Rufous-cheeked Nightjar *Caprimulgus rufigena* behaviour during the breeding season in Zimbabwe

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Summary.—Behaviour of Rufous-cheeked Nightjar *Caprimulgus rufigena*, a summer visitor to southern Africa, was studied in Zimbabwe during two breeding seasons, using radiotracking to follow individuals and locate nests. Males defend territories by regular singing at potential nest sites. Females and other males are attracted to these sites; intruding males are challenged vocally on the ground and during aerial chases; females test possible nest spots, while the resident male watches, sings and/or follows and displays. No nest is prepared; the eggs, usually two, are laid directly onto the ground. Egg losses are high but replacement clutches are sometimes laid. Females incubate by day, males at night; both may feed or roost outside the territory. Flying insects are caught in short flights from the ground.

Caprimulgidae by virtue of their crepuscular and nocturnal habits, and their cryptic coloration, are difficult to study in the field. While museum specimens of Afrotropical nightjars provide much information concerning their distribution, biometrics, food, relationships, mortality and moult (Jackson 1978, 2000a,b, 2002b,c, 2008), they reveal little about behaviour. Data from captive nightjars can provide clues to natural behaviour (Jackson 2009), but ideally field studies of wild birds are required.

Field studies in Zimbabwe have provided data on five of the seven species occurring there: Fiery-necked Nightjar *Caprimulgus pectoralis* (Jackson 1985, 1987, 2002a,d), Freckled Nightjar *C. tristigma* (Steyn 1971, Jackson 1973a,b, 1985), Square-tailed Nightjar *C. fossii* (Jackson 1985, 1987, 2003), Swamp Nightjar *C. natalensis* (Jackson 1987, Hustler & Carson 1996, Hustler 1997, 2003, Hustler & Mitchell 1997) and Pennant-winged Nightjar *Macrodipteryx vexillarius* (Shaw 1993, Jackson 2003, 2004). As European Nightjar *C. europaeus* does not breed in Zimbabwe, the only local breeder not addressed by these studies is Rufous-cheeked Nightjar *C. rufigena*, a trans-equatorial summer visitor.

Here I describe the breeding-season behaviour of Rufous-cheeked Nightjar, based on radiotracking and Betalights to follow individuals and locate nests. These aids were successfully used in England to study the behaviour of European Nightjar (Cresswell 1985); birds carrying radio packs and Betalights bred normally (B. Cresswell *in litt*. 1986).

Methods

Study area.—Quiet Waters Nature Reserve (20°18′S, 29°59′E) is owned and administered, as part of its conservation scheme, by Falcon College, near Esigodini, Zimbabwe. Descriptions and maps of the geology and topography of the reserve, with checklists of the flora and fauna, by Cunningham (1996) form the basis of this brief summary. Most of the 220-ha reserve (Fig. 1) is underlain by greenstone schists, heavily fractured and impregnated by many quartz veins and a few dolerite dykes. The major feature in the north of the reserve is the Usandisa massif, a prominent steep-sided, boulder-strewn granite kopje with a series of elevated benches and outcrops. South of Usandisa is a gently sloping area of deep, white sandy soils, and to the east of this is a pan, which was almost dry in 1988–89.

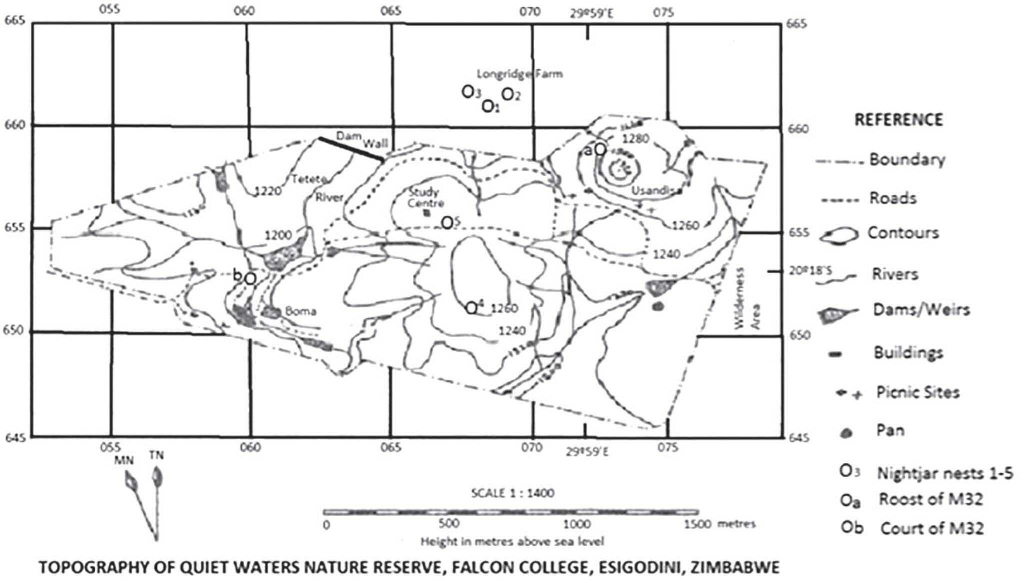

Figure 1. Map of Quiet Waters Nature Reserve, Falcon College, Esigodini, Zimbabwe, adapted from Cunningham (1996), with nightjar data added.

In the centre of the reserve is an oval-shaped hill covered with fragments of white quartz weathered from exposed quartz veins. A study centre, containing natural history specimens and other didactic material, is sited there. The drainage is dominated by the south-flowing Tetete River. Within the reserve the river is dammed in three places and some of its tributaries also have small earth weirs, providing extensive surface water when rains are good.

On schist soils the woody vegetation is fairly uniform, dominated by *Combretum*, *Acacia*, *Diplorhynchus* and *Euclea* spp. Tree species on granite and sandveld are far more diverse and include *Ficus*, *Terminalia*, *Burkea*, *Pterocarpus*, *Parinari* and *Strychnos*. On alluvial soils the riverine vegetation is typified by *Salix* and *Rhus*, while the commonest large tree on the pan is *Acacia sieberana*. Dominant grasses on the sandveld are *Eragrostis* spp., while those on the schist/clay complex are *Themeda*, *Heteropogon* and *Aristida* spp.

Nightjar research.—Some 375 hours, over 49 nights, from mid-September to mid-November 1988 and 1989, were spent in the reserve (Table 1), capturing, ringing, tagging, then tracking and observing nightjars during the breeding season. Observations were made from a vehicle parked 10–15 m from the bird using binoculars, or from a small canvas hide. I glued Betalights (Biotrack, UK), which emit an omnidirectional faint green glow in the dark, to the crowns of some individuals. These devices are tritium-filled capsules, lined with phosphorescent paint; they shine continuously and require no power source. Detailed notes were dictated into a pocket recorder and subsequently transcribed. Night lighting (Jackson 1984) was used to find and trap nightjars. Mist-nets and song playback were also

TABLE 1
Periods during which nightjar research was undertaken in Quiet Waters Nature Reserve.

1988		1989	
September	25–28	September	13–17
October	2–5		19–25
	9–11	October	10–20
	16–18	November	9–17
	23–26		
November	6–9		
	13–15		

used. All birds trapped were ringed for individual identification and weighed to the nearest gram using a Pesola spring balance before release at the capture point.

Radiotracking.—Some Rufous-cheeked Nightjars were also fitted with 2-g radio transmitters (Biotrack, UK) in the 173.2–173.35 MHz frequency band. Transmitter packages were glued to the base of the two central rectrices. I deployed five transmitters in 1988, all on females, specifically to find nests. In 1989 one radio-tagged male was monitored for most of the season. Radiotracking was performed using a Mariner-57 receiver and three-element Yagi antenna. The reserve boundary fence is electrified, so the current had to be turned off before a bird could be tracked across it.

