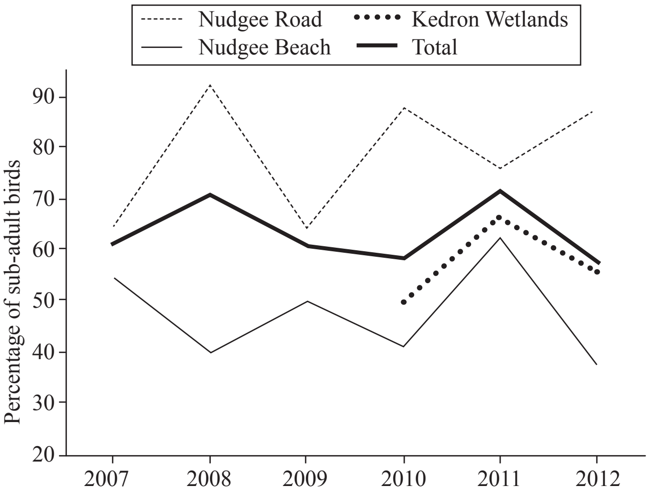

Figure 5. *Mean annual percentage of sub-adult Mangrove Gerygones banded at each location in each year of the study in Brisbane.*

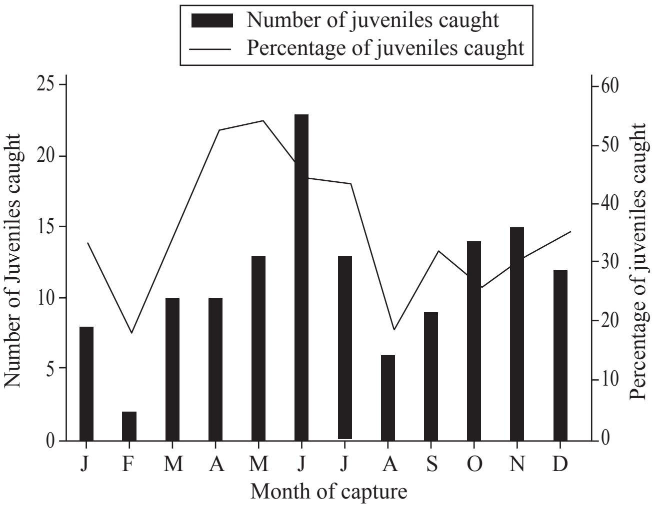

Figure 6. *Number of juvenile (age code 1) Mangrove Gerygones caught in each month of the study period in Brisbane (bars) and expressed as a percentage of the total birds caught in that month in all years (line).*

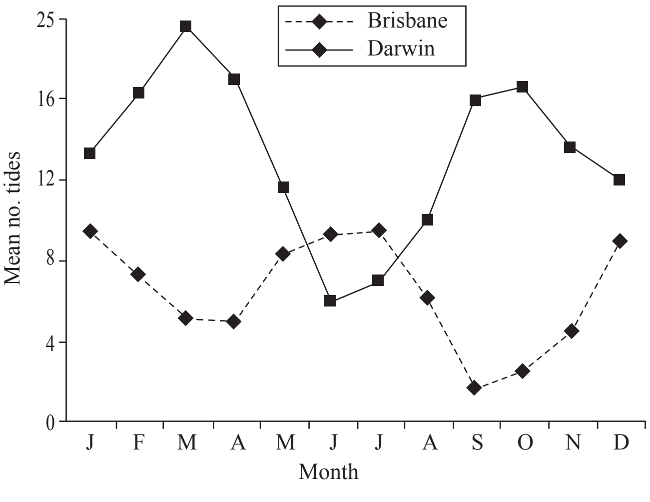

Figure 7. *Mean number of high spring tides by month for (a) Darwin Harbour, 1986-2009, where high spring tide => 7.0 m; and (b) Brisbane, 2007-2012, where high spring tide =>2.4 m. Source of data, Australian Bureau of Meteorology, December 2018.*

late dry season (August), when the abundance of *Anopheles* mosquitoes is also highest (Russell 1987; Franklin and Whelan 2009). The abundance of the Northern Salt-marsh Mosquito *Aides vigilax*, on the other hand, peaks when high tides and rain events coincide, mainly during the 'build-up' (September-November) (Jacups *et al.* 2011). Sessile insects in mangroves around Darwin also showed a biannual pattern of abundance, peaking in July and October (Mohd-Azlan *et al.* 2014).

The bimodal pattern of abundance of small insects in Darwin cannot be explained solely by rainfall, which is unimodal (see Fig. 1), but may be related to the seasonality of high spring tides which inundate salt flats (Noske 2013). The frequency of such tides is markedly biannual, being most frequent in March-April and September-October, and least frequent in June-July (Fig. 7). The frequency of high spring tides in Brisbane also shows a biannual pattern, but it is the converse of the pattern in Darwin, with peaks in June-July and December-January, about 2-3 months after the corresponding peaks in Darwin (Fig. 7). As gerygone fledglings in Darwin are probably most numerous in May and October, the Brisbane population appears to lag about 1-2 months behind the Darwin population in breeding phenology.

