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Breeding biology of the Northern Fantail, including brood parasitism by the Brush Cuckoo

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Abstract. Very little is known about the breeding biology of the Northern Fantail *Rhipidura isura*, despite it being an abundant species of forests and woodlands in tropical Australia and New Guinea. I collated breeding records of the species from personal observations and those of other birdwatchers in the Northern Territory (NT), the Western Australian Museum in Western Australia (WA), BirdLife Australia's Nest Record Scheme and Atlas Scheme, and the literature. In the NT, eggs were laid from May to January, with a peak in October, and in WA from June to February, with a peak in December. Nests were built in a wide range of tree species and at heights above the ground ranging from 0.9 to 10 m, with a mean height of 3.3 m in both the NT and WA. At least five (42%) of 12 nests built in the mangroves lost their eggs after they were flooded by high spring tides. Clutch size was usually two, the mean (1.98) being slightly smaller than those of the three fantail species that breed in temperate south-eastern Australia. The incubation period of *c.*14 days (*n* = 1) and nestling period of 12–13 days (*n* = 2) are comparable with those of the species that breed in temperate Australia. One of the two eggs in one nest was larger than, but similar in appearance to, the other (Fantail) egg. This nest subsequently contained a single nestling Brush Cuckoo *Cacomantis variolosus*, providing the first confirmed record of this species parasitising broods of the Northern Fantail. This record and observations of young Brush Cuckoos being provisioned by Northern Fantails advance the known breeding season of this Cuckoo in the NT and WA forward by 2 months.

Introduction

The family Rhipiduridae comprises four genera, of which *Rhipidura* is the largest, with 60 species (Winkler *et al.* 2020). Of these 60 species, six are found in Australia, though none are endemic, most species being shared with New Guinea. Although the breeding biology of the three species occurring in temperate south-eastern Australia – Willie Wagtail *R. leucophrys*, Rufous Fantail *R. rufifrons* and Grey Fantail *R. albiscapa* – is well understood (Marchant 1971; Ford 1981; Sedgwick 1983; McFarland 1984; Ashton 1987; Goodey & Lill 1993; Maxwell & Calver 1998; Munro 2007; Berger-Tal *et al.* 2010; Hoffman *et al.* 2010; Beckmann & Martin 2016), that of the three species restricted to the tropics is very poorly known.

Despite being common in a wide variety of forest and woodland habitats across northern Australia, New Guinea and eastern Indonesia, the Northern Fantail *R. isura* has received little attention in over a century. Almost nothing is known about its breeding biology apart from the structure and composition of its nests, and the size and appearance of its eggs, all of which were described in the late 19th and early 20th century (Ramsay 1886; Campbell 1887; MacGillivray 1918). The breeding season in the Northern Territory (NT) was summarised by Noske & Franklin (1999) and McCrie & Noske (2015), but the incubation and nestling periods and nestling characteristics are hitherto undescribed (Boles 1988; Higgins *et al.* 2006). Higgins *et al.* (2006) calculated the mean clutch size in the Kimberley region, Western Australia (WA) and North Queensland combined (2.1 ± 0.55 eggs; *n* = 20), but there were no acceptably complete clutches among the 12 Nest Record Scheme (NRS) records from the NT.

This paper summarises opportunistic observations of nesting by the species in northern NT (the 'Top End'), mostly in the Darwin region, and compares its breeding biology with that of other fantails studied to date. Although there are several reports of Northern Fantails feeding young Brush Cuckoos *Cacomantis variolosus*, Brooker & Brooker (1989) listed the former only as a potential host because of the lack of records involving nestlings. The present paper includes observations of at least one Northern Fantail nest that was parasitised by the Brush Cuckoo, and reviews the breeding season and egg and nestling characteristics of the latter in NT and WA.

Methods

I collated breeding records of Northern Fantails in the NT from opportunistic observations by myself (*n* = 30) and other birdwatchers in the Top End (*n* = 15) up to 2016, supplemented by records from BirdLife Australia's Nest Record Scheme (NRS; *n* = 12); BirdLife Australia's Atlas Scheme (*n* = 31, excluding duplicates from other sources) and the literature (*n* = 17), including ten records by William McLennan (White 1917), and the single records of Sedgwick (1947), Rix (1970), Boekel (1976) and Brooker & Parker (1985). Breeding records from the Kimberley, WA, were extracted from the Storr–Johnstone Bird Data Base at the Western Australian Museum (*n* = 46). Most NT records are from the Darwin region, including the mangroves around the suburb of Nightcliff, where 12 nests were found.

The breeding season is defined as the months in which egg-laying occurred. Dates of laying were calculated from the dates of observations of eggs, nestlings or fledglings, taking into account the incubation and nestling periods (see Results). If laying was estimated to occur in either the last week of month X or the first week of month X + 1, both months scored 0.5. Despite the common incidence of birds

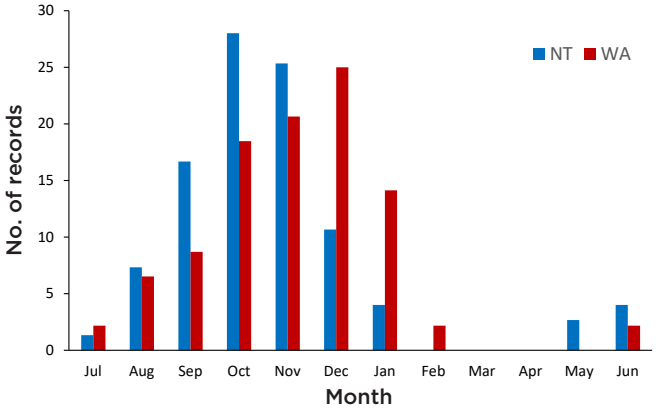

Figure 1. Estimated egg-laying months of the Northern Fantail in the Northern Territory (NT) (*n* = 75) and Western Australia (WA) (*n* = 46), over the fiscal year starting in July to accentuate breeding peaks. Records of building included (see Methods).

