Australian Field Ornithology 2015, **32**, 38–52

The ecology of the Australian sandstone *Meliphaga* honeyeater species

Eliot T. Miller[1,2]* *and Sarah K. Wagner*[3]

[1]Harris World Ecology Center, 1 University Boulevard, Department of Biology, University of Missouri, St Louis, Missouri 63121, United States of America
[2]Department of Biological Sciences, Macquarie University, Balaclava Road, North Ryde NSW 2109, Australia
[3]Ecology and Evolutionary Biology Department, Ramaley N122, University of Colorado, Boulder, Colorado 80309, United States of America
*Corresponding author. Email: eliotmiller@umsl.edu

Summary. Two of the five Australian *Meliphaga* species, the White-lined *M. albilineata* and Kimberley *M. fordiana* Honeyeaters, are endemic to sandstone habitats in the Northern Territory and Western Australia, respectively. Little is known of their ecology, and their taxonomic status remains debated. We addressed this information gap by studying the foraging ecology and interspecific interactions of both taxa in the field. When compared with other Australian honeyeaters, both species were infrequently found in flocks, and foraged low in the canopy. Within their respective local assemblages, however, the White-lined Honeyeater foraged relatively higher in the forest strata than most species, whereas the Kimberley Honeyeater foraged lower than all other co-occurring honeyeaters. The results presented here fill in some of the gaps in knowledge about these species' ecologies, and support the retention of the Kimberley Honeyeater as a distinct species.

Introduction

According to Christidis & Boles (2008), there are two species of *Meliphaga* honeyeaters in the Top End of the Northern Territory and the Kimberley in Western Australia, both of which are poorly known. One of these, the White-lined Honeyeater *M. albilineata*, was first collected in the early part of the twentieth century by William McLennan, while exploring the King River region in the Northern Territory. This taxon was initially named *Ptilotis albilineata* (White 1917a,b,c). To date, very little published information is available about this species (Schodde & Mason 1975), including almost nothing of its ecology beyond sparse details of breeding biology and some comments on its general foraging behaviour (Freeman 1971; Longmore 1983; Higgins *et al.* 2001). Though its presence is occasionally noted by birdwatchers in the Kakadu area, the White-lined Honeyeater has a reputation of being difficult to observe (Deignan 1964; Lendon 1966; Rix 1970; Freeman 1971; Schodde & Mason 1975).

The taxon now called the Kimberley Honeyeater *M. fordiana* was not known to science until 1972, when a bird then identified as *M. albilineata* was first noted on islands in the Bonaparte Archipelago and in the Mitchell River area of the Kimberley (Smith & Johnstone 1974; Smith *et al.* 1978). Schodde (1988) elevated this population to the level of subspecies (*M. a. fordiana*) based on small plumage differences, though these characters were later noted to overlap (Johnstone & Storr 2004). Christidis & Boles (2008) elevated it to the level of species based on large genetic distances between the taxa (Christidis & Schodde 1993; Norman *et al.* 2007), but this decision remains contentious (e.g. BirdLife International 2012). Like the White-lined Honeyeater, the Kimberley Honeyeater is considered difficult to observe (Smith & Johnstone 1974), and little is known about it (Ford 1978, 1987; Storr 1980; Johnstone & Burbidge 1991; Johnstone & Storr 2004).

We recently demonstrated that the taxa were completely separable based on elements of their vocalisations (Miller & Wagner 2014). Such differences do not necessarily merit recognising similar allopatric taxa ('allospecies': Mayr 1942) as unique species but, in combination with other differences such as those in morphology or ecology, recognition as separate species is warranted (Helbig *et al.* 2002; Edwards *et al.* 2005). White-lined and Kimberley Honeyeaters both occur in rugged sandstone country (see Figures 1–2), characterised by deep ravines, ledges, boulders, spinifex *Triodia* spp., sparse shrubs and scattered trees, and in adjacent woodland and riparian, paperbark, and monsoon forests (White 1917b; Deignan 1964; Lendon 1966; Rix 1970; Smith & Johnstone 1974; Schodde & Mason 1975; Ford 1978, 1987; Smith *et al.* 1978; Kikkawa *et al.* 1981; Woinarski 1993; Johnstone 1995). Though these are broadly similar environments, it remains unknown whether these taxa differ ecologically (e.g. in usage of different habitat types, food sources, interspecific interactions, and foraging behaviours).

We investigated the ecology of both taxa in an effort to address this lack of knowledge. Our work was carried out in the context of a larger study of the foraging ecology of the Australian Meliphagidae (ETM & SKW unpublished data). Here, we present information pertinent to these two taxa. To provide context, we also provide comparable information for the three other Australian *Meliphaga* species. Specifically, we report descriptions of the habitats where we found the species, quantitative foraging data, and interspecific interactions, including flocking behaviour. If, as suggested by differences in genetics and vocalisations, White-lined and Kimberley Honeyeaters are indeed sufficiently divergent to merit species status, they may also exhibit ecological differences in foraging and other behaviours. Conversely, allopatric congeners can forage similarly (Ford & Paton 1976), and this situation could characterise the sandstone *Meliphaga* honeyeaters. Inasmuch as the data allow, we draw such comparisons here. We consider the foraging data in a phylogenetic context, discuss the species' ecology with respect to other Meliphagidae species with which they were encountered, and make brief comments on the species status of the Kimberley Honeyeater.

