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New insights on the breeding biology of the Crow Honeyeater *Gymnomyza aubryana* suggest convergence with the Mao *G. samoensis*

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Abstract. Phylogenetic study of the honeyeater family shows that the four insular species of the genus *Gymnomyza* are polyphyletic, with the largest, the Crow Honeyeater *G. aubryana*, being a distinct and ancient lineage. The Critically Endangered Crow Honeyeater is a secretive species that lives in the rainforest of New Caledonia. For two breeding seasons (S1 in 2019 and S2 in 2020) we studied its breeding biology in the Parc Provincial de la Rivière Bleue. In S1, three nests (N1, N2, N3) were found and one nest (N4) in S2. Three dismantled nests (N1, N2 and N4) revealed four distinct layers; detailed measurements showed that Nest N2 consisted of 507 pieces of nest material and weighed 103 g. The female built the nest and incubated the one-egg clutch for 75% of time over a 24-hour period. The female rolled the egg each 33 minutes ($n = 50$) during the day and 118 minutes ($n = 23$) at night. The nest was 9.5 m above ground in a small tree (trunk 12 cm in diameter) and the trees and shrubs within 10 m mainly had trunks $\leqslant$10 cm in diameter ($n = 4$). Laying occurred during the dry season (August–October). The feeding rate of the nestling was 2.6 times/h. Animal prey items accounted for 74.7% by number, of which 66.5% were orthopterans; indeterminate 9.7%, fruit 12.4% and only 3.2% was nectar ($n = 1788$). Prey items in the size range 21–40 mm in length constituted 59% of the nestlings' food by number. The number of faecal sacs produced per nestling averaged 1.7/h ($n = 956$). The young fledged at 25.5 days (mean for two nests) and did not return to the nest, but was fed for another 2.6 months. One juvenile, from an unknown nest, remained at least 16.5 months in the adults' territory. The home range of a male during 2.6 months (September to early December) was 24 ha. The Crow Honeyeater has a slow life history for breeding biology, as found also for the Mao *G. samoensis*. Both species evolved on tropical islands and show a convergent adaptation.

Introduction

The avian family Meliphagidae (honeyeaters) originated in Australia in the late Oligocene–early Miocene (25 Mya: Marki *et al*. 2016). It includes four large insular species in the genus *Gymnomyza*: Mao *G. samoensis* in Samoa, Yellow-billed Honeyeater *G. viridis* and Giant Honeyeater *G. bruneirostris* in Fiji, and Crow Honeyeater *G. aubryana* in New Caledonia (del Hoyo 2020). All *Gymnomyza* species have the same type of morphology, a slim body, long tail and curved beak. However, the Crow Honeyeater is somewhat apart from the other *Gymnomyza* species, being predominantly black instead of green. It is the largest species of this genus, with a wing-length 16.5% and 22.5% greater than in the Mao and Yellow-billed Honeyeater, respectively (measurements from Keast 1985). Also, it is the only one of the genus with bare skin around the eye and between the eye and ear, a pattern found with great variability in another group of honeyeaters, *Melidectes* from New Guinea. Based on biometry and feathering of the face, the Crow Honeyeater is more different from the three other *Gymnomyza* species (Fiji and Samoa) than those three species differ from each other. It seems likely that *Gymnomyza* is a descendant of *Melidectes*, with the first colonisation of the remote Pacific islands of Fiji and Samoa by a *Melidectes* ancestor from New Guinea, from where further colonisation then reached New Caledonia (Mayr 1944).

Phylogenetic analysis has revealed that the genus *Gymnomyza* is polyphyletic, with the Crow Honeyeater being a distinct and ancient lineage for which phylogenetic relationships appear difficult to resolve (Marki *et al*. 2016; Andersen *et al*. 2019). The three remaining *Gymnomyza* species are part of a less inclusive clade that also includes the genera *Nesoptilotis*, *Entomyzon*, *Melithreptus*, *Meliarchus*, *Guadalcanaria*, *Meliphacator* and *Foulehaio* (Marki *et al*. 2016). In this latter clade, the two Fijian species are sister-species but not directly related to the Samoan species. Hence, the four *Gymnomyza* species consist of three independent evolutionary lineages. Estimates of divergence times suggest that the large species of Fijian honeyeaters diverged from their closest relatives between 7 and 15.6 Mya and the Mao diverged from *Foulehaio* 4–7.3 Mya (Figure 1; see also Marki *et al*. 2016 and Yabaki *et al*. 2016; differences in divergence estimates are due to different calibration strategies). Marki *et al.* (2016) estimated the divergence between the New Caledonian Crow Honeyeater and its sister-species to be around 15 Mya. Yabaki *et al*. (2016) did not include the Crow Honeyeater in their analyses.