In Brisbane, the proportion of juveniles was higher at the less frequently inundated than at the regularly inundated (intertidal) sites. As there was no evidence of movements among sites (Coleman and Noske 2017), this disparity does not seem to be due to the dispersal of juveniles from the former to the latter habitat, although if juvenile birds forage in a different stratum of the vegetation it is possible that their dispersal could be undetected with the sampling methods used. It seems more likely, however, that the disparity reflects higher breeding success in the less frequently inundated sites. It is noteworthy that in Darwin and the Top End generally, this species shows a distinct preference for infrequently inundated mangroves surrounding salt flats, whereas the Large-billed Gerygone prefers taller, frequently inundated mangroves along tidal creeks (Noske 1996; Mulyani 2004).

Moult and Adjusted Body Mass

Like breeding, moulting is quite energy-consuming, so overlap in the timing of moult and breeding is rare in temperate birds (Ginn and Melville 1983; Barta *et al.* 2006) and in most Australian species studied to date, although there are exceptions (Ford 1980; Gardner *et al.* 2008). In Darwin, the incidence of primary wing moult among Mangrove Gerygones peaked in October, overlapping with the second annual pulse of egg-laying, but one month after its September peak (Mulyani 2004). Primary moult was still prevalent in birds captured in November, and to a lesser extent December, but egg-laying was not recorded in either of these months. In January and February, most birds had new primaries with little wear, but by March primaries began showing slight to moderate wear. Four birds showed active primary moult in the first five months of the year – one in February, two in April and one in May. The latter two months correspond to the first annual peak in egg-laying, so it is possible that one or more of these individuals were immature birds hatched during the second annual breeding pulse and undergoing their first moult. Moreover, the absence of birds showing wing moult in the months after the first annual breeding pulse suggests that post-breeding moult is largely limited to the second pulse.

In Brisbane, the earliest records of wing moult were in November, coinciding with the spring peak in the occurrence of juveniles. However, the months with the highest proportions of adults showing wing moult were February and March, 3-4 months after that peak and 4 months before the 'winter peak in juveniles'. Thus, although the Brisbane population appears to lag about 1-2 months behind the Darwin population in breeding phenology (see above), moult appears to lag by c.4 months (cf. Fig. 3a and 3b).

The apparently protracted period over which Mangrove Gerygones moult their primaries in Brisbane is consistent with a long breeding season, as suggested by the year-round presence of juveniles. Virtually all (>95%) the birds recorded in primary moult were adults or sub-adults entering their first complete moult. Notwithstanding the possibility that the age of some birds was incorrectly assessed at the time of banding, the small number of juveniles recorded in moult supports the conclusion of Higgins and Peter (2002) that juvenile birds undergo only a partial post-juvenile moult. Only nine (20%) of the 46 birds recorded as having obvious cloacal protuberances or brood patches were in wing moult, suggesting that in most cases adult birds moult either before or after breeding, rather than the two activities overlapping or occurring concurrently. This supports the suggestion by Higgins and Peter (2002) that adult moult typically occurs post-breeding.

Adjusted body mass in Brisbane was greatest just after moulting (when birds were presumably not breeding) and lowest in May (when the proportion of sub-adults was highest).

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Abstracts, ABSA Conference

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Painted Honeyeaters - nomads or migrants?

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A banding project was initiated in September 2017 at a small (~1 ha) patch of Weeping Myall *Acacia pendula* woodland heavily infested with Grey Mistletoe *Amyema quandang* just north-west of Ungarie (33.6415° S, 146.9747° E), central NSW. The site had been identified as a hotspot for Painted Honeyeaters *Grantiella picta*, which are a specialist frugivores that strongly favour the fruit of this mistletoe. The aim of the project was to study the ecology of this poorly known species (listed as Vulnerable), particularly the question of whether they return to the same site each year after their annual movement north (to inland Queensland) over winter. The study included colour marking of individual Painted Honeyeaters to increase the data return from banded individuals. To date, 19 banding trips have been made to the site, with 430 birds of 34 species being banded and 94 subsequent recaptures being made. Forty-five Painted Honeyeaters have been banded, with 7 recaptures plus 23 re-sightings of colour-marked individuals being made. Of the 39 Painted Honeyeaters banded in the first summer at the site (2017-18), six returned to the same location in the following summer (2018-19), suggesting that at least some degree of site fidelity is shown by this species. Our preliminary conclusion is that small patches of high-quality habitat, such as this site, constitute a very important resource for Painted Honeyeaters, which are present in substantial numbers and breed at the site, despite intense competition for the food resource from other frugivores, such as Mistletoebirds *Dicaeum hirundaceum*. We note that habitat patches like this one are thinly dispersed and are rarely subject to formal protection in National Parks and Nature Reserves. Obtaining a better understanding of how Painted Honeyeaters utilise such habitat patches across their entire annual range and identifying key patches for protection is critical to developing an effective conservation strategy for this iconic honeyeater species.

A new digital tool for managing and analysing bird banding and other ornithological data

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The process of banding and recapturing birds generates a vast and valuable source of ecological data. Unfortunately, data collection, curation and storage protocols vary wildly both within and among countries, severely limiting the usefulness of these data for addressing research questions and informing conservation decisions. Here, we describe a digital tool that we have developed that is highly customisable, relational and which can be used by individual bird banders to safely store, explore and visualise their bird banding data. The quality of the summary data and data visualisations that we can produce depends entirely on the type and quality of data that is inputted into the system, providing a positive reinforcement mechanism that will help promote the collection of high-quality data that are consistent across banders. Ultimately, we hope that this tool will provide new capabilities for, and enhance the experience of, individual bird banders, as well as increase the quality, safety and useability of bird banding data both in Australia and overseas. More details of the digital tool can be obtained from the authors.

