

THE NESTING BIOLOGY OF THE BROWN HONEYEATER *Lichmera indistincta* IN THE DARWIN REGION OF NORTHERN AUSTRALIA, WITH NOTES ON TIDAL FLOODING OF NESTS

DONALD C. FRANKLIN¹ and RICHARD A. NOSKE²

¹P.O. Box 987, Nightcliff, Northern Territory, Australia 0814. E-mail: monsoon@topend.com.au

²Science Faculty, Northern Territory University, Darwin, Northern Territory, Australia 0909

Received: 16 May, 2000

In the Darwin region of northern Australia, the Brown Honeyeater nests in mangals (mangrove communities), woodlands and urban areas. Based on observations of 75 nests whose laying date could be estimated, the breeding season extends from April to September, a pattern that is consistent across years and habitats. Nests are usually built in shrubs and low twiggy growth of small trees, with a median nest height of 1.1 metre above the ground. The modal clutch size was 2, with a mean of 1.84, a small clutch size for such a small species (10 g), even by Australian standards. Both the incubation and nestling periods were approximately 13 to 13.5 days, slightly shorter than the 14 days previously reported. Females alone build, incubate and brood, but both sexes feed the young. Nest success was estimated to be 42 per cent, with most egg or nestling failures being the result of predation of the entire nest contents, or of flooding. Ten mangal nests were flooded by sea water during spring high tides. The period between full lunar cycle spring tide sequences (29–30 days) is slightly less than the time it takes a Brown Honeyeater to build a nest, lay and incubate the eggs and fledge the young. As a consequence, all nests built in mangals below about 7.4 metres Chart Datum would have been flooded. In mangals, Brown Honeyeaters may therefore only nest successfully in landward zones that are on higher ground and are thus subject to less deep inundation. At least three mangrove-endemic bird species are also obligate shrub-nesters, so preservation of landward mangrove zones may be critical for the conservation of mangrove bird communities.

INTRODUCTION

The Brown Honeyeater *Lichmera indistincta* is one of the most widely-distributed of all honeyeater (Meliphagidae) species. Its distribution includes much of Australia north of 30° latitude as well as some more southerly locations, and also New Guinea (Beehler *et al.* 1986) and eastern Indonesia (Coates and Bishop 1997). Within Australia, it occurs from the temperate south-west to the monsoonal tropics, and from the wet tropics to some of the most arid deserts (Blakers *et al.* 1984). In the monsoonal tropics of northern Australia, it commonly occurs in a wide range of treed habitats including savannah woodland, open eucalypt forest, riparian forest, monsoon rainforest, mangal (mangrove communities) and urban areas (Woinarski *et al.* 1988; Tidemann and Wilson 1992; Woinarski 1993; Noske 1996; Franklin and Noske 1998), and in many of these situations is among the most abundant bird species.

Not surprisingly then, it is also one of the better-studied honeyeaters. There is considerable information available concerning its ecophysiology (e.g. Collins 1981; Collins *et al.* 1980), a moderate amount of information concerning its ecology (e.g. Collins and Briffa 1982; Robertson and Woodall 1987; Franklin and Noske 1998) and morphology and plumage (Robertson 1966, 1969; Liddy 1989). However, there have been very few published observations and no formal studies of the reproductive behaviour of the Brown Honeyeater. Cassels (1961) and Ford (1998) provided observations at one nest each, with contradictory findings as to whether both sexes, or only the female feeds the young.

In this paper we provide data on the nesting biology of the Brown Honeyeater based on 83 nests in mangal,

woodland and urban habitats in and near Darwin in the Northern Territory. We also draw attention to the unresolved issue of small clutch size in a highly seasonal environment, and to the unexplored implications of shrub-nesting by birds for conservation of mangrove bird communities.

METHODS

Study area

Nest records were collected in the northern quarter of the Northern Territory, mostly close to Darwin (12°22'S, 130°52'E). The climate of this area is monsoonal tropical, with warm to hot temperatures throughout the year but a very marked seasonality of rainfall. In Darwin, the mean annual rainfall is 1 650 mm, over 95 per cent of which falls between October and April inclusive. Natural habitats in the vicinity of Darwin include eucalypt woodland/open forest, monsoon rainforest, paperbark riparian forest, mangal and wetlands.

In 1999, search effort was concentrated in mangal adjacent to the Darwin suburbs of Nightcliff and Rapid Creek, particularly within the less-frequently inundated communities of the landward fringe. The mangal in the Rapid Creek study area were commonly 1.5–4 metres high, comprising dense stands of Spurred Mangrove *Ceriops australis* and Grey Mangrove *Avicennia marina* alternating with bare saltflats. At Nightcliff, mixed-species mangal occupied a narrow fairly open band between foreshore parkland and rock shelves in the intertidal zone.