Results

Population density and variety.—In each of the two seasons, the reserve supported *c*.6 pairs of Rufous-cheeked, three pairs of Fiery-necked and two pairs of Freckled Nightjars, based on the dusk song of males in different parts of the reserve. No Square-tailed Nightjar song was heard, despite apparently suitable habitat in the reserve. Insect-like song thought to belong to Pennant-winged Nightjar was actually produced by a small cricket (Gryllidae, *Cophogryllus* sp.). Up to five male Pennant-winged Nightjars were displaying along 1 km of the main road west of the reserve, but none was seen in the reserve. A European Nightjar was observed perched on the boundary fence. Thirteen nightjars were trapped and ringed in the reserve, nine Rufous-cheeked (two males, seven females; Table 2), three Fiery-necked (two males, one female) and one Freckled (female). The brood patch was bare on one male Rufous-cheeked and one male Fiery-necked, while all the females, except Fiery-necked, had a bare brood patch; the body mass of four females suggested that each was carrying a well-developed egg. None ringed in 1988 was retrapped in 1989. Two of the five females fitted with radio transmitters were tracked to nests with eggs; a third shed her transmitter within hours, while the signals from the other two were never heard again after the birds were released.

Behaviour of female F27.—Trapped on 27 September 1988 at 19.15 h, on a road opposite the small dam on the Tetete River at *c*.1,200 m, when released at 21.00 h she flew west. Tracking her signal showed that she then moved south slowly, probably feeding, toward

TABLE 2

Rufous-cheeked Nightjars *Caprimulgus rufigena* trapped, weighed and ringed in Quiet Waters Nature Reserve. M = male, F = female. Some were fitted with radio transmitters (tags) and/or Betalights. Contents of nests 1–5 are shown. c/1, c/2 = clutches of one, two eggs. Neither bird was captured at nest 5.

Ring no.	Ref. No.	Mass (g)	Tag no.	Betalight	Egg size and mass
BB 08327	F27	59	230		Nest 1. c/2, not measured Nest 2. c/1, 28.3 × 20.9 mm; 6.5 g Nest 3. c/1, not measured
BB 08329	F29	60, 61	280		Nest 4. c/2, 26.9 × 20.3 mm, 26.0 × 19.9 mm; clutch mass 10 g
BB 08330	F30	64 (egg?)	310		
BB 08331	F31	66 (egg?)	310		
BB 08332	M32	54, 49	220	Yes	
BB 08335	F35	66 (egg?)			
BB 08336	F36	55	250		
BB 08337	M37	49			
BB 08338	F38	60		Yes	
?	?				Nest 5. c/2, not measured

the boma (livestock enclosure). The following morning, she was roosting, perhaps nesting, on a hill overlooking the upper Tetete River, where it flows into the large dam on Longridge Farm, well outside the reserve. At sunset on 2 October F27 was on the same hillside. For the duration of twilight she moved slowly toward the boma, the fluctuating signal indicating that she was feeding. By 20.00 h, when it was dark, she was back on the hillside, remaining there even after the half-moon rose above Usandisa Kopje at 01.15 h. On 3 October at 15.00 h I got within 20 m of her; she was perched *c.*20 m below the summit of the tall hill, which has slopes of 30–45° covered in open woodland, with lots of leaf litter, quartz pebbles and some grass. The trees present were small, with an occasional large individual every *c.*100 m.

With her back to the sun, she crouched with head held lower than most nightjars, giving a hunchbacked appearance. With eyelids closed to slits, she watched me closely, but by moving casually I approached to 2 m behind her. She teetered forward in pre-flight attitude, revealing two eggs aligned parallel to her body. She took off east, circled clockwise, landed 20 m downslope, facing me. This nest ('O1' in Fig. 1) was 1.05 km from where she was captured and 1.45 km from where she was feeding near the boma.

On 4 October at 16.00 h she was sitting facing away from the sun. The eggs, pink in ground colour and evenly marked with large dark freckles, were on a small patch of bare ground. A 10-cm cube of quartz was just below the nest, while a small tree to the west provided afternoon shade. On 11 October at 07.45 h the eggs had disappeared, with no sign of predation or hatching. The last signal for F27 from the nest area was on 9 October at 20.20 h. On 11 October at 16.00 h, she was tracked to the foot of the hill on the west side. Judging by the droppings at the base of a tall tree, she regularly roosted there; no chicks were found in the vicinity.

On 18 October at 05.45 h she was on a single egg at a new nest ('O2' in Fig. 1), on the east side of the hill, *c.*75 m north-east of, but on the same contour as, the old nest. When checked again at 16.20 h there was still only one egg. On each occasion that she flushed, she flew *c.*5 m to settle briefly with head up and eyes open, then flew a further 20–30 m.

On the overcast day of 24 October at 11.30 h she was facing downslope into the wind. Her eyelids were narrow slits but on closer approach narrowed even further. There was still only one egg, brownish pink, with lilac and brown blotches and freckles, evenly distributed with a clear patch of 5 mm diameter. The egg's mass was 6.5 g and measurements 28.3 × 20.9 mm. A good signal from F27 came from the nest area on 26 October at 07.00 h.

There was no sign of the female in the vicinity of the nest on 7 November at 16.30 h. Bits of eggshell, with edges nibbled by tooth or bill, suggested predation. On 8 November at 09.10 h F27 was tracked to a new nest ('O3' in Fig. 1), *c.*100 m north-west of the first, and on approximately the same contour as the first two. She flushed off a single egg and flew north in a series of short (5–10 m) flights until she settled out of sight. At 09.30 h she flew back low over the ground (1 m) to land 5 m from the nest. She was very alert, bobbing her head up and down, eyes wide open. She flipped 2 m nearer, looked around, flipped another 2 m nearer, paused, ran rapidly towards the nest, stopped short of it, paused, then sidled onto the egg without any probing or shuffling. She had her head slightly up, facing downhill with her back to the sun. On 9 November at 08.30 h there was still only one egg.

F27 was still incubating on 13 November at 17.00 h. She returned to the nest at 17.40 h after being flushed, but did not stay long. I remained observing until 19.10 h while the nest was unattended. On 14 November at 17.25 h both female and egg were present. By 19.00 h, when dusk twilight had almost faded, there was no bird at the nest and no eyeshine in the vicinity. At 19.10 h a male called near the nest with three *Q-whoop* coughs followed by five seconds of churring. I located his eye-shine 1 m west of the nest. The song sequence was repeated five minutes later but he did not return to the nest and was still there at

19.30 h when I left. F27 was in the vicinity of the nest on 15 November at 20.45 h when my observations ended.

Behaviour of female F29.—Trapped 350 m east of the study centre, on 4 October 1988 at 19.30 h, she was released at 20.10 h after being fitted with a radio transmitter. On 9 October at 16.45 h she was tracked to a nest ('O4' in Fig. 1) on the south-west slope of the hill south-east of the study centre, at about the same altitude as the latter. I must have walked past her several times, once within 3 m, without flushing her; only when the Yagi antenna passed over her did she take off, flying 5 m south-east along the contour to settle behind a rock. Two eggs, which scattered 5 cm apart on take-off, were in the same position when I returned at 18.00 h, and the female was still behind the rock.

On 10 October at 16.00 h F29 was on the nest, facing downhill. She flushed east and flew in a semicircle 10 m west of the nest, on the same contour. The nest was <1 m uphill from a narrow game trail, used mainly by Plains Zebras *Equus quagga*. The eggs lay on bare earth surrounded by small angular pebbles of schist and quartzite. A large block of quartzite with a dead branch over it provided some protection one side of the nest. The eggs were less pink, more brown, than those of F27, well freckled throughout, measuring 26.9 × 20.3 mm and 26.0 × 19.9 mm, with a clutch mass of 10 g. On 11 October at 16.40 h she was on the nest. At 18.25 h she flew slowly downhill toward the boma, apparently feeding. She settled at 18.40 h in light rain.

