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Breeding behaviour, home range and habitat selection in Rock Firefinches *Lagonosticta sanguinodorsalis* in the wet and dry season in central Nigeria

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Knowledge of a species' movement behaviour and habitat choice is a prerequisite for assessing its ecological requirements to plan successful conservation strategies. Little is known about these factors in the Rock Firefinch, a recently described species which is probably endemic to the Jos Plateau in central Nigeria. We investigated home range size, habitat use and breeding behaviour of the Rock Firefinch in Amurum forest reserve in central Nigeria during the wet (August–October) and the dry season (November–December) using radio-tracking. Birds showed high site fidelity. They mainly moved alone or in pairs but did not have exclusive home ranges. Home range size tended to be larger during the dry season due to long movements to water sources. Birds generally preferred inselberg habitat and avoided farmland. During the dry season they additionally utilized gallery forests where water was readily available, and as a result of having to cross scrub savannah to get to water, scrub savannah was also more heavily used during the dry season. Birds bred between the late rainy (September–October) and the early dry season (November). Nest-sites were associated with rocky boulders. Both sexes contributed to incubation. Daily egg survival rate calculated using the Mayfield method was 0.89 (0.83–0.95 95% confidence interval); no nests failed during the chick stage, but sample size was only four nests. Of all 14 nests found, 50% were depredated and only 29% of breeding attempts succeeded in producing Rock Firefinch chicks. A second breeding attempt was recorded when the first one failed. Chick production just about compensated adult mortality (measured in a separate study at the site) such that the population is probably stable at present. However, given the large uncertainty in our underlying assumptions, more data are needed to confirm this. We suggest that the presence of inselberg habitat in close proximity to water sources is the essential and limiting resource for this species.

Keywords: breeding, habitat selection, home range, Rock Firefinch, tropics.

Food abundance, availability and distribution have been described as some of the main factors influencing home range size and habitat use in a variety of animal species (Krebs & Davies 1993, McIntyre & Wiens 1999, DeVault *et al.* 2004, Eide *et al.* 2004, Prange *et al.* 2004, Wauters *et al.* 2005). Many granivorous bird species inhabiting desert or savannah habitats, where the occurrence of rain and associated seed availability is highly unpredictable and patchily distributed, have been reported to show extensive nomadic movements (Davies 1984, Dean 1997), whereas under more predictable conditions, more resident species occur (Dean 1997). Little is known about such movements in response to the wet and dry season in West Africa in the Rock Firefinch *Lagonosticta sanguinodorsalis*, a recently described species (Payne 1998), which is probably endemic to the Jos Plateau in central Nigeria. Knowledge of movement behaviour and habitat choice is therefore a prerequisite for assessing its ecological requirements to plan any successful conservation strategies.

The Rock Firefinch is brood parasitized by the Jos Plateau Indigobird *Vidua maryae* (Payne 1998). The species is thought to be endemic to the Jos Plateau in central Nigeria, although a few observations have been reported off the Jos Plateau in similar rocky habitat (Payne 1998). Wright and Jones (2005) found

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Rock Firefinches to be associated with inselberg habitat (elevations consisting of granite rocks vegetated with scrub and grass) and granite outcrops, and to be negatively associated with more open farmland and scrub savannah. However, their study was carried out during the beginning of the wet season (May–July) and differences during the dry season (November–April) are likely. No Rock Firefinch nests in the wild have been described prior to this study (Fry *et al.* 2004) and we know almost nothing about its breeding behaviour. Even though the Rock Firefinch and its brood parasite the Jos Plateau Indigobird were listed by the IUCN in 2007 as species of least concern, their restricted distribution and negative association with farmland make them potentially vulnerable species to habitat loss and disturbance. This is especially true as the human population in Nigeria is growing rapidly and natural habitats shrink as farmland encroaches and activities such as grazing and the cutting of firewood increase (Manu *et al.* 2007). Only if the ecological requirements of a species are known will we be able to assess its conservation status and take conservation measures if necessary. It is essential, therefore, that we gain more information on the habitat requirements, movement patterns and breeding biology of the Rock Firefinch to ensure its and the Jos Plateau Indigobird's long-term survival.