The Crow Honeyeater is a rare and poorly known monogamous species. Although it may be curious and sometimes come to check a visitor, it usually disappears quickly and stays out of sight. It is shy and its low density makes encounters rare and unpredictable. All these characteristics have made collection of data difficult, and the available information is scarce.

In this work, we aimed to gather information from two seasons of field study on the breeding biology of this Critically Endangered species (BirdLife International 2018): nest and nest site, egg and clutch size, nestling care and

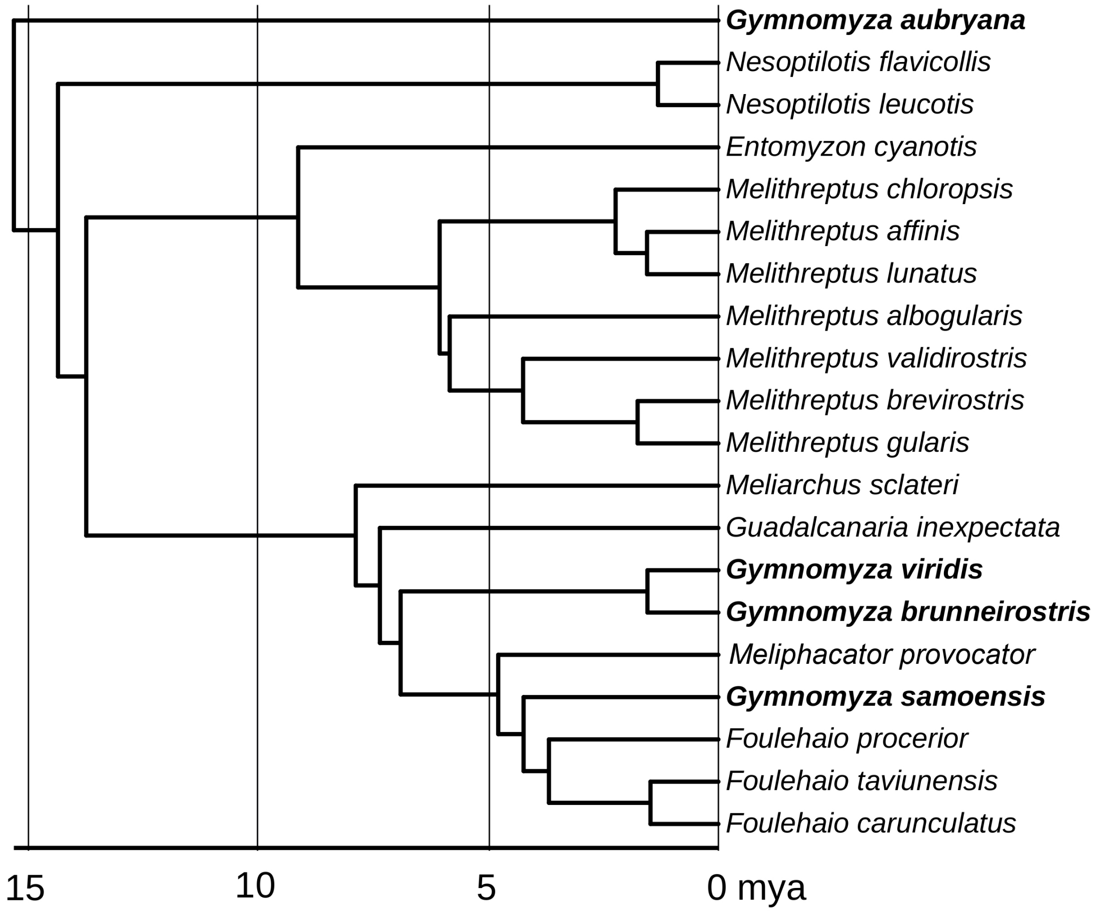

Figure 1. Phylogenetic relationships and estimates of divergence times for some honeyeater species. *Gymnomyza* species are shown in bold. Modified from Marki *et al*. (2016). The tree was drawn using iTOL v4 (Letunic & Bork 2019).

time from fledging to independence. We also compared reproduction parameters of the Crow Honeyeater with those of the large *Gymnomyza* species present in Samoa, the Mao, to see if they share prolonged parental care (i.e. long incubation, nestling and post-fledging periods: Stirnemann *et al*. 2016) and the same breeding strategy (Russell 2000) as a possible correlate of insular tropical environments.