On 17 October at 09.15 h the nest was empty. There were no eggs or eggshells, no chicks or droppings, and no sign of predation. I tracked F29 well down the slope, *c.*200 m due south of the nest. On approach I saw a bird in the shade of a small bush next to a footpath, facing downhill with its back to the sun. It flushed to settle 10 m further on, the bright patches in the plumage identifying it as a male. F29 flushed from 3 m beyond where the male had been; it flew 30–40 m before perching on a low (1 m) branch (2 cm diameter) at the same contour level. No eggs or young were found where either bird had been. At 18.05 h her signal came from where she had settled earlier and for the next 20 minutes she moved steadily west, while male song started nearby. On 18 October at 17.00 h she was at the foot of a large tree on a termitarium 75 m south-east of the nest; sitting on leaf litter but with no eggs. An intermittent signal at 18.25–18.35 h indicated that she was moving downslope towards a small weir south of the boma, with male song coming from the same direction but across the boundary fence.

On 23 October at 17.00 h F29 was roosting 8 m south of a previous roost (see 17 October at 09.15 h), sitting with her back to the sun on leaf litter (no eggs) between two trees providing some shade. She flew horizontally into a strong headwind and tried to perch on a branch 1.5 m high in a small tree, gave up and flew further uphill, turned and glided 30–40 m downwind to settle on the ground east of the roost. On 24 October at 16.30 h she was roosting 100 m west of this position, with her back 45° to the sun on an open patch of pebbly ground (no eggs) with a block of quartzite and thorny shrubs behind her. Acacias a few metres away provided some dappled shade. She flushed *c.*10 m downhill to perch 2.5 m up on a steeply sloping (60°) branch, crosswise back-on. After ten minutes she bobbed her head a few times toward another branch at the same level, 1 m further on, flew there to perch crossways on this 5-mm diameter twig, with her back to me, but head turned. After ten minutes she flew 30 m east to perch 2 m up in the middle of a tree, atop a bow-shaped branch (15–20 mm thick). Seen in bright sunlight, she appeared very grey with dark scapulars and a definite rufous cheek; her posture was upright, with tail at 45°. On 25 October at 18.00 h she was roosting 10 m south-east of the previous day's roost, on a flat stone in dense grass (20 cm high). She again flushed 10 m downhill to perch in a small tree, 2–3 m up, and after two minutes flew to roost on virtually the same spot as the previous day.

On 6 November at 17.00–18.40 h her signal consistently came from beyond the boundary fence south of the boma, in the area where her presumed mate was singing on 18 October. I tracked the transmitter (but no bird) there next morning, on the ground below the fence of a horse paddock, *c*.0.5 km south-west of the roost area and 1 km from where she was captured.

On 14 November at 20.30 h F29 was retrapped on the road 150 m east of where she had first been captured. All rectrices were intact, so the transmitter had come off cleanly; it was reattached before she was released. On 15 November at 09.00 h she was 100 m south of the usual roost, beside a small tree in a rocky area with large trees. She flew 4 m to settle and watch me (no distraction display) before flying another 30 m; there were no eggs or young where she had flushed.

Behaviour of a pair at the study centre.—On 10 November 1989 at 04.30 h a male was churring near the study centre. Walking along the road toward it, the churring stopped when I was opposite 'O5' (Fig. 1). As I moved away the churring resumed, but stopped again as I returned. A female then flew in with loud *Q!-Q!-Q!* calls and settled on the road 10 m from me, her wings held in a V; each time I walked up to her, she flew up with a *Q*-call to land a few metres further with wings up; this was repeated several times until she had led me well away from the study centre, when she circled round and flew back toward it.

At 20.05 h a male was found on a nest ('O5' in Fig. 1) at the point where the churring had come from earlier, 5 m north of the road among low shrubs. The nest, on bare ground, contained two eggs, dark pink and mottled with numerous darker freckles; the eggs were not handled.

On 11 November at 16.30 h the female was on the nest, facing north-west. She was still there at 18.15 h. She had her back to me, but turned her head 30° to watch me. At 18.37 h she took off silently and flew east; 25 minutes later the male flew in silently from the east, landed directly on the nest and shuffled slightly. Taking a photograph with flash yielded a dramatic reaction; the female appeared almost immediately, uttering *Q*-calls in flight, while the male commenced churring, but remained on the nest. Every flash triggered the same response. The male was on the nest when I left and was still there at 02.00 h, yet at 06.00 h the eggs had gone; no sign of hatching or predation, the only tracks being those of Impala *Aepyceros melampus* 1 m away. Neither bird was captured at the nest, and no new nest was found within their presumed territory.

Description of a nest outside Quiet Waters.—T. Marais showed me colour photographs of a nest found 2 km north of Quiet Waters in November 1980. It was on a rocky outcrop beside a road. Habitat surrounding the nest was mainly rubble, with two tufts of tall grass and several short tufts between rocks 30–40 cm from the nest. Pale buff edges to the outer rectrices of the bird on the nest, with its back to the sun, revealed it to be female. She was incubating two eggs, oriented longitudinally either side of her keel. They were pinkish brown, heavily freckled and mottled throughout, laid on fine gravel with a dozen small quartz pebbles within 5 cm, leaf and grass debris beyond. Two chicks were subsequently seen in the nest, but two days later they had moved 2 m to the foot of the outcrop, on scree of quartzite chips. They were highly cryptic, looking much like small grass tufts, without a definite outline, due to hair-like filoplumes projecting in all directions. Dark transverse bands across crown, back and rump also disrupted the outline. General colour was dark brown and grey, with paler spots, giving them a grizzled appearance. Counter-shading was evident, the buff sides being paler than the dorsal plumage. A whitish W, formed by the eyebrows and two dorsal stripes, provided a further disruptive pattern. Tubular nostrils were prominent on the bill. Blue-grey skin showed on apteria on the rump, lower back and either side of the upper back. Pale feathers encircled the vent.

Behaviour of male M32.—The only male fitted with a radio transmitter was tracked and observed extensively, but never tended a nest. He was not followed when he flew across the boundary fence onto adjoining Longridge Farm. However, radio signals from there indicated he was feeding or passing through. Male M32 was captured on 15 September 1989 at 03.00 h in a mist-net in the study centre car park. Body mass was 54 g and he was fitted with a tail-mounted radio transmitter and a crown-mounted Betalight. He flew off strongly when released.

Roosting.—Radiotracking revealed that M32 spent the daylight roosting on the ground, usually (n = 10) on the north-west slopes of Usandisa Kopje in the north-east corner of the reserve, or (n = 4) *c*.200–300 m north-west, on adjoining Longridge Farm. A regular roost site ('Oa' in Fig. 1) was located due north-west of Usandisa, just below a footpath on the lower slopes, at *c*.1,280 m. Despite the radio transmitter signal, it initially took almost one hour to spot him, on an exposed area of sparse leaf litter on a small, flat granite outcrop, which was half below a broken tree on one side and flanked by a tall (1 m) tuft of grass on the other. This provided some shade in the morning. Immediately nearby was a block of quartz, slightly larger than the bird. Numerous droppings showed that he had roosted there frequently; I found him in the same spot on five other days.

When first found, he did not fly until I spotted him, then glided downhill. On subsequent visits, when I did not approach closer than 10 m, my presence did not cause him to flush. He did not assume the hunchback posture often seen during incubation, but adopted the typical nightjar pose, with body flattened and eyes closed to narrow slits. He faced the sunrise but turned his back to the sun for the rest of the day. When it was windy, he faced the wind.

Once he was found roosting on his courtship site ('Ob' in Fig. 1), *c*.1.7 km south-west of his regular roost. At the time when he would normally have left for the roost at Usandisa, it was dark (the moon set at midnight), overcast (8/8 cloud) and raining heavily. Although the rain gradually eased, these conditions, along with misty mornings, prevailed for three days, during which time he was found at three different roosts on Longridge Farm, *c*.200–300 m from the regular roost. On the fourth day, after the rain had ceased, he was again at the usual roost.