Figure 2. Adult Northern Fantail sitting on nest in Stilt-root Mangrove, Darwin. Photo: Richard A. Noske

abandoning nests before laying eggs, I included nests observed only at the building stage as they comprised a small percentage (16% and 20% in the NT and WA, respectively) of the total. I estimated the laying date of such records by adding 7 days to allow for the completion of the nest and clutch, based on minimum periods given by Higgins *et al.* (2006) for other fantail species, and the typical clutch size for the Northern Fantail of two eggs (see below). As the stage of breeding is unknown for Atlas Scheme records, I collated these separately. Two-tailed *t*-tests assuming equal variances were used to compare clutch sizes between the NT and WA.

On 8 September 2007, I video-recorded incubation behaviour for 54 minutes at a nest with two eggs using a SONY camcorder.

Results

In the NT, estimated egg-laying months of the Northern Fantail ranged from May to January, peaking in October (Figure 1; *n* = 75, including 12 nest-building-only records; Appendix 1). In WA, estimated laying months were from June to February, peaking in December (Figure 1; *n* = 46, including 9 building-only records; Appendix 2), suggesting that the breeding season lagged 1–2 months behind that of the NT. Of 31 additional breeding records (unspecified stage) for the species in the Atlas Scheme database, 24 (77%) occurred from August to October, but most records were from the NT, with few records from WA (*n* = 4) or Queensland (*n* = 6).

Table 1. Plants in which Northern Fantails built nests in the Northern Territory (NT) and Western Australia (WA).

Plant taxa	*No. species*	*NT*	*WA*
Mangroves	3	14	–
Eucalypts	7	5	7
Paperbarks	3	6	4
Acacias	2	7	2
Sandpaper Fig	1	-	5
Tropical Banksia	1	1	3
Others	10	3	11
	27	36	32

All nests had the typical wine-glass shape of most fantail species, with pendulous 'tails'. Nests were built in at least 27 species of trees and shrubs (Table 1). Over a third of the nests found in the NT were built in mangroves, especially the Stilt-root Mangrove *Rhizophora stylosa* (*n* = 11; Figure 2), a reflection of the habitat adjacent to my place of residence. In WA, on the other hand, most nests were found in eucalypts (mostly bloodwoods *Corymbia* spp.) or Sandpaper Figs *Ficus opposita*. Paperbarks *Melaleuca* spp., wattles *Acacia* spp. and Tropical Banksias *Banksia dentata* were used in both regions. The height above ground of 39 nests in the NT ranged from 1.2 to 10.0 m (mean 3.32 ± standard deviation 2.19 m) and in WA from 0.9 to 9.0 m (mean 3.36 ± 1.80 m). The estimated heights of 16 nest trees in the NT ranged from 2.4 to 25 m, and the relative height above ground of the nests within them ranged from 5% to 85% of the plant height, with a mean of 41%, i.e. slightly lower than half of the plant height.

The clutch and brood sizes of Northern Fantails were typically two in both the NT and WA (Figure 3). Although clutches of three were found only in the NT (*n* = 3), both the NT and WA had one record of a brood of three. Clutches of one were more commonly found in WA (*n* = 3) but broods of one were more common in the NT (*n* = 4), though these could have been the result of brood parasitism (see below). There was no significant difference between the NT and WA in either clutch size (t = 1.669; n = 24, 26; P = 0.101) or brood size (t = – 1.845; n = 14, 5; P = 0.082). Combining data from both regions, the mean clutch size was 1.98 ± 0.43 eggs. Nest attentiveness at the video-recorded nest was 97%, with complete incubation bouts lasting from 6.6 to 15.4 minutes (mean 12.0 min., *n* = 4), and complete off-bouts lasting from 12 to 35 seconds (mean 20.7 sec.; *n* = 4). Although change-overs were not seen at the nest, the brevity of off-bouts strongly suggests that the two adults shared incubation.

In 2006, Nest 13 was empty on 20 October, had one egg on 21 October and two eggs by 0930 h on 22 October. One chick hatched before 0830 h on 5 November (Figure 4) and both chicks had hatched by 0800 h the following day. The median incubation period was 14 days 22 h ± 22.5 h but, given the similar size of both nestlings, it seems likely