Field work

Nest records were collected opportunistically from 1985 to 1999 ($n = 53$ nests) in the course of various field studies conducted throughout the year. During 1999, wide-ranging year-round nest searches (Noske and Franklin 1999) continued, but efforts to locate Brown Honeyeater nests were intensified during the breeding season and concentrated in the Nightcliff and Rapid Creek mangals ($n = 30$ nests). For each nest, we identified the habitat and nest plant species and estimated or measured the height of the nest above ground. On each visit we recorded the contents of nests and made notes about the activity of adults where possible. During 1999 we made a particular effort to

return to nests at appropriate intervals to document success or failure, laying times and incubation and nestling periods. We also include data collected from a small number of nests by other observers, for which however, some aspects of the data set may be incomplete; for example, the habitat is not adequately described for six nests.

Adults were identified by the presence of a prominent yellow patch behind the eye and sexed on gape and crown colour — a black gape and grey head indicates a breeding adult male, whereas adult female Brown Honeyeaters usually have olive heads and all Brown Honeyeaters other than breeding adult males have yellow gapes (Robertson 1969; Liddy 1989; Noske and Franklin, unpubl. data).

Analysis

A clutch was considered to be complete if the nest was active and contained the same number of eggs at an interval greater than the laying interval (see Results), or if it contained eggs on the first occasion and nestlings after a subsequent interval of less than the incubation period (see Results). The incubation period was defined as beginning with the laying of the final egg and ending with the hatching of the first egg. The laying date was defined as the date of laying of the final egg, and in the absence of detail permitting more accurate dating was estimated to be 7 or 20 days prior to the date of observation for nests with eggs or nestlings respectively (see Results for incubation and nestling periods).

Nest success was calculated using the method of Mayfield (1975). To minimise uncertainty about whether a nest was at the egg or nestling stage, nest success was calculated using only visits at intervals of no more than three days. Data from all habitats were combined and the incubation and nestling periods were each assumed to be 13 days (see Results). For the purpose of estimation of nest success, a nest attempt is defined as a nest with a full clutch of eggs.

Tide heights are predictions for Darwin Harbour by the National Tidal Facility, Flinders University of South Australia and provided to us by the Marine Branch of the Department of Transport and Works, Darwin. They are expressed in standard form as heights Chart Datum (CD). Chart Datum is the height above the expected lowest tide (as computed and known as the Lowest Astronomical Tide). In Darwin, the Lowest Astronomical Tide is 4.00 metres below mean sea level (David Williams, pers. comm.). Although there can be differences between actual and predicted tide heights, and between Darwin Harbour, Nightcliff and Rapid Creek, such differences are likely to be slight for spring high tides (David Williams, pers. comm.).

RESULTS

This analysis is based on 484 visits to 83 nest attempts. The mean number of visits per nest was 5.83, eighteen nests were visited only once and fifteen nests were visited more than ten times. Sixty-two nests were in or near Darwin (12°25'S, 130°50'E), fifteen at Berry Springs (12°45'S, 131°02'E) and six in other areas of the Top End of the Northern Territory. Fifty-nine nest attempts were in natural vegetation (mangal — 39; woodland — 20) and 18 were in urban areas.

Breeding season

Brown Honeyeaters were recorded laying from early April until mid to late August, a trend that was consistent across years and habitats (Fig. 1). Figure 1a in particular was derived from searches conducted throughout the year (Noske and Franklin 1999). Apparent differences between years and habitats in the distribution of nesting effort through the season are most likely an artifact of variation in search effort.

Nest structure and placement

Nests were moderately deep cups slightly narrower in diameter at the rim than below, with an irregular

margin. The dimensions (mean \pm s.d.) of eight nests were: outer depth 48.9 \pm 5.0 millimetres; outer diameter 52.0 \pm 2.7 millimetres; inner depth 40.6 \pm 4.1 millimetres; and inner diameter at the top of the cup 41.9 \pm 2.4 millimetres. Nests were built of fibrous plant material such as bark and fine leaves, often with spider egg sacs and other material woven in and bound together with spider web. They were sparsely to moderately lined, often with fine fibrous material.

Nests were invariably suspended by the rim from twigs. Most frequently, the nest was suspended at several points along the rim to each of two or three horizontal twigs which had diverged from a common branchlet within