Roost departure.—I observed the waking sequence once. The first sign of activity was a sideways shake of the head 12 minutes after sunset, and again five minutes later, perhaps attempting to dislodge the Betalight. After two minutes, he raised both wings vertically, while stretching his head and neck forward, then paused before closing his wings, turning and scuttling a few paces to hide behind a tuft of grass. He took off three minutes later, 22 minutes after sunset. M32 left the roost 17–25 minutes after sunset (mean 20.5 ± 2.4, n = 10), towards the end of twilight. However, during the four days of rain, he left the roost significantly earlier ($p < 0.001$), 0–11 minutes after sunset (mean 7.3 ± 5.0, n = 4). The zero value relates to the day he rose at sunset after roosting in the rain at the courtship site. On another occasion, not included above, he left the roost at Usandisa 12 minutes after sunset, when a strong north-east wind was blowing, and flew directly to his courtship site in two minutes. This fast (*c*.51 km/hour) wind-assisted flight took him over the study centre, where he was seen flying at a height of *c*.5 m.

Search for a territory.—Early in the season M32 tried to establish a breeding territory in the vicinity of his roost, but the incumbent males prevented him from doing so. When a sound-recording of song was played at the first picnic site below Usandisa (i.e. south-west of M32's roost) on 15 September at 01.00 h, two males arrived almost simultaneously, with repeated *Q*-calls and flying around fast in tandem *c*.3–5 m above ground. They ranged far and wide for >100 m, flying in formation one above the other, or side by side, with many *Q*-calls and some *oar!-oar!-oar!* calls. Eventually they settled on the ground 1 m apart to cough (*Q-whoop*) and churr at each other. Singing bouts then occurred at several points around and within the road loop to the south. They continued their churring and formation flights for almost two hours before one bird flew off toward the study centre, while the other, presumably the victor, continued churring at the picnic sites. The presumed vanquished male was trapped in a mist-net at the study centre at 03.00 h; he was ringed and radiotagged as M32.

When the first nightjar song started at dusk on 16 September at 18.15 h, it was M32 churring non-stop for five minutes *c.*150 m west of his roost site, halfway toward the fence. A second male started churring in the vicinity of the picnic sites, followed by a third just across the fence to the north-west. Wedged between these two males, M32 returned to his roost briefly and then (18.20–18.30 h) moved steadily west towards Longridge Dam. He spent much of the night (00.30–03.45 h) on the road opposite the dam north-west of the study centre, sitting quietly or feeding, but at 03.00 h he started churring in earnest, immediately attracting a challenger from the south; this caused him to move further east along the road, accompanied by *Q*-calls from both. The same scenario was repeated several times until 03.45 h, when the two birds performed fast formation flights with *Q*-calls, and much *Q*-whooping and churring on the ground. M32 then flew east, while the other male remained on the road still churring. At 04.00 h M32 was 50 m inside Longridge Farm, across the fence from his roost, singing frequently, on occasions churring non-stop for >5 minutes. He crossed the fence at least twice to sing in the reserve, once accompanied by a second bird.

Establishing a territory.—Subsequent observations in September showed that while M32 often fed on Longridge Farm shortly after leaving the roost, he no longer sang there but moved steadily south-west along the Tetete River towards the small dam and beyond. He spent much of the night, especially moonlit hours, on or near Hayfield B ('Ob' in Fig. 1), in the south-west corner of the reserve. He was present for 49.4–77.7% (mean 62.9 ± 10.1, $n = 6$ nights) of the moonlit period between sunset and sunrise in September, and for 85.3–96.4% (mean 92.9 ± 4.6, $n = 7$ nights) of this period in October. There, *c.*1.7 km south-west of his regular roost at Usandisa, and *c.* 80 m lower in elevation, he defended an area of *c.*3.4 ha.

Fig. 2 shows M32's times of initial arrival on, and final departure from, his territory, in relation to sunset, moonrise, moonset and sunrise. In September, apart from one early arrival, he did not appear on his territory until 0.80–2.25 hours after moonrise (mean 1.63 ± 0.59, $n = 7$ nights), having spent the dark period on Longridge Farm, inactive except for a brief feeding bout at the end of twilight. On 10 October, he was already on his territory at sunset, after roosting there all day; subsequently, he arrived 22–39 minutes after sunset (mean 30.6 ± 6.4, $n = 8$ nights), i.e. after the 22-minute dusk twilight, having fed several times en route from the roost. Final departure from his territory was 19–111 minutes before sunrise (mean 47.7 ± 31.5, $n = 13$), i.e. usually well before dawn twilight. However, during the first half of October, when moonset preceded sunrise, his departure was significantly later ($p = < 0.01$), 17–27 minutes before sunrise (mean 19.4 ± 5.1, $n = 4$), having waited for dawn twilight before leaving.

Song points defining M32's territory.—A bare patch of ground in the hayfield ('Ob' in Fig. 1) was the focus of M32's territory. This small area, *c.*25 m in diameter, is where he spent most of the night, did most of his singing, and attracted most visits by females (Table 3c), so I refer to it as the courtship site ('court'). The major song point within this area was marked by a 6-cm quartzite pebble, which appeared bright in the moonlight. While he particularly favoured this pebble, visiting females appeared more interested in a sandy area around a similar pebble 12 m to the west; so much so that M32 gradually shifted his

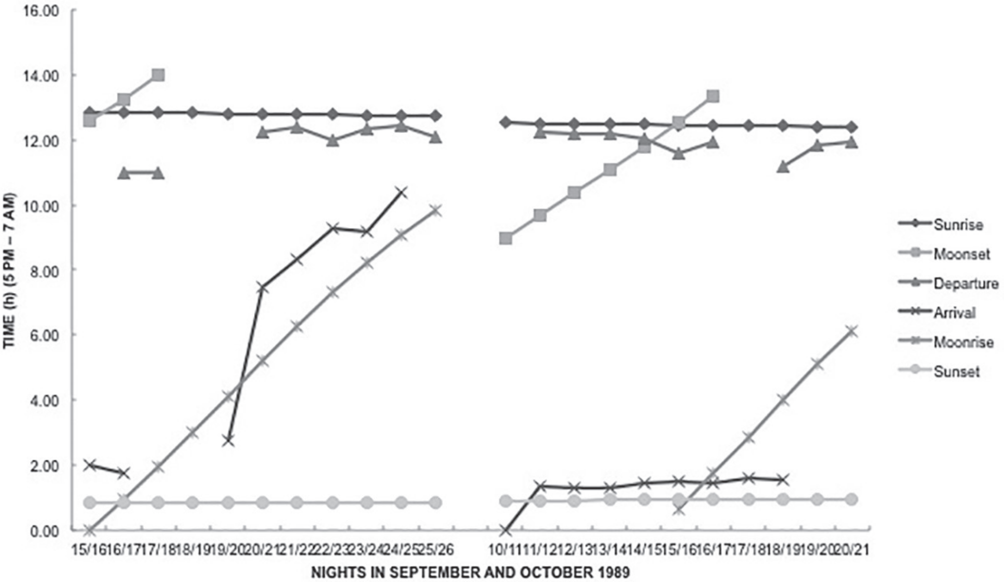

Figure 2. Initial arrival and final departure times of male Rufous-cheeked Nightjar *Caprimulgus rufigena* (M32) on his court, in relation to sunset, moonrise, moonset and sunrise.

attention there and to a point midway between the two pebbles. A concrete culvert on the north edge of the court provided another regular song point, used frequently when my vehicle was parked too close to the south edge of the court. Mean duration of song at the culvert was greater than at any other point (Table 3c).

The gravel roads and concrete ruins surrounding the hayfield provided several song points used more or less regularly; an inner ring of five, enclosing an area of *c*.3.4 ha (Table 3b), and an outer ring of four, enclosing an area of *c*.17 ha (Table 3a). During my observation periods, M32 visited song points on the outer ring 16 times, those on the inner ring 38 times, and those within the court 125 times (Table 3).