The strategic importance of the Lower Hunter Valley woodlands

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The woodlands of temperate south-eastern Australia are among the most endangered ecosystems in the country. This is because between 80-85% of them have been cleared, with much of the remaining 15-20% being highly fragmented and degraded, which severely diminishes their ability to provide habitat for obligate woodland bird species. The woodland bird assemblage that thrives in these temperate forests comprises a suite of species that are showing declines across the board, with up to 20% of them already being considered threatened.

The dry open forests of the Lower Hunter Valley (situated in the Cessnock LGA) are large remnants of lowland forests that were, perhaps ironically, retained to support the underground coal mines for which the area is well known. As a result, these large, intact remnants provide habitat for a large range of threatened and declining bird species, as well many other flora and fauna species. However, it is not just the fact that they are remnants in an over-cleared landscape that makes these forests so diverse and important. They are situated at the eastern extent of the broad, west-sweeping Hunter Valley, which itself is a haven for threatened woodland birds and has a very strong “western influence” in its biodiversity. This influence is derived from the Goulburn River catchment, which makes up 40% of the Hunter River catchment, due to there being a distinct gap in the Great Dividing Range at a very westerly longitude (e.g. Ulan is as far inland as Gunnedah).

This “western influence” stretches all the way to the Lower Hunter woodlands and in effect they are a large remnant containing habitats resembling those found on the western slopes of New South Wales, but all within 40km of the coast. Hence, not only are they very diverse and offer habitat for a range of threatened species, but they are also strategically important in the light of contemporary threats to woodland birds. As they are large, forested remnants with very minor fragmentation, they are largely Noisy Miner *Manorhina melanocephala*-free. Further, being close to the coast they potentially will be more resilient to the future impacts of climate change and associated severe droughts.

Rufous Scrub-birds in the Gloucester Tops, New South Wales

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A study of the Rufous Scrub-bird *Atrichornis rufescens* in the Gloucester Tops (32.0662° S, 151.6196° E) was initially focussed on monitoring the status of the population within an area known to be core habitat for the species, located at 1,100-1,300m altitude. The study now includes investigations into the behaviour of individual birds.

The density of territories within the core habitat was found to resemble that reported in a previous study in 1980-81, suggesting that the Gloucester Tops population is stable. However, birds are no longer recorded at altitudes below 1,000m where previously some territories were known to occur. When spring conditions were dry, many Rufous Scrub-birds ceased advertising their territories and hence might not have bred. After a major fire in 2010, it took six years for any Scrub-birds to reappear in the area which had been burnt, and an additional year before a male established a territory.

Automated recording units (ARUs) are being used to investigate daily and seasonal variability in the singing behaviour of male Rufous Scrub-birds. A rapid, semi-automated method for analysing the recordings has been developed. This new capability will allow suspected territories to be checked thoroughly for the presence of a singing male. Males have been found to sing all day in the breeding season, although with occasional and unpredictable breaks. Outside of the breeding season, the rate at which they sing decreases markedly. Some results from the study of Rufous Scrub-bird singing behaviour are presented. The size of the singing area of the male Scrub-bird was small, with birds being restricted to singing areas of 0.5-1.7 ha. It is not known whether this corresponds to the size of the bird’s territory, as it is not yet possible to know the location of a Scrub-bird when it is not singing.

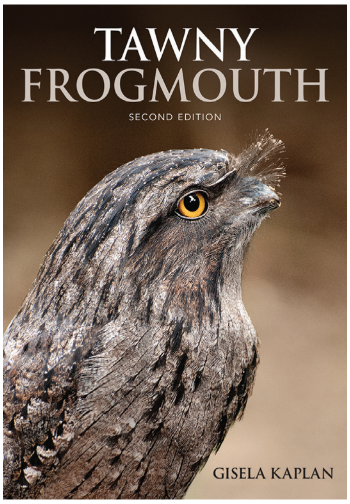
Initial results from a banding program are reported, including description of a method for catching male Rufous Scrub-birds in the breeding season. However, the method is less effective at other times of the year.

Other talks were given by:

Emily Mowat:
A year with the Albatrosses on Macquarie Island

Thomas Clarke:
Shorebird Habitat Restoration in the Hunter Estuary

Book Review



Tawny Frogmouth, 2nd Edition

Gisela Kaplan 2018. CSIRO Publishing. Soft-cover. 160 pp, black and white photographs. ISBN: 9781486308163. RRP $A 30.95

I must disclose at the very start that I am an enormous Tawny Frogmouth fan. Even after finishing a PhD on their ecology and behavior in 2016, my interest in them has never waned. So naturally I was delighted to see a follow-up to the first edition of the publication *Tawny Frogmouth* and even more delighted that I was asked to review this 2nd edition.