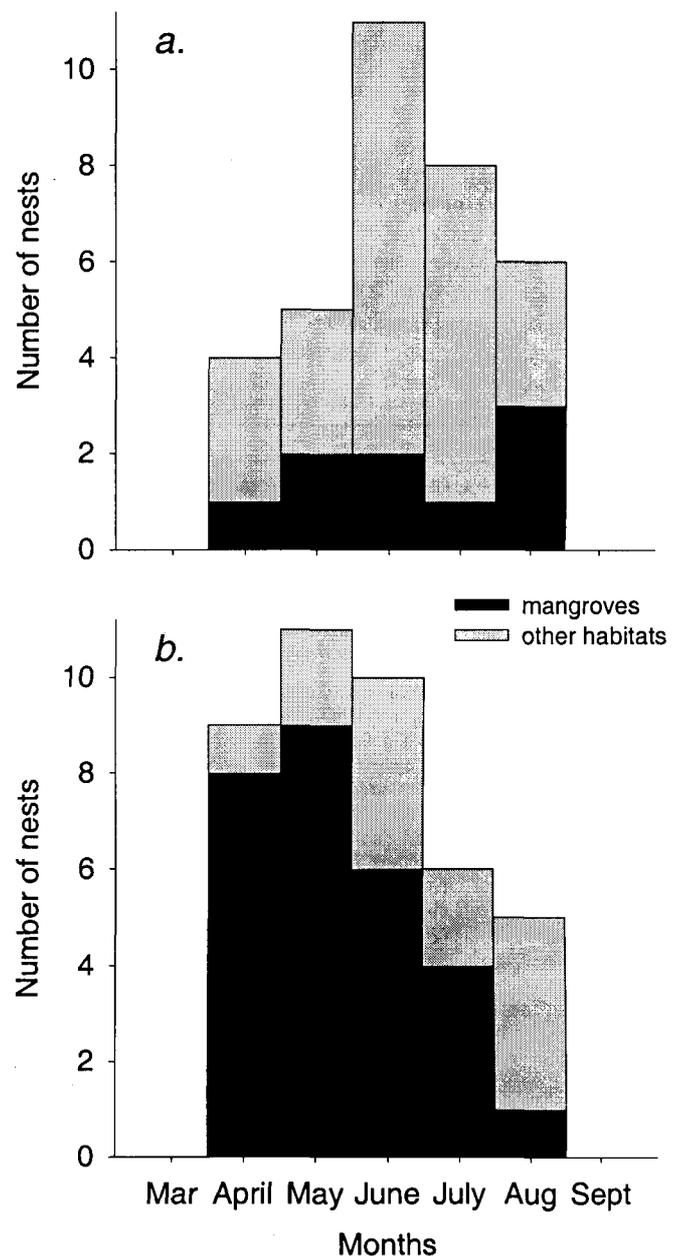


Figure 1. Laying dates of nests of the Brown Honeyeater near Darwin, Northern Territory: a. nests located during general nest searches and other field work conducted throughout the year, 1985 to 1998; b. nests located during targeted searches, 1999.

10 centimetres of the nest. However, a variety of arrangements were noted including attachment to vertical (both ascending and weeping, although the latter rarely) twigs, and attachment to up to ten different twigs, sometimes from quite separate branches of the plant. The median diameter of the largest twig immediately above the first point of attachment was 3.2 millimetres (range 2.4–7.4 mm, $n = 13$).

Nests were built in a wide variety of shrubs and small trees including saplings of larger tree species, or less commonly in larger trees or woody vines (Table 1). In the mangals, 39 nests were recorded in seven mangrove species, but 67 per cent were in Grey Mangrove and 18 per cent were in Spurred Mangrove, a proportion that may approximately reflect the relative abundance of the species in the areas we searched. In the woodlands, 16 nests were placed in 13 different named species, with the use of tree saplings particularly frequent. In urban areas, 14 nests in named plants were in six native and three exotic species.

Most nests were well-concealed amongst foliage and twigs, but others were fully visible to the observer at distances of several metres or more. The median distance from the nest to the edge of plants/thickets, for the 36 nests for which this dimension was recorded, was 0.3 metres, with a range from 0 to 2.0 metres. However, they were

usually placed amongst rigid twigs and never high in the outer foliage of trees.

Nests were 0.4–9.0 metres above the ground, but the median height was 1.1 metres and 86 per cent of nests were 2.0 metres or less above the ground. There was significant variation between habitats in the median height of nests above the ground (Fig. 2; Kruskal-Wallis $H = 9.4$; $n = 37, 19, 15$; χ^2 approximation, d.f. = 2, $P < 0.01$), with those of urban areas highest (median = 2.0 m, $n = 15$), those of woodland lowest (median = 0.9 m, $n = 19$) and those of the mangals intermediate (median = 1.1 m, $n = 37$). Nest height was strongly correlated with plant height for all habitats combined ($r_s = 0.65$, $n = 59$, $P \ll 0.001$), as it was for each habitat separately (r_s from 0.47 to 0.96, $P \leq 0.05$). However, the position of the nest relative to plant height was highly variable, ranging from 5 to 100 per cent of the plant height (median = 58%), and this proportion did not vary significantly between habitats (Kruskal-Wallis $H = 0.4$; $n = 30, 18, 11$; χ^2 approximation, d.f. = 2, $P > 0.75$).

The nest cycle

Nest construction took a minimum of three days ($n = 1$) and a maximum of five days ($n = 2$). There was a minimum of five days from the commencement of construction to the

TABLE 1

Plant species in which nests of the Brown Honeyeater were recorded. An asterisk indicates a non-native species.

