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Fiery-necked Nightjar *Caprimulgus pectoralis* development and behaviour from hatching to fledging, including attendant parental care

by H. D. Jackson

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Summary.—Four pairs of Fiery-necked Nightjars *Caprimulgus pectoralis*, each with two young, were observed from hatching to fledging at four different localities in Zimbabwe, two pairs of *C. p. fervidus* in Mashonaland and two pairs of *C. p. crepusculans* in Manicaland. Development of the young was measured and their behaviour recorded daily, as was adult behaviour. My observations provided corrections and additions to the literature. *C. p. pectoralis* and *C. p. fervidus* remove eggshells from the nest area after hatching, but *C. p. crepusculans* does not. Chicks provide a feeding stimulus by grasping the adult's bill in its own. By not responding until this stimulus, the adult ensures that each chick receives its fair share of food. Chicks do not return to the nest to be fed. They move towards a calling adult, on or off the nest. The 'wooting' call is not a warning call, but is used by adults to summon their chicks, which respond immediately by running towards the sound. Rictal bristles appear on day 18, and are only 2 mm long on day 19, providing no protection for the eyes during the first days of flight. On days 18–19, when the middle claw is 3–4 mm long, the inner flange splits to form a comb of four teeth 1 mm deep, the start of the pectinate claw. Primaries emerge centrifugally, as in adult moult pattern, wherein primaries moult descendantly. Adults leave their territories soon after breeding, whereas chicks, which become independent at 19–23 days, remain in their natal areas.

This paper is a sequel to Jackson (1985a) which dealt with those aspects of the breeding biology of Fiery-necked Nightjar *Caprimulgus pectoralis* prior to the hatching of the eggs, thus it deals with hatching to fledging. These aspects include development of the chicks and all aspects of their behaviour, as well as adult behaviour toward the chicks, especially brooding, feeding and distraction displays.

Methods

Study areas.—Research was conducted at the following four localities in Zimbabwe on the dates shown, with the number of hours of observation in brackets, and a very brief habitat description. **Nest 1**. 17 September–7 October 1969 (30.25 hours). Atlantica Ecological Research Station, now Boulton Atlantica Centre for Conservation Education, Zimbabwe National Parks and Wildlife Management Authority (17°49′S, 30°49′E, 1,397 m), 25 km south-west of Salisbury (now Harare). Miombo woodland (*Brachystegia–Julbernardia*) with termitaria thickets. **Nest 2**. 15 October–2 November 1969 (12.25 hours). Retreat Farm (17°55′S, 31°02′E, 1,460 m), 9 km south of Harare. Bluegum *Eucalyptus globulus* plantation (full habitat description in Jackson 2002a). **Nest 3**. 21 November–9 December 1971 (47.75 hours). Muneni River (18°59′S, 32°41′E, 990 m), Umtali (now Mutare). Miombo woodland (*Brachystegia–Julbernardia*) on a 30° slope adjacent to riparian forest (full habitat description

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in Jackson 1972). **Nest 4**. 7 November–9 December 1975 (17.75 hours). Ranelia Farm (19°22'S, 32°37'E, 885 m), 45 km south of Mutare. Miombo woodland (*Brachystegia–Julbernardia*) with numerous granitic outcrops and termitaria thickets (full habitat description in Jackson 1985a).

Nightjar research.—Night lighting (Jackson 1984) was used to find and capture Fiery-necked Nightjars on the nest at night. Their mates were captured during the day by flushing them from the nest into mist-nets erected nearby. Most birds trapped were ringed for individual identification and weighed to the nearest gram, using a Pesola spring balance, before release at the capture point. Four nests, which permitted chick development to be followed from hatching to fledging, were the subject of this study.

The aim was to record the physical development of the chicks on a daily basis, by weighing them with a Pesola spring balance and measuring their wing, tail, tarsus and culmen (to nostril) lengths with callipers. This was achieved at Retreat and Muneni alone, while the Ranelia chicks were weighed daily but measured only on day 19 (day 1 = day of hatching). The Atlantica chicks were neither weighed nor measured, but their vocalisations, and those of the adults, were taped using an Uher tape recorder and a microphone placed near the nest. Copies of the recordings are lodged in the Fitzpatrick Bird Communication Library, Transvaal Museum (now Ditsong National Museum of Natural History), Pretoria, South Africa. Rectal body temperatures of one of the Muneni chicks were measured daily with a clinical thermometer, from day 3 to day 16, between 11.00 h and noon, immediately after the brooding female was flushed.

The behaviour of the chicks and the adults was observed for a total of 108 hours, usually from a small canvas hide placed 2–3 m from the nest. An assistant accompanied the observer to the hide at the start of an observation period and then left the area, returning later to 'release' the observer. At times the nest was surrounded by a wire mesh fence, 15 cm high and 1 m distant, to prevent the chicks from leaving the nest area. Detailed notes were dictated quietly into a pocket recorder at the time of observation and subsequently transcribed.

No night vision equipment was used, other than a Starlight Scope (AN/PVS-2) that was available for just two nights (at Ranelia), so lamps fitted with red filters were attached to the top of the hide to illuminate the nest area at night. The Starlight Scope is a night vision image-intensifier that produces a light amplification of *c*.1,000. It was quite bulky and required moonlight to function properly but nevertheless provided valuable data. Windows in the hide enabled use of binoculars and cameras, with remote flash-guns fixed to the top of the hide.

Results

Hatching.—At Retreat the chicks hatched on successive days. When the female was flushed from the nest at 17.50 h, a damp chick that must have stuck to her breast feathers was thrown a short distance from the nest, which contained an egg showing a few tiny cracks. Next day at 05.56 h the egg showed signs of chipping, with the shell lifting in two areas, one star-shaped, the other like a small trapdoor. By 13.20 h these had developed into two holes and by 17.40 h the chick had emerged. By then its down was much drier than on the other chick when first seen, so it must have hatched earlier than its sibling, but both clearly hatched in the late afternoon. At Muneni both chicks hatched on the same day, one between 04.30 h and 14.50 h, probably in the morning, the other in the afternoon between 15.45 h and 16.45 h. At Ranelia there were two young in the nest at 15.15 h, one showing a damp dorsum, so here too it is probable that both chicks hatched on the same day, one probably in the morning, the other in the afternoon.