In the field of ecological research, long-term studies are both immensely valuable but unfortunately quite rare. Here, Gisela Kaplan, one of Australia's leading authorities on animal behaviour and native birds, provides a study of a single species spanning 20 years. In *Tawny Frogmouth*, Professor Kaplan provides important information on the behaviour and ecology of one of Australia's most elusive and interesting nocturnal bird species. The first edition of *Tawny Frogmouth* was published in 2007 by CSIRO as part of its Australian Natural History Series. Based primarily on 20 years of systematic observations, scientific writings and information from bird surveys, it continues to hold enormous and wide appeal to readers.

Particularly appealing is the overall style of the book. Scientific facts and information are punctuated with Professor Kaplan's often affectionate comments and personal observations about Tawny Frogmouths. Whilst she received some criticism regarding her anthropomorphizing of the species e.g. attributing to them human qualities, such as emotions and loyalty, I think that this is one of the factors that have led to the book's wide appeal, readability and a second edition.

In this second edition, Professor Kaplan continues in a similar vein, integrating scientific research and her own long-term observations and knowledge to reveal many more interesting and appealing facts about one of Australia's most unusual birds. Whether you are a scientific researcher, have an interest in birds and avian behaviour or just enjoy observing and listening to birds, this book will have great appeal for you.

The second edition provides an excellent update of new knowledge gained since the first edition. Since the mid-2000's, research has provided new and interesting facts about the Tawny Frogmouth; particularly, it has yielded new information about breeding behavior, habitat use and the species' response to habitat fragmentation caused by urbanization. A welcome addition to the "what and where they are" chapter is a table showing nightjar and frogmouth family groups separated into geographical regions across the southern hemisphere. This table will be especially useful for avian researchers or to those who are curious about the evolutionary relationships between these two important groups.

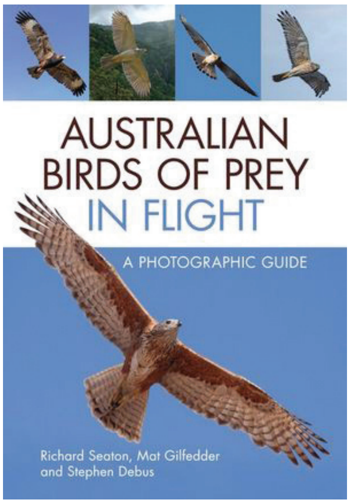
The organization of this edition resembles that of the first edition in that facts and information are organized into the following chapters: what and where Tawny Frogmouths are, general anatomy, the brain and the senses, daily life and adaptations, feeding and territory, bonding and breeding, development and emotions, vocal behavior and communication. This allows the reader to easily and quickly navigate to the section of most interest. Another welcome addition is the inclusion of subheadings under these main headings, providing greater detail of what aspects will be covered. Whilst the photographs are of good quality and are well produced, I was disappointed that aside from the front and back covers, all the photographs are black and white. The first edition contained a substantial number of colour photographs which illustrated so well how Tawny Frogmouth plumage is one of the species' most important attributes for avoiding detection from predators.

One minor annoyance is the organization of references. Instead of the format used here where references occur at the end of the book for ease of reading, I would much prefer a reference section at the end of each chapter.

The threats that rapid and wide-scale urbanization pose to global biodiversity is acknowledged in the book's epilogue. Increasingly these days we read how more and more native species are adversely affected by, and are in decline because of, habitat loss and fragmentation by urbanization. Here we finish on a happier note. Professor Kaplan paints a more optimistic future for the Tawny Frogmouth, attributing its apparent resilience to urbanization to its generalist habitat requirements and behavioural adaptations to urban living. My final comment is to commend this book to readers, as in my opinion it makes an important contribution to our knowledge of, and appreciation for, a unique Australian bird species.

Marian Weaving

Book Review



Australian Birds of Prey in Flight, a photographic guide. Richard Seaton, Mat Gilfedder and Stephen Debus. 2019. CSIRO Publishing. Paperback, 256 pp. ISBN 9781486308668. RRP AU$39.99.

When Richard Seaton and Stephen Debus told me of their idea to publish a book of photographs of Australian birds of prey in flight, I was most interested. As a raptor enthusiast and member of the Australasian Raptor Association, I frequently meet people who struggle to identify these amazing birds. Some raptors can even be difficult to identify when viewed in good light while perching, but when in flight many can be most challenging to identify. Field guides are of some assistance, but can only illustrate the 'typical' poses, and something more is required. This 'something more' is this book, which illustrates, with several of photos of each species, the twenty-four raptors native to Australia and the two vagrants recorded here. With the echoes of Paul Kelly's song 'From little things big things grow' ringing in my ears, I consider the resulting book to be much more than I expected when first mooted. I expected that a small number of raptor enthusiasts and photographers would have contributed images, but the list of contributors is impressive. As an ecologist with a camera, I also submitted a few photos, but in retrospect they were nothing like the quality of those in the finished product.

There is a quick reference plate at the beginning of the book which shows a single photo of each species with the relevant species profile page number. Then there is a forward by Hugh Possingham, the Chief Scientist of the Nature Conservancy and Australian Research Council Laureate Fellow at the University of Queensland, followed by acknowledgements and an introduction which includes tips on using the book and discusses GISS (General Impression of Size and Shape). The individual species' profiles follow; these include six photos of each species in flight, with supporting text concentrating on identification characters, and a distribution map.