Study site and methods

The study site was the Parc Provincial de la Rivière Bleue (22°6′S, 166°40′E) on the island of Grande Terre, 60 km north-east of the capital city Nouméa, New Caledonia. The park covers 220.7 km^2 and has 116 km^2 of rainforest, the habitat of the Crow Honeyeater. In 2019 and 2020, the total annual rainfall recorded 3.6 km from the core of our study site was 2713 mm and 3206 mm, respectively. Field work was carried out from 9 September 2019 to 3 December 2020 and included two breeding seasons (S1 in 2019 and S2 in 2020), with four nests found – N1, N2 and N3 in S1 and N4 in S2 (Figure 2). The species is sexually monomorphic in plumage. Males are heavier than females (Higgins *et al*. 2008) but this is difficult to assess in the field. To facilitate the recognition of individuals, nine birds caught in mist-nets were colour-banded.

To obtain data on nest structure, we dismantled three nests, after predation (N1) or successful breeding (N2, N4), and counted and measured each element of nest material in each layer for one of them (N2). We also described the vegetation surrounding the nest sites (n = 4) and, within a 10-m radius of each nest, counted and measured each shrub and tree that had a trunk diameter >1cm and height >1m.

To monitor the behaviour of Crow Honeyeaters at a nest, we used a small infrared micro-camera and recorded continuously the nestling in each of two nests: in S1, from Day 10 until fledging on Day 27 (4–21 October 2019, N2); and in S2, the entire nestling period (3–26 September 2020, N4), for 235 and 322.5 hours, respectively. In addition, the last part of the incubation period was monitored (28 August–3 September 2020, N4). Whenever possible, we identified the prey given to the nestling to at least the taxonomic order from footage from the infrared camera. Prey was classified into five categories: very small (<5 mm), small (5–20 mm), medium (21–30 mm), large (31–40 mm) and very large (>40 mm). The beak of the adult bird was used as a benchmark when estimating prey size.

To find out the area of rainforest used during the breeding season, a radio-transmitter with a harness (Karl & Clout 1987) was attached to a male Crow Honeyeater, from 15 September to 2 December 2020 (2.6 months), and the bird was followed on foot. Using a GIS (QGIS 2018), its movements were mapped to assess the area covered.

Figure 2. Four nests of the Crow Honeyeater studied during this research: (a) N1 (female on nest), (b) N2 (female on nest), (c) N3 and (d) N4. Photos: Pascal Villard

Results

During the two breeding seasons studied (S1 in 2019, Nests N1–N3; and S2 in 2020, Nest N4), reproduction started with nest building in late July and incubation and feeding of nestlings lasted until early December.

Nest and nest site

Three dismantled nests (N1, N2 and N4) each consisted of four layers. The detailed composition of Nest N2 is shown in Table 1 and Figure 3. The first or outer layer of the nest was made of rather thin elements, 1–2 mm in diameter and 45.3 ± 23.1 cm long, and had four main components: aerial roots (66.5%; appeared to be from an orchid), palm-leaf filaments (20.1%), dry inflorescence stems (11%) and plant filaments of unknown origin (2.4%). Internal to this, the second layer was made of dry leaves, decomposed to some extent, to form the bottom of the nest cup. The third layer consisted of dry but intact leaves from *Calophyllum caledonicum* and pieces of dry fern leaves (Austral Bracken *Pteridium esculentum*, Shiny Fan Fern *Sticherus flabellatus* and Old World Forked Fern *Dicranopteris linearis*). Finally, the innermost layer consisted of dry stems of tree inflorescences of 1–2-mm diameter and 21.7 ± 11.9 cm long (possibly *Macaranga alchorneoides*); no feathers or soft material was added. Filaments and sticks of the outermost layer were loosely intertwined and only four or five were tied around the branches and/or lianas supporting the nest. However, they were bound together with a very sticky material, apparently derived from spider webs, which was not used for the other three layers. The three collected nests shared the same structure, but the composition varied (e.g. more or less

Table 1. Number (*n*) and total length of pieces of nesting material and weight of each layer for Crow Honeyeater Nest N2. See also Figure 3.

Layer	*n*	*Length (m)*	*Weight (g)*
1	164	74.3	41
2	37	4.7	10
3a	80	10.9	32
3b	20	1.4	3
4	206	44.7	17
Total	**507**	**136**	**103**