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Figure 1. Three pieces of abandoned eggshell (arrowed), the largest immediately in front of the adult Fiery-necked Nightjar *Caprimulgus pectoralis* tending the chicks on day 1 at Muneni, a smaller piece in the lower centre and a very small piece in front of the stones to the right (H. D. Jackson)

Egg tooth.—Once a chick had hatched, it no longer needed the small straw-coloured or off-white egg tooth on the tip of the maxilla, used for cutting its way out of the shell, and so could shed it immediately. The chicks at Atlantica had shed their egg teeth by day 5 and those at Muneni by day 6, so it is remarkable that at Retreat egg teeth were still visible on both chicks on day 12 and persisted on chick 1 until day 15.

Eggshells.—At Ranelia and Muneni the broken eggshells were not removed from the nest area, despite being extremely conspicuous, and remained scattered 10–50 cm from the nest for up to nine days. On day 1 eggshells could even be seen on or beside the nest (Fig. 1). At Muneni the sitting female, with a chick and egg in the nest, was very restless, rocking from side to side. Half an eggshell lay 10 cm in front of her and the other half was underneath her right side. One of the violent rocking spells ejected it on her left side, where it remained against her body. At Ranelia too, the sitting female was seen with half an eggshell against her body but neither bird made any effort to remove it.

At dusk on day 3 at Muneni, when the male arrived for the first changeover at 18.30 h, he appeared to settle on an old eggshell that was lying convex side up. A few seconds later the female on the nest flew off and the chicks started calling, so he ran towards them. The concave side of the eggshell was now facing up.

Only once was a nightjar observed to remove an eggshell from the nest area and this was under unnatural circumstances. A small fence had been erected below the nest at Muneni on day 9 to prevent the chick moving too far, but the female settled outside it and called the chick, which reached the fence and ran back and forth along it while the female continued calling. Eventually she moved towards it but was stopped by the fence, where she too moved back and forth searching for a way through. At 18.30 h she flew up and landed inside the fenced area, and the chick immediately ran to her and was brooded. This was *c.*10 cm from the third of an old eggshell. The female stretched over, picked up the eggshell in her bill, paused for a few seconds with her head up and her back to me, so that when she tilted her head I could see the whole eggshell above her bill. She then took off,

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Figure 2. Fiery-necked Nightjar *Caprimulgus pectoralis* chick 2 on day 4 at Muneni, showing the well-developed legs (H. D. Jackson)

apparently dropping the eggshell somewhere, for she had returned within a few seconds, minus the eggshell, landing next to the chick before brooding it.

At Retreat, when I flushed the bird off the nest at 17.50 h on day 1, it appeared to be carrying an egg between its legs as it flew away. In the nest there was just one egg. However, 40 cm from the nest, where it could easily have been overlooked among the leaf litter, lay a newly hatched chick, still damp and sticky. It had probably been briefly stuck to the adult during take-off. Meanwhile the adult had flown 5 m to perch on a thin branch and was tugging at an eggshell stuck to its breast. The shell came free and dropped to the ground, before the bird flew to a higher perch further from the nest. Adhering to the sticky albumen on the inside of the shell were several adult breast feathers. On day 2 at 17.55 h there was no eggshell in the immediate vicinity of the nest and on day 13 I found an eggshell 12 m east of the nest site, where it had probably been dropped by an adult.

The Atlantica nest was found by one of the Research Station staff, who at 12.00 h on day 1 reported that the eggs had hatched, and that when he flushed the bird from the nest it carried an eggshell between its legs, dropping it 3–5 m away. I first visited this nest on day 4 at 16.00 h, when no eggshells were present. Not having seen their removal, I cannot be certain but I suspect that the eggshell observed being carried away from the nest between the legs of an adult had been stuck there briefly, as happened at Retreat. Although it is uncertain whether the adults at Retreat and Atlantica deliberately removed any eggshells after hatching, as some were accidentally removed, they probably did so.

Hatchlings.—The hatchlings were no larger than my thumb, measuring < 50 mm in length and weighing just 5–6 g. At first they appeared naked, but after drying out could be seen to possess downy plumes up to 4 mm long in some areas. Most obvious were the dark brown stripes running from the lores through the eyes, then across the wings and along the dorsal tracts to join a cluster of plumes around the preen gland. There were many russet plumes around the face and on the wings, while the crown was adorned with fuzzy pale buff plumes.

The egg tooth was conspicuous at the tip of the culmen. While there was no sign of a rictal bristle or a tail, and the wings were rudimentary, the legs were already extremely well developed (Fig. 2), with the toes having claws of 1–2 mm, but without pectination on the claw of the middle toe. The hatchlings could move well in short runs and while walking

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around on the palm of my hand could climb a slope of *c*.50°. While standing, their heads often wobbled from side to side as they had difficulty holding them up.

The hatchlings were already gular fluttering whenever they became hot. Their eyes were still closed, so there was no evidence of them attempting to adopt the cryptic posture in response to movement, instead they responded to sound. As I worked on one and it cheeped, so the other in the nest gradually worked its way over obstacles towards the one I was holding. While they could not see, they vocalised loudly in response to the sound of an adult.

Vocalisations.—Not only did the chicks call well on day 1, they could be heard calling inside the egg prior to hatching. The normal cheeping of the chick was a quiet *wee-you* repeated at *c*.1-second intervals, with the bill closed. When handled, most chicks became more vocal, their cheeping increasing in volume and duration. As they grew older, they protested more violently at being handled by opening their gapes wide and uttering a variety of subdued shrieks, hoarse growls, wheezy squawks and harsh hisses. The adult that had been flushed from the chicks, and was watching from a nearby perch, responded to the distress calls by uttering a series of *chuck* calls, either when perched or flying nearer.

The *chuck* call served mainly as an alarm, so that whenever chicks moving on the ground heard it they immediately froze into immobility. Adults foraging in woodland uttered a *chuck* or *chuck-chuck* each time they pursued an insect, and whenever they came across an owl they would mob it with a continuous series of rapid staccato chucks. Quite frequently, when an adult at Muneni arrived with food, it would utter two or three chucks on approach. The sitting bird would then take off and the chicks would run towards the sound, cheeping loudly. In contrast, a Ranelia bird seldom chucked when arriving with food. The first sound I heard was usually the wing-flapping as it landed close to the nest. A Muneni chick uttered a few soft chucks in flight on day 18, while one at Retreat did so on day 19.

In the evenings, at *c*.18.30 h, *chuck* calls nearby would sometimes be followed by quiet squawks from the bird on the nest. Once the brooding bird took off and flew up to a perch where it uttered a deep squawk while its mate fed the chicks. Occasionally the adults indulged in aerial chases 10–20 m from the nest, accompanied by much loud calling (both chucks and some squawks). Once, when one was giving rapid and continuous *chuck* calls from a low branch, the other adult perched next to it and uttered a peculiar squawk. Another time, as an adult approached with many *chuck* calls, a perched bird uttered two or three deep squawks and the approaching bird appeared to settle either on top of or next to the perched individual, resulting in both taking off. While both birds gave *chuck* notes, it appeared that only the female squawked.