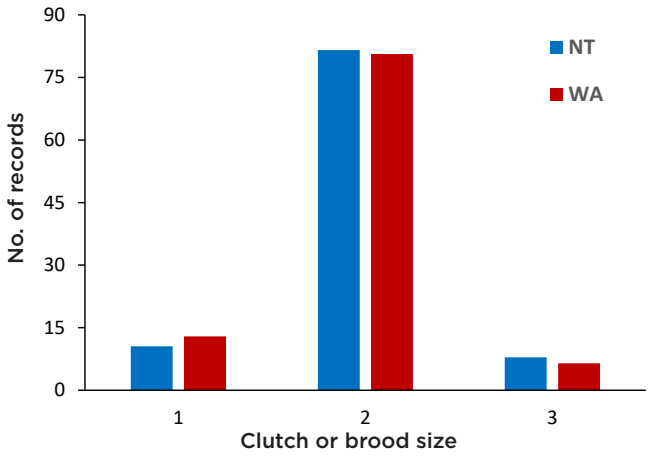

Figure 3. Clutch or brood size of Northern Fantails in the Northern Territory (NT) (*n* = 38) and Western Australia (WA) (*n* = 31).

that the second chick hatched later on the same day as the first, suggesting that the incubation period was close to the minimum (14.0 days). On 15 and 18 November, only one nestling was present, but by 0930 h on 19 November the nest was empty. Assuming that the chick was not depredated, the median nestling period was 13 days ± 24 h. In 1996, Nest 5 had two eggs at 1330 h on 4 November but by 1300 h on the following day, two hatchlings were present. Both nestlings were still present at 1830 h on 16 November, but the nest was empty 24 h later. Assuming that the chicks fledged successfully, the median nestling period was 12 days 5.5 h ± 24 h. At another nest, Northern Fantails were first observed sitting on 19 November 2005, and the nestlings were last observed on 14 December, giving a minimum nest cycle of 25 days (data supplied by S. Forsstrom).

At Nest 13, the hatchlings were naked with bright-pink skin, except for wisps of whitish natal down (neossoptiles) in the occipital, dorsal (back) and secondary (elbow) areas of the body (Figure 4), and greyish skin around the eyes. The bill was pinkish cream, rictal flanges (gape) cream and mouth bright yellow. The hatchling at Nest 18 had additional sparse down in the coronal, pectoral and caudal regions. At Nest 10, two chicks that were <5 days old were still blind and largely naked except for small greyish-blue pins on the wings and mantle (Figure 5). On Day 7 post-hatching, the wings of the chicks in Nest 5 had long pins that erupted on the following day, and the eyes were half open. On Day 10 post-hatching, the single nestling in Nest 13 had open eyes, long black pins on the crown, feathered lesser and median wing-coverts, blue wing quills sprouting blackish-brown feathers broadly edged pale cinnamon-brown in the terminal third, and blue tail quills sprouting cinnamon-brown feathers for almost half their length (Figure 6). At 12 days, the chick had white supercilia (eye-brows) and the wing quills were no longer visible, but the tail quills were still less than a quarter grown (Figure 7).

In two nests one egg was noticeably different from the other in the clutch. In Nest 11, one egg was more elongated and slightly wider than the other (Fantail) egg, though similar in colour and markings (Figure 8). In Nest 18, one egg had a distinct pale-olive band between the larger end and the middle, overlain with light mauve-grey blotches and dark-grey dots, and the rest of the egg was sparingly marked with diffuse grey and olive spots (Figure 9).

Figure 4. Northern Fantail egg and hatchling at Nest 13, Darwin. Photo: Richard A. Noske

Figure 5. Northern Fantail nestlings, <5 days old, at Nest 5. Photo: Richard A. Noske

Although I suspected that the latter egg was that of a Brush Cuckoo, the single nestling that was photographed soon after hatching was a Fantail, with typical anisodactylous feet. On the other hand, 17 days after its discovery, Nest 11 contained a large naked chick with zygodactylous feet and rounded nostrils, two characteristics of nestling cuckoos (Brooker & Brooker 1991). Its skin was dull pinkish brown

Figure 6. Northern Fantail nestling, 10 days old, at Nest 13. Note the tilt of the nest because of flooding. Photo: Richard A. Noske

Figure 7. Northern Fantail chick, 12 days old, at the same nest (Nest 13) as Figure 6. Photo: Richard A. Noske

Figure 8. Northern Fantail Nest 11 with eggs of Fantail (lower) and Brush Cuckoo (upper). Photo: Richard A. Noske

Figure 9. Northern Fantail Nest 18 with eggs of Fantail (left) and possible Brush Cuckoo (right). Photo: Richard A. Noske

Figure 10. Northern Fantail Nest 11 with Brush Cuckoo chick, probably 6–7 days old. Photo: Richard A. Noske

Figure 11. Same Brush Cuckoo chick as in Figure 10, probably 10–11 days old. Photo: Richard A. Noske

Figure 12. Brush Cuckoo chick photographed on same day as in Figure 11. Photo: Richard A. Noske

Figure 13. Displaced Northern Fantail Nest 16A/B after inundation by high tides, with two eggs absent. Photo: Richard A. Noske

over most of the body and dark grey around the eyes and future feather tracts, with short tufts of whitish down on the superciliary and occipital regions of the head, thighs and shoulders, and tiny pins emerging on the wings (Figure 10). Four days later, the chick's eyes were fully open and the body was partly feathered (Figures 11–12). The crown, neck and back had short black pins, and the scapulars and wing-coverts had long pins that were mostly greyish black, fading to pale grey distally, and were sprouting cinnamon feathers on the wing-coverts, and blackish feathers on the primaries, which were up to 25 mm long (including the pin). The short tail (~6 mm) consisted of grey-black pins except for the outermost pair, which were white.