Study areas and methods

We recorded data on foraging and other behaviour from dawn to dusk during all days in the field. As already noted, the present study is focussed on the two sandstone *Meliphaga* species, but we also present data for the three other Australian members of the genus to facilitate interpretation. We provide general study areas and dates for all *Meliphaga* species in Table 1, and we describe in detail the habitats of the sandstone species in the results. Here, we also detail the general study areas and dates for the sandstone species. On 17–19 August 2009 and 17–25 September 2011, we observed birds in Kakadu National Park, NT. Locations

Table 1. General study areas, co-ordinates, and dates of observations on foraging of the five Australian *Meliphaga* honeyeater species. NP = National Park; co-ordinates are latitude and longitude.

Species	*Site*	*Co-ordinates*	*Date(s)*
White-lined Honeyeater *Meliphaga albilineata*	Nourlangie Rock	12°52′S, 132°49′E	17–19 Aug. 2009 17–25 Sep. 2011
	Gunlom Falls	13°26′S, 132°25′E	17–25 Sep. 2011
Kimberley Honeyeater *Meliphaga fordiana*	Little Mertens Falls	14°49′S, 125°43′E	1–4 Oct. 2011 20–22 May 2014
	Mitchell Falls Lookout	14°49′S, 125°42′E	1–4 Oct. 2011 20–22 May 2014
Graceful Honeyeater *Meliphaga gracilis*	Murray Falls	18°08′S, 145°48′E	Late Oct. 2010
	Iron Range NP	12°40′S, 143°20′E	Early Nov. 2010
	Kingfisher Park, Julatten	16°35′S, 145°20′E	Mid Nov. 2010 Late Nov.– early Dec. 2011
	Mt Lewis NP	16°31′S, 145°16′E	Late Nov. 2011
Lewin's Honeyeater *Meliphaga lewinii*	Lane Cove NP	33°46′S, 151°07′E	Mid Jun. 2009
	Ku-Ring-Gai Chase NP	33°40′S, 151°16′E	Mid Jul. 2009
	Wollemi NP	33°10′S, 150°14′E	Late Jul. 2009
	Royal NP	34°13′S, 151°01′E	Late Aug. 2009 Early May 2011
	Myocum, NSW	28°35′S, 153°28′E	Mid Oct. 2010 Late May 2011
	Eungella NP	21°02′S, 148°36′E	Late Oct. 2010 Early Nov. 2011
	Mt Lewis NP	16°31′S, 145°16′E	Mid Nov.–mid Dec. 2010 Mid–late Nov. 2011
	Myall Lakes NP	32°25′S, 152°27′E	Late Dec. 2011
Yellow-spotted Honeyeater *Meliphaga notata*	Iron Range NP	12°40′S, 143°20′E	Early Nov. 2010
	Kingfisher Park, Julatten	16°35′S, 145°20′E	Mid Nov. 2010 Late Nov.–early Dec. 2011
	Mt Lewis NP	16°31′S, 145°16′E	Early Dec. 2010

where we encountered White-lined Honeyeaters were Nourlangie Rock and Gunlom Falls (Figure 1). On 1–4 October 2011 and 20–22 May 2014, we observed birds in Mitchell River National Park, WA. We encountered Kimberley Honeyeaters in several locations from the top of Little Mertens Falls (Figure 2) through to the lookout for Mitchell Falls, though we found the birds to be concentrated primarily around Little Mertens Falls and the narrow gorge above Big Mertens Falls. Because this study was done in the context of a larger study on the foraging ecology of all Australian honeyeaters, we travelled extensively throughout the study areas, recording data for all individuals of all species that we encountered. During this process, we made efforts to sample all habitat types. This allows us, with acknowledged temporal limitations, to provide some assertions about the habitat types in which these taxa are found.

We used trails and natural features to walk transects through the study sites, and generally worked together. When separate, we communicated with walkie-talkies to ensure that we were not observing the same birds. Upon encountering a honeyeater, if we found the bird by its vocalisations or while it was not foraging, we recorded the first observation that we saw. If, however, the first foraging manoeuvre was what drew our attention to the bird, then we discarded this observation, to avoid a bias towards conspicuous manoeuvres or locations (Wagner 1981). Unlike other researchers (Hejl *et al.* 1990; Naoki 2003), we recorded serial observations. However, we did not treat each such observation as independent; rather, we weighted these observations by the reciprocal of the number of observations in the series, such that a series of observations on the same individual in sum carried the same weight as a single observation from a different individual. Finally, we attempted to ensure that we did not resample birds in a given day; for instance, after recording data for all birds in a given foraging group, we followed by sight and sound that group's movements as we continued our transect, and we did not return to areas that we had previously sampled that day. Thus, we consider an independent data point to be a single observation or series of observations from a single bird from a single day. The final dataset consists of 9595 total observations, 7302 of which are independent, across 74 species (minimum: n = 20 independent observations for Green-backed Honeyeater *Glycichaera fallax*; maximum: n = 459 for Brown Honeyeater *Lichmera indistincta*).

Foraging behaviour was quantified according to standardised protocols (Remsen & Robinson 1990), with slight modifications. For each observation, we recorded the date, time, and general location within the study site, the bird species and the bird's age and sex if these could be determined. We recorded whether the bird was in a cohesive mixed species flock, a monotypic species flock, a loose foraging association, or simply as a pair or alone, and used this to derive a metric of flocking propensity. For this study, we assigned both 'monospecific flocks' and 'mixed species flocks' a score of 1, a 'loose association' a score of 0.5, and a single bird or pair of birds a score of 0. Most of our observations come from birds in flocks (66%) or loose associations (16%), and only 18% from solitary birds or pairs.