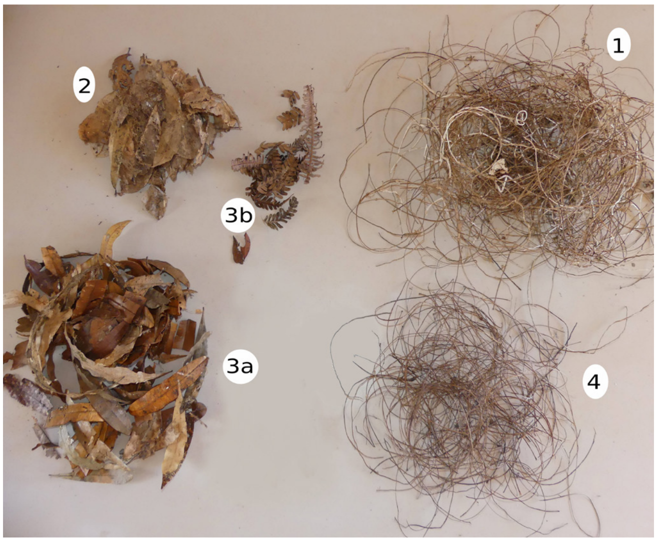

Figure 3. Different layers of Crow Honeyeater Nest N2 (indicated by numbers). See text and Table 1 for further details. Photo: Pascal Villard

fern) depending on what was available around the nest site. In S2, the nest found (N4) was not so enclosed between branches and creepers but was partly suspended and had 19 links to lianas. All nests were oval in shape, with internal dimensions of 12.8 ± 1.8 cm on the longest side, were 10.0 ± 0 cm wide, 9.7 ± 0.6 cm deep, and weighed 105.5 ± 10.3 g (*n* = 3). Each nest was located in a tree with a thin trunk and a small crown (Table 2).

In the vegetation sample plots within a radius of 10 m of each nest (*n* = 4), the two smallest stem diameter classes ⩽10 cm (D1 and D2) represented 91% of the stems (Table 3).

Laying, clutch size and incubation

Laying dates were calculated for four nests using an incubation period of 21 days (Mériot & Létocart 2005): 13 August 2020 (N4), 4 September 2019 (N2), 18 September 2019 (N1) and 21 October 2019 (N3). Clutch size for each nest was one egg (*n* = 4). Each egg had a flesh-coloured background and brown blotches especially on the blunt end. Only the female incubated. In S2, we followed incubation for 6 days at Nest N4. After hatching, the female carried away two large pieces of eggshell (Figure 4) and swallowed two very small pieces. She spent 53.7% of the daylight period incubating but, including the night, 75% of the time incubating over a 24-hour period. Inside the nest, she sometimes rolled the egg with her beak, at average intervals of 33 minutes (*n* = 50, 27.2-h survey) during the day and 118 minutes (*n* = 23, 45.2-h survey) during the night. After the long night spent at the nest incubating (average 11.1 h ± 13.1 min., *n* = 6), the first morning absence of the female was on average 4.7 times longer than the next absence that morning [27.1 ± 9.0 min. (*n* = 6) vs 5.8 ± 4.0 min. (*n* = 5)]. In the morning, she left the nest 8 minutes before dawn, and in the evening she returned to spend the night 1 minute before the end of the day (defined as 30 minutes after sunset). On three occasions, she was seen licking raindrops from the nest before sitting down.

Figure 4. Female Crow Honeyeater holds the last large piece of eggshell before taking it away at Nest N2 (IR camera image). Photo: Pascal Villard

Nestling and parental care

The chick in Nest N4 hatched with a few lines of black natal down, on spinal (pelvic) tract, humeral tract, capital tracts, and uppertail-coverts (Figure 5; see Proctor & Lynch 1993). The first prey item, a very small spider, was brought 4.9 hours after hatching. The nestling's first faecal sac was produced 52 minutes after hatching, and was swallowed by the female. Over the next 5 days, all faecal sacs were swallowed by the female. On Day 6, for the first faecal sac of the day, she swallowed the white part and left the nest with the larger dark part. The next day, and until fledging, all faecal sacs were swallowed except for the first one produced after the night. Despite the envelope of the faecal sac, it was sometimes very soft and dripping, in which case the adult cleaned up any marks in the nest. The mean number of faecal sacs produced per day was 22.4 (S1) and 25.1 (S2). On average, the number produced

Table 2. Details on supports of four Crow Honeyeater nests. DBH = diameter at breast height of nest tree, nest height = height of nest above the ground, and Fc = closure of forest canopy above the crown with the nest.

Nest no.	*Nest tree species*	*DBH (cm)*	*Nest height (m)*	*Tree height (m)*	*Fc (%)*
N1	*Codia jaffrei*	11.0	8.3	9.4	10
N2	*Codia jaffrei*	16.0	8.6	10.7	0
N3	*Garcinia balansae*	10.0	11.7	15.0	5
N4	*Planchonella kuebiniensis*	10.8	9.4	11.3	80
Mean		**12.0 ± 2.7**	**9.5 ± 1.5**	**11.6 ± 2.4**	**23.8 ± 37.7**

Table 3. Number of stems of vegetation of seven different class sizes (D1–D7) in area (total = 314.2 m²) around four Crow Honeyeater nests.