Of 13 nests built in mangroves, at least five (38.5%) lost their eggs after high spring tides (>7.6 m) inundated the nest, causing displacement of the nest in some cases (Figure 13). These five nests represented 4 years (2005–2008 inclusive) and 3 months (September, October and November) and, in three cases, the high tide occurred during the evening preceding the loss of eggs. On the other hand, at least one brood survived partial flooding. In 2006, Nest 13 was apparently partially flooded on the two evenings following the hatching of the chicks (6 and 7 November, when high tides peaked at 7.6 and 7.8 m, respectively). Thereafter the nest was tilted at ~30° from horizontal, and the 'tail' of the nest was partly wrapped around a vertical twig (see Figures 6–7). Although two nestlings were present on 9 November, only one remained by 15 November, presumably a victim of nest predation. However at least two nests in the mangroves were successful in producing fledglings. One fledgling was found close to Nest 10, 11 days after the two young nestlings were photographed, and two fledglings were found 30 m from Nest 17B, where there had been two well-developed nestlings 8 days previously.

Discussion

Breeding season, nest sites and clutch size

During 4 months of collecting birds and eggs around the King River in western Arnhem Land, NT, from 26 September 1915 to 24 January 1916, William McLennan found no fewer than nine Northern Fantail nests, though three were deserted during 3 days of heavy rain (White 1917; Noske 2017). Storr (1967) defined the egg-laying season of this species in the NT as the 4 months from October to January, but later (Storr 1977) corrected this to 9 months (June–February). My dataset confirms that the laying season in the NT is long, though laying began and finished a month earlier (May and January, respectively) than Storr (1977) stated. In WA, laying peaked in December (Figure 1), suggesting that the breeding season lagged 1–2 months behind that of the NT. In northern Queensland, laying has been recorded in July and from October to December (Bravery 1970; Lavery 1986), and the Atlas included 'breeding' records for August (n = 1) and September (n = 2). Thus, laying in Queensland appears to extend from July to December, suggesting that the breeding season in the east of the species' range starts and ends earlier than in the west, though there are insufficient data to draw firm conclusions. Breeding records in Papua New Guinea, which lies north of Queensland, also indicate a peak in September and October (Coates 1990).

Most closely related to the Rufous Fantail of eastern Australia, the Arafura Fantail *R. dryas* occurs across the three northern Australian states and territories, but its range does not extend to Cape York or the eastern seaboard as does that of the Northern Fantail. Moreover, it is more specialised in its habitat requirements, occurring mainly in monsoon rainforests, mangroves and riparian forests, where it is generally uncommon (McCrie & Noske 2015). Combining nest data from WA and the NT, Noske & Johnstone (2018) showed that the laying season of the Arafura Fantail extends from September to March, a slightly longer period than in the Rufous Fantail, but possibly shorter and later than in the Northern Fantail, which may relate to the predilection of the Arafura Fantail for habitats that are prone to inundation from rains during the mid to late wet season.

Table 2. Breeding characteristics of Australian fantails, based on data in Higgins *et al.* (2006), except for Northern Fantail (present study) and Arafura Fantail (Noske & Johnstone 2018). Species are listed in order of decreasing number of Nest Record Scheme (NRS) records. Values shown are range (mean in parentheses) except where indicated; nr = no record, nest height = height of nest above the ground.

Species	*Mass (g)*	*No. NRS records*	*Nest height (m)*	*Clutch size*	*Incubation period (days)*	*Nestling period (days)*
Willie Wagtail	18	3560	0.25–30.0 (3.1)	1–5 (3.05)	13–15 (14.1)	12–15 (14.0)
Grey Fantail	8	1367	0–30.0 (3.3)	1–4 (2.66)	13–14 (13.8)	11–14 (12.3)
Rufous Fantail	10	126	0.34–6.0 (1.6)	2–4 (2.10)	14–17 (14.9)	11–17[#]
Northern Fantail	13	13	0.9–10.0 (3.3)	1–3 (1.98)	14–15*	12.2–13.0**
Mangrove Fantail	7	nr	1.0–3.0[#]	1–3 (2.17)	nr	nr
Arafura Fantail	9	0	1.0–3.0 (1.8)	2 (2.0)	nr	nr

[#]Insufficient data to calculate mean
**n* = 1 (see text)
***Median (*n* = 2)

The diversity of plant species and heights of nests above the ground found in this study is consistent with the literature. Of ten records in the NRS, four were in paperbarks *Melaleuca* spp., two in eucalypts, two in dead trees, one in a Leichhardt Tree *Nauclea orientalis* and one in a vine tangle (Higgins *et al.* 2006). In the Kimberley, Hill (1911, p. 275) noted "No decided preference in the choice of nesting sites was noticed. Some nests were built in an acacia scrub 3 or 4 feet [0.9–1.2 m] from the ground, while others were found at a height of from 70 to 75 feet [21–23 m]". The mean height of nests of Northern Fantails in the present study is identical to that of the Grey Fantail, but is apparently higher than nests of Rufous and Arafura Fantails (Table 2).