For every foraging observation, we classified the attack type as one of 17 mutually exclusive behaviours. Definitions of these behaviours follow Remsen & Robinson (1990). Some were much more commonly observed than others (Figure 3, third row). We occasionally refer to composite variables. 'Complex bill manoeuvres' are any attack that was a flake, gape, hammer, peck, pull or probe to a non-floral resource. 'Wing-powered manoeuvres' are any attacks that were either a flush-pursue, flutter-chase, sally-glide, sally-hover, sally-pounce, sally-stall, sally-strike or screen. Any of the non-wing-powered manoeuvres could be performed while hanging. Four directions of hang were considered possible: hang up, hang down, hang sideways, and hang upside-down (Remsen & Robinson 1990).

For every foraging manoeuvre, we recorded the substrate that the bird attacked, and the plant species if known. If the attack was to a flower for nectar, then we measured the functional length of the corolla (the effective floral tube through which a bird would have to penetrate to access nectar). We did this with callipers, estimated it in the field, or determined it later with photographs and image analysis (Schneider *et al.* 2012). Ten such mutually exclusive substrates were considered (Figure 3, fourth row).

We visually estimated the height of the attack, and standardised our estimates to each other's and by periodic checks with a laser rangefinder (Opti-Logic Insight, Tennessee, USA). We did the same for the average height of the canopy in a 2-m-diameter circle around the attack site. The dataset-wide distributions of these two measures were right-skewed (Figure 3, first row; attack height, not shown, was similarly distributed).

For each attack, we recorded the foliage density in a 1-m-diameter sphere around the attack site on an ordinal scale of 0–5, where 0 indicates that 0% of light passing through that sphere would be intercepted, and 5 indicates that 100% would be blocked (Figure 3, fifth row). We also noted the distance of the attack from the trunk on an ordinal scale of 1–4, where 1 indicates along the trunk or just adjacent to it, and 4 indicates outside the canopy, e.g. a sally-strike well beyond the canopy, or a glean from bare ground (Figure 3, sixth row).

We used the weighting system described above to convert these raw observations into descriptors of species' foraging niches. For nominal variables (e.g. glean, probe, air), we expressed species' averages as a percentage of total observations. For example, if 15 of 30 independent observations were of feeding on nectar, then we considered the species to be 50% nectarivorous. For continuous variables, the weighting system was used to calculate the average and 25 and 75% quartiles of the species-specific trait in question. Because relative foraging height (height of attack/height of canopy) ranges from zero to infinity (e.g. an attack at 10 m above bare rock), all extreme values were rounded down to 110%.

In addition to quantitative foraging data, we recorded interspecific behaviours, particularly displacements and chases, and the winner (dominant species) of such disputes. We do not include nest-defence interactions, or multiple individuals of one species chasing another species, as these are difficult to interpret. We included four interactions not observed by us but documented in the literature (Higgins *et al.* 2001). All of these interactions are represented in a directed graph, where nodes (vertices) are species and arrows (directed edges) connect dominant to displaced species.

We opportunistically used a Sony HDR-CX100 digital video camera to film foraging and other behaviours of Kimberley Honeyeaters. Clips of this footage are archived in the Internet Bird Collection (http://ibc.lynxeds.com/).

Results

Habitat description

The areas where we encountered White-lined Honeyeaters were the sandstone bluffs, boulders, and escarpments of Kakadu National Park. Specifically, we found small groups near the Anbangbang Shelter at Nourlangie Rock and ranging along the narrow ravine that forms the start of the Barrk sandstone bushwalk. This area is a combination of tall, eucalypt-dominated woodland and monsoon vine forest along the base of the bluff. Most of our observations of this species, however, come from the top of Gunlom Falls. This area is described by Thomas *et al.* (2011). We found the birds to be concentrated primarily in the wide valley hemmed in by large sandstone bluffs (Figure 1), though they did also regularly visit the thin strip of monsoon rainforest that lined Gunlom Creek above the falls. This strip was composed largely of Screw Pine *Pandanus* spp. and An-binik *Allosyncarpia ternata*. The much drier valley supports extensive woodland of species such as Kakadu Woollybutt *Eucalyptus* cf. *gigantangion* and other myrtaceous trees and shrubs (Centre for Plant Biodiversity Research 2006). Tall grasses grow along the dry creek, spinifex is found throughout the area, particularly amongst the boulders and ledges, and tangles of vines and denser vegetation can be found in sites of higher water availability (e.g. the head of the valley). Within (and across) this valley the birds travelled widely, and it was difficult to observe them at length.

The areas where we located Kimberley Honeyeaters were largely similar in appearance to those for the White-lined Honeyeater (Figure 2). There was a strip, broader than that at Gunlom Creek, of monsoon vine forest that the birds visited regularly. Nevertheless, as at Gunlom, the birds seemed to consider this strip merely as a component of their habitat matrix. They ranged widely throughout their seemingly extensive home-ranges, spending much of their time amongst the Rock Figs *Ficus* cf. *platypoda* and Sandstone Cocky Apples *Planchonia rupestris* that grew in and around the large sandstone boulders on top of the escarpment. In general, this area was a drier, flatter area more like the top of Nourlangie Rock than the valley above Gunlom Falls or the base of Nourlangie Rock. Spinifex covered most of the landscape, fairly deep channels dissected the sandstone plateau, and the dry woodland, where it existed, did not seem to be frequented by Kimberley Honeyeaters. We also found small groups of Kimberley Honeyeaters in grassy areas somewhat away from the larger boulders of the escarpment; even during the heat of the day they passed through these areas foraging on species such as Silver-leaf Grevillea *Grevillea refracta*.