Habitat	Plant species	Species growth habit	No. of nests	
mangal	Grey Mangrove <i>Avicennia marina</i>	shrub or tree	26	
	Spurred Mangrove <i>Ceriops australis</i>	shrub or small tree	7	
	White-flowered Black Mangrove <i>Lumnitzera racemosa</i>	shrub or bushy tree	2	
	Club Mangrove <i>Aegialitis annulata</i>	shrub	1	
	River Mangrove <i>Aegiceras corniculatum</i>	shrub or small tree	1	
	Myrtle Mangrove <i>Osbornia octodonta</i>	shrub or small tree	1	
	Star Mangrove <i>Sonneratia alba</i>	tree	1	
	woodland	Swamp Box <i>Lophostemon lactifluus</i>	tree	3
		Milkwood <i>Alstonia actinophylla</i>	tree	2
Darwin Black Wattle <i>Acacia auriculiformis</i>		tree	1	
Sandpaper Fig <i>Ficus opposita</i>		shrub or small tree	1	
Weeping Ti-tree <i>Leptospermum longifolium</i>		small tree	1	
*Coffee Bush <i>Leucaena leucocephala</i>		small tree	1	
Sand Palm <i>Livistona humilis</i>		palm, mostly < 3 m	1	
Weeping Paperbark <i>Melaleuca leucadendra</i>		large tree	1	
Yellow-barked Paperbark <i>Melaleuca nervosa</i>		small tree	1	
Broad-leaved Paperbark <i>Melaleuca viridiflora</i>		tree	1	
Quinine Tree <i>Petalostigma pubescens</i>		shrub	1	
Cocky Apple <i>Planchonia careya</i>		shrub	1	
Cunningham's Feather-flower <i>Verticordia cunninghamii</i>		shrub	1	
not named			4	
urban		Liniment Tree <i>Asteromyrtus symphyocarpa</i>	shrub	4
	Weeping Paperbark <i>Melaleuca leucadendra</i>	large tree	3	
	*Chain-of-love <i>Antigone</i> sp.	climber	1	
	*Bougainvillea <i>Bougainvillea</i> sp.	large scrambler	1	
	Weeping Fig <i>Ficus benjamina</i>	tree	1	
	a paperbark, <i>Melaleuca</i> sp.	tree	1	
	<i>Mimusops</i> sp.**	tree	1	
	*Waterfall Plant <i>Phyllanthus minutifolia</i>	shrub	1	
	Umbrella Tree <i>Schefflera actinophylla</i>	tree	1	
	not named		4	
	not named		6	

**Planted. Not the local native form of *M. elengi*. Species and origin unclear.

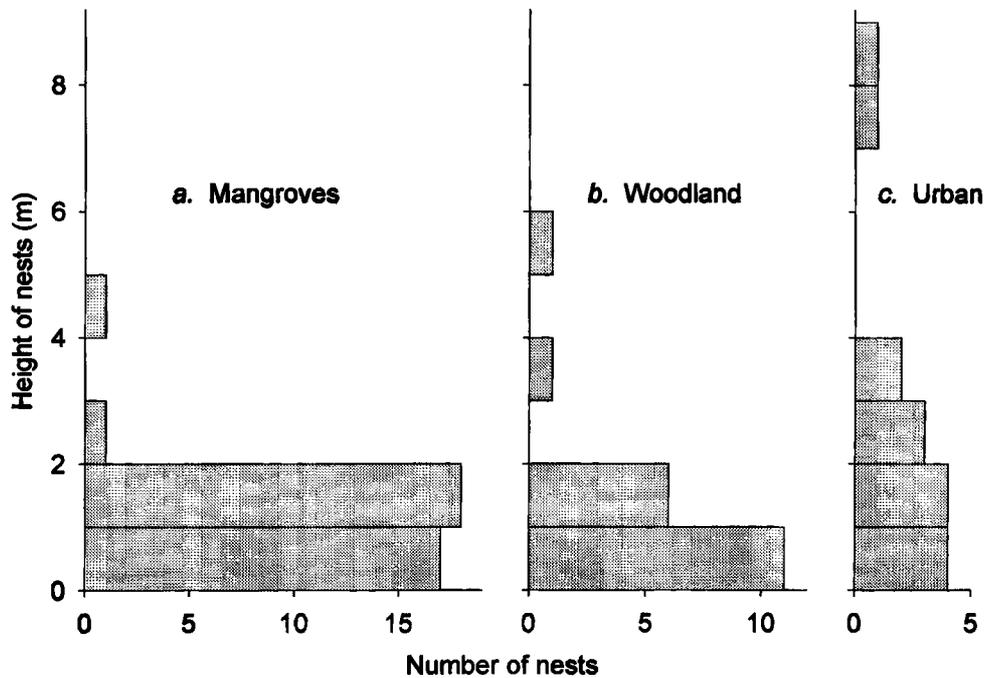


Figure 2. Heights of nests of the Brown Honeyeater in three habitats near Darwin, Northern Territory.

laying of the first egg ($n = 4$) and a minimum of eight days in another nest. Laying commenced one to two days after the completion of lining of the nest. Eggs were laid between evening and morning and at *c.* 24-hour intervals (Table 2), with observations at one nest (# 11) providing evidence that laying takes place early in the morning.