The mean clutch size of the Northern Fantail appears to be smaller than in the Willie Wagtail and Grey Fantail in temperate south-eastern Australia (Table 2), but typical for tropical lowland fantails in New Guinea (Donaghey 2015), as well as the Arafura Fantail (Noske & Johnstone 2018). The clutch size of at least two montane fantail species in New Guinea is one, though this is common there, where few passerines lay clutches greater than two (Freeman & Mason 2014; Donaghey 2015). As in other fantail species, incubation in the Northern Fantail is apparently shared by both the male and female. The incubation period (*c*. 14 days) and nestling period (*c*. 12–13 days) are comparable with those of the temperate Australian-breeding species (Table 1).

Although there are no previous descriptions of nestlings of the Northern Fantail, nestling Grey Fantails are said to have pink skin (at least ventrally) with a few tufts of dark-brown down on the top of the head and upperparts (Higgins *et al.* 2006), whereas New Zealand Fantails *R. fuliginosa* (formerly considered conspecific with the Grey Fantail) are described as being sparsely covered in brown down at hatching (Powlesland 1982). Nestling Rufous Fantails have dark orange-rufous or pinkish skin with sparse grey-black down on the centre of the crown (Higgins *et al.* 2006). By contrast, newly hatched Willie Wagtails have dark red-black skin with dense pale-brown down in eight major patches (coronal, occipital, dorsal, humeral, secondary, femoral, pectoral and latero-abdominal) and sparse down in five minor patches (ocular, primary, caudal, crural and jugular) (Gill 1982). In the present study, the hatchling Northern Fantail in Nest 13 (Figure 4) had sparse down in only three of these major patches (occipital, dorsal and secondary), though the Nest 18 hatchling had additional sparse down in two other major areas (coronal and caudal). Nevertheless, neonate Northern Fantails are clearly more similar to the smaller Grey and Rufous Fantails than to the larger Willie Wagtail in having sparse down and pinkish skin. Nestlings of all four species have pale-yellow or cream rictal flanges (gape), though the bill and mouth of the Northern Fantail appear to be yellower than the greyish bill and orange or yellow-orange mouth of the other three species (Boles & Longmore 1985; Higgins *et al.* 2006). In the New Zealand Fantail, the wing quills measured 5–10 mm by Day 4, and feathers erupted from them by Day 7; by Day 10, feathers were well developed everywhere except the tail, where they protruded only ~5 mm (Powlesland 1982). My observations of nestling Northern Fantails are broadly consistent with these stages of development.

Brood parasitism by the Brush Cuckoo

In the Top End and Kimberley, most records of brood parasitism by Brush Cuckoos involve the dome-nesting Bar-breasted Honeyeater *Ramsayornis fasciatus*, but this cuckoo has also been recorded parasitising the open-cup-nesting White-throated Honeyeater *Melithreptus albogularis*, Rufous-banded Honeyeater *Conopophila albogularis*, Yellow-tinted Honeyeater *Ptilotula flavescens*, Broad-billed Flycatcher *Myiagra ruficollis* and Paperbark Flycatcher *M. nana* (Thompson 1982; Brooker & Brooker 1989; Johnstone & Storr 2004; McCrie & Noske 2015). Brooker & Brooker (1989) found seven records of brood

parasitism involving the Northern Fantail, six of which concerned the Brush Cuckoo, and the other, the Little Bronze-Cuckoo *Chalcites minutillus*, but they considered both these cuckoo species only as potential brood parasites because of the lack of records involving nestlings. Of the six species of brood-parasitic cuckoos known to breed in the Top End of the NT, four lay eggs that are demonstrably larger than those of the Northern Fantail. Of the remaining two species, the resident Little Bronze-Cuckoo normally lays its uniformly dark olive or brown eggs only in nests of gerygones (Brooker & Brooker 1989), and the migratory Horsfield's Bronze-Cuckoo *C. basalis* lays eggs that are finely spotted and freckled all over with reddish brown (Beruldsen 1980), usually in enclosed (domed) nests, and is not known to breed in the Darwin region (Thompson 1982; McCrie & Noske 2015). Therefore, these two bronze-cuckoo species are unlikely to parasitise the broods of Northern Fantails.

My observations and photographs of the large egg and ensuing nestling in Nest 11 confirm that nests of the Northern Fantail are at least occasionally parasitised by the Brush Cuckoo. Moreover, Northern Fantails were recorded feeding a fledgling Brush Cuckoo in monsoon rainforest at East Point on 20 November 2005 (N. McCrie pers. comm.), and a juvenile Brush Cuckoo in mangroves in Ludmilla on 9 November 2005 (RAN pers. obs.). In addition, Brooker & Parker (1985) observed Northern Fantails feeding a juvenile Brush Cuckoo in Kakadu National Park, ~300 km east of Darwin. McLennan's observation of Northern Fantails feeding a young cuckoo, identified as a Fan-tailed Cuckoo *Cacomantis flabelliformis*, on the King River, Arnhem Land, on 25 December 1915 (White 1917), most likely involved the Brush Cuckoo, given that the range of the Fan-tailed Cuckoo does not extend west of Cape York. It is also possible that the strangely patterned egg photographed in Nest 18 (Figure 9) in the present study was laid by a Brush Cuckoo but subsequently ejected by one of the Fantails. In experiments using model eggs, Langmore *et al.* (2005) found that all Grey Fantails and Willie Wagtails ejected non-mimetic eggs that matched the host eggs in size but not in colour.