Stem diameter (cm)	*Nest no.*				*Total*	*%*
	N1	*N2*	*N3*	*N4*		
D1 (1.0–5.0)	316	362	174	243	1095	71
D2 (5.1–10.0)	114	70	66	53	303	20
D3 (10.1–20.0)	40	21	46	16	123	8
D4 (20.1–30.0)	2	4	5	4	15	1
D5 (30.1–40.0)	0	0	2	2	4	0
D6 (40.1–50.0)	0	1	0	0	1	0
D7 (50.1–60.0)	0	1	0	0	1	0

per hour was 1.6 ± 0.6 (*n* = 377) and 1.8 ± 0.6 (*n* = 579) during breeding seasons S1 and S2, respectively.

Nests N2 and N4 were made by the same pair of Crow Honeyeaters (in breeding seasons S1 and S2). The female was banded in January 2020 and the male, easy to recognise based on his wattles, was banded in April 2020. The two nests were 95 m apart. During S1, the male appeared on Day 11 for a single feeding of the nestling, and thereafter he fed the nestling every day until the juvenile left the nest. In contrast, in S2, the same male never came to the nest, although he was seen and heard in the immediate vicinity.

During 9 days, after feeding, the male (in season S1) sometimes tugged the chick's beak and a few times its tongue (*n* = 109), which was never done by the female. The chick did not seem to be affected by the treatment and fledged from the nest. While brooding the nestling during the night, the female woke up on average 13.8 times (Week 2), 15.6 (Week 3), 20.2 (Week 4) in S1 (*n* = 299, 18 nights), and 39.8 times (Week 1), 26.6 (Week 2), 11.7 (Week 3), 5.0 (Week 4) in S2 (*n* = 464, 20 nights). The mean number of visits by the female to the nest to feed the nestling (all hours combined) was 2.7 ± 0.6/h (*n* = 635) and 2.6 ± 0.9/h (*n* = 851) in S1 and S2, respectively. For the male, it was 1.5 ± 0.7/h (*n* = 302) in S1. In S1, on average, the first feeding occurred at 0524h ± 14 minutes and 0654h ± 71 minutes, by the female and male, respectively, sunrise being at 0523h ± 4 minutes. In S2, on average, the first feeding by the female occurred at 0541h ± 10 minutes (sunrise at 0549h ± 7 minutes). For S1 and S2 combined, the food items provided to nestlings were: nectar 3.2%, indeterminate 9.7%, fruit 12.4% and vertebrate and invertebrate prey 74.7% (*n* = 1788) (see Table 4 for prey items). During our study, the Crow Honeyeaters visited flowers of 12 plant species for nectar, but mostly the first three species (*Geissois hirsuta*, *Syzygium austrocaledonicum*, *Crossostylis grandiflora*, *Myodocarpus fraxinifolius*, *Thiollierea montana*, *Psychotria gabriellae*, *Dracophyllum verticillatum*, *Oxera palmatinervia*, *Montrouziera gabriellae*, *Pleurocalyptus pancheri*, *Tristaniopsis guillainii* and *Amyema scandens*), and three species for fruit (*Crossostylis grandiflora, Ilex sebertii* and *Hibbertia lucens*).

The food items provided to the nestlings were 5.1% very small, 32.9% small, 42.5% medium, 18.2% large and 1.3% very large (*n* = 544) for S1, and 5.3% very small, 34.5% small, 38.7% medium, 18.9% large and 2.6% very large (*n* = 837) for S2.

In S1, during the last 3 days before fledging, the juvenile climbed five, 19 and 33 times onto the nest rim for the following total times: 0.9 minute, 16.2 minutes (51 sec. on a branch) and 60.3 minutes (47 sec. on a branch), respectively, sometimes stretching the wings. In S2, in the last 2 days before fledging, the juvenile climbed four and 10 times onto the nest rim for total times of 0.8 minute and 4.5 minutes, respectively, sometimes stretching its wings. Young fledged after 25.5 days (mean for two nests), and did not return to the nest.

Post-fledging period

We made the following observations on the fledgling from Nest N2. Times shown are times since fledging.

2.6 months. The female fed the fledgling twice (325 m from Nest N2) (Figure 6).

3.6 months. The fledgling foraged for prey in dead palm leaves, the female licked the flowers of *Geissois hirsuta*. The fledgling flew to the female and they left together.

5.9–6.2 months. The fledgling made plaintive submissive calls when close to another Crow Honeyeater. On one occasion, it was chased by an unbanded, unidentified adult to 620 m from Nest N2.