The sound heard most frequently from the female was made when she was calling the chicks to her after they had been weighed and measured in the morning. We usually returned the chicks to the nest, but the female more often than not settled a few metres away and called until the chicks reached her. While calling, the two gular patches fluttered prominently, so could have acted as a guide for the chicks once their eyes had opened. However, they responded immediately on day 1, when still blind, by running towards her and were clearly guided by the sound alone.

Her calling was described variously as a continuous *woot-woot-woot*, *what-what-what*, *cube-cube-cube* or *cue-cue-cue*, perhaps reflecting some minor differences between the four females or, more likely, changes in my hearing over the six years. These calls I refer to as 'wooting'. Whenever the chicks became restless during brooding, the female would utter a quiet *woot* or *woot-woot* and they would immediately settle down. The male also used 'wooting' to call the chicks to him or to settle them.

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Fig. 3. Male Fiery-necked Nightjar *Caprimulgus pectoralis* at Muneni singing from an elevated perch while a female flies around, during the courtship stage (H. D. Jackson)

The microphone near the Atlantica nest sometimes detected quiet sounds that were inaudible to me in the hide <3 m away. For example, on day 14 at *c*.22.00 h the chicks were being brooded by an adult and were very restless. Through headphones I could hear them tittering continuously, and the adult soothing them with quiet 'wooting'. Without the headphones I could hear none of this. As the chicks grew older their cheeping grew deeper and could better be described as chirping, which they not only uttered from the ground, but also in flight. On day 16 at 11.50 h the remaining Muneni chick called 120 times at fairly regular intervals of 1.0–1.5 seconds, while looking around with its eyes three-quarters open and rocking from side to side. The calling was not loud, but was huskier and deeper than previously.

The liquid whistling song of the species was heard in the vicinity of the nest only once at Retreat (day 1 = 15 October), Ranelia (day 4 = 10 November) and Muneni (day 10 = 30 November), but more often at Atlantica (days 7, 9, 14 and 18 = 23 September–4 October). It appears that the earlier breeding at Atlantica accounts for the higher incidence of song there, perhaps a carry-over from the courtship phase. The phrase 'Good Lord, deliver us' aptly captures the song's cadence. All songs were given from elevated perches (Fig. 3) apart from one from the ground at Atlantica on day 9 at 18.10 h, and a remarkable record of five songs in quick succession by a female on the nest at Muneni on day 5 at 18.27 h. This was the only occasion on which a female was heard singing. I had entered the hide overlooking her nest at 17.45 h, when she was quietly brooding the remaining chick. Aside from occasionally opening her eyes slightly, nothing happened until 18.20 h, when she became restless, then at 18.27 h she called five times from the nest, the complete 'Good Lord, deliver us' song, but very quietly. Shortly afterwards, *chuck* notes were heard nearby and the male arrived.

Solicitation, feeding and defecation.—At all nests, chicks became restless when the light faded at *c*.18.20 h, often emerging from below the brooding females and soliciting

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Figure 4. Male Fiery-necked Nightjar *Caprimulgus pectoralis* at Ranelia feeding chicks (arrowed) at 18.40 h on day 6; the chick on the left has been fed and is settled, while that on the right is stretching up to grasp the male's bill to provide the feeding stimulus (H. D. Jackson)

food by seizing their bills, but with no food forthcoming crawled underneath the adult again. Males arrived with the first feed at *c*.18.30 h and the females departed to go hunting; they then took turns to tend the chicks, and while one adult was away hunting the other was usually feeding or brooding the chicks. Sitting birds occasionally took off vertically to capture a flying insect, and sometimes the chicks were left alone, but they started calling after a few minutes and this brought a parent back.

Whenever there was a changeover at the nest, the chicks immediately stood tall, craning upwards and looking towards the arriving bird. Any movement by the adult caused a frenzy of excitement, the young calling noisily while moving towards the adult and standing upright against its chest trying to get a grip on its bill (Fig. 4, on day 6). The adult always waited until a chick, presumably the hungrier of the two, had grasped its bill tip, before feeding the young. Once the chick secured a firm grip with its own bill, the adult tipped its head vertically down, raising its neck simultaneously, and, with a rapid series of up-and-down head movements, regurgitated food into the chick's throat. This movement was extremely rapid, with the adult's bill clearly well inside the chick's gape, at times accompanied by a low growling.

Once a chick had been fed it was brooded and settled down for a while before starting to solicit again. The adult sat up with its head held high and its bill rapidly opening and closing *c*.2 mm, while its throat pulsated in rhythm to the movement of the mandibles. This may have served to settle the food still in the crop, perhaps working the items into a food ball to transmit during the next feed. The feeding performance was repeated several times until the adult had no more food. The chicks continued their frenzied activity until the adult 'wooted' quietly, on which signal they submitted to brooding. Gentle palpation of their stomachs revealed that they were often full by 20.00 h. The adults continued hunting after twilight whenever there was sufficient moonlight. For example, on day 1 at Ranelia, when

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the half-moon set at *c*.22.30 h, there was a changeover at the nest at 21.40 h, with the new bird feeding the chicks before settling to brood them.

On day 4 at Ranelia one of the chicks reversed out from under the female at 14.25 h, backed away a few paces, elevated its posterior and deposited a dropping, a dark brown coil with a white centre, 4 cm from the adult, then scuttled back underneath. I had previously noticed this behaviour at other nests and recorded it again at Ranelia on day 16 at 18.20 h. The number of characteristic small droppings around most nests revealed that this was a regular occurrence. Occasionally there was a much larger dropping in the nest, clearly from an adult, so it was clear that the adults practised little or no nest sanitation. At no stage did I see an adult carrying faeces away from the nest, but ants were regularly observed doing so and this helped to keep the nest clean.

When finding the female and chicks each day, they had often moved well away from the nest area, but each spot where they had roosted for a while was easily identified by the droppings, the number indicating how much time they had spent there and the freshness how recently they had moved on. Fresh droppings were soft and friable, but dried rapidly in the sun. Only once did I find what appeared to be a pellet of hard insect parts that might have been regurgitated by an adult.