The skin of a hatchling Brush Cuckoo in a nest of the Rufous Fantail was described as being "of dark flesh colour and entirely devoid of down" (Hindwood 1930, p. 19), and that of a 2–3-day-old Brush Cuckoo nestling as "blackish and shiny" (E.S. Hoskin in Brooker & Brooker 1989, p. 20). The quills emerged at 7–8 days, and the feathers began to erupt at 9–10 days (E.S. Hoskin in Brooker & Brooker 1989). The skin colour of the young chick that I photographed in Nest 11 (Figure 10) was more consistent with Hindwood's (1930) description than with Hoskin's, but the short neossoptiles on the head, wings and thighs contradict Hindwood's claim of the skin being entirely naked. Assuming that Hoskin's statements on feather development apply to the cuckoo chick in Nest 11, it was probably *c*. 6–7 days old when photographed on 27 November (Figure 10) and *c*. 10–11 days old on 1 December (Figures 11–12).

The incubation period for Brush Cuckoo eggs laid in the nests of Grey Fantails is 12–13 days (n = 2; Marchant 1980; NRS in Higgins 1999), which is 1 day shorter than for the host. The nestling period of the Brush Cuckoo was calculated as 17 days ± 4 h (Marchant 1980), and estimated as 16 and 19 days at two other nests (E.S. Hoskin in Brooker & Brooker 1989; NRS in Higgins 1999). The nestling period therefore probably exceeds that of the Northern Fantail by *c.* 4–5 days. Combining these incubation and nestling periods gives a nest cycle of *c*. 30 days. The Brush Cuckoo egg in the present study must therefore have been laid in early November 2005, and the two records of Northern Fantails feeding fledgling or juvenile Brush Cuckoos in Darwin suggest that the Cuckoos' eggs were laid in September and mid October, respectively. Of 70 breeding records for the Brush Cuckoo in the Top End and Kimberley (Table 6 in Brooker & Brooker 1989), however, 56 (80%) involved eggs being laid from January to March, with the earliest records in November (n = 1) and the latest in May (n = 1). Assuming that most of these records involved eggs laid in nests of the riparian-associated Bar-breasted Honeyeater, which breeds mainly in January and February (McCrie & Noske 2015), my records suggest an earlier breeding season for Brush Cuckoos parasitising Northern Fantails, from September through December. On the other hand, Brooker & Parker (1985) reported Northern Fantails feeding a juvenile Brush Cuckoo in Kakadu National Park on 28 February 1982, suggesting that the Cuckoo egg had been laid in December or January.

Because of its wide range through northern and eastern Australia, New Guinea and eastern Indonesia, the Brush Cuckoo has many hosts, including 60 species in Australia alone (Brooker & Brooker 1989; De Geest & Leitão 2017; Johnsen 2021). In Australia, geographical differences in host use have led to the evolution of at least two egg morphs (Beruldsen 1980; Abernathy & Liang 2020). One of these morphs closely resembles the eggs of the Leaden Flycatcher *Myiagra rubecula* (Beruldsen's Type 'A'), but another (Type 'B') is said to resemble those of the Grey Fantail, both these species being major hosts in eastern Australia. In the present study, the Brush Cuckoo egg in Nest 11 (Figure 8) was similar in appearance to those of both the Grey Fantail and Northern Fantail, but was noticeably longer, supporting the conclusion of Abernathy & Liang (2020) that Brush Cuckoo eggs laid in fantail nests are significantly larger than fantail eggs. This contrasts with the findings of Attard *et al.* (2017), who concluded that the eggs of Brush Cuckoos mimicked those of their hosts in size, and showed greater mimicry of egg shape when parasitising open-cup-nesting hosts (like fantails) than when parasitising hosts with domed nests.

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Appendix 1. Breeding records of the Northern Fantail from the Top End of the Northern Territory. Stage: B = building, E = eggs, N = nestlings, E/N = adult brooding but contents of nest unknown, F = fledglings, J = dependent juveniles. Laying month is estimated – see Methods. Location: Ck = creek, CDU = Charles Darwin University (Casuarina campus unless stated otherwise), NP = National Park, Pk = park, R = river, Res. = Reserve, WTP = Wastewater Treatment Plant; S = south, W = west. Observer/source: NRS = Nest Record Scheme.