6.2 months. The fledgling and the male in the same tree both licked the flowers of *Geissois hirsuta*, and the fledgling emitted high-pitched, plaintive submissive calls.

7.7 months. The fledgling flew to the female, and they perched side by side (300 m from N2).

8.7 months. The fledgling and female foraged together (78 m from N2).

9.4 months. The fledgling was last seen. It was foraging in a dead branch (83 m from future Nest N4, where the estimated laying date was 16 days later).

In both seasons S1 and S2, the breeding success (i.e. number of fledglings in relation to number of nests) was 0.5 (*n* = 4 nests, each with one egg; two eggs predated, two fledglings). Monitoring of nests with a mini-camera has provided evidence that the Black Rat *Rattus rattus* is

Figure 5. Crow Honeyeater nestlings at various stages of development: (a) 2 days (Nest N4), (b) 11 days (Nest N2) and (c) 16 days old (N2). Photos: Pascal Villard

Figure 6. The Crow Honeyeater fledgling (on left), 2.6 months after fledging, still being fed by the adult female (on right). Note the ear-covert is lighter coloured in the fledgling than in the adult. Photo: Pascal Villard

a predator at Crow Honeyeater nests (Villard *et al.* 2022). Two fledglings were observed in S1 (from Nest N2 and from an unknown nest) and four in S2 (from nest N4 and from three unknown nests).

Home range during breeding season

For a pair of Crow Honeyeaters that did not successfully raise a fledgling (Nest N3), during the incubation period the female was injured by a Black Rat and lost her nest (Villard *et al*. 2022). In the present study, on 16 days (on average 5.0 ± 2.7 days apart), 19 monitoring sequences were carried out for a total of 41.1 h on a male equipped with a radio-transmitter. The cumulative surface area during this monitoring was ~24 ha. At the furthest point, the male was 380 m from the nest.

Discussion

Construction of the nest

The nest consisted solely of plant material except for silk, probably from spider web. Unlike the Regent Honeyeater *Anthochaera phrygia*, which does not have well-defined layers in its nest (Low *et al*. 2013), the Crow Honeyeater has four nest layers. The outer one (1) gives structure to the nest and is bound together with sticky silk, layers 2 and 3 (made of leaves) should insulate the nest contents, and the innermost layer (4) is looser and allows water to drain out, keeping the chick dry. The nest has a solid construction; when removed from its support, its parts still hold together well. In windy weather, we have seen the nest being shaken but, because of the deep inner cup, the egg or chick is safe and should not be expelled. In addition, the deep cup allows the female to sleep on the nest even when the juvenile fills it completely before fledging (Figure 7). At night, the juvenile's beak can often be seen between the edge of the nest and the female's body, probably in order to breathe better.

Figure 7. Adult female Crow Honeyeater at Nest N4 with nestling 3 days before it fledged (IR camera image). Photo: Pascal Villard

Nests N2 and N4 were made by the same female, showing some plasticity in nest building as she modified nest attachment according to the structure of the support. Nest N2 was tightly inserted between the branches and lianas whereas N4 was partly suspended with some swinging, and in the latter case the female put 15 more ties than for N2 (only four links) to keep her nest safely attached to the supporting tree.

The Crow Honeyeater's nest construction corresponds to the main type for 74 species of honeyeaters, for which 77% are attached between branches, 15% attached by the rim and 8% are suspended (Higgins *et al*. 2001). At our study site, in a tall rainforest, the female built her nest in a micro-habitat within young trees, with a high density of stems and a relatively open canopy. Of the four nests found, three were difficult to see from the ground.

For safety reasons, birds may have an interest in placing their nests in a wider variety of sites (Ford 1999). The four Crow Honeyeater nests that we studied were in a fairly similar type of vegetation structure, thus having a similar chance of being predated.

Laying, clutch size and incubation

All four Crow Honeyeater nests found had the egg laid between August and October, i.e. not during the wettest season. This species is one of the eight New Caledonian species with a one-egg clutch, including the Barred Honeyeater *Glycifohia undulata* (Hannecart & Létocart 1980, 1983). A small clutch size is frequent in birds of tropical islands; in New Guinea, 39 species, including five honeyeaters, have a one-egg clutch, and it has been suggested that biotic factors specific to New Guinea, such as parasitism or predation, would have led to the evolution of small clutch size in New Guinea passerines (Freeman & Mason 2014). Incubation in the Crow Honeyeater is carried out only by the female; she spent 53.7% of daylight in the nest (this study), compared with 69% in the Regent Honeyeater (Ley & Williams 1998). If nighttime incubation is included (Sofaer *et al*. 2020), the female Crow Honeyeater spends 75% of her time incubating in a 24-h period.