The Amurum forest reserve, located on the Jos Plateau in central Nigeria, is subject to a distinct dry (November–April) and rainy season (May–October) and seed abundance and water availability differ greatly between the seasons. This might have implications for the birds' habitat choice and movement patterns and consequently for its habitat requirements. The objectives of this paper are to assess the Rock Firefinch's: (1) home range size and movement patterns, (2) habitat requirements and possible seasonal changes, (3) nest-site characteristics and breeding behaviour, and (4) annual reproductive output in order to infer population trends.

METHODS

Study area

The study was carried out in Amurum forest reserve located on the Jos Plateau 15 km northeast of Jos city in central Nigeria (09.87°N, 08.98°E). The reserve is approximately 300 ha in size. It comprises an area of mainly scrub savannah interspersed with patches of gallery forest, granite outcrops and inselbergs (elevations of granite rock rising from a relatively even landscape up to a height of *c.* 40 m within the reserve). The reserve is surrounded by both extensively used and abandoned farmland, and small villages. Logging and hunting are prohibited within the reserve, and the cutting of grass is limited to a period after seed fall has taken place, whereas outside the reserve all these activities are widespread. The climate in our study area is characterized by a drastic change between the wet and the dry season. The wet season, during which heavy rains are frequent, lasts from May to October and the dry season, during which almost no rain occurs, lasts from November to April. We collected weather data during our study period with a Davis Vantage Pro2 weather station. Rains were frequent up to 19 October 2005, after which rain completely ceased (Fig. 1). Within a few days after the rain ceased, water sources in the rock ponds of the inselberg habitat dried out. We therefore categorized birds tracked until 14 October 2005 as being part of the wet season cohort and birds tracked after this as part of the dry season cohort.

Bird trapping and handling

Birds were caught in mist-nets at four different places within Amurum forest reserve between 19 August 2005 and 7 December 2005. Four to eight nets were placed at each trapping site. Three sites were trapped regularly and an effort was made to trap a similar number of birds for radiotracking on each of these sites during each season. A fourth site within the reserve was only trapped over four continuous days for logistical reasons but a Rock Firefinch female trapped there was also radiotracked (locations of trapping sites can be seen in Figure 2). Nets were checked every 45 min during the morning and afternoon but at more frequent intervals during midday hours when temperatures were high. Usually trapping occurred between 06:00–11:00 h and 16:00–18:00 h and only occasionally during midday. Birds were ringed with a uniquely numbered metal ring provided by SAFRING and a unique colour ring combination. Rock Firefinches were fitted with a radio-transmitter (Biotrack Ltd, Wareham, Dorset, UK) weighing about 0.5 g, which was about 5% of a Rock Firefinch's body weight (10.5 ± 0.9 g, $n = 125$). The transmitter was glued on to the feather-base on a bird's back after feathers were slightly trimmed. Birds were released directly after the glue had dried. During our study period, 41 adult Rock Firefinches were caught, of which 21 were fitted with transmitters.