Vocalisations.—A general account of the vocal behaviour of Rufous-cheeked Nightjars, including M32, observed during this study has been published (Jackson 2002d), so here I discuss in more detail the performance by M32 (Table 4). The most-frequently heard vocalisation, and the major activity while in his territory, was the steady churring song, delivered from the ground for up to ten minutes at a time without pause; sometimes, while churring, he faced in a new direction and shuffled sideways. Mean song duration was 82 ± 103 seconds (2–600; *n* = 224); the mean varied from 59 to 90 seconds between song points within the court (Table 3c). There was a noticeable slowing down in churring rate towards the end of a session, thus the finish could often be anticipated.

Churring was mostly heard at dusk and dawn, immediately upon arrival at the court in the evening and intensively again just prior to departure for roost in the morning. During the rest of the night the amount of churring depended mostly on the moonlight available; no moon meant no song, as he did not sing in the dark. The state of the moon also influenced his arrival time and departure from the court (Fig. 2). Once, after leaving the roost, he spent 15–20 minutes feeding on Longridge Farm during twilight, then remained there until moonrise before moving to the court. There was often no activity between the end of twilight and moonrise; even then, sustained churring did not start until the moon was at least 10° above the horizon.

TABLE 3

Number of observed visits paid by a male Rufous-cheeked Nightjar *Caprimulgus rufigena* (M32) to various song points defining (a) the boundary of his larger territory, (b) the boundary of his smaller territory, and (c) the central court. Visits to these song points by other males or females are indicated by ♂ or ♀ respectively. The location of each song point in relation to the grid lines in Fig. 1 is shown in brackets. Also shown is the mean song duration at each point in the court.

(a) Outer song points enclosing *c.*17 ha

Song point (Ref. in Fig. 1)	Number of observed visits	Direction from court	Neighbour in that direction	Neighbour's song noted (*n*)
Ridge ruins (656/061)	3	N		
Steep Road (655/065)	4 ♂♂	NE	Causeway on road	4
Road at boma (651/061)	2 ♂	S		
Road at west gate (652/057)	7	W		
Totals	16 3 ♂			

(b) Inner song points enclosing *c.*3.4 ha

Song point (Ref. in Fig. 1)	Number of observed visits	Direction from court	Neighbour in that direction	Neighbour's song noted (*n*)
Car park at dam (6535/0605)	14 ♂♂♀	NE	Longridge dam (distant)	3
Road east of dam (653/062)	13 ♂♀	E	Study Centre	1
Road to boma (652/0605)	6 ♂♂	SE	Old claims	8
Concrete floor (6515/060)	3 ♂♂♂	S	Mine dumps (distant)	5
Road to west gate (653/058)	2	W		
Totals	38 8 ♂, **2** ♀			

(c) Song points within the *c.*25-m diameter court

Song point	Number of observed visits	Direction from court centre	Duration of song (s) mean ± SD	Range (s) and number
Culvert	27 ♀	N	90 ± 105	(3–480) 66
East pebble	45 ♂♂♂♀	E	77 ± 100	(2–480) 46
Midway	18 ♂♀♀♀	S	59 ± 80	(2–300) 20
West pebble	19 ♂♀♀♀♀♀♀♀♀♀	W	80 ± 112	(5–420) 20
Other	16 ♂♂♀♀	random	75 ± 87	(2–330) 67
Totals	125 7 ♂, 16 ♀			

Cloud cover, cold, wind, mist and rain all inhibited song. On several occasions M32 stopped churring as a cloud obscured the moon, then re-started immediately after the cloud had passed. On other occasions, when there was extensive cloud cover, he started singing each time a break permitted moonlight to shine through. Surprisingly, a bright moon overhead on a clear night also appeared to inhibit churring, as if there was too much light. When it was cold and windy M32 faced the wind, huddled up; on a particularly cold night he appeared to leave the valley for higher ground, his radio signal coming from the ridge above the small dam. A noticeable drop in temperature usually resulted in diminished activity. Mist and rain also inhibited churring by M32; once, heavy rain prevented him from leaving the court for his roost, so he spent the day there.

Churring was usually preceded by a few preliminary coughs, with slight pauses, e.g. *Q-whoop ... Q-whoop ...Q-whoop ...* churring. The bird had its head down and tucked in while uttering the coughs, then stretched forward head up while churring, prominently exposing the white throat patches. My impression was that the preliminary coughs were a means of gulping air into a reservoir, to fuel the churring; however, the duration of churring did not seem dependent on the number of coughs. Sometimes (15%) churring started without any preliminary coughs. Emphasis in the cough was on the first element, which is a less explosive version of the *Q*-call. As many as nine preliminary coughs were noted, but mean was 4.3 ± 2.2 (1–9; $n = 140$).

The steady churring song of M32 changed tone in response to the arrival of another male or a female. Males were greeted with a continuous series of much louder, harsher *oaroaroar* notes, while females provoked a continuous series of more mellow, purring notes. A change in tone alerted the observer to the arrival of another bird. M32 occasionally appeared to mistake the sex of the visitor, so that churring turned to purring to oaring in a single continuum. The oaring and purring are simple variations on the territorial song, each being uttered as a continuation of, and at the same rate as, the churring.

These vocalisations were all performed while M32 was on the ground; in-flight vocalisations comprised two distinct calls, an explosive, staccato *Q!-Q!-Q!* and a guttural *oar!-oar!-oar! Q*-calls were frequently heard during feeding flights, mainly on take-off, occasionally on landing, and often during formation flights with a female. *Oar*-calls, as many as 30, with some *Q*-calls interspersed, were heard mostly during aerial skirmishes with other males. Subjectively, the *Q*-call sounds excited, the *Oar*-call aggressive. The former is a scaled up version of the first element in the preliminary cough (*Q-whoop*), while the latter is derived from oaring by breaking up the continuous *oaroaroar* series into separate *oar!-oar!-oar!* notes.

Reaction to intruders.—The largest intruder into M32's territory was the vehicle used as a mobile hide; this was normally parked, prior to his arrival at dusk, on the south edge of the court and facing, at a distance of 10–15 m, the two pebbles used as song points. Switching on parking lights triggered a churring response, while dimmed headlights caused him to move to sing elsewhere on the court, so virtually all observations were made in moonlight alone. Once, when caught in the beam of a headlight at *c*.3 m, he turned sideways through 180° a few times, broadside on, then faced the light, put his head down as if to peck the ground, and flew off.

M32 responded to movements and sounds from the vehicle, such as the radiotracking *kips* made by the receiver, by flying straight towards the cab with repeated *Oar*-calls before returning to his song point. The vehicle's proximity seemed to cause him to spend less time singing near the east pebble, his favourite song point, and more time 20 m north on the culvert song point, where mean song duration was greatest (Table 3c). The mean for the court as a whole, with the vehicle present, was 89 ± 104 seconds (2–480; $n = 165$). To check whether the vehicle inhibited singing, I parked behind a tree on the boma road, 85 m from the court, from dusk to midnight on 15 October. Contrary to expectation, mean song duration decreased to 46 ± 60 seconds (2–270; *n* = 54).

Several times, when viewed through binoculars, M32 deliberately hid from view behind a tuft of grass, remaining absolutely still for some time before flying directly towards the cab with *Q*- and *Oar*-calls. The bird was clearly aware of me, especially during bright moonlight, despite screening the windows. He was also aware of ungulate activity at the west of the hayfield, where cattle and wild game congregated at the Duncan Applicator, which provided tick control. Whenever a commotion occurred, M32 flew over the animals uttering many *Q*- and *Oar*-calls, before returning to his song post. The bare court was created by the hooves of these ungulates, while the applicator was at the east end of the hayfield.