A particularly valuable feature is the comparison with other species that can be confused with the one being described. Details here reminded me of my own experience with very pale Brown Falcons *Falco berigora* that were at first thought to be Grey Falcons *F. hypoleucos*. Luckily someone photographed them and the experts could then correctly identify them. Nankeen Kestrels *F. cenchroides* soaring at a great height can also look a little like Grey Falcons. Species such as Brown Falcons and Nankeen Kestrels can look quite different in the arid zone where they are much paler. Of interest also, are the sections on identifying age and sex. Young raptors can appear very different to adults, particularly in colouration and sometimes markings. Towards the back of the book is a section on species comparisons, where black and white photographs are used to directly compare species that are easily confused.

With this guide to raptors in flight with them, birdwatchers can now have a good chance of identifying those often hard-to-identify raptors gliding, hovering or soaring overhead. I recommend this attractive little book with its great photographs to anyone who is interested in birds, as to lump raptors in the 'too hard basket' along with 'little brown birds' and shorebirds is to miss out on a whole world of remarkable, beautiful and powerful, but delicate, birds. I commend this book to anyone with even the slightest interest in birds and it is a must for those keen to sort out the raptors of Australia.

Greg Clancy
Coutts Crossing, NSW

Corella 2019, 43: 118-120

RECOVERY ROUND-UP

This section is prepared with the co-operation of the Secretary, Australian Bird and Bat Banding Schemes, Australian Nature Conservation Agency. The recoveries are only a selection of the thousands received each year; they are not a complete list and should not be analysed in full or part without prior consent of the banders concerned. Longevity and distance records refer to the ABBBS unless otherwise stated. The distance is the shortest distance in kilometres along the direct line joining the place of banding and recovery; the compass direction refers to the same direct line. (There is no implication regarding the distance flown or the route followed by the bird). Where available ABBBS age codes have been included in the banding data.

Recovery or longevity items may be submitted directly to me whereupon their merits for inclusion will be considered.

Hon. Editor

The following abbreviations appear in this issue:

ANPWS-DOE –ANPWS Coral Sea Project.

AWSG - Australasian Wader Study Group.

Australian Brush-turkey *Alectura lathami*

132-31722. Adult (2-) banded by J. T. Coleman at Iron Range National Park, Cape York Peninsula, Qld. on 23 Nov. 1911. Recaptured, released alive with band at banding place by R. P. Allen on 21 Nov. 2018, 7 years after banding.

Wedge-tailed Shearwater *Ardenna pacifica*

162-44325. Adult (1+) banded by L.W. Nicholson on Varanus Island and Satellites, WA on 8 Dec. 1998. Recaptured, released alive with band at banding place on 1 Nov. 2018, over 19 years, 10 months after banding.

Great Frigatebird *Fregata minor*

210-03689. Nestling banded by ANPWS-DOE Coral Sea Project at Coringa Islet, Coral Sea, Qld. on 18 Sep. 1985. Recovered sick or injured, was mercy killed at South Mission Beach, Qld. on 4 Feb. 2019, over 33 years, 4 months after banding. 422 km WSW.

(This is the oldest and longest movement recorded for the species.)

Royal Spoonbill *Platalea regia*

131-70053. Nestling banded by C.D.T. Minton at Torry Plains Station, near Balranald, NSW on 10 Dec. 1996. Recovered sick, later died at Tarwoona Road, 27 km NW of Texas, NSW by M. Bassington on 18 Jan. 2019, over 22 years, 1 month after banding. 915 km NE.

(This is the oldest recorded for the species.)

Australian Pied Oystercatcher *Haematopus longirostris*

101-27751 plus engraved leg flag: L Yellow D5. Nestling banded by G.P. Clancy at Brunswick River, Brunswick Heads, NSW on 30 Oct. 2007. Colour marking sighted in field, band number inferred at Bonville Creek, south of Sawtell, NSW on 3 Jun. 2019, over 11 years, 7 month after banding. 214 km S.

101-27759 plus engraved leg flag: R Yellow E4. Nestling banded by G.P. Clancy at Bombing Range Site 1, Bundjalung National Park, NSW on 21 Nov. 2007. Colour marking sighted in field, band number inferred at Killick Beach near Crescent Head, NSW on 25 Dec. 2018, over 11 years, 1 month after banding. 224 km S.

Black-winged Stilt *Himantopus himantopus*

083-22839. Adult (2) banded by AWSG at Beaches Crab Creek Road, Roebuck Bay, Broome on 1 Aug. 2006. Recaptured, released alive with band at banding place on 19 Feb. 2019, over 12 years, 5 months after banding.

Masked Lapwing *Vanellus miles*

083-02406. Nestling banded by A. N. Boyle at Lake McIntyre, Millicent, SA on 8 Nov. 1998. Band number read in field twice (bird not trapped) at banding place the last occasion on 5 Jul. 2019, over 20 years, 7 months after banding

(This is the oldest recorded for the species.)

Bar-tailed Godwit *Limosa lapponica*

072-55884. Adult (2) banded by AWSG at Beaches Crab Creek Road, Roebuck Bay, Broome on 6 Mar. 1996. Recaptured, released alive with band at banding place twice the last occasion on 22 Feb. 2019, over 22 years, 11 months after banding.

Ruddy Turnstone *Arenaria interpres*

052-40145. Immature (1) banded by AWSG at Beaches Crab Creek Road, Roebuck Bay, Broome on 26 Jun. 2005. Recaptured, released alive with band at banding place three times the last occassion on 21 Feb. 2019, over 13 years, 8 months after banding.