Incubation did not usually begin until the final egg was laid (one exception was observed), but assuming an early morning laying, commenced no more than an hour after completion of the clutch. The incubation period was at least 13 days at two nests and less than 14 days at two nests, with the most precise estimate for any nest being 13 days 11 hours \pm 13 hours. If we assume that incubation commenced at 0700 hours following the laying of the final egg, then the incubation period was between 13 days and 13 days 9 hours, with the most precise estimate for any nest being 13 days 5 hours \pm 5 hours.

Broken egg shell from a successful hatching was observed in the nest only on the day of hatching. Young hatched naked and blind, down being prominent by *c.* 2 days. At this age also, dark areas under the skin indicated the development of incipient feather tracts. At *c.* 3 days, the wing pins emerged from the skin, the eyes opened at *c.* 5–6 days, the crown pins emerged at *c.* 7 days, the vanes of the wing feathers began to open at *c.* 8 days, the vanes of the crown pins began to open at *c.* 9 days and by *c.* 10 days the young were well-feathered except on the head. Fledging was preceded by wing- and leg-exercising and preening. It occurred (in the absence of any human disturbance) both with and without obvious agitation and encouragement by adults. The nestling period was at least 12 days 22 hours at one nest and no more than 13 days 17 hours at another.

To our ears and by comparison with other honeyeaters we have studied, nestling Brown Honeyeaters either did

not beg audibly or did so very faintly. This persisted for several days after fledging, but the volume increased noticeably within four days of fledging, coinciding with more confident movements by the fledglings.

TABLE 2

Details of records of Brown Honeyeater nest contents relevant to the determination of laying time and interval.

Nest Number	Clutch size	Day	Time
11	0	1	0700
	2	2	0740
41	0	1	1800
	1	2	1700
	2	3	0900
45	0	1	1800
	1	2	1500
	2	3	0745
49	1	1	1730
	2	2	1300
57	0	1	0930
	1	2	0900
	2	3	0930
60	1	1	0900
	1	1	1745
	2	2	0800
64	0	1	1715
	1	2	0815
	1	2	1805
	2	3	0730
67	0	1	0750
	1	2	0715
	0*	2	1750
	1	3	0800
68	0	1	0750
	1	2	0720
	1	2	1800
	2	3	0800

*An unusual case of apparent predation during laying.

Given the above data, the nest cycle from the commencement of nest construction to fledging must take at least 32 days, with 33–35 days a more likely norm.

Nest productivity

Clutch sizes were of two, and less frequently (16% of nests) one egg, but one nest was found to contain three nestlings. The mean size of the 25 complete clutches was 1.84 eggs. There was no evidence of cuckoo parasitism. The mean brood size of active nest attempts immediately after hatching was 1.61 ($n = 18$ nests), and the mean brood size of active nest attempts at or shortly before fledging was 1.74 ($n = 19$ nests). The cause of the increase in brood size from hatching to fledging is unclear and may be an artifact of sampling.

We estimate that 42 per cent of nest attempts produced fledglings. This rate comprises a 77 per cent success rate during incubation and 54 per cent during the nestling period, but the data were of insufficient quantity to formally compare rates during the respective periods. The mean number of young fledged from all nest attempts is estimated to be 0.73 (1.74×0.42).

Symptoms and causes of nest failure

Of 26 nests known to have failed, ten had been flooded, four had been damaged or were gone, two contained abandoned eggs and one contained dead nestlings (not known to have been flooded), one was burnt by a wildfire, the partial remains of a nestling were found close to one and the remaining seven were found empty before sufficient time had elapsed for fledging. Of the twelve nests presumed to have been predated (seven empty, four damaged or gone, one with dismembered nestling nearby), two were known to have failed during daylight hours, both in the same mangal patch on the same day. The ten flooded nests were all in mangals and flooded by high tides. Drowned nests were most often found wet and empty, but in one case each a dead nestling and two eggs remained in the nest. Other nests survived narrowly — on one occasion we watched adults feed advanced nestlings (which subsequently fledged) as a minor swell lapped 8 to 15 centimetres below the base of the nest.

The ten drowned nests ranged from 0.4 to 1.3 metres above the ground, with eight below and two above the median height of all mangal nests. Of more consequence is the height Chart Datum (CD). Three drowned nests were estimated from known tide heights to be 7.1, 7.3 and 7.45 metres CD. High tides ranging from 7.08 to 7.80 metres CD, including two definitely below 7.40 metres and another below 7.60 metres CD, were responsible for drowning of the remaining seven nests. The nine nest floodings recorded during the 1999 breeding season occurred during five of the nine half or full lunar cycle spring-tide sequences that exceeded 7.0 metres CD (Table 3). Flooding of nests occurred even with fairly unexceptional spring high tides.

Most loss of eggs or nestlings involved the failure of the entire nest ($n = 26$ above). Partial nest failures ($n = 7$) recorded were: a single egg missing, presumed predated, before laying of the second egg (# 67, Table 2), three cases where one of two eggs failed to hatch, two cases where a nestling died during hatching and one where a nestling died at *c.* 10 days of age.