Greater Kudus *Tragelaphus strepsiceros*, up to ten but usually <5, often crossed his court, sometimes browsing on the trees next to the culvert song point. They seldom caused him to fly, but he stopped singing, although he occasionally gave some preliminary coughs without churring, only resuming when they left. He crouched down in cryptic posture, even when some kudus passed as close as 1 m. Once, while churring from the normal tarsus squat, he swung round to face a kudu approaching 10 m away, rose onto his toes and churred at it strongly, behaviour repeated towards a rival male nightjar on another occasion.

When a group of Bushpigs *Potamochoerus larvatus* spent 30 minutes in the north-east corner of the hayfield, squealing loudly, M32 continued churring with lengthy songs on at least ten occasions. He also continued churring for 84 seconds despite the raucous song of a Water Thick-knee *Burhinus vermiculatus* a short distance away. A Scrub Hare *Lepus saxatilis* approaching the east pebble caused him to spin round to face it, before flying up to land 2 m beyond it, without any *Q*- or *Oar*-calls; facing the hare, he continued feeding with short flights into the air. On separate occasions, while M32 was away, a Side-striped Jackal *Canis adustus* and a Serval *Leptailurus serval* (both potential predators) crossed his court.

Reaction to conspecifics.—When a Rufous-cheeked Nightjar was heard singing in the distance, M32 faced that direction and churred steadily. However, song anywhere within his territory caused him to immediately fly towards it, giving *Q*-calls. Three times, while M32 was absent, an intruder flew to the court, sat for a while, coughed a few times and churred. The radio signal immediately revealed that M32 was returning, with *Q*-calls being heard. Both then flew around in formation, with many *Q*-calls, before the intruder left and M32 returned to the court to churr for several minutes; once, however, the two birds first hopped around each other, flipping towards each other, before taking off. M32 took no notice of Fiery-necked and Freckled Nightjars—whistlers not churrers—that regularly sang in his territory.

Conspecifics flying silently over the court triggered a steady churring from M32, apparently serving as both a warning to males and invitation to females; when close enough to identify, his churring changed to loud oaring if it was a male, or to subdued purring for a female (Table 4). A nightjar landing on his court immediately provoked M32 to take off with *Q*-calls, fly at the intruder, quite often over it, and land nearby with wings in a dihedral V, the white bars being conspicuous. Subsequent behaviour depended on the response of the intruder. Males usually took off with *Q*-calls and flew away, in which case M32 followed, also with *Q*-calls, to evict them from his territory, before returning to sing on his court. However, twice the intruder flipped towards M32 with *Q*-calls, both birds then repeatedly flipping at each other while calling, before taking off.

Females on the court seldom moved towards M32 if he was wearing the radio transmitter, but often ran or flew toward him when he was wearing the crown-mounted

TABLE 4
Vocalisations uttered by a male Rufous-cheeked Nightjar *Caprimulgus rufigena* (M32) and the context in which they occurred. No recordings were made of these vocalisations, so no sonograms are available.

Vocalisation	**Sound**	**Description**	**Context**
Preliminary coughing	*Q-whoop* … *Q-whoop* … *Q-whoop* … with slight pauses between coughs.	Like kick-starting a vintage motorcycle a few times before it fires. Emphasis on the first syllable. Terrestrial only.	Churring song is usually (but not always) preceded by some of these coughs.
Churring	*RRRRRRRRRRRR…* continuous.	Like the steady, rather high-pitched firing of a two-stroke engine. Terrestrial only.	Proclaimed from song points defining M32's territory, especially in the court, to warn off males and attract females.
Oaring	*oaroaroaroaroaroar…* continuous.	A louder, more guttural version of churring song. Terrestrial only.	Churring songs usually ended in oaring when a male arrived in the vicinity of M32.
Purring	*rrrrrrrrrrrrrrrrrrrrrrrrrr…* continuous.	Subdued form of churring song, at a lower pitch. Terrestrial only.	Churring songs usually ended in purring when a female arrived in the vicinity of M32.
Q-call	*Q!-Q!-Q!-Q!* … staccato with very slight pauses between calls.	A more explosive form of the first syllable (*Q*-) in the preliminary call. Like striking a metal pipe with a wooden stick. Mainly aerial but also terrestrial.	An excited call given during feeding flights; during formation flights with other males in territory defence, and courtship flights with females.
Oar-call	*oar!-oar!-oar!-oar!* … with very slight pauses between calls.	Similar to oaring, but with individual, rather than continuous notes. Mainly aerial but also terrestrial.	Aggressive call given on take-off or after landing. Often interspersed with *Q*-calls in flight.
Protesting	Rasping hissing	A low, hoarse, rasping, growling hiss. In-hand only.	Whenever handled, M32 gaped widely and repeatedly uttered this protest.

Betalight. With this exception, the behaviour of females, and of M32, appeared identical whether he was wearing the transmitter or the Betalight alone. A female usually sat quietly when M32 landed next to her, then walked or ran around, as if looking for a suitable nest site, sometimes shuffling or turning around on the spot, while M32 sat quietly watching her, occasionally flipping nearer. Each flip started with a *Q*-call and ended with a wings-up landing. She was quiet but he occasionally coughed and churred briefly between flips. During an extended walkabout by a female, M32 flew around her, making *Q*-calls, landed some metres away and started churring. Often, the female ran or flew to him. At times, they performed an 'advance and retreat' display, by hopping around or flipping to and fro with *Q*-calls. Whenever he landed right behind her, she spun round to face him.

Copulation was never observed and no nest was found on or near the court. All female visits ended with her flying away, usually (12/16) followed by M32, with both giving *Q*-calls. He (10/12) returned to the court within 20 minutes to resume churring. Once it was the female who returned, after 13 minutes, with M32 following. On another occasion, he was accompanied by a new female (F38) as he flew in from the east at dusk, heading for the court; they were flying in formation, 3 m apart, when they were both caught in a mist-net next to the culvert M32 used as a song point (Table 3c). She was not radio-tagged but a Betalight was glued to her crown; while being handled she gave a number of quiet *oar-oar-oar* notes and, when my fingers approached her crown, she gaped upward and hissed. She weighed 60 g prior to voiding a huge dropping, so had already fed. Released at 19.45 h, she sat for two minutes, turning her head slowly sideways, then shaking it horizontally, trying to dislodge the Betalight. She ran a few steps, stopped and shook her head again; after repeating this several times over a distance of 3 m, she took off silently towards the main gate. She did not attempt to remove the Betalight with her foot. At 21.13 h she was seen near the main gate, with the Betalight still in place. She was not seen again. It is unlikely that they were paired; while her brood patch was devoid of feathers, his was not. Also, during his absences from the court at night, radiotracking showed him to be feeding elsewhere, not attending a nest.

Feeding.—After leaving the roost in the evening, M32 spent much of the dusk twilight (22 minutes) feeding, either on Longridge Farm or en route to his court. Once there, the main activity was singing, but his head movements suggested that he kept constant watch for passing insects. When spotting one flying over, he took off with *Q*-calls to catch it, sometimes with an audible snap of the bill, before gliding back to the same spot, often with another *Q*-call, then immediately resumed churring. At times he left the court to feed near the small dam, his favoured observation platform being the adjoining road to the east, next to some thorn trees.

Feeding flights, up to 25 in five minutes, seldom (<50%) reached a height of >1 m, and did not exceed 5 m. Most flights were simply out and back, but a few involved aerobatics in a figure eight, with sharp twists and turns. On landing he sometimes ran a few steps, and occasionally he bent over hunched as if processing prey, but he was not seen chasing insects on the ground. When first trapped, on 15 September at 03.00 h, M32's body mass was 54 g. When recaptured, on 18 October at 18.35 h, it was only 49 g, with stomach *c*.25% full.