(This bird has also had its leg flag sighted 26 times in areas adjacent to the banding place and three times in Taiwan in 2014.)

Great Knot *Calidris tenuirostris*

062-09414. Adult (1+) banded by AWSG at Beaches Crab Creek Road, Roebuck Bay, Broome, WA on 28 Jul. 1994. Recaptured, released alive with band at banding place three times the last occasion on 22 Feb. 2019, over 24 years, 7 months after banding.

(This bird has also had its leg flag sighted 102 times in areas adjacent to the banding place)

(This is the oldest recorded for the species.)

Red Knot *Calidris canutus*

(a) C78481* plus leg flag white BJR. Adult (3+) banded by A. Riegen at Miranda, Firth of Thames, New Zealand (37^{0}11'S 175^{0}20'E) on 18 Oct. 2008. Leg flag recorded seven times in the Firth of Thames, NZ area until the 26 Feb. 2011. Recaptured, released alive with band at Thompsons Beach, Third Creek, SA (34^{0}29'S 138^{0}17'E) on 22 Nov. 2017, over 9 years 11 months after banding. 3332 km WSW.

*New Zealand Banding Scheme band.

(b) 051-28979 plus colour bands: Lbyy. Adult (2+) banded by V.W. Smith at Princes Royal Harbour, Albany, WA on 17 Mar. 2001. Recaptured, released alive with band at Beaches Crab Creek Road, Roebuck Bay, Broome, WA on 23 Sep. 2018, over 17 years, 6 months after banding. 1950 km N.

(c) 052-00657. Imature (1) banded by AWSG at Beaches Crab Creek Road, Roebuck Bay, Broome on 30 May. 2000. Recaptured, released alive with band at 80 Mile Beach, WA on 12 Feb. 2019, over 18 years, 8 months after banding.

Laughing Kookaburra *Dacelo novaeguineae*

200-07169. Adult (1+) male banded by A. J. Leishman at The Australian Botanic Garden, Mount Annan, near Campbelltown, NSW on 28 Mar. 2009. Recaptured, released alive with band at banding place twice, the last occasion on 11 Dec. 2018, over 9 years, 8 months after banding.

Superb Fairy-wren *Malurus cyaneus*

019-79986. Adult (1+) female banded by J. W. Hardy at Scheyville National Park, near Windsor, NSW, on 11 Sep. 2011. Recaptured, released alive at banding place three times the last occasion by A. Hunt on 24 Mar. 2019, over 7 years, 7 months after banding.

Tropical Scrubwren *Sericornis beccarii*

019-40405. Adult (1+) banded by R. P. Allen at Iron Range National Park, Cape York Peninsula, Qld. on 22 Nov. 2005. Recaptured, released alive with band at banding place by R. P. Allen on 20 Nov. 2018, 13 years after banding.

(This is the oldest recorded for the species.)

026-60699. Adult (1+) banded by J. T. Coleman at Iron Range National Park, Cape York Peninsula, Qld. on 12 Nov. 2008. Recaptured, released alive with band at banding by R. P. Allen on 23 Nov. 2018, 10 years after banding.

Fairy Gerygone *Gerygone palpebrosa*

019-75092. Adult (2+) banded by A. J. Leishman at Iron Range National Park, Cape York Peninsula, Qld. on 20 Nov. 2011. Recaptured, released alive with band at banding place by E. Mulder on 21 Nov. 2018, 7 years after banding.

(This is the oldest recorded for the species.)

Striated Thornbill *Acanthiza lineata*

019-33702. Adult (2+) banded by A. J. Leishman at Munghorn Gap Nature Reserve, near Mudgee, NSW on 2 Oct. 2005. Recaptured, released alive with band at banding place four times, the last occasion by G. Fry on 23 Aug. 2019, over 13 years, 1 month after banding.

(The bird was also banded with band no. 019-95213.)

Eastern Spinebill *Acanthorhynchus tenuirostris*

018-87226. Juvenile banded by G. Fry at Munghorn Gap Nature Reserve, near Mudgee, NSW on 19 Feb. 2009. Recaptured, released alive with band at banding place ten times, the last occasion on 23 Aug. 2019, over 10 years, 6 month after banding.

(The bird was also banded with band no. 019-95835.)

Lewin's Honeyeater *Meliphaga lewinii*

043-00381. Immature (1) banded by G. P. Clancy at Iluka Nature Reserve, Iluka NSW on 26 Aug. 2012. Recaptured, released alive with band at banding place on 21 Sep. 2018, over 6 years after banding.

Yellow-spotted Honeyeater *Meliphaga notata*

042-49619. Adult (1+) banded by S. Rae at Iron Range National Park, Cape York Peninsula, Qld. on 9 Nov. 2008. Recaptured, released alive with band at banding place by P. T. Webster on 19 Nov. 2018, 10 years after banding.

042-59738. Adult (2+) banded by J. T. Coleman at Iron Range National Park, Cape York Peninsula, Qld. on 18 Nov. 2011. Recaptured, released alive with band at banding place twice, the last occasion by J. T. Coleman on 20 Nov. 2018, 7 years after banding.