Gender roles

Only females were observed to build nests (13 observations at 11 nests), incubate (51 observations at 23 nests) and brood (15 observations at 9 nests). Both sexes were observed to feed young at five nests where observations were adequate. Although not quantified, only males were noted singing (the 'shrill, clear warbling song' of Longmore 1991) and only in the breeding season, whereas both sexes used single-noted apparent contact calls (the 'simple, repeated calls' of Longmore 1991).

Helpers and multi-broodedness

In the absence of colour-banded individuals, the occurrence or incidence of helpers at the nest and of multi-broodedness was not reliably determined. Nevertheless, we saw no evidence to suggest that birds other than the breeding pair attended the nest. Areas of mangal at Nightcliff and Rapid Creek checked throughout the 1999 breeding season appeared to be occupied by territorial pairs, and if this is so, then multi-broodedness (defined as re-nesting after a successful nest) was commonplace.

TABLE 3

Dates of spring tide sequences (7.0 metres CD or greater) for Darwin Harbour, and the number of recorded nest drownings during the 1999 breeding season of the Brown Honeyeater.

No. of nests drowned	Dates Month	≥7.0 m	≥7.2 m	≥7.4 m	≥7.6 m	≥7.8 m
2	April	15–21	16–20	17–20	17–19	18
1	May	1–3				
3	May	15–20	15–19	16–19	16–18	17
0	June	13–18	14–17	14–17	14–16	
2	July	13–17	13–16	14–16		
0	July-August	30–1				
1	August	11–15	12–15	13–14		
0	August	28–31	29–30			
0	September	10–13	10–12			

DISCUSSION

The little published information on the nesting biology of the Brown Honeyeater is nevertheless remarkably inconsistent in its findings. We found that both sexes fed the young, consistent with Ford (1998) but not Cassels (1961). Contrary to Longmore (1991), we found no evidence that males are involved in nest construction. Our data suggest a slightly shorter incubation and nestling period than the 14 days for each reported by Cassels (1961) and Longmore (1991). Whereas we recorded laying in the Darwin area from April to August, Longmore (1991) reported breeding from April to November, the latter perhaps reflecting a collection of records from both temperate and tropical areas. Our data on the timing of breeding are consistent, however, with Liddy's (1989) data that black-gaped individuals near Brisbane, Queensland, occur only from March to October and mostly from April to September. Black gapes are thought to be a feature of breeding condition in adult males (Robertson 1969; Liddy 1989).

The April to August laying season documented in this study contrasts almost diametrically with the August to May laying season documented by Noske (1998) for the Rufous-banded Honeyeater *Conopophila albogularis* in Darwin. These two species are of similar size and commonly occur together in mangal/coastal vine thicket interface, urban/mangal interface and urban habitats. A range of other patterns of seasonality have been documented for other honeyeater species in the Darwin area (Noske and Franklin 1999) and near Townsville in Queensland (Maher 1988), which shares with Darwin a tropical wet-dry climate with a similarly-timed wet season. This intriguing variability between species in the face of an intensely seasonal environment is not readily attributable to any simple dichotomy between relatively nectarivorous and relatively insectivorous diets (Noske and Franklin 1999). This study provides evidence of consistency in breeding season between habitats and years, going some way to ruling out one potential explanation — intra-specific variability related to habitat and annual variation in climate — for the reported diversity of patterns.

The Brown Honeyeater has a small clutch size, a moderate nest success rate but high survival of individual eggs/nestlings in successful nests, and is probably also markedly multi-brooded. This set of traits is consistent with general trends amongst honeyeaters and other old endemic Australian passerines in general (Yom-Tov 1987; Rowley and Russell 1991; but see Ford and Tremont 2000). Egg-laying at 24-hour intervals may be a universal feature of honeyeater (Meliphagidae) biology (Ford and Tremont 2000), but contrasts with longer laying intervals in at least some members of another old-endemic Australasian family, the Pardalotidae (Marchant 1985). Nevertheless, a mean clutch size of 1.84 eggs appears particularly extreme given that small birds often lay larger clutches (Yom-Tov 1987; Reiss 1991). Indeed, even by temperate Australian standards and certainly by those of the northern hemisphere, the sight of a 10 gram bird sitting on (sometimes) a single egg appears almost absurd!

Small clutches are to be expected in the tropics along with the temperate southern hemisphere (Skutch 1949;

Martin 1996), and indeed are a feature of a range of small passerines of the monsoonal tropics of north-western Australia (Noske 1998, 1999, unpubl. data). However, the most widely accepted explanation for this — that seasonal fluctuations in food supply are slight, producing little relative excess during the breeding season — seems hardly to apply in the monsoonal tropics where seasonality is extreme (McDonald and McAlpine 1991). An alternative explanation, that they are a response to high rates of nest predation, is not strongly consistent with our finding of a moderate nest success rate of 42 per cent, but may nevertheless warrant further investigation. Another hypothesis, that small clutch and brood size in the tropics helps prevent over-heating remains, so far as we know, untested.