Quantitative foraging behaviour

We recorded 55 and 119 total and 68 and 133 independent foraging observations (after accounting for serial observations) of White-lined and Kimberley Honeyeaters, respectively. Quantitative foraging data for all Australian *Meliphaga* species are presented in Table 2. Rank is from least to most of the trait in question, with respect to our entire honeyeater dataset (74 of 75 Australian species), and is an average.

Compared with other honeyeaters, all *Meliphaga* species were infrequent members of flocks (both monotypic and mixed-species: Table 2). Four of the species foraged considerably lower in the available strata than the rest of the Australian Meliphagidae. The White-lined Honeyeater stands out with respect to the other four species and, according to our limited data, foraged relatively higher than the rest of the *Meliphaga* species. The five species generally foraged closer to the trunk, in less leafy vegetation, than most other Australian Meliphagidae, though the Graceful Honeyeater foraged in more leafy areas than the other *Meliphaga* species (Table 2). In terms of specific foraging manoeuvres and substrates, four of the species stood out (excluding the Kimberley Honeyeater) in their use of complex bill manoeuvres; the White-lined and Lewin's *M. lewinii* Honeyeaters, in particular, were frequent probers of branches. All *Meliphaga* honeyeaters infrequently or only occasionally made foraging attacks to leaves,

Figure 1. Habitat of the White-lined Honeyeater. This scene is from the sandstone-boulder-strewn valley adjacent to Gunlom Falls, Kakadu National Park, Northern Territory. Photo: Eliot T. Miller

Figure 2. Habitat of the Kimberley Honeyeater. This scene is from the dissected sandstone escarpment adjacent to Little Mertens Falls, Mitchell River National Park, Western Australia. Photo: Eliot T. Miller

Table 2. Quantitative foraging data for the two sandstone honeyeaters (White-lined and Kimberley) and the three other (Graceful, Lewin's and Yellow-spotted) Australian *Meliphaga* honeyeaters: mean frequencies and associated data for different foraging behaviour (see text). Rank is from least to most for the trait in question and with respect to our entire honeyeater dataset (unpublished, 74 of 75 species). It is also an average, e.g. though the White-lined Honeyeater is 0% frugivorous in our dataset, its rank is 25.5 because there were 51 such 0% frugivorous species. Where appropriate, 25 and 75% quartiles are also calculated, and shown in parentheses. For nominal variables like gleaning, the frequencies are given as the percentage of total attacks.

Data on foraging	*Honeyeater species*									
	White-lined		*Kimberley*		*Graceful*		*Lewin's*		*Yellow-spotted*	
	Mean (25%, 75% quartiles)	*Rank*	*Mean (25%, 75% quartiles)*	*Rank*	*Mean (25%, 75% quartiles)*	*Rank*	*Mean (25%, 75% quartiles)*	*Rank*	*Mean (25%, 75% quartiles)*	*Rank*
Flocking (%)	60	14	46	8	47	9	42	4	42	5
Attack height (m)	7.6 (3, 11.3)	40	3.4 (1.7, 5)	13	11.5 (6, 16)	58	7.7 (2.6, 12)	41	8.9 (5, 12)	47
Canopy height (m)	10.4 (6, 14.3)	40	5.5 (3.5, 7)	14	19.0 (14, 24)	64	13.9 (7.3, 20)	50	17.0 (12, 19)	59
Relative foraging height (%)	72 (58, 93)	42	63 (49, 80)	19	61 (40, 87)	13	56 (33, 81)	8	53 (29, 80)	5
Foliage density (0–5)	2.0 (1, 3)	18	2.2 (1, 3)	40	2.3 (2, 3)	43	2.1 (1, 3)	26	2.2 (1, 3)	33
Distance from trunk (1–4)	2.3 (2, 3)	7	2.6 (2, 3)	33	2.5 (2, 3)	19	2.4 (2, 3)	15	2.4 (2, 3)	11
Hanging (%)	16	28	30	58	0.5	6	14	22	4	9
Gleaning (%)	30	28	35	35	34	33	40	43	58	60
Complex bill manoeuvres (%)	15	60	3	30	6	41	14	58	6	40
Sally-hovering (%)	1	34	4	48	11	70	9	68	4	55
Wing-powered (%)	17	37	15	34	23	61	27	69	20	46
Nectarivory (%)	38	43	49	51	37	42	19	19	19	18
Frugivory (%)	0	25.5	18	71	8	68	25	72	27	73
Attack to air (%)	12	47	6	25	9	36	9	38	4	21
Attack to branch (%)	31	68	4	14	4	15	18	60	9	35
Attack to leaf (%)	20	23	24	30	39	52	27	33	34	46
Mean corolla length (cm)	0.5 (0.2, 0.9)	13	1.8 (1.5, 2.8)	58	1.0 (0.5, 1.3)	35	1.0 (0.4, 1.4)	37.5	0.6 (0.4, 0.6)	15