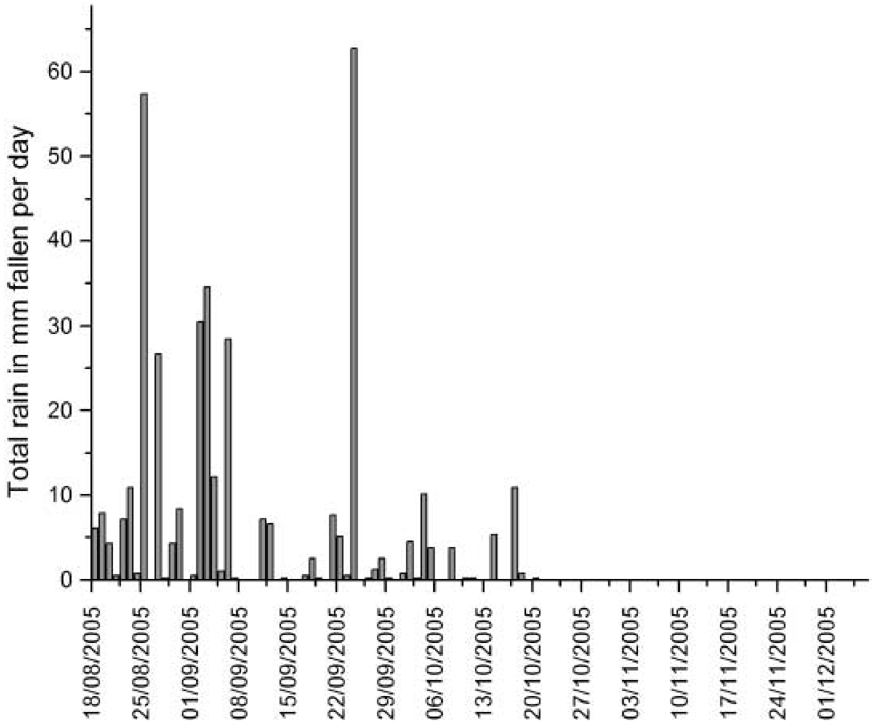

Figure 1. Total rain in mm falling per day during the study period.

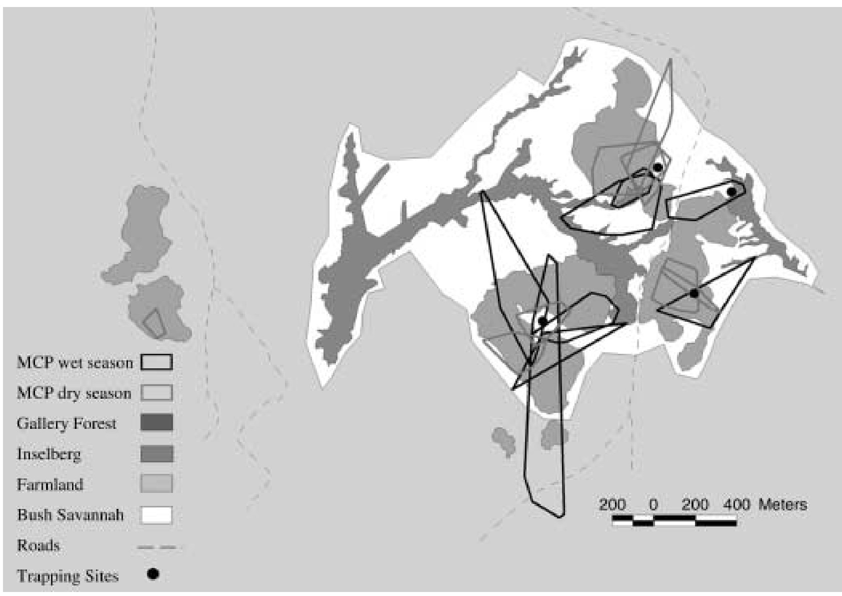

Figure 2. Map of the study area and 100% MCP home ranges of Rock Firefinches during the dry and the wet season.

Fifteen yielded data for analysis (one bird was fitted with a transmitter twice). One bird was not found again either because it had left the study area or because the transmitter failed, and five lost their transmitter before we could collect any radiotracking data. One of our aims was to find nests of Rock Firefinches and because we assumed females incubated the eggs we focused on radiotracking females at first. However, when we found that males incubate as well, we also fitted two males with transmitters. As birds were mostly observed in pairs and sexes do not differ significantly in weight ($t_{135,124} = -1.85$, $P = 0.07$, with males weighing on average 10.58 g ($n = 135$) and females 10.78 g ($n = 124$)), we believe that there is no reason for assuming differences between sexes in terms of habitat choice and therefore have combined the data for the following analyses.