Date day.month.year	*Stage*	*Laying month*	*Location*	*No. eggs (e) or nestlings (n)*	*Nest height (m)*	*Observer/source*
25.11.1898	E	Nov.	Katherine region	2e	3.0	Le Souëf (1899)
31.10.1915	E	Oct.	King R, Arnhem Land		1.5	White (1917)
7.11.1915	B	Nov.	King R, Arnhem Land		1.5	White (1917)
10.11.1915	N	Oct.	King R, Arnhem Land		9.0	White (1917)
13.11.1915	E	Nov.	King R, Arnhem Land	1e	1.8	White (1917)
28.11.1915	E	Nov.	King R, Arnhem Land	2e		White (1917)
3.12.1915	B	Dec.	King R, Arnhem Land		2.4	White (1917)
12.12.1915	B	Dec.	King R, Arnhem Land			White (1917)
13.12.1915	E	Dec.	King R, Arnhem Land	2e		White (1917)
25.12.1915	F	Nov.	King R, Arnhem Land			White (1917)
5.1.1916	E	Dec./Jan.	King R, Arnhem Land	2e		White (1917)
12.11.1944	B	Nov.	Batchelor		3.0	Sedgwick (1947)
10.7.1967	N	Jun.	East Point, Darwin	2n		Rix (1970)
30.8.1974	E/N	Aug.	Gove, Arnhem Land			Boekel (1976)
14.10.1978	F	Sep.	Howard Springs			NRS 34178
29.10.1978	E/N	Oct.	Humpty Doo–Adelaide R		2.1	NRS 34179
5.10.1979	E/N	Sep./Oct.	Near Gunn Point	2n	3.0	NRS 34184
12.12.1979	N	Nov.	South Alligator R	2n	8.0	NRS 34180
13.12.1979	E	Dec.	South Alligator R	3e	1.5	NRS 34182
14.12.1979	E	Dec.	Gunlom Falls, Kakadu NP	3e	1.2	NRS 34181
2.9. 1980	E/N	Aug./Sep.	Kakadu NP			Brooker & Parker (1985)
18.10.1980	E	Oct.	Gunlom Falls, Kakadu NP	3e	4.5	NRS 34185
26.11.1980	E	Nov.	Cannon Hill, East Alligator R		1.8	NRS 34186
29.8.1981	B	Sep.	S of Bynoe		3.0	NRS 34187
29.8.1981	B	Sep.	South Alligator R		7.0	NRS 34188
27.10.1981	E	Oct.	Kakadu NP			Brooker & Parker (1985)
28.2.1982	F	Jan.	Kakadu NP			Brooker & Parker (1985)
16.10.1985	B	Oct.	Kapalga, Kadadu NP		10.0	T. Hertog
16.11.1985	N	Oct./Nov.	Howard Springs		7.0	NRS 34177 (RAN)
3.12.1985	B	Dec.	Kapalga, Kadadu NP		4.0	T. Hertog
30. 10.1988	E	Oct.	CDU			RAN/01
12.11.1988	N	Oct.	CDU			M. Guinea
6.11.1989	E	Nov.	CDU			RAN/02
26.5.1991	N	May	Palmerston WTP			RAN/03
10.12.1994	N	Nov.	East Point, Darwin			K. & L. Fisher
19.10.1995	E	Oct.	Holmes Jungle Nature Pk	2e	1.5	K. Ueda
29.10.1996	E	Oct.	Buffalo Ck, Darwin region			G. Smith
4.11.1996	N	Oct./Nov.	CDU	2e	1.8	RAN/05
17.11.1996	N	Oct./Nov.	Territory Wildlife Pk	2n	1.2	RAN/04
2.11.1997	E	Oct.	Darwin High School		3.0	RAN/06
16.11.1997	N	Oct.	Territory Wildlife Pk	1n	6.0	NRS 34189
2.10.1998	E	Sep./Oct.	Gove, Arnhem Land	2e	2.1	RAN/07
4.11.1998	E	Oct./Nov.	Groote Eylandt	2e	3.6	Noske & Brennan (2002)

Appendix 1 continued

Date day.month.year	*Stage*	*Laying month*	*Location*	*No. eggs (e) or nestlings (n)*	*Nest height (m)*	*Observer/source*
8.8.1999	E/N	Jul./Aug.	Holmes Jungle Nature Pk			G. O'Brien
29.7.2000	J	Jun.	Mary R			RAN/08B
25.9.2000	E	Sep.	Murganella, Arnhem Land	2e	5.4	RAN/08A
12.9.2001	F	Aug.	Marrakai Crossing	2n		D.C. Franklin
10.9.2002	F	Aug.	CDU, Palmerston campus	2n		RAN/08C
1.3.2003	J	Jan.	Casuarina Coastal Res., Darwin			RAN/08D
14.10.2005	E	Oct.	Nightcliff, Darwin	2e	2.2	RAN/09
9.11.2005	J	Oct.	Ludmilla Pipeline			RAN/12A
10.11.2005	E	Nov.	Nightcliff, Darwin	2e	2.5	RAN/10
10.11.2005	E	Nov.	Nightcliff, Darwin	2e		RAN/11
19.11.2005	E	Nov.	Darwin Botanic Gardens	2n	4.0	S. Forsstrom
20.11. 2005	F	Oct.	East Point, Darwin			N. McCrie
4.9.2006	E	Aug./Sep.	Nightcliff, Darwin	2e	2.0	RAN/12B
22.10.2006	E	Oct.	Nightcliff, Darwin	2e	2.4	RAN/13
9.1.2007	J	Nov.	CDU			RAN/14A
12.6.2007	B	Jun.	Robertson Ck, Darwin		10.0	RAN/14B
8.9.2007	E	Aug./Sep.	Nightcliff, Darwin	2e		RAN/14C
15.9.2007	E	Sep.	Nightcliff, Darwin	2e	2.4	RAN/14D
30.10.2007	N	Oct.	Buffalo Ck, Darwin	2e	2.4	RAN/14E
17.9.2008	E	Sep.	Nightcliff, Darwin	2e	2.1	RAN/17A
25.9.2008	B	Sep./Oct.	Buffalo Ck, Darwin		3.0	J. Estbergs
5.10.2008	E	Sep./Oct.	Nightcliff, Darwin	2e	2.2	RAN/15
8.11.2008	B	Nov.	Nightcliff, Darwin		2.2	RAN/16
29.11.2008	N	Nov.	Nightcliff, Darwin	2n	3.6	RAN/17B
4.1.2009	E	Dec.	Kulaluk Crab Farm, Darwin	2e		RAN/18
8.9.2009	E	Sep.	Darwin			NT Birds
16.9.2009	E	Sep.	Nightcliff, Darwin			I. Hance
4.8.2011	E/N	Jul./Aug.	East Point, Darwin		3.0	B. Hensen
28.9.2011	E/N	Sep.	Casuarina Coastal Res.			B. Hensen
31.10.2011	B	Nov.	East Point, Darwin		2.5	J. Rawsthorne
7.2.2012	J	Dec./Jan.	East Point, Darwin			J. Rawsthorne
20.5.2016	E	May	Howard Springs		6.5	J. Cameron