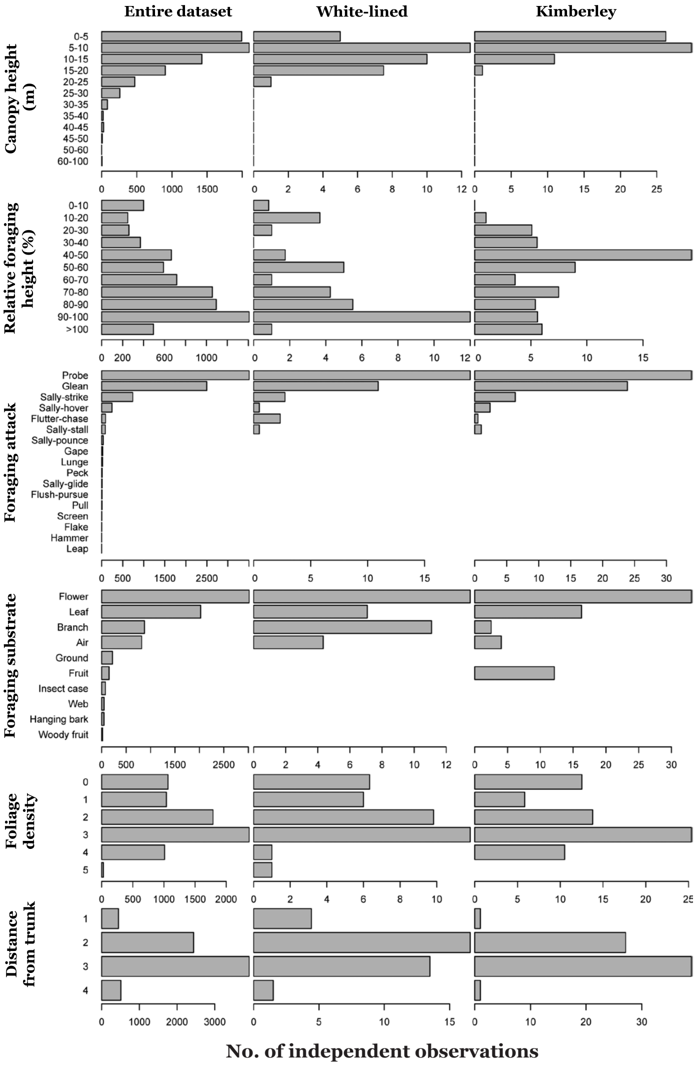

Figure 3. Distributions for the entire dataset (for 74 of 75 Australian honeyeater species) (column 1), White-lined (column 2), and Kimberley Honeyeaters (column 3), of canopy height (row 1), relative foraging height in canopy (row 2), foraging attack manoeuvre (row 3), foraging substrate (row 4), foliage density (row 5) and distance from trunk (row 6). For the first two rows, second values are break points, e.g. a canopy height of 5–10 m includes all observations of >5 m and ≤10 m. In foraging substrate, fruit refers to fleshy fruits, insect case refers to invertebrate shelters e.g. those of Psychidae (bagworms) and various leaf-tying Lepidoptera, web refers specifically to those of Araneae (spiders), and woody fruit refers to woody fruits e.g. of *Eucalyptus* and *Banksia*. Foliage density is based on amount of light estimated to pass through a 1-m-diameter sphere centred on the site of the foraging attack, and is on an ordinal scale where 5 is the densest foliage. Distance from trunk is also an ordinal measurement based on visual estimation, where 4 refers to attacks well beyond the canopy.

though (in keeping with its leafy foraging strata) the Graceful Honeyeater stood out from the others in its more frequent use of leaves as foraging substrate. All were capable of hovering, particularly Graceful and Lewin's Honeyeaters (see also videos of the Kimberley Honeyeater uploaded to http://ibc.lynxeds.com/).

The sandstone *Meliphaga* honeyeaters—White-lined and Kimberley—were more nectarivorous than most honeyeaters (Figure 3) (i.e. >57% of other Australian honeyeaters: ETM & SKW unpublished data). Species of flowers from which nectar was taken by White-lined Honeyeaters were: Rock Grevillea *Grevillea* cf. *heliosperma* and Ferny-leaved Grevillea *G. pteridifolia* (Proteaceae); Kakadu Woollybutt, *Melaleuca* cf. *viridiflora*, and An-binik (Myrtaceae); a mistletoe species (Loranthaceae); and an unknown species whose identity we could not establish (photographs available upon request). For the Kimberley Honeyeater, plant species were: Silver-leaf Grevillea (Proteaceae); a possible *Syzygium* species, and a single attack to Darwin Woollybutt *Eucalyptus* cf. *miniata* (Myrtaceae); *Brachychiton* cf. *fitzgeraldianus* (Malvaceae); and the Kimberley endemic Sandstone Cocky Apple (Lecythidaceae: Barrett 2006). In general, all *Meliphaga* species took at least some nectar, though Lewin's and Yellow-spotted Honeyeaters did so infrequently compared with other Australian Meliphagidae species. These two species were particularly frugivorous, but all Australian *Meliphaga* species consume fruit; four of the five species (excluding White-lined Honeyeater) were within the top seven most frugivorous species of Australian Meliphagidae according to our dataset, and frugivory in the White-lined Honeyeater has been documented by others (see discussion). We observed Kimberley Honeyeaters consuming fruits of Rock Fig (Moraceae), Freshwater Mangrove *Carallia brachiata* (Rhizophoraceae) and another unidentified shrub with small, cauliflorous fruits.

Additional ecological observations

We saw a White-lined Honeyeater displaced by an individual of the sandstone subspecies of the Helmeted Friarbird *Philemon buceroides ammitophila*. We also observed a White-gaped Honeyeater *Stomiopera unicolor* (see taxonomy of Nyári & Joseph 2011) displace an individual Kimberley Honeyeater from a Sandstone Cocky Apple flower, and another White-gaped Honeyeater displace a different individual Kimberley Honeyeater from the flowers of a Silver-leaf Grevillea. Individual Kimberley Honeyeaters twice displaced individual Bar-breasted Honeyeaters *Ramsayornis fasciatus* from flowers of Silver-leaf Grevillea. We summarise these and all other indirect interspecific interactions one degree removed from the focal species as a directed network graph (Figure 4).