Singing Honeyeater *Lichenostomus virescens*

036-33021. Immature (1) banded by J. E. Lewis at Minyirr Coastal Park near Margin, WA on 29 Jan. 2005. Recovered dead (collided with building, non-wire fence, immobile vehicle) at banding place on 18 Mar. 2018, over 13 years, 1 month after banding.

(This is the oldest recorded for the species.)

Fuscous Honeyeater *Lichenostomus fuscus*

026-30627. Adult (2+) male banded by J. Farrell at Scheyville National Park near Windsor, NSW on 14 Oct. 2007. Recaptured, released alive with band at banding place by A. Hunt on 28 Jul. 2019, over 11 years, 9 months after banding.

White-plumed Honeyeater *Lichenostomus penicillatus*

026-10984. Adult (2+) banded by G. Fry at Munghorn Gap Nature Reserve, Mudgee, NSW on 5 Aug. 2009. Recaptured, released alive with band at banding place twice, the last occasion by R. Kyte on 24 Aug. 2019, over 10 years after banding.

(The bird was also banded with band no. 027-35224.)

Tawny-breasted Honeyeater *Xanthotis flaviventer*

052-06719. Adult (1+) banded by S. Newberry at Iron Range National Park, Cape York Peninsula, Qld. on 21 Nov. 2005. Recaptured, released alive with band at banding place by R. P. Allen on 21 Nov. 2018, 13 years after banding.

(This is the oldest recorded for the species.)

Golden Whistler *Pachycephala pectoralis*

(a) 034-37388. Adult (2+) banded by A & A Leishman at Camden Airport, NSW on 27 Aug. 2007. Recaptured, released alive with band four times (full male plumage) the last occasion on 18 Dec. 2018, over 11 years 2 months after banding.

(The bird was also banded with band no. 035-26650.)

(b) 034-37389. Adult (2+) female banded by A. & A. Leishman at Camden Airport, NSW on 10 Sep. 2007. Recaptured, released alive with two bands at banding place six times the last occasion on 14 Jan. 2019, over 11 years, 4 months after banding.

(The bird was also banded with band no. 035-26621.)

Little Shrike-thrush *Colluricincla megarhyncha*

(a) 041-05866. Adult (1+) banded by C. Rich at Iron Range National Park, Cape York Peninsula, Qld. on 17 Nov. 1990. Recaptured, released alive with band at banding place three times, the last occasion by P. T. Webster on 19 Nov. 2018, 28 years after banding.

(This is the oldest recorded for the species.)

(b) 042-02190. Adult (1+) banded by B. Chaffey at Iron Range National Park, Cape York Peninsula, Qld. on 18 Nov. 2002. Recaptured, released alive with band at banding place by P. T. Webster on 19 Nov. 2018, 16 years after banding.

(c) 042-10740. Adult (1+) banded by P. Ewin at Iron Range National Park, Cape York Peninsula, Qld. on 6 Nov. 1999. Recaptured, released alive with band at banding place twice, the last occasion by R. P. Allen on 19 Nov. 2018, 19 years after banding.

(d) 042-39014. Adult (1+) banded by B. Pascoe at Iron Range National Park, Cape York Peninsula, Qld. on 21 Nov. 2002. Recaptured, released alive with band at banding place four times, the last occasion by J. T. Coleman on 20 Nov. 2018, 16 years after banding.

Torresian Crow *Corvus orru*

101-37622. Immature (1) banded by J. T. Coleman at Shailer Park, Qld. on 3 Feb. 2018. Recovered dead at Robertson, Brisbane, Qld. on 9 Aug. 2018. 14 km WSW.

Spectacled Monarch *Symposiarchus trivirgatus*

(a) 024-82081. Adult (2+) banded by W. Goulding at Iron Range National Park, Cape York Peninsula, Qld. on 9 Nov. 2008. Recaptured, released alive with band at banding place by P. T. Webster on 19 Nov. 2018, 10 years after banding.

(b) 025-83025. Adult (1+) banded by S. Newberry at Iron Range National Park, Cape York Peninsula, Qld. on 18 Nov. 2005. Recaptured, released alive with band at banding place twice, the last occasion by A. Hunt on 20 Nov. 2018, 13 years after banding.

(c) 026-28606. Adult (2+) banded by C. Rich at Iron Range National Park, Cape York Peninsula, Qld. on 21 Nov. 2005. Recaptured, released alive with band at banding place by P. T. Webster on 19 Nov. 2018, 13 years after banding.

Magnificent Riflebird *Ptiloris magnificus*

073-33162. Adult (1+) banded by J. T. Coleman at Iron Range National Park, Cape York Peninsula, Qld. on 9 Nov. 2008. Recaptured, released alive with band at banding place on 20 Nov. 2018, 10 years after banding.

White-faced Robin *Tregellasia leucops*

(a) 026-09481. Adult (1+) banded by B. Pascoe at Iron Range National Park, Cape York Peninsula, Qld. on 21 Nov. 2002. Recaptured, released alive with band at banding place by J. T. Coleman on 20 Nov. 2018, 16 years after banding.

(b) 026-35607. Adult (2-) banded by A. Leavesley at Iron Range National Park, Cape York Peninsula, Qld. on 20 Nov. 2005. Recaptured, released alive with band at banding place by J. T. Coleman on 20 Nov. 2018, 13 years after banding.