Although nests of the Brown Honeyeater were occasionally recorded at heights of greater than 3 metres and rarely greater than 6 metres, the considerable majority of nests were below 2 metres. They were never attached to major branches of trees, nor suspended amongst highly unstable foliage. We believe, therefore, that it is appropriate to characterize the Brown Honeyeater as an 'obligate shrub-nester'. Wykes (1982) noted a relatively clear dichotomy amongst *Lichenostomus* honeyeaters between shrub-nesting and tree-nesting species, and suggested that the dichotomy reflected an evolutionary history in shrubby compared with grassy woodland habitats. The evolutionary implications of this for the Brown Honeyeater are unclear. What is clear is that shrub-nesting has major ramifications for a species that nests in mangal.

Our finding that a substantial proportion (possibly more than half) of nest failures in mangal were the result of flooding by spring high tides is apparently without parallel in the literature (but see Noske in press). Our data may have somewhat over-represented the incidence because we concentrated much of our search effort in the outer mangal zone where the vegetation is usually quite short (mostly less than 3 metres). Nevertheless, we have shown that the Brown Honeyeater is a shrub-nesting species even in woodland areas with available taller vegetation. The taller inner (seaward) mangals in which we made little search effort are subject to much deeper and more frequent flooding than the outer (landward) zones, and are therefore unlikely to provide any suitable shrub nest sites. Successful nest attempts in the areas we searched demonstrate that suitable above-tide options for nest sites were available. Clearly, Brown Honeyeaters were unable to anticipate the considerable fluctuations in the height of high tides, which in Darwin Harbour ranged from at least 5.0 to 7.34 metres CD in the course of each lunar cycle during the breeding season of the Brown Honeyeater. Although it was our impression that pairs that suffered nest loss by inundation subsequently built nests higher (though we did not have individually marked birds), losses continued to occur throughout much of the nesting season, suggesting limited learning capacity on the part of Brown Honeyeaters.

The interval between spring tide sequences is *c.* 29.5 days (the lunar cycle), with a secondary peak in high tides approximately every 15 days (the half-lunar cycle). This is less than the 32 days minimum time required for

Brown Honeyeaters to fledge young. Thus, any nest built at any time during the breeding season at less than 7.4 metres CD, and in the first half of the breeding season at less than 7.6 metres CD, would inevitably have been inundated.

The Brown Honeyeater is one of a number of obligate shrub-nesting birds that breed in mangal. Others include the mangal endemic Yellow White-eye *Zosterops luteus*, Red-headed Honeyeater and Mangrove Gerygone *Gerygone levigaster*, all of which usually nest 3.0 metres or less above the ground in outer mangal zones (Noske 1999, in press, and unpubl. data). The Mangrove Gerygone, at least, also suffers a moderate incidence of nest failures due to inundation (Noske, in press), demonstrating that even mangal-endemic species have not fully solved the problem of dealing with tide fluctuations and cycles. If, as appears plausible, the inner mangal zones cannot provide nest sites for these species because of frequent deep inundation, then conservation of landward mangal zones may be of critical importance for a range of mangal-endemic birds. In the light of proposed and actual development in Darwin Harbour and the possibility that these landward mangal zones may be identified as 'unproductive' because of lower primary productivity, and targeted for development as they have elsewhere (e.g. Malaysia, Noske 1995), the topic appears to warrant urgent investigation.

ACKNOWLEDGMENTS

We are grateful to Heather Ryan, Terry Barnes, Keisuke Ueda, Ross McDonald and Niven McRie who located and monitored some of the nests. David Williams of the Resource Assessment Branch of the NT Department of Lands Planning and Environment provided most helpful explanations of tidal patterns. Hugh Ford provided constructive comment on an earlier draft.