Eight species of honeyeaters were recorded in the same sites as foraging White-lined Honeyeaters: Blue-faced *Entomyzon cyanotis*, White-gaped, Brown *Lichmera indistinta*, White-throated *Melithreptus albogularis*, and Dusky Honeyeaters *Myzomela obscura*, and Silver-crowned *Philemon argenticeps*, Helmeted *P. buceroides ammitophila*, and Little Friarbirds *P. citreogularis*. Four other honeyeaters that we studied in Kakadu were not observed near White-lined Honeyeaters: Yellow-throated Miner *Manorina flavigula*, and Bar-breasted,

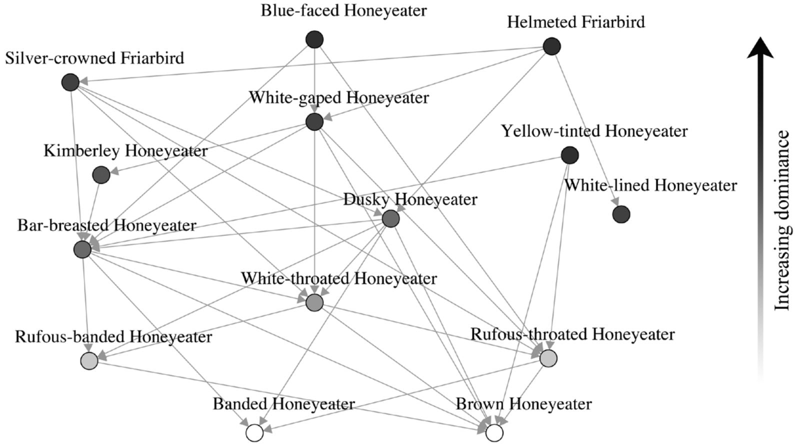

Figure 4. A directed graph depicting the interspecific interactions among the focal species—White-lined and Kimberley Honeyeaters—and those with which they interacted directly and indirectly (separated by one degree). The figure is restricted to species that co-occur with the focal species. Nodes are species, color-coded from dark grey (most dominant) to white (least dominant). Arrows depict observed interactions, and run from displacing species towards those that they displaced. Although many possible interactions among the illustrated species were not observed, the figure nevertheless suggests a strict linear dominance hierarchy among these species, with the focal species being mid-ranked.

Rufous-banded *Conopophila albogularis*, and Rufous-throated *C. rufogularis* Honeyeaters. The Blue-faced Honeyeaters and Little Friarbirds that we studied were seen at the base of Gunlom Falls; they were not seen in the specific areas where we encountered White-lined Honeyeaters.

Nine species of honeyeaters were recorded in the immediate vicinity of foraging Kimberley Honeyeaters: Yellow-tinted *Ptilotula flavescens* (see Nyári & Joseph 2011), White-gaped, Brown, White-throated, Blue-faced, Rufous-throated and Bar-breasted Honeyeaters, and Silver-crowned and Little Friarbirds. The Yellow-tinted Honeyeater was very infrequently observed in the area, but the other species were all regularly seen foraging near individual Kimberley Honeyeaters.

Discussion

White-lined and Kimberley Honeyeaters are two poorly known sister species endemic to the sandstone escarpments of, respectively, the northern Northern Territory and Western Australia. They were recently classified as distinct species based largely on molecular evidence. However, the two taxa are phenotypically similar, and acceptance of the split has not been unanimous. This has been hindered by the fact that ecological and vocal data that might shed light on their debated taxonomic status have been limited. We recently demonstrated that these taxa differ in vocalisations (Miller & Wagner 2014). Here we are primarily concerned with reporting details of the ecology of these species.

The foraging behaviours of the White-lined and Kimberley Honeyeaters were broadly similar (Table 2, Figure 3); see differences below. Both species are more nectarivorous than many other honeyeaters, tend to forage closer to the trunk and in less dense foliage, infrequently glean from leaves, and are both (presumably: see below) more frugivorous than most other Australian honeyeaters.

Like other Australian members of the genus *Meliphaga*, these two sandstone species were less gregarious than most honeyeaters, and they were comparatively infrequently found in mixed-species flocks (Table 2; cf. Schodde & Mason 1975). *Meliphaga* honeyeaters seem to shy away from aggressive encounters; we rarely recorded interactions involving these species. Body mass generally predicts dominance among close relatives, but these relationships grow harder to predict with increasing phylogenetic distance (Martin & Ghalambor unpublished data). For example, species such as Bridled *Bolemoreus frenatus* (see Nyári & Joseph 2011) and White-cheeked *Phylidonyris nigra* Honeyeaters, near or well below the mass of Lewin's Honeyeater, readily displaced that species from foraging areas (ETM & SKW unpublished data). We expect that both sandstone taxa are subordinate to the medium-to-large honeyeaters with which they co-occur (e.g. all *Philemon*, *Entomyzon*, and *Stomiopera* species). In a dominance hierarchy of co-occurring species (Figure 4), that would put these species above only such smaller honeyeaters as Bar-breasted, Dusky, White-throated and, if they seasonally or occasionally overlap, Banded Honeyeater *Cissomela pectoralis* and perhaps Black-chinned Honeyeater (Golden-backed subspecies) *Melithreptus gularis laetior*.