Eastern Yellow Robin *Eopsaltria australis*

(a) 024-94110. Adult (1+) male banded by J. W. Hardy at Scheyville National Park, near Windsor, NSW, on 12 Aug. 2007. Recaptured, released alive with band at banding place five times the last occasion by A. Hunt on 24 Mar. 2019, over 11 years, 7 months after banding.

(b) 025-79538. Adult (1+) banded by A. Overs at Iluka Nature Reserve, Iluka, NSW on 5 May 2009. Retrapped, released alive with band at banding place four times the last occasion by G. P. Clancy on 12 Aug. 2019, over 10 years, 3 months after banding.

(c) 025-97517. Adult (2+) banded by A. J. Leishman at Iluka Nature Reserve, Iluka, NSW on 1 Jul. 2007. Retrapped, released alive with band at banding place twice the last occasion by G. P. Clancy on 21 Sep. 2018, over 11 years, 2 months after banding.

Common Myna *Sturnus tristis*

073-48272. Adult (1+) male banded by J. T. Coleman at Shailer Park, Qld. on 7 Jan. 2006. Recovered dead near banding place on 11 Sep. 2018, over 11 years, 9 months after banding.

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Notice to Contributors

Manuscripts relating to any form of avian research will be considered for publication. Field studies are preferred, whether they involve identification of individual birds, as by banding, or are on unmarked individuals. Some broad areas of research which do not necessarily require individual identification include morphometric analyses, techniques, species diversity and density studies, as well as behavioural investigations. Behavioural, plumage and breeding studies that are conducted in captivity are also welcome, but must provide basic ornithological knowledge rather than just having avicultural interest.

Manuscripts are classified as either major articles (more than 1500 words) or minor articles (500 to 1500 words). Minor articles need no summary. Shorter notes relating to almost any aspect of ornithology are welcomed, but must adhere to the aims of the Association. Species lists or sightings which are not discussed in relation to historical evidence or scientific parameters are not suitable for publication in *Corella.* Authors proposing to prepare Seabird Island items should contact the Assistant Editor Seabird Islands.

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Contributors are requested to observe the following points when submitting articles and notes for publication in *Corella*.

Manuscripts:

A guide to the format required for tables, figures and manuscripts can be attained by reference to a recent edition of the journal and more specifically to the Publication Style found on the ABSA website.

Articles or notes should be sent via email to the editor as a .doc or .docx or .rtf file. Double spacing is required. Margins of not less than 25 mm width at the left-hand side and top, with similar or slightly smaller at the right-hand side of the page are required. Line numbers should be added consecutively throughout the manuscript.

All pages of the manuscript must be numbered consecutively, including those containing references, tables and captions to illustrations, the latter placed in after the text. No underlining and no abbreviations should be used within the text (except those outlined in the 'Guide to Authors'). Values should be given in SI units e.g. 100 mm, 20 km.

The *Style Manual for Authors, Editors and Printers* (6th edition 2002; John Wiley & Sons Australia, Ltd.) is the guide for this journal. Spelling generally follows the Macquarie Dictionary. Authors are urged to conduct a spelling and grammar check before submitting their manuscript.

Nomenclature and Classifications follow:

Christidis, L. and Boles, W. E. (2008). *Systematics and Taxonomy of Australian Birds*. CSIRO, Collingwood, Victoria.

Proper nouns, particularly place and bird names must commence with a capital letter.

Headings are as follows:	**HEADING – capitals and bold** (e.g. **RESULTS**)
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Referencing:

References to other articles should be shown in the text – '. . . Bell and Ferrier (1985) stated that . . .'or '…. this is consistent with other studies (Jones 1983; Bell and Ferrier 1985).'– and in the Reference Section as:

Bell, H. L. and Ferrier, S. (1985). The reliability of estimates of density from transect counts. *Corella* **9**: 3-13.

Jones, J. C. (1983). *Sampling Techniques in Ornithology*. Surrey Beatty and Sons, Chipping Norton, NSW.

Figures (Maps and Graphs) and Tables:

The printable area of the page is 18 cm x 24 cm; double column figures/tables will be 18 cm across; single column figures/tables will be 8.5 cm across; widths between one column and double column can also be accommodated.

The captions for figures should be typed on a page separate from the figure.

Maps

Maps should be clear and relevant to the study and can be submitted in a variety of formats (.tif, .eps, .pcx) but the recommended one is a high resolution .jpg file (colour is acceptable). In some instances simply listing the latitude and longitude may suffice instead of a published map. Maps should only show necessary information. Excessive labelling (including names of towns, roads, rivers) will clutter the figure making it difficult to locate key place names. Photocopies of original hand drawn maps are not suitable for publication. They should be submitted only initially. When the paper is accepted for publication, the originals must be submitted so that they can be scanned into an appropriate electronic format.

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Lines should be thick and dark and any fill used should show a clear distinction between sets of data (colour fills are acceptable). Borders around the graph and the key are not necessary. The recommended format is an .xls or .xlsx file – this makes it very easy to adjust fills, thickness of lines etc, if necessary.

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FOR MORE DETAILED INFORMATION OR ASSISTANCE IN THE PREPARATION OF FIGURES PLEASE CONTACT THE PRODUCTION EDITOR.

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Seabird Islands

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