Radiotracking

Radiotracking began the day after capture. Birds were followed between 5 and 12 h a day and located approximately once every hour with at least 1 h between consequent fixes using a Mariner Receiver and a hand-held Yaggi antenna. This method was adopted to make individual observations more independent and to minimize potential disturbance. Birds were located by slowly homing in on the suspected location of the bird while trying not to flush the bird. After the bird had left, the location was determined with a Garmin GPS 12 and the coordinates recorded in UTM format. For each location we recorded the GPS error as indicated by the instrument and estimated an observer error when the bird was seen (comparing the location of visual contact to the location where the bird was thought to be from the radio fix). The average GPS error was 7.8 ± 4.1 m and observer error was about 4.5 ± 6 m. In total we managed to radiotrack 15 individuals (two males and 13 females). One female was caught and tracked during the wet and again during the dry season. Due to a long time span between these two periods and the birds' home range having shifted slightly we treated these periods independently, giving a total sample size of 16 (eight during the wet and eight during the dry season). A total of 582 locations were obtained over a period of 102 days of radiotracking with 36.4 ± 17.4 locations and 5.9 ± 2.8 days per individual ($n = 15$ individuals, but effectively $n = 16$, see above).

Habitat mapping

To create habitat maps we discriminated between four different habitat categories. Inselbergs were characterized by rocky outcrops dominated by boulders with grasses and scrub growing between them. Scrub savannah was characterized by long grasses (mostly > 1 m) interspersed with scrub of several bushes; this habitat mainly occurred within the reserve. Gallery forest consisted of many densely growing trees mostly higher than 2–3 m, growing along natural deep wet gullies (formed by rivers during the wet season). Farmland was much more open land around the reserve with shorter grasses (due to grazing, cutting or burning) and less scrub. Part of this farmland was abandoned and part of it was still being used for growing various crops. Habitat was mapped by walking along the boundaries of inselbergs and gallery forest with a Garmin GPS 12 using its tracking function. Data were then downloaded to a computer to create a digital map using ArcView 3.1 (Environmental Systems Research Institute). Where borders between scrub savannah and farmland were non-linear, they were mapped by using the tracking function. We then completed the map by visually estimating clear linear borders between farmland and scrub savannah from the top of inselbergs and drawing them on top of the habitat map already showing the features mapped with the tracking function. With an average error of 7.8 m, as indicated by the GPS instrument during radiotracking, this map can be treated as fairly accurate.

Nest checks

If a Rock Firefinch nest was found we briefly checked how many eggs or chicks were present and left again as quickly as possible. Nests were then checked again 4–8 days later unless we knew from radiotracking that the bird was still incubating. This infrequent checking of nests was adopted to minimize disturbance and any effects on nest predation. We knew from radiotracking that in most cases when a nest was depredated the bird stopped incubating some days after the first nest check. It therefore seems very unlikely that the checking of nests should have directly caused nest predation. When the nest was abandoned we measured the size of the ball-formed nests (length, height and entrance diameter). If the nests were still completely intact, we recorded the material it was made from and assessed the following habitat parameters: general habitat of nest site (inselberg, scrub savannah or farmland), height above ground, feature the nest was attached to, nearest distance to rocky boulder (where a boulder was defined as at least 0.5 × 0.5 × 0.5 m), nearest distance to bush cover (where a bush was any shrub at least 1 × 1 × 1 m) and nearest distance to grass cover (where grass was at least 0.5 m high).

Analyses of movement

To test for site fidelity we used the site fidelity test option available in the ArcView 3.1 extension Animal

Movement (Hooge & Eichenlaub 2000, Alaska Science Center – Biological Science Office, U.S. Geological Survey, Anchorage, AK, USA).

We calculated home ranges as 100% minimum convex polygon (MCP). Home range size and diameter of home ranges (longest distance within MCPs) were calculated using the software program RangesV (R. Kenward & K. H. Hodder, Institute of Terrestrial Ecology, Wareham, UK). To test for saturation of home ranges we applied the bootstrap sampling technique (using 100 replicates for each fix with a starting sample of five) offered in the module Animal Movement and then fitted a quadratic function to test whether the area of MCPs levelled off during the period a bird was studied. General linear models (GLMs) were applied to test for seasonal differences in home range size and in diameter of home ranges. Number of locations was entered as a covariate and season as a fixed factor. All parameters are given as mean ± sd.