In our dataset, White-lined and Kimberley Honeyeaters differ from each other in three notable ways: average relative foraging height, frequency of attacks to branches, and degree of frugivory (Figure 3). The first of these had ramifications in terms of which species the White-lined and Kimberley Honeyeaters foraged amongst. In our experience, this difference seems real; Kimberley Honeyeaters generally foraged below the canopy, whereas White-lined Honeyeaters often foraged well into the canopy. It is possible that our conclusion could be influenced by availability of floral resources, as Kakadu Woollybutt was flowering during some of our observations of White-lined Honeyeaters. However, despite widespread flowering of Darwin Woollybutt (May 2014), commonly visited by all other local honeyeater species, we recorded only a single, very quick visit of a Kimberley Honeyeater to these flowers. The degree to which the species differed in attacks to branches warrants further study as it might, if corroborated, indicate large differences in resource use. In terms of differences in frugivory, the members of the genus *Meliphaga* are among the most frugivorous of all species that we studied (Table 2). Though we did not observe the White-lined Honeyeater take any fruits, its consumption, particularly of *Ficus* fruit, has been noted by others (White 1917a,c; Deignan 1964; Storr 1977). In our dataset, four out of seven of the most frugivorous Australian honeyeater species are members of the genus *Meliphaga*, and we suspect that temporally less restricted data would show the White-lined Honeyeater to be comparably frugivorous.

Another approach is to make assemblage-level comparisons of foraging niche. We take the previously noted species [including Black-chinned (Golden-backed subspecies) and Banded Honeyeaters] to be those that co-occur with the present taxa. Doing so, the difference in relative foraging height between the *Meliphaga* species (Table 2) becomes apparent, with the White-lined Honeyeater foraging amongst the highest-foraging honeyeaters, and the Kimberley Honeyeater foraging lower than all co-occurring species. The latter seems most similar to the White-gaped Honeyeater, which tends to forage even closer to the trunk and in generally denser vegetation. White-gaped Honeyeaters focus many of their attacks on branches, leaves and substrates like dead leaves and invertebrate shelters, whereas Kimberley Honeyeaters tend to be more nectarivorous, frugivorous and, when foraging on invertebrates, focussed on flying prey taken in aerial manoeuvres. The White-lined Honeyeater, in contrast, seems most similar to the Helmeted and Silver-crowned Friarbirds, particularly the latter. In these comparisons, White-lined Honeyeaters tend to forage closer to the trunk, and in less leafy vegetation; Helmeted Friarbirds tend to forage lower than either of the other species, and also to be less nectarivorous. Silver-crowned Friarbirds are notably more nectarivorous than either species and, like the Kimberley Honeyeater, White-lined Honeyeaters focus more on flying prey taken in aerial manoeuvres (the White-lined Honeyeater was the dataset-wide leader in frequency of flutter-chases: ETM & SKW unpublished data). White-lined Honeyeaters also make many more attacks to branches than either of the friarbird species.

In summary, foraging and other ecological characteristics are largely similar between White-lined and Kimberley Honeyeaters, and the species resemble other members of the genus in many respects. That said, they differ from each other in a few notable ways, and differences between the species are comparable to those among sympatric *Meliphaga* species (Table 2). Thus, though our interest here has been to document the ecology of these species, we note that our results show subtle differences between the species which, combined with vocal (Miller & Wagner 2014), genetic (Christidis & Schodde 1993; Norman *et al.* 2007), and morphological differences (Schodde 1988), suggest that these taxa should be recognised as separate species.

Acknowledgements

We thank Bryan Suson for help studying the Queensland *Meliphaga* honeyeaters, Garry Sankowski, Russell Barrett, and Lyn Craven for help with plant identification; the Westoby Lab at Macquarie University for logistical support; Iris Levin, Vincenzo Ellis, Matthew Medeiros, Toshi Tsunekage, Ben Freeman and Eloisa Sari for helpful discussion; and Hugh Ford, anonymous reviewers and the editors of *AFO* for comments on previous versions of this manuscript. This work was funded in part by the National Science Foundation (GRFP #1051698), St Louis Audubon Society, Harris World Ecology Center, and Macquarie University Higher Degree Research Office.

References

Barrett, R.L. (2006). A review of *Planchonia* (Lecythidaceae) in Australia. *Australian Systematic Botany* **19**, 147–153.

BirdLife International (2012). Species factsheet: White-lined Honeyeater *Meliphaga albilineata*. BirdLife International. Available at: http://www.birdlife.org/datazone/speciesfactsheet.php?id=5272 (retrieved 17 August 2012).

Centre for Plant Biodiversity Research (2006). *EUCLID: Eucalypts of Australia*. 3rd edn. CSIRO Publishing, Melbourne.

Christidis, L. & Boles, W.E. (2008). *Systematics and Taxonomy of Australian Birds*. CSIRO Publishing, Melbourne.

Christidis, L. & Schodde, R. (1993). Relationships and radiations in the meliphagine honeyeaters, *Meliphaga*, *Lichenostomus* and *Xanthotis* (Aves: Meliphagidae): Protein evidence and its integration with morphology and ecogeography. *Australian Journal of Zoology* **41**, 293–316.

Deignan, H.G. (1964). Birds of the Arnhem Land Expedition. In: Mountford, C.P. (Ed.). *Records of the American–Australian Scientific Expedition to Arnhem Land, Volume 4*, pp. 345–425. Melbourne University Press, Melbourne.

Edwards, S.V., Kingan, S.B., Calkins, J.D., Balakrishnan, C.N., Jennings, W.B., Swanson, W.J. & Sorenson, M.D. (2005). Speciation in birds: Genes, geography, and sexual selection. *Proceedings of the National Academy of Sciences of the United States of America* **102**, 6550–6557.

Ford, H.A. & Paton, D.C. (1976). Resource partitioning and competition in honeyeaters of the genus *Meliphaga*. *Australian Journal of Ecology* **1**, 281–287.