During the daylight period, the Dusky Honeyeater *Myzomela obscura* (13 g) rolled its two eggs more often (on average every 7.4 minutes: Noske & Carlson 2011) than the bigger (146 g) Crow Honeyeater rolled its egg (every 33 minutes: this study).

During incubation, the female Crow Honeyeater was not fed at the nest by the male, but she had time to forage herself – she was away from the nest for 6 hours a day. In an experiment conducted in South Africa, attentiveness of female Karoo Prinias *Prinia maculosa* that had been fed was 8% higher than in control females (Chalfoun & Martin 2007). This rather small percentage increase indicates that food is a factor affecting attentiveness, but only within certain limits. The long incubation period of the Crow Honeyeater could result from less nest attentiveness; a shorter stay in the nest could lower the temperature of the egg and potentially slow down embryonic development, but no support was found of an association between the number or duration of stays outside the nest and the incubation period (Tieleman *et al*. 2004).

Although the Crow Honeyeater's egg is not brightly coloured, it is easily visible to aerial predators (e.g. New Caledonian Crow *Corvus moneduloides*) and one might expect that a more subdued coloration would have been selected. However, Zima *et al*. (2021) found that visually oriented predators visited empty nests and nests with eggs at similar frequencies, regardless of shell colour.

Nestling and parental care

The nest was always kept clean, preventing the nestling from being soiled, reducing the visual attraction to predators of the white spot from the faecal sac. The number of times that the nestling was fed per hour by the female was similar for breeding seasons S1 and S2, even when the male was also feeding in S1. Is this evidence that the feeding male was very unusual? An intriguing unresolved question is why for the same pair in different seasons, the male that fed the nestling in season S1 (Nest N2) did not come to Nest N4 in S2. The feeding rate of the Dusky Honeyeater (largely on nectar) has been described as very low (8.9 feeds/h: Noske & Carlson 2011) but for two large Australian Honeyeaters (the Red Wattlebird *Anthochaera carunculata* and Noisy Friarbird *Philemon corniculatus*) it is 5.4 and 6.6 feeds/h, respectively (Tokue & Ford 2007), and in our study it is only 2.7 feeds/h for the female Crow Honeyeater. In S1, prey items 21–40 mm long constituted

Table 4. Prey items (number and percentage of total) brought by female (F) and male (M) Crow Honeyeaters to the nestling at Nests N2 and N4.

Prey	*Nest no.*					
	N2				*N4*	
	F	*M*	*Total F + M*	*%*	*F*	*%*
Orthopteran	282	207	489	72.0	361	60.2
Spider	107	25	132	19.4	201	33.5
Moth	17	0	17	2.5	6	1.0
Adult insect	7	9	16	2.4	4	0.7
Larval insect	12	1	13	1.9	15	2.5
Millipede	2	1	3	0.4	–	–
Scorpion	1	2	3	0.4	–	–
Caterpillar	2	0	2	0.3	–	–
Centipede	0	1	1	0.1	1	0.2
Gecko	3	0	3	0.4	12	2.0
Total	**433**	**246**	**679**	**100**	**600**	**100**

61% of the animal items brought by the pair to the nestling, with an average feeding rate of 4.2 times/h (male and female combined). The large prey size could compensate for lower delivery rates. From the time that the nestling was 6 days old, all faecal sacs were swallowed (an average of 24/day), except for the first one in the morning, which was taken away by the female; perhaps it contained more toxins and/or was unappetising. The average removal rate of faecal sacs (1.7 sacs/h) was similar in the Dusky Honeyeater (1.6 sacs/h: Noske & Carlson 2011) but much lower in the Red Wattlebird (0.3 sac/h) and Noisy Friarbird (0.9 sac/h) (Tokue & Ford 2007).

Orthopterans, the staple food for the nestling, constituted 66.5% by number of the prey items brought to Crow Honeyeater nestlings in our study. Geckos, the largest, and only vertebrate, prey item constituted only 1.2% by number (Table 4). Vertebrates do not appear to have been previously reported in the diet of the Crow Honeyeater (Higgins *et al.* 2020).

From egg-laying to fledging, the female Crow Honeyeater spent every night lying in the nest with her beak buried in the feathers of her back (Figure 8), keeping warm the egg or nestling. In the last days before fledging, the young climbed onto the edge of the nest for total times of 1.3 hours (Nest N2) and 5.3 minutes (N4). In contrast, in the Mao, fledging took place over several days, with the young being on the branches during the day and returning to the nest at night (Stirnemann 2015).