Habitat selection

Habitat selection was tested on a landscape level following the suggestions of White and Garrott (1990). We calculated the proportion of each habitat within home ranges (use) and the proportion of each habitat within a larger area (availability), which we defined as follows. As we could not assume that the whole study area was available to all birds and birds tracked came from four different sampling locations, we had to adopt a more complicated procedure to define habitat availability. We defined available habitat as the area within a circle around the centre of the trapping site just containing the outermost point where a resident bird (caught at that site) had been located. Thus we created four circles around the four trapping locations. Birds were assigned to the circle around the trapping site where they were caught. However, birds three and eight were not included in this because bird no. 3 left the study area after trapping and was found to be resident 2.5 km away from the trapping site 1 week after trapping, and bird no. 8 had an unusually large home range compared to the other birds and did not show significant site fidelity. For bird no. 8 we defined habitat availability separately because it moved over a much larger scale, and we could not assume that the space available to this bird was also available to the others. For bird no. 3 we defined availability as the area within a circle just containing the trapping location and the outermost location of this bird, assuming that the area from the trapping spot to the furthest point the bird flew was available to this bird. Habitat maps were digitized and analysed using ArcView GIS Version 3.1.

We tested for divergence from random habitat use using compositional analyses as described by Aebischer and Robertson (1993), due to potential problems with using dependent proportions in the analysis. Habitats that were not selected were given the value 0.01 as recommended by Aebischer and Robertson (1993) because analysis cannot be calculated from zero values. We calculated the log ratios for all habitat types and then used multivariate GLMs to test whether habitat use differed from random and whether there were seasonal differences in the habitat preference relative to each other. We tested for seasonal differences in the extent to which different habitats were used by dividing the proportion of each habitat used by the proportion available and comparing these values between seasons using a non-parametric Kruskal–Wallis test for several independent samples. All statistical procedures were carried out using the software-package spss 12.

Nest survival

Fourteen nests of Rock Firefinches were found on the Jos Plateau in central Nigeria between September and November 2005 (see Table 3). Four nests were found when adult birds were flushed from the nest and 10 were found via radiotracking of two adult males and six adult females (two females making two breeding attempts). We calculated nest survival rates following Mayfield (Mayfield, in Johnson 1979) with confidence intervals following Johnson (1979). As most nests were completely depredated rather than just some eggs removed, we assumed that once a nest was depredated the whole clutch failed. We therefore used the number of nests rather than the number of eggs as the sample unit. If we did not know when a nest was depredated or when chicks hatched, the midpoint of the period between nest checks and the date of predation or hatching was used as the failure date. In some cases we knew from radiotracking that a bird was incubating up to the point the radio was lost or the bird was no longer tracked. Such days were then counted as nest still active with eggs, and the midpoint of the period following it until the nest was known to be depredated was used as the failure date. Nests that only contained Indigobird chicks but initially had more eggs were also counted as having failed.

Incubation periods

Incubation periods were recorded as any 15-min period during which a bird was known to be present on the nest either from observation or from one or more radio fixes. If only one radio fix was taken, the 15-min period in which this time fell was counted. When we radiotracked an incubating bird on the nest for longer we sat at a distance from the nest enabling us to know when exactly the bird left or entered. Then only those 15-min periods during which a bird was constantly on the nest were counted as incubation periods. To compare the incubation behaviour of males with females, we calculated the proportion that each individual was present during each period and then calculated a mean for the two sexes over these values. Note, however, that sample sizes are not equal for each time period because individual birds were not tracked the same amount of time. Also the sample size for males is based on only two individuals, so these estimates have to be treated carefully. During visual observations, sexes of Rock Firefinches were easily distinguishable by plumage using binoculars.

RESULTS

Trapping

Between 12 February 2004 and 7 December 2005, 149 first caught Rock Firefinches were trapped and ringed at four different trapping sites. Of these, 127 were adult birds, 9 subadults and 13 juveniles. Of the 127 adults, 62 were females and 65 were males, giving a sex ratio of roughly 1 : 1. During the trapping period for this study (19 August 2005–7 December 2005) 23 first caught adult Rock Firefinches and 17 adult Rock Firefinches ringed during previous trapping periods, 3 subadults and 2 juveniles were caught. Of the 41 adult birds caught, 17 were females and 24 were males. We trapped 27 birds at site one, 8 birds at site two and 10 birds at site three. One bird was trapped at site four, which was not regularly used. We recaptured 7 of these 46 birds (15.2%) during this study period with 3–55 days between captures. Only one bird was captured at a different site; all other recaptures occurred at the same site from where they were first caught.