Brooding and role of the sexes.—Females, whose plumage is even more cryptic than that of males, performed all brooding by day, while males roosted some distance away. At 04.45 h on day 2 at Muneni the female landed 0.5 m from the nest to take over the day shift, and the male took off shortly afterwards. She then moved to the nest and for the next 15 minutes rocked from side to side, while rotating left or right, before finally settling to brood. Much of the day was spent in low profile, with her head held just above mantle level and her eyes closed to a narrow slit. All brooding females slept sometimes by day. At such times their eyelids were closed to the point of touching in the centre, but on either side a small slit remained open. The whole eyelid occasionally would droop rapidly and when this happened the head tipped forward 4–5 mm. Quite frequently this would be sufficient to cause her to wake up suddenly.

Despite dozing, brooding females were alert to sounds and movements in their surroundings, opening their eyes slightly whenever a noisy bird flock, group of people, car or train passed by. At Muneni at 11.45 h the female opened her eyes and rocked sideways as a millipede gradually approached her at a distance of *c*.40 cm. After the millipede moved away she settled down with eyes closed again. This female always showed great concern whenever a noisy flock of Helmeted Guineafowl *Numida meleagris* roosted nearby in the evening. She turned her head to look in their direction and crouched slightly, as she also did whenever medium- to large-sized mammals passed nearby. A large raptor flying over, or settling in the canopy above the nest area, caused a brooding female to crouch down to the maximum, her plumage sleeked and her eyes narrowed to a slit. She would freeze like this until the danger passed.

Once in the brooding position, the female sat very still, but occasionally the chicks became restless and heaved, causing her to lift slightly. When this occurred, she ruffled her feathers, rocked sideways, made the comforting noise and they all settled down again. However, when it was very hot, she spent much time gular fluttering and only stopped when alarmed. While gular fluttering, her bill was held open *c*.2–4 mm and her throat patches flickered rather conspicuously. At Ranelia on day 4 at 13.15 h the chicks were clearly feeling the heat and before the female covered them they too were gular fluttering regularly. At 13.55 h the female rocked several times, yawned, turned and walked away from the chicks. She probed the fence with her bill a few times, stopped, turned and returned to the chicks, fluffing out her plumage over them. One chick sat in front of her, but they both very

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Figure 5. While brooding at night, the male Fiery-necked Nightjar *Caprimulgus pectoralis* at Muneni stretched its right wing and spread its tail after rocking from side to side (H. D. Jackson)

soon started gular fluttering again. The body temperature of chick 2 at Muneni was taken daily between 11.00 h and noon from day 3 to day 16 just after the female had flushed. This ranged from 39.2–40.6°C (mean 39.6°C), but rose as high as 42.6°C if the chick had been handled or had exerted itself.

Brooding females occasionally preened the breast feathers and the upper and lower surfaces of the scapulars during the heat of the day, between bouts of gular fluttering. While preening, they fluffed out their plumage and rocked sideways. Sudden rocking frequently coincided with gusts of wind, as shown, for example, by the female at Muneni: 'At 15.40 h she rocked eight times and bobbed her head as the wind blew. Again at 15.45 h she rocked six times because of the wind and then closed her eyes. 16.05 h rocked four times with wind blowing and eyes closed. 16.15 h rocked seven times with eyes closed when wind blew. No noise. 16.26 h rocked six times with wind blowing, eyes closed.' Once, on day 2 at 13.46 h, in response to a strong gust of wind, the Ranelia female stretched upwards and yawned with her gape wide open.

Some unusual rocking by the female at Muneni occurred on day 1 at 14.50 h after it had been drizzling for some time. She stood and rocked violently from side to side, while shaking her head repeatedly and bending forward, presumably to clear water. At the same time she performed frequent minor bill-claps. By 17.03 h it was raining heavily and she bent her head over to peer down at the chicks, but did not poke them with her bill. She spread her wings slightly over them and rocked sideways. She jerked each time a heavy raindrop hit her. When the male arrived to relieve her at 18.20 h he was remarkably dry and did not feed the chicks, so had apparently not been hunting. He immediately brooded them and this seemed to calm them, as they had been cold, wet and restless under the female.

During evening twilight and early moonlight, adults took turns to feed and brood the chicks but once they had settled down in the dark of the night, it was usually the male that

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Figure 6. Cryptic posture adopted by female Fiery-necked Nightjars *Caprimulgus pectoralis* by day when they felt threatened, flattening the body into the substrate as far as possible, closing the eyes to a slit, sleeking the plumage and remaining immobile (H. D. Jackson)

Figure 7. An approaching hand at Muneni on day 12 at 11.10 h caused Fiery-necked Nightjar *Caprimulgus pectoralis* chick 2 to lunge aggressively at the fingers, with wings spread and gape wide open, while hissing (H. D. Jackson)

brooded. The brooding female typically waited for the male to arrive with the first feed of the evening before departing to hunt. At Ranelia on day 1 at 18.15 h, when the male arrived

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Figure 8. Further provocation of the Muneni Fiery-necked Nightjar chick 2 (circled upper right) on day 12 at 11.25 h caused it to run away with wings held up (circled lower left) (H. D. Jackson)

and fed the chicks for the first time, he then, while brooding, showed great interest in flying insects silhouetted against the moon. At no stage did he take off after an insect, or even give a flight intention movement, but his head swung from side to side and occasionally arced up and over slowly as he followed an insect. While brooding the chicks at Muneni, the male made some wing and tail stretches after rocking from side to side (Fig. 5).

While an adult was brooding the chicks between feeds, its large eyes were wide open, each forming an almost complete circle, with the pupil fully dilated. It was the adult's eye-shine that enabled me to find the family in the dark. Although both chicks were being brooded, one under each wing, their heads emerging under the adult's breast, their eyes did not reflect well, so I had to approach closely to be sure both were present. At times the chicks were very restless. For example, on day 14 at Atlantica, after being brooded for more than an hour, the chicks emerged several times after 22.00 h, once even flapping their wings and walking all over and around the male.

Responses to threats.—Brooding adults initially responded to an approaching human by hugging the ground, adopting a cryptic posture with the plumage sleeked, the head withdrawn level with the mantle, and the eyes closed to a very narrow slit (Fig. 6). They remained immobile until the threat had receded. The superb camouflage of the cryptic plumage against the surrounding leaf litter made it extremely difficult to find the brooding bird by day. At night it was relatively easy to find the eye-shine of an adult in a spotlight. The confidence shown by brooding females in their camouflage was almost complete. At all four nests my assistants and I often walked within 1 m of a female without flushing her. At Ranelia on day 1 at 15.15 h, the female was in full cryptic posture as an assistant on hands and knees approached her from directly behind. He had to touch her on the tail and lift her once or twice before she took flight. Brooding females sat tight in the cryptic posture while we searched back and forth, but if one of us paused within 2–3 m and looked at the bird, it would flush off the chicks 3–10 m and perform a distraction display, usually on the ground but sometimes on an overhead branch. There was no distraction display on day 1 and only a

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mild display on day 2 at any of the four nests. It should be noted that no female performed a distraction display when flushed from eggs earlier in the season.