Resting and preening.—There were many periods of inactivity during the night, when M32 did little feeding or singing, especially if there was no moon, or it was cloudy, cold or windy. He sat quietly, without moving, for 30 minutes or more at times. This usually coincided with a general lack of nightjar activity anywhere in Quiet Waters. It was during these periods that he occasionally preened, an activity observed just eight times and never involving the flight feathers. He concentrated on the ventral plumage, mainly on the breast and belly.

Discussion

Comprehensive summaries of published data for Rufous-cheeked Nightjars are presented in two monographs of the Caprimulgiformes (Cleere 1998, Holyoak 2001) and in *Roberts VII* (Spottiswoode & Jackson 2005). Much of what was discovered during the Quiet Waters study confirms the information in these summaries, but some new observations require discussion.

Lunar effects.—All nightjar species at Quiet Waters were active mainly during the twilight periods. Nocturnal activity was observed only when sufficient moonlight was available; the brighter the moon, the more activity; with no moon, there was no singing or feeding; the birds just sat quietly. Even a temporary reduction in moonlight inhibited activity temporarily, as when M32 ceased churring as a cloud obscured the moon, only to resume immediately it passed. Shaw (1998) observed avian behaviour during a total lunar eclipse, noting that a Square-tailed Nightjar that had been singing fell silent during it, not singing again until half the moon face was exposed.

Several nightjar species synchronise breeding with the lunar cycle (Holyoak 2001). In Africa Fiery-necked, Freckled, Square-tailed and Pennant-winged Nightjars lay during the week following full moon (Jackson 1985), but this has not been demonstrated for Rufous-cheeked Nightjar. The full-moon dates relevant to the nests in this study were 25 September and 24 October 1988, 14 October and 12 November 1989. The incubation period being 15–17 days (Fry & Harwin 1988), it is probable that the eggs found on 3 October 1988 (F27) and 9 October 1988 (F29) were laid during the week following the 25 September full moon, but it is also possible that F29 did not lay until the second week after full moon. Neither of the two replacement clutches laid by F27 could have been laid during the first week after the 24 October full moon; the first was found on 18 October and the second, found on 8 November, was still there on 15th. The nest at the study centre already had eggs two days prior to the 12 November full moon. Replacement clutches and late nests are less likely to be synchronised with the lunar cycle, so the early clutches laid by F27 and F29 provide the best evidence that Rufous-cheeked Nightjars also synchronise their breeding with the lunar cycle. Further research is required to confirm this. With regard to their closest relatives, Perrins & Crick (1996) showed that European Nightjars that arrive relatively early on the breeding grounds (i.e. in May) appear to start nesting as soon as possible, but the rest, which initiate nesting between early and mid June, tend to synchronise nesting with the lunar cycle.

Jetz *et al*. (2003) studied the effects of light and prey availability on nocturnal, lunar and seasonal activity in West Africa of Long-tailed Nightjar *C. climacurus* and Standard-winged Nightjar *M. longipennis*. They demonstrated the distinct nocturnal, lunar and seasonal pattern of both light availability and aerial insect biomass, and highlighted the significance of moonlight above and beyond prey availability. They demonstrated that the lunar cycle affects short-term timing of foraging activity and breeding, while prey biomass, modulated by patterns of rainfall, governs presence and seasonality of breeding. Nocturnal foraging was positively correlated with lunar light levels and ceased below *c*.0.03 mW m^{-2}. White-winged Nightjar *Eleothreptus candicans* nesting attempts in Paraguay exhibited remarkable synchrony with the full moon; the first egg was laid within two days of full moon for all seven clutches where laying date was confirmed (Pople 2014).

Nests, eggs and young.—Crypsis is a recurrent theme in the lifecycle of all nightjars. The superb camouflage provided by the cryptically coloured plumage, which has evolved to blend perfectly with the preferred substrate, protects the adult both at roost and while on the nest. The counter-shading, disruptive pattern and hair-like filoplumes of the downy chicks make them extremely difficult to see (Uys 1984, Steyn 1996), especially when they are immobile. Even the eggs are cryptically coloured, as noted for this species by Hoesch & Niethammer (1940). The eggs are laid directly onto the substrate, so the nest is invisible. With no nest structure to direct attention to the site, how do the owners find it? I suggest that they use the quartzite blocks often found near the nest for navigation. The behaviour of M32, using a quartzite pebble as a song point, supports this suggestion, as does the block of quartz at his roost, and those at many roosts of F29.

Carlyon (2011) noted that when Rufous-cheeked Nightjars select a nest site, moist areas are avoided, with elevated sites such as hillsides or ridges being preferred. Each of the six nests in the Quiet Waters area was near the summit of a hill or on a ridge. That none of the females visiting M32's court accepted the site for nesting may have been due to its low-lying, rather moist situation. As in some other nightjars (Jackson 1985), females incubated the eggs by day, males at night. Males occasionally sit during the day, e.g. one photographed at Olifantsfontein by W. Tarboton (*in litt*. 1969) and a Fiery-necked Nightjar captured on Ranelia Farm, Chipinga (Jackson 1985).

Double-brooding by Rufous-cheeked Nightjars has never been recorded, and neither have replacement clutches, so it is significant that F27 laid two successive replacement clutches. In contrast, F29 did not lay a replacement clutch after her eggs disappeared in mid October, well before the end of the breeding season; radiotracking revealed that she and her mate remained in his territory, but had not moved her eggs to a new location (*cf*. Jackson

2007 for a discussion of nightjar nest translocation). While F27's behaviour shows that the birds sometimes replace lost clutches, it also suggests that some females raise two broods in a season. Clutch size is 1–2 (Cleere 1998), but single-egg clutches are rare (Holyoak 2001), <3% (Spottiswoode & Jackson 2005). They may well be commoner in replacement clutches, as the only single-egg clutches found in this study were the two replacement clutches laid by F27.

***Territory, monogamy and fidelity*.**—This study confirms that Rufous-cheeked Nightjar is a solitary, monogamous breeder and that males defend a territory during the breeding season. Ownership is proclaimed and territory defined by churring from terrestrial song points around and within the area. Females attracted by the singing inspect potential nest sites within the territory and once one of them accepts a nest site, breeding may commence. As noticed by Carlyon (2011), while males sing frequently within their territories, they become silent once breeding has commenced. Breeding males in this study sang briefly at dusk as they assumed incubation from the females; singing while on the nest could attract the attention of predators. The inordinate amount of singing by M32 suggested he was a bachelor, especially as radiotracking failed to lead to a nest.

Because only half of the 220-ha reserve provided suitable breeding habitat for this species, the mean size of the six territories identified could have been no more than *c*.18 ha. The outer song points used by M32 enclosed *c*.17 ha (Table 3a), but these were visited only 16 times, compared to 38 visits to the inner points, which enclosed *c*.3.4 ha (Table 3b), and 125 visits to those within the *c*.25-m diameter court (Table 3c). These results, which beg the question as to what constitutes the territory, show that territory defence is strongest in a small central display area (court), gradually diminishing outwards. White-winged Nightjars in eastern Paraguay also have a small display arena at the centre of a much larger territory (Pople 2014).

Birds were found roosting or feeding well outside their territories. M32 regularly roosted 1.7 km from his court, and frequently foraged in rival territories while en route between roost and court. F27 was captured 1.05 km from her nest, and was subsequently seen foraging 1.45 km from it. R. Earlé (*in litt*. 1988), while radiotracking Square-tailed Nightjars in Kruger National Park, South Africa, found that one travelled >3 km between its roost site and foraging area at dusk. Radio-tagged European Nightjars in Dorset travelled a mean 3.1 km from their nesting areas at night to atypical habitats, presumably to feed (Alexander & Cresswell 1990).

None of the birds captured in 1988 was recaptured in 1989, so my data provide no information on site or mate fidelity. However, breeders in the Transvaal were recaptured in three successive years (Tarboton *et al*. 1987), demonstrating site fidelity, perhaps even mate fidelity. Another, ringed in Nylsvlei Nature Reserve, and recaptured in exactly the same area 14 months later, suggested to van Eeden (2005) that this intra-African migrant returns to breed in a preferred area each year.