Movement patterns

The site fidelity test in the ArcView Module Animal Movement revealed that movement paths of 15 of 16 birds were significantly more constrained than 100 randomly created paths (all $P < 0.05$), so all these birds apart from no. 12 showed high site fidelity. Home range size, calculated as 100% MCP (minimum convex polygon) area, levelled off at 20–30 locations as shown by a bootstrap sampling procedure. Saturation of MCP home range size was not achieved for five individuals (nos. 3, 7, 8, 13, 14). Because exclusion of these animals would have severely compromised sample size we instead statistically controlled for variation in the number of fixes by including it in the model as a covariate when testing for the influence of season on MCP home range size. Information on radiotracked birds is summarized in Table 1. Home ranges tended

Table 1. Summary of movement patterns of Rock Firefinches radiotracked. Note that birds nos. 1 and 10 are the same bird.

ID	Sex	Trapping site	Period tracked	Season	No of fixes	MCP in ha	Diameter of MCP in m
1	F	1	20/08–09/09	wet	63	3.94	302
2	F	1	21/08–27/08	wet	41	7.28	395
3	F	1	31/08–06/09	wet	39	0.76	142
4	F	2	10/09–16/09	wet	51	2.98	249
5	F	2	12/09–28/09	wet	25	3.67	304
6	F	3	01/10–06/10	wet	40	4.17	294
7	F	3	11/10–12/10	wet	9	1.09	355
8	F	1	12/10–14/10	wet	17	5.03	645
9	M	2	02/11–11/11	dry	69	5.10	633
10 (1)	F	1	09/11–16/11	dry	38	9.07	506
11	F	2	22/11–23/11	dry	20	5.17	438
12	F	2	10/11–21/11	dry	46	16.81	1269
13	F	2	10/11–15/11	dry	25	10.68	875
14	F	3	16/11–17/11	dry	11	5.27	540
15	F	4	29/11–06/12	dry	46	3.91	390
16	M	1	19/10–27/10	dry	42	2.01	243

Table 2. The percentage of each habitat type available to a bird (calculated as the area within a circle around the trapping location containing the outermost point of the MCP home range of the outermost resident bird) and percentage of each habitat type within MCP home ranges of birds.

		% availability				% use (habitat within MCP home range)				% use/% availability			
Bird ID	Season	I	G	S	F	I	G	S	F	I	G	S	F
1	1	32	11	42	15	78	3	20	0	2.41	0.25	0.47	0.00
2	1	32	11	42	15	90	3	7	0	2.78	0.29	0.18	0.00
3	1	11	7	19	63	100	0	0	0	8.94	0.00	0.00	0.00
4	1	24	9	33	34	48	0	52	0	1.99	0.00	1.58	0.00
5	1	24	9	33	34	89	0	11	0	3.66	0.00	0.34	0.00
6	1	43	5	36	15	100	0	0	0	2.31	0.00	0.00	0.00
7	1	43	5	36	15	95	0	5	0	2.19	0.00	0.14	0.00
8	1	32	11	42	15	52	0	43	5	1.62	0.00	1.02	0.35
9	2	24	9	33	34	63	0	36	0	2.60	0.03	1.11	0.00
10	2	32	11	42	15	29	18	54	0	0.89	1.59	1.28	0.00
11	2	61	1	33	5	67	4	29	0	2.77	0.42	0.88	0.00
12	2	20	9	29	42	48	0	18	34	2.36	0.00	0.63	0.81
13	2	24	9	33	34	53	1	46	0	2.19	0.13	1.40	0.00
14	2	43	5	36	15	57	0	43	0	1.31	0.08	1.19	0.00
15	2	19	11	42	28	53	10	37	0	2.85	0.88	0.89	0.00
16	2	32	11	42	15	68	31	1	0	2.10	2.81	0.03	0.00