When the adult flushed, the chicks immediately adopted the cryptic posture flat on the ground, necks stretched out and eyes closed, remaining immobile. On days 1–5 they showed no reaction to my approaching hand, other than to breathe more rapidly, and permitted me to pick them up without any aggression. On day 6 the first sign of aggression was made when one of the chicks turned its head towards my hand and gaped. As my hand approached, it raised its breast off the ground slightly, stretched its neck and lunged repeatedly, but silently, at my fingers. No aggressive display was seen again until day 12, despite my provoking all of the chicks. They maintained their frozen attitude despite being prodded with a finger, depressing their bills or tilting their heads up. One chick on day 9 eventually made a quiet *cheep*, raised its wings and stood, then turned and tried to move away with a small hop. On day 12 some chicks hissed while striking very snake-like with an open gape (Fig. 7) but others ran away with their wings held up (Fig. 8). Another on day 13 half stood and moved away slightly with a wheezy call, then hopped sideways, but permitted me to pick it up without any aggression. On day 16 two chicks kept their eyes closed to slits as my hand reached down to pick them up, then suddenly both gaped with heads up and gapes wide open, followed immediately by spreading their wings fully. The culmination was a series of hops off the ground, gapes and wings still open, lunging at my hand and even striking it. By day 18 the chicks were capable of flight, so readily took off with the female when she flushed, but occasionally one remained behind in the cryptic posture, only flushing later.

On day 14 at 17.09 h I flushed the Retreat female off its chicks and found that they were completely surrounded by cattle tracks, which I followed in both directions to find that the herd had passed through the gum plantation without stopping. There is no doubt that the chicks were there when the cattle passed because many of their droppings were very dry. There was a hoof print 46 cm south-west of the chicks and another 22 cm north-west, evidence of a lucky escape. The female may have flushed during such a close encounter, but the chicks would certainly have frozen into immobility while the cattle passed. The only casualty among the chicks was the elder Muneni chick, which vanished before 11.00 h on day 6, probably taken by an avian predator. It was the more aggressive and adventurous of the two chicks and would sometimes run away while its sibling froze immobile, so it was more likely to be noticed.

Distraction display.—Distraction displays were performed by both adults, but those seen most frequently were performed during the day by females. My notes on the distraction display of the Muneni female, after being flushed on day 3 at 11.00 h, are representative of the behaviour of all four females: 'She flew directly away from my line of approach and flopped down onto the ground at a distance of about 5 m from the nest. As soon as she landed, somewhat hidden by the grass, she started thrashing around violently with wings and tail spread. At the same time she uttered a high-pitched rapid growling call. Both the sound and the movement attracted my attention immediately, and would presumably do the same for a predator. I followed her and when she saw that I was approaching she took off, flew about 10 m and settled on a thick, horizontal branch of about 10 cm diameter. She straddled it lengthways with wings drooping, one on each side, and tail fully spread. In this position she repeated the distraction display quite violently, moving the wings alternately up and down in a chopping motion. She was facing me and when I continued my advance toward her she took off and settled in another tree, on a thin branch, further down the slope. This happened several times, the intensity of the display diminishing according to

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TABLE 1
Daily mean measurements of Fiery-necked Nightjar *Caprimulgus pectoralis* chicks from hatching to fledging. Sample sizes shown in brackets.

Day	Wing	Mass	Tail	Tarsus	Culmen
1	10.3 (1)	5.3 (2)	0.0	7.5 (1)	1.8 (1)
2	13.6 (4)	6.2 (6)	0.0	10.2 (3)	1.8 (4)
3	14.0 (4)	8.2 (6)	0.0	10.1 (4)	1.6 (4)
4	16.9 (4)	10.2 (6)	0.0	12.1 (4)	2.0 (4)
5	21.9 (4)	13.1 (6)	1.1 (2)	12.2 (4)	1.9 (4)
6	28.3 (3)	15.4 (5)	4.7 (3)	12.6 (3)	2.1 (3)
7	35.3 (3)	18.6 (5)	6.8 (3)	13.4 (3)	2.2 (3)
8	41.1 (3)	20.9 (5)	7.8 (3)	13.6 (3)	2.4 (3)
9	47.9 (3)	23.4 (5)	10.8 (3)	13.3 (3)	2.7 (3)
10	53.1 (3)	25.5 (5)	13.7 (3)	15.1 (2)	2.9 (2)
11	61.3 (3)	27.2 (5)	17.5 (3)	15.0 (1)	3.5 (1)
12	66.5 (3)	29.4 (5)	18.0 (2)	16.5 (1)	3.5 (1)
13	71.7 (3)	30.1 (5)	22.8 (3)	15.6 (2)	3.1 (2)
14	77.7 (3)	33.0 (5)	27.7 (3)	15.3 (3)	3.5 (3)
15	83.6 (2)	34.7 (4)	26.5 (1)	15.9 (1)	3.1 (1)
16	88.1 (3)	35.2 (5)	30.0 (1)	17.5 (1)	3.5 (1)
17	93.7 (1)	37.1 (3)	34.1 (1)	17.0 (1)	3.8 (1)
18	94.4 (2)	36.6 (4)	38.3 (2)	17.3 (2)	4.1 (2)
19	95.3 (2)	39.1 (3)	39.8 (2)	19.0 (2)	4.5 (2)
20	102.0 (1)	40.0 (2)	43.0 (1)	18.0 (1)	5.0 (1)

our distance from the nest, until eventually, when we were 30–40 m from the nest, she flew off and landed at the bottom of a small gully, hidden from view.'

The most intensive distraction displays were performed by females that had been in the cryptic posture for lengthy periods while we searched for them. The longer the search continued, the more violent the initial display when she was discovered. Subsequent displays diminished in intensity according to our distance from the chicks, but immediately increased if we turned back towards them. Once we started handling the chicks, the females flew to a perch nearby and watched from there, while regularly giving *chuck* notes. When I completed my examination of the chicks I replaced them in the nest and immediately left. The female usually returned to the chicks shortly afterwards, landing nearby and calling them to her, but sometimes she walked back to the nest from some distance. At Muneni on day 4 at 11.05 h the female was on the ground *c*.20 m from the nest when I left. At 11.07 h she flew halfway towards the nest and then walked 8 m towards it before settling 2 m away and calling the chicks. The first part of the walk was in alert posture, with head up and eyes open, but she gradually adopted a more skulking posture, with head down and eyes half-closed. Initially this was a slow waddle but gradually became faster as she approached the chicks.