Appendix 2. Breeding records of the Northern Fantail from the Kimberley region of Western Australia, supplied by R.E. Johnstone. Rd = road, Stn = station; E = east; SW = south-west; other abbreviations as in Appendix 1. Weaner Creek is located 30 km west of Kununurra.

Date day.month.year	*Stage*	*Laying month*	*Location*	*No. eggs (e) or nestlings (n)*	*Nest height (m)*	*Observer/source*
15.10.1886	E	Oct.	Derby			North (1901–1904)
23.10.1909	N	Oct.	Wyndham	2n		Mathews (1909)
12.1.1925	E	Jan.	Fitzroy Crossing	3e		Whitlock (1925)
29.5.1955	B	Jun.	Kimberley Research Stn			Slater (1959)
23.9.1959	E	Sep.	King R, W of Wyndham	2e		I.C. Carnaby
23.9.1959	E	Sep.	King R, W of Wyndham	1e	1.2	I.C. Carnaby
25.9.1959	E	Sep.	King R, W of Wyndham	1e		I.C. Carnaby
23.10.1959	E	Oct.	King R, W of Wyndham	2e		I.C. Carnaby
23.10.1959	E	Oct.	King R, W of Wyndham	2e	1.2	I.C. Carnaby
22.11.1959	N	Oct./Nov.	King R, W of Wyndham			I.C. Carnaby
1.1.1963	E	Dec.	Kununurra	2e	1.2	I.C. Carnaby
2.1.1963	E	Dec.	Kununurra	2e	2.7	I.C. Carnaby
13.1.1963	E	Jan.	Kununurra	2e	6.0	I.C. Carnaby
3.2.1963	E	Jan./Feb.	Kununurra	2e	3.6	I.C. Carnaby
12.12.1964	E	Dec.	48 km E of Wyndham	2e	5.4	I.C. Carnaby
19.12.1964	E	Dec.	48 km E of Wyndham	1e	2.4	I.C. Carnaby
26.12.1964	E	Dec.	48 km E of Wyndham	1e	2.7	I.C. Carnaby
25.12.1965	E	Dec.	48 km E of Wyndham	2e	3.0	I.C. Carnaby
19.11.1972	B	Nov.	Mitchell Plateau			J.A. Smith
24.8.1974	E	Aug.	Prince Regent R Res.		2.7	J. Dell
29.8.1974	N	Aug.	Prince Regent R Res.	3n	2.4	R.E. Johnstone
6.8.1975	E	Jul./Aug.	Prince Regent R Res.	2e		J. Dell
7.8.1975	E	Jul./Aug.	Prince Regent R Res.		3.0	J. Dell
6.1.1981	E/N	Dec./Jan.	Dunham R			G. Lodge
4.2.1983	E	Jan./Feb.	Flying Fox Rd, Kununurra	2e	7.5	G. Lodge
12.9.1995	E	Sep.	Weaner Ck	2e	3.6	G. Lodge
8.10.1995	B	Oct.	Weaner Ck			G. Lodge
5.11.1995	B	Nov.	Weaner Ck		5.4	G. Lodge
7.11.1995	B	Nov.	Weaner Ck		0.9	G. Lodge
15.11.1995	B	Nov.	70 km SW of Kununurra		3.6	G. Lodge
18.11.1995	E	Nov.	Weaner Ck	2e	3.0	G. Lodge
24.11.1995	E	Nov.	Weaner Ck			G. Lodge
24.11.1995	E	Nov.	Weaner Ck	2e	3.6	G. Lodge
28.12.1996	E	Dec.	70 km SW of Kununurra	2e	2.4	G. Lodge
30.12.1996	B	Jan.	Cooliman Ck, Ord R		4.5	G. Lodge
5.1.1997	E	Jan.	Weaner Ck	2e	3.0	G. Lodge
27.9.1997	B	Oct.	Weaner Ck		1.8	G. Lodge
17.12.1997	N	Nov.	Cooliman Ck, Ord R	2n		G. Lodge
28.12.1997	E	Dec.	Weaner Ck	2e	3.0	G. Lodge
26.10.1998	E	Oct.	Weaner Ck	2e	3.6	G. Lodge
9.12.1998	E	Nov.	Weaner Ck	2e	4.5	G. Lodge
10.12.1999	E	Dec.	Cooliman Ck, Ord R	2e	2.4	G. Lodge
22.12.1999	N	Dec.	Cooliman Ck, Ord R	2n		G. Lodge
31.10.2003	E	Oct.	Cooliman Ck, Ord R	2e	2.4	G. Lodge
5.1.2006	B	Jan.	Cooliman Ck, Ord R		9.0	G. Lodge
14.1.2006	N	Dec.	Weaner Ck	2n	2.4	G. Lodge