REFERENCES

- Beehler, B. M., Pratt, T. K. and Zimmerman, D. A. (1986). 'Birds of New Guinea.' (Princeton University Press: Princeton, New Jersey.)
- Blakers, M., Davies, S. J. J. F. and Reilly, P. N. (1984). 'The Atlas of Australian Birds.' (Melbourne University Press: Carlton.)
- Cassels, M. L. (1961). Field notes on the nesting of the brown honeyeater. *Aust. Bird Watcher* 1: 174–176.
- Coates, B. J. and Bishop, K. D. (1997). 'A Field Guide to the Birds of Wallacea: Sulawesi, the Moluccas and Lesser Sunda Islands, Indonesia.' (Dove Publications: Alderley, Brisbane.)
- Collins, B. G. (1981). Nectar intake and water balance for two species of Australian honeyeater, *Lichmera indistincta* and *Acanthorhynchus superciliosus*. *Physiol. Zool.* 54: 1–13.
- Collins, B. G. and Briffa, P. (1982). Seasonal variation of abundance and foraging of three species of Australian honeyeaters. *Aust. Wildl. Res.* 9: 557–569.
- Collins, B. G., Cary, G. and Payne, S. (1980). Metabolism, thermoregulation and evaporative water loss in two species of Australian nectar-feeding birds (family Meliphagidae). *Comp. Biochem. Physiol.* 67A: 629–635.
- Ford, H. A. (1998). Biparental care in the Brown Honeyeater *Lichmera indistincta*. *Aust. Bird Watcher* 17: 308–309.
- Ford, H. A. and Tremont, S. (2000). Life history characteristics of two Australian honeyeaters (Meliphagidae). *Aust. J. Zool.* 48: 21–32.
- Franklin, D. C. and Noske, R. A. (1998). Local movements of honeyeaters in a sub-coastal vegetation mosaic in the Northern Territory. *Corella* 22: 97–103.
- Liddy, J. (1989). Brown Honeyeaters *Lichmera indistincta* at a banding station in south-eastern Queensland. *Corella* 13: 65–72.
- Longmore, W. (1991). 'Honeyeaters and their Allies of Australia.' (Angus and Robertson: Sydney.)
- Maher, W. J. (1988). Breeding biology of the Brown-backed Honeyeater *Ramsayornis modestus* (Meliphagidae) in northern Queensland. *Emu* 88: 190–194.
- Marchant, S. (1985). Long laying intervals. *Auk* 103: 247.
- Martin, T. E. (1996). Life history evolution in tropical and south temperate birds: What do we really know? *J. Avian Biol.* 27: 263–272.
- Mayfield, H. A. (1975). Suggestions for calculating nest success. *Wilson Bull.* 87: 456–466.
- McDonald, N. S. and McAlpine, J. (1991). Floods and droughts: the northern climate. In 'Monsoonal Australia. Landscape, ecology and man in the northern lowlands' (Eds C. D. Haynes, M. G. Ridpath and M. A. J. Williams) Pp. 19–29. (A. A. Balkema: Rotterdam.)
- Noske, R. A. (1995). The ecology of mangrove forest birds in Peninsular Malaysia. *Ibis* 137: 250–263.
- Noske, R. A. (1996). Abundance, zonation and foraging ecology of birds in mangroves of Darwin Harbour, Northern Territory. *Wildl. Res.* 23: 443–474.
- Noske, R. A. (1998). Breeding biology, demography and success of the rufous-banded honeyeater *Conopophila albogularis*, in Darwin, a monsoonal, tropical city. *Wildl. Res.* 25: 339–356.
- Noske, R. A. (1999). Notes on the breeding biology of the tropical mangrove-dwelling Yellow White-eye *Zosterops luteus*. *Aust. Bird Watcher* 18: 3–7.
- Noske, R. A. (in press). The breeding biology of the Mangrove Gerygone *Gerygone levigaster* in the Darwin region, with notes on nest-parasitism by the Little Bronze-cuckoo *Chrysococcyx minutillus*. *Emu*.
- Noske, R. A. and Franklin, D. C. (1999). Breeding seasons of land birds in the Australian monsoonal tropics: diverse responses to a highly seasonal environment. *Aust. Biol.* 12: 72–90.
- Reiss, M. J. (1991). 'The allometry of growth and reproduction.' (Cambridge University Press: Cambridge.)
- Robertson, J. S. (1966). Honeyeater size variation. *Aust. Bird Bander Sept.* 1966: 50–52.
- Robertson, J. S. (1969). The significance of gape colour in Brown Honeyeaters. *Aust. Bird Bander* 7: 51–55.
- Robertson, J. S. and Woodall, P. F. (1987). Survival of Brown Honeyeaters in south-east Queensland. *Emu* 87: 137–142.
- Rowley, I. and Russell, E. (1991). Demography of passerines in the temperate southern hemisphere. In 'Bird population studies. Relevance to conservation and management.' (Eds C. M. Perrins, J. D. Lebreton and G. J. M. Hirs.) Pp. 22–44. (Oxford University Press: Oxford.)
- Skutch, A. F. (1949). Do tropical birds rear as many young as they can nourish? *Ibis* 91: 430–455.
- Tidemann, S. C. and Wilson, B. A. (1992). Bird assemblages in relation to habitat measures in Gregory National Park, Northern Territory. *J. Roy. Soc. WA* 75: 9–18.
- Woinarski, J. C. Z. (1993). A cut-and-paste community: birds of monsoon rainforests in Kakadu National Park, Northern Territory. *Emu* 93: 100–120.
- Woinarski, J. C. Z., Tidemann, S. C. and Kerin, S. (1988). Birds in a tropical mosaic: the distribution of bird species in relation to vegetation patterns. *Aust. Wildl. Res.* 15: 171–196.
- Wykes, B. J. (1982). Resource partitioning and the role of competition in structuring *Lichenostomus* honeyeater (and *Manorina melanophrys*) communities in southern Victoria. Ph.D. thesis, Monash University, Melbourne.
- Yom-Tov, Y. (1987). The reproductive rates of Australian passerines. *Aust. Wildl. Res.* 14: 319–330.