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Figure 9. On day 6 at Muneni the fence shown in the background prevented the Fiery-necked Nightjar *Caprimulgus pectoralis* chicks from reaching the adult; as soon as the adult flipped over the fence the chicks ran across to be fed (H. D. Jackson)

Figure 10. Fiery-necked Nightjar *Caprimulgus pectoralis* chick 2 at Muneni on day 10, showing the growth of the flight feathers (H. D. Jackson)

During distraction displays the birds maintained a bold upright stance, standing and rocking sideways, sometimes even bouncing up and down as much as 5 cm, especially when perched on a branch. The eyes were wide open, the head held upright, the breast off the ground and the plumage raised. The tail and both wings were usually spread fully, but sometimes just one wing was spread. The *chuck* call was regularly used to warn the chicks to remain immobile. When being approached, the perched birds often bobbed their heads. After day 18, when the chicks were able to fly, the adults no longer performed distraction displays, but instead flew towards me and hovered nearby.

Relocation and locomotion.—At Muneni on day 4 at 18.25 h the female appeared to be alarmed by a camera lens projecting from the hide, taking off and flying 2–3 m downslope to settle on the ground, from where she called the chicks with the *woot-woot-woot* call. While doing so, she faced them and rocked violently from side to side, the gular patches fluttering when she called. The chicks immediately made their way downslope to her and snuggled

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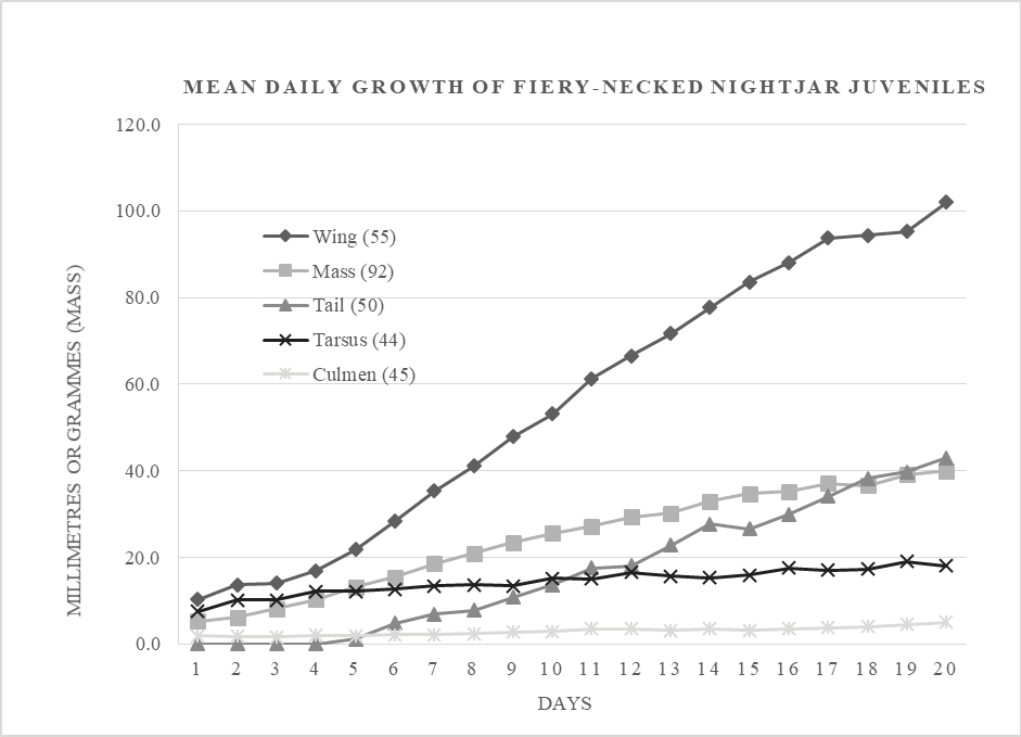

Figure 11. Mean daily growth of young Fiery-necked Nightjars *Caprimulgus pectoralis*. The figures in brackets are the number of measurements for each character.

under her wings, entering from the front, then turning round to face out either side of her breast.

When the adult tending the chicks decided to move them from a perceived threat, such as the hide, it invariably did so by first moving itself and then calling the chicks. All chicks had very well-developed legs at hatching (Table 1, Figs. 2 and 11) and were already highly mobile on day 1, so readily responded when females called them. The small fences placed around three of the nests for a few days prevented the chicks from reaching the female. They ran back and forth along the fence until the female flew into the enclosure to join them, when they would run up to her to be brooded (Fig. 9). No adult was observed taking a chick in its mouth to move it or 'airlift' it to a new location.

Growth rates of chicks.—Chicks were weighed and measured daily for 20 days after hatching (Table 1, Fig. 11). Body mass reached 80% of adult mass by day 20. At Ranelia I continued to weigh one of the chicks daily for another 12 days, by which time it was fully independent. An adult was last seen with this chick on day 19 and its sibling was last seen with it on day 22. Its body mass on days 20, 21, 22 and 23 was, with a full stomach on each occasion, 41, 44, 47 and 49 g, i.e. just below the adult mean of 50 g. On days 28, 29, 30, 31 and 32, with stomach half to full, its body mass was 58, 54, 54, 54 and 55 g, well above typical adult mass.

At hatching the tarsi already were almost half adult length and the toes had claws of *c*.1 mm. By day 6 the claw on the middle toe was 1.5 mm and slightly downcurved. On day 13 it was just over 2 mm and distinctly concave below. When it was 3–4 mm long on days 18–19, the inner edge split to form a comb of four teeth with a depth of 1 mm, the so-called pectinate claw. No adult was seen preening its rictal bristles with a pectinate claw, but this

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could have occurred away from the nest. Rictal bristles did not appear until day 18, when small pin-feathers were evident at the base of the maxilla of the Atlantica and Muneni chicks. On day 19 at Muneni they were emerging from the sheath and were *c*.2 mm long. The contour plumage appeared to be complete by day 16.

The wings and tails of the chicks at hatching were 6% and 0% of adult lengths. By day 10 they had reached 33% and 11% respectively (Fig. 10), and on day 20 they had grown to 63% and 36% respectively. The remiges appeared on day 4, breaking their sheaths on days 8–9. By days 11–12 the primaries and secondaries projected 10–25 mm from the sheaths, while the tertials were just breaking clear. By days 16–19 the remiges were half-grown, with all of the upperwing-coverts in place, but there was no sign of the underwing-coverts. The primaries grew centrifugally from the mid-wing outwards, so the outermost primary did not break sheath until day 19. The rectrices did grow evenly, first appearing on day 5 and a few breaking sheath on day 8; by day 11 they were clear and by days 16–18 projected 1–3 cm.