***Vocalisation and wing-clapping*.**—The male's basic song is a prolonged steady churring at between 31 notes/second (Walker 1969) and 32–37.5 notes/second (Fry 1988). One Quiet Waters male, timed by stopwatch, churred without pause for 20 minutes, eight seconds (Jackson 2002d), a performance of 37,448–45,300 notes! Churring tends to slow towards the end of a sustained singing session, but not to the extent that Fry & Harwin (1988) claim, repeated by Cleere (1998) and Holyoak (2001); the series of slower, lower-pitched units, *wha wha wha wha wha wha wha wha* that they describe is unlike anything heard at Quiet Waters (Table 4), but is similar to the monotonous wooting call of Fiery-necked Nightjar, often heard there (Jackson 2002d); clearly a case of mistaken identity. The churring song serves to proclaim the territory to other males, and probably invites females to breed.

Any conspecific visitor is greeted with oaring, in the case of a male, or purring, for a female (Table 4). The deimatic oaring and epigamic purring are variations on the territorial song, each being uttered as a continuation of, and at the same rate as, the churring.

Two distinct flight calls are heard; an excited staccato *Q!-Q!-Q!-Q!* … with very slight pauses, and an aggressive *oar!-oar!-oar!-oar!* … also with very slight pauses. The former is a more explosive version of the first element in the preliminary coughs (*Q-whoop … Q-whoop … Q-whoop …*) usually given prior to churring, while the latter is derived from oaring song. Ranft & Cleere (1998) provided a sound-recording that includes several preliminary coughs, sustained churring and a few *Q*-calls. Sonograms in Fry (1988), sound-recordings in Chappuis (1981) and the FitzPatrick Bird Communications Library, depict the preliminary cough and sustained churring of a Rufous-cheeked Nightjar. None of the sonograms that I have seen, or recordings that I have heard, has captured either the oaring or purring extension to the song.

According to Cleere (1998) males clap their wings in flight during courtship displays, or when pursuing males that enter their territory. This behaviour was not observed during 375 hours of observation at Quiet Waters. Wing-clapping was observed just once, in a different context, when a male taking off from a 7–8 m-high tree gave two explosive wing-claps (Jackson 2002d). Wing-clapping is common in European Nightjars, mainly by males in aggressive contexts, courtship display and even on take-off when flushed from the ground (Holyoak 2001), but is uncommon in Rufous-cheeked Nightjar, despite their close relationship.

Courtship and breeding status of male M32.—Interested females responded to the churring song of M32 by flying into his court and landing nearby. As she approached, his churring changed to purring and he flew towards her with *Q*-calls, landing with his wings in a dihedral V (displaying the white wingbars) before folding them. Initially the female sat still before searching for a suitable nest site, even turning around and shuffling sideways to get the feel of it. M32 sat watching her, singing occasionally and performing short horizontal flips. Some females left at this stage, flying off with M32 in pursuit, both giving *Q*-calls. Others responded by approaching and interacting with him in an 'advance and retreat' display, each bird performing short vertical hops and flips. None of these displays culminated in copulation; whenever M32 landed behind a female, she spun round to face him.

The reason M32 failed to secure a mate could be due to one or more factors, the most obvious being that during courtship encounters he was wearing either a radio transmitter or a Betalight. Females appeared to be attracted by the Betalight, as they flew or ran towards M32 more often when he was wearing it; perhaps they were simply curious about this unusual glow in the semi-dark. As European Nightjars wearing identical transmitters and Betalights bred and foraged normally (Cresswell 1985), it is unlikely that those on M32 inhibited courtship or copulation.

On 15 September, M32 weighed 54 g, but on 18 October only 49 g. This loss of mass was thought to be due either to the energy lost during the enormous amount of singing that he did, or due to the radio transmitter and/or Betalight he was carrying during this period (33 days). However, another male (M37), not wearing either, and caught in the same mist-net as M32 a few minutes earlier, also weighed 49 g. Palpation showed that both their stomachs were virtually empty in the early evening, so M32 may well have had a full stomach on 15 September at 03.00 h, but it was unfortunately not palpated. Since his brood patch was feathered, he may have been an inexperienced first-year, less likely to attract a mate.

The most likely reason for his lack of success, however, was the unsuitability of his territory, especially the moist, low-lying courtship area, for nesting. Observations of courtship by a pair of Rufous-cheeked Nightjars in South Africa (Tyler 1992) showed behaviour very similar to that observed in this study, suggesting that M32 was behaving in a manner representative of the species. Females were attracted and interacted with him, but rejected his territory, which he occupied only after challenging unsuccessfully for more suitable territories uphill in the vicinity of his roost.

Superspecies comparisons.—European, Rufous-cheeked and Sombre Nightjars *C. fraenatus* form a superspecies (Fry 1988). The behaviour of Rufous-cheeked, as displayed by M32, can be expected to be similar to that of its two allospecies. While little has been published on the behaviour of Sombre Nightjar, the literature on European Nightjar is extensive. European Nightjar is a trans-continental migrant, Rufous-cheeked Nightjar a trans-equatorial migrant and Sombre Nightjar mainly resident, with local movements according to the state of the vegetation (Holyoak 2001).

As discussed by Holyoak (2001), Sombre Nightjar is variously believed to be a whistler (Dowsett & Dowsett-Lemaire 1993) or a churrer (Cleere 1998). Afrotropical *Caprimulgus* have adapted both their songs and degree of p9 emargination to their habitat; the whistlers, which have stronger emargination, occur in more closed habitats, while the churrers, which have weaker emargination, occur in more open areas (Jackson 2002d). Sombre Nightjar, which occurs in open habitats (Holyoak 2001), was placed in the churring group on the basis of its weak p9 emargination (Jackson 2002b). A sound-recording of the churring song (Ranft & Cleere 1998) is extremely similar to Rufous-cheeked Nightjar (Cleere 1998), even ending in three *Oar*-calls. The recording of a European Nightjar's churring differs from both in constant changes of speed and pitch, alternating between a faster, lower pitched churr and a slower, higher pitched one, in much the same way that Square-tailed Nightjar song does.

Comparing the territorial and breeding behaviour of European Nightjars (Holyoak 2001) with Rufous-cheeked Nightjar (this study), there are many similarities in territory establishment, size and defence, but the latter performs much less wing-clapping and less volplaning with wings in a V, seldom sings from arboreal perches and does not roost there. Both species are monogamous (Sombre Nightjar too, probably), with adults sharing nest duties, but while in Afrotropical species the female attends by day and male at night, in European Nightjar, which has evolved overlapping broods in response to the short Palearctic summer, females incubate the second clutch day and night, while males tend the first brood night and day (Jackson 1985). European and Sombre Nightjars feed mainly in sustained flight (Holyoak 2001), while Rufous-cheeked Nightjar forages mostly by short sallies from a terrestrial perch (this study).

Radiotracking and Betalights.—A primary purpose of my study was to test the effectiveness of radiotracking and Betalights as aids for studying nightjars. Despite some limitations, radiotracking proved an invaluable tool. Without radiotracking, the roost site of M32 and the nests of most females would not have been found. The Betalight was helpful while observing courtship, feeding or preening, but I recommend that it be mounted on the radio transmitter body or antenna, as shown in Hayward (1987), rather than on the nightjar's crown.

Conclusion

The shortcomings of this study are obvious; too few observers ($n = 1$), too few observer nights/hours ($n = 49/375$), too few radio transmitters ($n = 5$), too few study individuals (*c.*12), small sample sizes, no night-vision binoculars, no sensitive light meter, no tape-recorder and no GPS. Despite these limitations, new insights were obtained into the breeding-season behaviour of Rufous-cheeked Nightjar, especially its roosting, territory establishment and defence, vocalisations, courtship, nesting and feeding.

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