I = inselberg, G = gallery forest, S = scrub savannah, F = farmland.

to be larger during the dry (7.34 ± 4.78 ha, $n = 8$) than during the wet season (3.56 ± 2.04 ha, $n = 8$; $F_{1,13} = 3.9$, $P = 0.06$; including in the model number of locations $F_{1,13} = 0.1$, $P = 0.67$), and the diameter of these MCP home ranges was significantly longer during the dry (470 ± 278 m, $n = 8$) than during the wet season (329 ± 125 m, $n = 8$; $F_{1,13} = 5.0$, $P < 0.05$; including in the model number of locations $F_{1,13} = 0.03$, $P = 0.87$). When we removed bird no. 12 from this analysis, the differences between the size and diameter of MCP home ranges became weaker but the tendency remained ($F_{1,12} = 2.80$, $P = 0.12$ and $F_{1,12} = 4.15$, $P = 0.06$, respectively).

Birds showed linear movements to water sources in gullies in the gallery forest during the dry season but not during the wet season. Of 58 days of radiotracking during the wet season there was only 1 day when a bird moved to the gallery forest, whereas this occurred on 20 of 43 days during the dry season. When birds flew to the gallery forest they left the inselberg habitat along an almost straight line and very fast, such that we often had difficulties in keeping up with them. They then stayed in the gallery forest for about 30 min until they moved back to the inselberg. These trips usually occurred between late morning and early afternoon when temperatures were highest and birds had probably already foraged for some time.

Habitat selection

Habitat selection was found to be non-random during both seasons at the spatial scale we recorded it (wet: Wilks' Lamda = 0.05, $F_{3,5} = 30.14$, $P < 0.01$; dry: Wilks' Lamda = 0.05, $F_{3,5} = 30.30$, $P < 0.01$; see Table 2 for individual summaries). There was no seasonal difference in habitat selection relative to each other (Wilks' Lamda = 0.69, $F_{3,12} = 1.84$, $P = 0.19$). Habitat ranking was inselberg > scrub savannah > gallery forest > farmland during both seasons. However, as indicated by the following analysis, the extent to which each habitat was used differed between the seasons. Scrub savannah was selected during the dry but not the wet season ($\chi^2 = 5.30$, df = 1, $P < 0.05$; 0.74 ± 1.0 during the dry as opposed to 0.07 ± 0.12 during the wet season). There was a slight tendency for gallery forest to be used to a higher degree during the dry season ($\chi^2 = 2.83$, df = 1, $P = 0.09$; 0.93 ± 0.44 during the dry as opposed to 0.47 ± 0.56 during the wet season). Selection of inselberg habitat, however, did not differ between seasons ($\chi^2 = 0.54$, df = 1, $P = 0.46$; 2.13 ± 0.70 during the dry and 3.24 ± 2.38 during the wet season), and the usage of farmland also did not differ seasonally ($\chi^2 = 0.01$, df = 1, $P = 0.93$; 0.10 ± 0.29 during the dry and 0.04 ± 0.12 during the wet season).

Table 3. Summary of nest parameters of Rock Firefinches.

Nest no.	Date found	No eggs	Discovered by	Habitat	Height above ground	Fate	Note
1	01.09.05	2	Bird flushed	farmland, bush	0.7	predated (reptile?)	
2	10.09.05	5	Radiotracking	inselberg, grass between boulders	0.7	parasitized, 1 ROCFF, 3 IB fledged	
3	15.09.05	5	Bird flushed	inselberg, ground between boulders	0	predated (reptile?)	
4	15.09.05	5	Radiotracking	inselberg, in grass-tufts in gap of rock	5	predated (reptile?)	
5	16.09.05	5	Bird flushed	inselberg, grass between boulders	0.3	predated (rodents?)	
6	04.10.05	2	Bird flushed	garden, bush	0.4	abandoned	
7	05.10.05	3	Radiotracking	inselberg, ground between boulders	0	parasitized, 1 IB fledged	
8	06.10.05	2	Radiotracking	inselberg, in grass tufts in gap of rock	2	predated (reptile?)	
9	11.10.05	4 chicks	Radiotracking	inselberg, in bush between boulders	1.1	4 ROCFF fledged	
10	19.10.05	4	Radiotracking	inselberg, in grass tufts in gap of rock	2.3	4 ROCFF fledged	
11	03.11.05	4	Radiotracking	inselberg, grass between boulders	0.5	3 ROCFF fledged	
12	12.11.05	3	Radiotracking	inselberg, grass between boulders	0.5	abandoned	
13	10.11.05	?	Radiotracking	inselberg, in grass tufts in gap of rock	3	predated?	judged by bird's behaviour, nest not accessible
14	14.11.05	3	Radiotracking	farmland, bush between boulders	1.7	predated (reptile?)	