From day 13 the chicks often ran from my approaching hand, their wings held up at an angle of 70°. This was not a continuous movement, but a series of short hops, suggesting that they were trying to become airborne. On day 15 at Retreat at 17.30 h, the younger chick ran 20 cm, then ran further with wings up, before taking off and flying upwards 30 cm for 1 m. It immediately made a repeat flight of 5 m at a height of 1 m. Other chicks also made their first flights on days 14–15. On day 18 at 11.00 h the Muneni chick flew 2 m downslope, then 4 m upslope and finally 25 m along the slope, climbing *c*.2–3 m above ground, flying very strongly and landing with much hovering. While in flight it uttered a high-pitched chirruping sound, perhaps to guide the adults to its new location.

Discussion

Comprehensive summaries of published information concerning Fiery-necked Nightjar appear in two monographs dealing with the Caprimulgiformes (Cleere 1998, Holyoak 2001) and in *Roberts* (Vernon & Dean 2005). Many of the results of my study of the four Zimbabwe nests confirm the information in these works, but there are some corrections, observations and new insights. Data obtained by Carlyon (2011) at a nest observed near Grahamstown, South Africa, are very similar to my own.

Eggshell removal.—The remarkable behaviour of the adults at two nests in Manicaland (Ranelia and Muneni) in not removing eggshells post-hatching suggests that there is a regional difference in the species' behaviour. Manicaland birds are *C. p. crepusculans*, while those in Mashonaland (Retreat and Atlantica) are *C. p. fervidus*. The accidental removal at both Mashonaland nests, as a result of some eggshell sticking to the breast plumage is notable, but evidence suggests that Mashonaland birds also deliberately remove eggshells from the nest soon after hatching. If so, the two Zimbabwe subspecies behave differently when dealing with eggshells. There may also be a difference in the amount of albumen when the eggs hatch, as eggshells appear to be stickier in Mashonaland than in Manicaland, based on my limited data. The presence of sticky albumen at the time of hatching offers a plausible explanation for many alleged cases of transportation of eggs or young by caprimulgids (Jackson 1985b). These statements appear in the literature pertaining to Fiery-necked Nightjar: 'Eggshells removed immediately' (Langley 1984, Vernon & Dean 2005); 'Parent quickly removes eggshells' (Fry & Harwin 1988); 'The eggshells are removed from the nest-site by the adult' (Cleere 1998); and 'A parent quickly removes egg-shell from the nest site' (Holyoak 2001). All were based on Langley's (1984) observations at two nests of *C. p. pectoralis* in South Africa. There is survival value in removing the conspicuous eggshells

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(Fig. 1) from the nest site immediately after hatching, so it is strange that the Manicaland birds do not do so.

Feeding stimulus.—The method by which adults feed their chicks was determined in detail for the first time. The adult waited until a chick stretched up to grasp the tip of its bill in the chick's own (Fig. 4) before feeding it. Once the chick had a firm grip, the adult tipped its head vertically down, raising its neck and, with a rapid series of up-and-down head movements, regurgitated food into the chick's throat. This movement was extremely rapid, with the adult's bill clearly well inside the chick's gape. An excellent colour photograph of a chick soliciting food from a female appears in Carlyon (2011: 146), showing the chick's bill clearly engulfing that of the adult. Without this feeding stimulus from the chick, the adult was passive, thereby ensuring even distribution of food. Holyoak (2001: 86) noted that European Nightjar *C. europaeus* and several congeners use a similar method, but appeared unaware of the significance of the necessary feeding stimulus provided by the chick.

Return to nest for feeding.—Fry & Harwin (1988), after stating that chicks are brooded at increasing distances from the nest, added that they return to the nest to be fed. Cleere (1998) and Holyoak (2001) both repeated this with 'Return to nest to be fed'. The original source for this statement is Steyn & Myburgh (1975), who appear to have based it on the behaviour of two chicks they observed at Somerset West near Cape Town. However, since those chicks were never found >1.5 m from the nest during 42 days of observation, they had barely left the nest anyway. Twice, when 27 and 42 days old, they flew up with the female when approached, but returned to the nest at dusk. The question is whether the female was already at the nest, and calling them to her. At another nest near Cape Town (Langley 1984), the female regularly brooded the chick further away, until by day 28 they were *c.*14 m from the original site. Carlyon (2011) noted that movement around the vicinity of the nest is a feature of Fiery-necked Nightjar breeding behaviour and serves to prevent an excessive build-up of excreta in one spot.

None of the chicks in this study, or any other chicks that I have observed, some of which were relocated many metres from the nest by an adult, returned to the nest to be fed, unless an adult was there and was calling them. Firstly, there is no nest as such, i.e. no visible structure to guide a chick seeking to return to the nest. Secondly, it would not risk predation by moving to the nest, if by remaining immobile it would be exactly where the adult had left it, and to where the adult would return with food. Chick locomotion is in response to adult guidance (see below); when an adult calls, the chick moves in that direction. Only in the event of that adult being on the nest at the time can the chick be said to be returning to the nest to be fed, but it is actually returning to the adult, not to the nest.

Do nightjars sing?—Technically, only the perching birds (Passeriformes) are said to have true song. However, Holyoak (2001: 70) argued that 'this seems to be unduly restrictive, because many of the Caprimulgiformes produce elaborate, richly patterned sequences of sounds in a consistent manner and for purposes of territorial defence and attracting mates, closely similar to those termed songs in many passerines, not only in their complexity, but also in the manner of their delivery and their functions'. Throughout his monograph on the Caprimulgiformes, Holyoak (2001) referred to these sequences of sounds as 'songs', and so do I here. I cannot think of a more descriptive term for the liquid litany of Fiery-necked Nightjar.

'Wooting' call.—According to Fry & Harwin (1988) 'Warning call (of ♂ and ♀), 'woot-woot-woot …'; adults disturbed when feeding young utter nervous 'chuck' and growling notes (H. D. Jackson, pers. comm.).'. If I was quoted correctly, I was wrong concerning the 'wooting' call, which is not a warning or alarm call, but has subsequently been described as such by Cleere (1998) and Holyoak (2001), based on the statement attributed to me by Fry

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& Harwin (1988). It is in fact quite the opposite, an attraction call, used during the courtship phase, in response to the litany song (Jackson 2002b, Vernon & Dean 2005) and, during the brooding phase, to call the chicks to the adult (Jackson 1985b, Holyoak 2001, Jackson 2002a, where it was described as 'cue-cue-cue', followed by Vernon & Dean 2005, Jackson 2009, describing a captive chick at Ranelia that immediately responded to the 'wooting' of a distant adult by moving in that direction, and this study).