Ford, J. (1978). Geographical isolation and morphological and habitat differentiation between birds of the Kimberley and the Northern Territory. *Emu* **78**, 25–35.

Ford, J. (1987). Notes on Kimberley birds. *Western Australian Naturalist* **16**, 181–184.

Freeman, D.J. (1971). The nest of the White-lined Honeyeater. *Emu* **71**, 86–87.

Hejl, S.J., Verner, J. & Bell, G.W. (1990). Sequential versus initial observations in studies of avian foraging. In: Morrison, M.L., Ralph, C.J., Verner, J. & Jehl, J.R.J. (Eds). *Avian Foraging: Theory, Methodology, and Applications*, Studies in Avian Biology No. 13, pp. 166–173.

Helbig, A.J., Knox, A.G., Parkin, D.T., Sangster, G. & Collinson, M. (2002). Guidelines for assigning species rank. *Ibis* **144**, 518–525.

Higgins, P.J., Peter, J.M. & Steele, W.K. (2001). *Handbook of Australian, New Zealand & Antarctic Birds, Volume 5: Tyrant-flycatchers to Chats*. Oxford University Press, Melbourne.

Johnstone, R.A. (1995). Sexual selection, honest advertisement and the handicap principle: Reviewing the evidence. *Biological Reviews of the Cambridge Philosophical Society* **70**, 1–65.

Johnstone, R.E. & Burbidge, A.H. (1991). The avifauna of Kimberley rainforests. In: McKenzie, N.L., Johnston, R.B. & Kendrick, P.G. (Eds). *Kimberley Rainforests of Australia*, pp. 361–391. Surrey Beatty, Sydney.

Johnstone, R.E. & Storr, G.M. (2004). *Handbook of Western Australian Birds, Volume 2: Passerines*. Western Australian Museum, Perth.

Kikkawa, J., Webb, L.J., Dale, M.B., Monteith, G.B., Tracey, J.G. & Williams, W.T. (1981). Gradients and boundaries of monsoon forests in Australia. *Proceedings of the Ecological Society of Australia* **11**, 39–52.

Lendon, A. (1966). Notes on Northern Territory birds. *Australian Bird Watcher* **2**, 191–206.

Longmore, N.W. (1983). Nidification of the White-lined Honeyeater *Meliphaga albilineata*. *Emu* **83**, 275.

Mayr, E. (1942). *Systematics and the Origin of Species, from the Viewpoint of a Zoologist*. Harvard University Press, Cambridge, Massachusetts, USA.

Miller, E.T. & Wagner, S.K. (2014). The vocalisations and species status of the White-lined and Kimberley Honeyeaters. *Emu* **114**, 116–120.

Naoki, K. (2003). Evolution of Ecological Diversity in the Neotropical Tanagers of the Genus *Tangara* (Aves: Thraupidae). PhD thesis. Louisiana State University, Baton Rouge, Louisiana, USA. Available online: http://etd.lsu.edu/docs/available/etd-0710103-144206/ (retrieved 17 August 2012).

Norman, J.A., Rheindt, F.E., Rowe, D.L. & Christidis, L. (2007). Speciation dynamics in the Australo-Papuan *Meliphaga* honeyeaters. *Molecular Phylogenetics and Evolution* **42**, 80–91.

Nyári, A.S. & Joseph, L. (2011). Systematic fragmentation of *Lichenostomus* improves the basis for understanding relationships within the honeyeaters (Meliphagidae) and historical development of Australo-Papuan bird communities. *Emu* **111**, 202–211.

Remsen, J.V. & Robinson, S.K. (1990). A classification scheme for foraging behavior of birds in terrestrial habitats. *Studies in Avian Biology* **13**, 144–160.

Rix, C.E. (1970). Birds of the Northern Territory. *South Australian Ornithologist* **25**, 147–191.

Schneider, C.A., Rasband, W.S. & Eliceiri, K.W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* **9**, 671–675.

Schodde, R. (1988). New subspecies of Australian birds. *Canberra Bird Notes* **13**, 119–122.

Schodde, R. & Mason, I.J. (1975). Occurrence, nesting and affinities of the White-throated Grass-wren *Amytornis woodwardi* and White-lined Honeyeater *Meliphaga albilineata*. *Emu* **75**, 12–18.

Smith, L.A. & Johnstone, R.E. (1974). First record of White-lined Honeyeater in northern Kimberley, WA. *Emu* **74**, 58.

Smith, L.A., Johnstone, R.E. & Dell, J. (1978). Birds. *Wildlife Research Bulletin, Western Australia* 7, 29–41.

Storr, G.M. (1977). *Birds of the Northern Territory*. Western Australian Museum, Perth.

Storr, G.M. (1980). *Birds of the Kimberley Division, Western Australia*. Western Australian Museum, Perth.

Thomas, R., Thomas, S., Andrew, D. & McBride, A. (2011). *Birds of Australia*. 2nd edn. CSIRO Publishing, Melbourne.

Wagner, J.L. (1981). Visibility and bias in avian foraging data. *Condor* **83**, 263–264.

White, H.L. (1917a). Description of a new honeyeater of the genus *Ptilotis*, from north Australia. *Emu* **16**, 165.

White, H.L. (1917b). North Australian birds. Part 3. *Emu* **16**, 117–158.

White, H.L. (1917c). North Australian birds. Part 4. *Emu* **16**, 205–231.

Woinarski, J.C.Z. (1993). A cut-and-paste community: Birds of monsoon rainforests in Kakadu National Park, Northern Territory. *Emu* **93**, 100–120.

Received 10 August 2013 ■