Post-fledging period

After fledging, a juvenile was fed by the female Crow Honeyeater for 2.6 months. However, the fledgling (from Nest N2) was still in contact with the adult 8.7 months after fledging. Furthermore, a fledgling banded a few months after leaving the nest (not one of the four nests studied here) was seen in the adults' territory 16.5 months later (unpubl. data).

Figure 8. Adult female Crow Honeyeater sleeping (Nest N4) with her beak hidden in the feathers of her back (IR camera image). Photo: Pascal Villard

Table 5. Comparison of reproductive ecology of Crow Honeyeater and Mao. F = female, M = male. Source of data: Crow Honeyeater – this study and *Mériot *et al.* (2003); Mao – Butler & Stirnemann (2013), Stirnemann (2015) and Stirnemann *et al.* (2016).

Features	*Crow Honeyeater*	*Mao*
No. breeding attempts/year	1	1
Laying attempt	3-month period, outside wettest season	9–10-month period, outside or reduced in wettest season
Nest tree	Small (trunk diameter 12.0 ± 2.7 cm)	Large
Nest height (m above ground)	9.5 ± 1.5 (*n* = 4)	14.2 ± 3.7 (*n* = 10)
Nest cup internal diameter (cm)	12.8 ± 1.8 × 10.0 ± 0	14.0 ± 1.8 × 8.0 ± 1.5
Clutch size	1	1
Egg	Flesh-coloured; brown blotches mainly on blunt end	Buff-pink; pinkish-brown markings on blunt end
Incubation by	F	F
Incubation period (days)	21*	20
Incubation predation	A Black Rat jumped on F, which escaped with her egg	A Black Rat jumped on F and took the egg
Nestling period (days)	24–27	22–24
Faecal sacs	All consumed by F and M (S1) and F (S2) except the first each day	Discarded below nest or consumed
F resting at night	On nest until nestling fledged	Perched on branch above nest when chick *c*. 12 days old
Nestling fed by	F and M (only record of M feeding a nestling)	F and M
Fledging	Nestling fledged from nest and did not return to nest	Nestling gradually left nest during the day and returned for night
Reproductive success	0.5 (*n* = 4)	0.33 (*n* = 29)
Fledgling behaviour	Rather quiet	Very vocal in soliciting food
Post-fledgling dependency period (months)	2.6	2–2.5
Fledgling remains in adults' territory	16.5 months (*n* = 1)	Unknown

Contrary to the Mao (Stirnemann *et al*. 2016), the fledgling Crow Honeyeater is rather quiet, which makes encounters rather unpredictable and breeding success cannot be estimated without finding the nests.

Area cover during breeding season

The radio-tracking of a male Crow Honeyeater indicated a home range of ~24 ha, which is four times smaller than that found in 2001 during 25 days of tracking (100 ha: Delafenêtre *et al*. 2001). Although the monitoring by Delafenêtre *et al*. (2001) was also carried out in the Parc de la Rivière Bleue, it was on the White River where the quality of the rainforest is lower than in our study area, and their data collection (55 locations) was done by triangulation from 19 marked points in the surveyed area. This may have inflated the area estimated to have been occupied by the bird. These two very different estimates of home range highlight the need for caution when using these data to calculate the number of pairs of birds in the entire rainforest of the park. The quality of the forest, and extent of the slopes, influence the distribution of the Crow Honeyeater and may significantly skew calculations. Our study area, in a tall rainforest on flat land, appears to be a very suitable place for the species, with a good and long-lasting density.

Comparison of the reproductive biology of the Crow Honeyeater and Mao

Phylogenetic and evolutionary studies have shown that the Crow Honeyeater from New Caledonia and the Mao from Samoa are not very closely related and group with other, smaller species of honeyeaters that have different features of reproduction biology (Higgins *et al*. 2001). The *Gymnomyza* polyphyly, within the Meliphagidae, suggests the need for a thorough taxonomic revision (Marki *et al*. 2016; Andersen *et al*. 2019). Interestingly, these two large insular honeyeaters share several traits in their life history (Table 5): both the Crow Honeyeater and Mao, compared with other honeyeaters, have a longer incubation time [20 days (combined average for Crow Honeyeater and Mao) vs 12–17 days (other honeyeaters)], nestling period (24 vs 11–20 days) and fledgling care duration (10 vs 4–6 weeks)

(Winkler *et al*. 2015). The slow development (in incubation, nestling and post-fledging periods) found previously for the Mao (Stirnemann 2015), and now also for the Crow Honeyeater, appears to be the product of convergent evolution in a tropical insular environment. Therefore, these traits in life history will play an important role in extending any conservation plan to ensure the survival of these two large insular honeyeaters.

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