Chicks responded to the 'wooting' call as early as day 1, being guided by sound alone as their eyes were still closed. They must be highly mobile to reach the adult quickly. A feature of their semi-precocial development is their very well-developed legs (Fig. 2), the tarsus length at hatching already being almost half that of the adult (this study), so that they can walk strongly within four hours of hatching (Jackson 1983: 144).

The 'wooting' call was the only means by which an adult moved the chicks from perceived danger. No adult was observed to pick up and carry, or 'airlift', a chick to a new location. It invariably first moved itself and then called the chicks by wooting. They immediately responded by running towards it, even on day 1. I reviewed evidence for the translocation of eggs and young by nightjars and found that there is no satisfactory evidence of any nightjar deliberately 'airlifting' its eggs or young away from a disturbance (Jackson 2007a). Most of the evidence was based on hearsay, supposition, a misunderstanding of nightjar behaviour, or the repetition of a 200-year-old story dating from Le Vaillant and copied by Audubon. As noted by Holyoak (2001: 3) it has taken more than 100 years of observations to dispel this myth and some superstitions about nightjars.

Camouflage and flush distance.—Recent research in Zambia (Stevens *et al*. 2017) showed that individuals of some ground-nesting birds, including nightjars, appear able to assess the level of camouflage of their own plumage, and that they use this to select backgrounds that enhance their camouflage. As there is variation in plumage among individuals, they hypothesised that nesting birds choose microhabitats that improve their camouflage and predicted that birds should choose nest sites that improve their own specific camouflage compared to sites selected by conspecific individuals.

As predicted by Stevens *et al*. (2017), nightjar plumage (n = 98 adults) matched the pattern, luminance and colours of the individuals' chosen backgrounds better than those of their conspecifics' backgrounds. They also found that adult nightjars sit tight and flee from the nest only when a predator is nearby, their data showing a flush distance across three nightjar species, including Fiery-necked, of 1.9 ± 1.3 m (n = 38), meaning that nest survival should be more strongly affected by parental camouflage than by egg camouflage.

The camouflage of females at the four nests that I studied was so effective that often, while searching in daylight, we passed within 1 m of the sitting bird without flushing her. Throughout the search, she sat tight in the cryptic posture, depending totally on her camouflage. She was clearly aware of whether or not she had been seen. The act of flushing was triggered more by our behaviour than our distance from her. As soon as one of us suddenly stopped and looked at her, she took off and performed a distraction display a few metres from the nest. Only a direct approach towards the nest caused her to flush before we had spotted her.

Aggressive chick behaviour.—Reynolds (1968) described the display of a half-grown Fiery-necked Nightjar chick threatening a person by spreading its wings, opening its bill wide and lunging. This is illustrated in Fry & Harwin (1988) and photographically here (Fig. 7). The earliest full manifestation of this behaviour (which also includes hissing) that I noted, despite frequent provocation of the chicks, was on day 12, when the chicks were 60% grown. However, one chick already showed a mild example on day 6.

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Chick development.—Growth rates of the chicks were much as described by Vernon & Dean (2005), which is unsurprising as most of their data were from my Retreat nest (Jackson 2002a). Vernon & Dean (2005) made no mention of the rictal bristles or the pectinate claws, and neither do the accounts in Fry & Harwin (1988) or Cleere (1998). Holyoak (2001) noted that the bases of some larger rictal bristles were pale, while their tips were black, but did not mention the pectinate claws. I have previously (Jackson 2007c) drawn attention to the omission of these notable appendages by these authors, and have commented on their possible value to nightjars. In the current study, rictal bristles appeared as small pin-feathers on day 18 and by day 19 had broken sheath by 2 mm. Chicks can fly by day 18, perhaps even by day 14 (Carlyon 2011), so the bristles provide no protection for the eyes during the early days of flight. However, the rictal bristles of Fiery-necked Nightjar develop rapidly, the longest measuring 12 mm within one month, and when fully grown can reach 20 mm (Jackson 2007c). The claw on the middle toe was 1.5 mm long and slightly downcurved by day 6. On day 13 it was just over 2 mm and distinctly concave below, while on days 18–19, when it was 3–4 mm long, the inner flange had split to form a comb of four teeth with a depth of 1 mm, the so-called pectinate claw. As the claw grows, further splitting occurs with the result that the adult has *c*.9 teeth in each comb (Jackson 2007c).

The remiges appeared on day 4 and began to break sheath on days 8–9. By days 11–12 the primaries and secondaries projected 10–25 mm from the sheaths, while the tertials were just breaking clear. By days 16–19 the remiges were half-grown, with all of their upperwing-coverts in place, but there was no sign of the underwing-coverts. It is interesting to note that the primaries did not grow evenly, but centrifugally from the mid-wing outward, so that the outermost primary did not break sheath until day 19. This agrees with the moult pattern in adults, where the primaries moult descendantly in regular order, the inner primaries being new by the time the outer primaries start to moult (Jackson 2007b). The rectrices grew evenly, appearing on day 5 and a few breaking sheath on day 8. By day 11 they were clear and by days 16–18 projected 1–3 cm from the sheaths. These data are within 1–2 days of those given by Vernon & Dean (2005).

Independence.—Two chicks studied by Steyn & Myburgh (1975) were still with the female when 42 days old, but when flushed at 62 days no adult was present. Langley (1984) also studied a pair of Fiery-necked Nightjars breeding near Cape Town, in Rondevlei Bird Sanctuary. This pair was double-brooded, successfully raising one chick from each brood. An adult was last seen with the first chick when it was 39 days old, and Langley (1984) noted that the second chick 'was never seen in the company of an adult after the age of 23 days, with both adults having disappeared from the area when it was 30 days old, suggesting that it may have been independent at this age.' This chick disappeared four days later, probably having perished, as the first chick was still in the area when 152 days old.

At the four nests in Zimbabwe, adults were seen with chicks until days 19–21, after which the chicks appeared to be independent. At Ranelia, I continued to weigh one of the chicks daily for another 12 days, by which time it was fully independent. It reached adult body mass on day 23, with a full stomach, and regularly exceeded it on days 28–32, with a half-full to full stomach. It is evident from observations at the seven nests above that independence may be achieved as early as 19–23 days after hatching, but that chicks up to the age of 39–42 days may still accompany an adult, for whatever reason. On the available evidence, most adults leave their territories post-breeding, but most chicks remain in their natal areas.

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