One bird was caught at site one and located there several times on the day of release but not found again the day after. One week later we located it on a small inselberg where it had an active nest 2.5 km away from the place of capture. Between the reserve and this inselberg lie extensive areas of abundant and used farmland, which this bird must have crossed.

Nests, nest-sites and breeding success

The majority of the 14 Rock Firefinch nests (79%) were located on inselbergs within a bush savannah habitat with many rocks and boulders. Nests were ball-shaped and made from grass, about 9 cm in diameter with an approximately 5-cm-wide round hole as an entrance. They were woven from rough grasses on the outside and finer grasses on the inside. Thirteen nests (93%) also contained feathers as lining. Most nests were hidden in small tufts of grasses near the ground or on rocks in close proximity to big boulders providing shelter. Some were woven into longer grasses above the ground or built in dense bushes. Most were located in close proximity to inselbergs or granite outcrops. Details on nest locations can be found in Table 3.

When found, nests contained two ($n = 2$), three ($n = 3$), four ($n = 3$) or five ($n = 4$) eggs. Seven nests were depredated within 8 days of finding the nest, most probably still during the egg stage. Two nests were abandoned during the egg stage for unknown reasons. In five nests, chicks hatched and probably fledged. Of these, two were parasitized by Indigobirds (probably Jos Plateau Indigobirds). In one nest, only one Indigobird chick hatched despite three eggs initially being present, and in the other nest, three Indigobird chicks and one Rock Firefinch chick hatched and probably fledged despite five eggs being initially present. The Rock Firefinch chick was less developed than the Indigobird chick as apparent from weight and wing growth. In three cases, nests were not depredated or parasitized: in two nests, four Rock Firefinch chicks hatched (one had initially four eggs, the other nest was found when it already contained chicks) and in one nest, three Rock Firefinch chicks hatched and probably fledged (four eggs initially present). This gives a nest predation rate of

50% (seven of 14 nests depredated), a parasitism rate by Indigobirds of 40% (two of five nests parasitized), and 29% of nests produced Rock Firefinch chicks (four of 14 nests).

Nest survival rate was 0.89 ± 0.03 (se) during the egg stage (91.5 days of exposure, four of 14 nests survived) and a survival rate of 1.0 during the chick stage (37.5 days of exposure, four of four nests survived). Assuming 14 days until hatching (which is the time until hatching in the closely related Black-bellied Firefinch with a comparable weight of about 9.7 g (Fry *et al.* 2004) and which also seems to be reasonable for Rock Firefinches judging from our data), this gives a total nest survival rate of 0.20 (0.07–0.49 95% confidence interval). The two birds whose nests failed and which we were able to track long enough to witness a second breeding attempt both did so. It is therefore reasonable to assume that Rock Firefinches are able to at least make a second breeding attempt should the first one fail. Thus 0.20 pairs might successfully raise a brood during a first breeding attempt and a further 0.16 would succeed during a second breeding attempt. The chance of a pair to reproduce successfully would be 0.36 (0.14–0.74 95% confidence interval). With an average of three chicks per successful nest ($n = 4$) this gives an average of 1.08 (0.42–2.22 95% confidence interval) chicks per breeding pair per year. Given an annual survival rate of 0.65 in Rock Firefinches (McGregor *et al.* 2007), and assuming that juvenile survival is the same as adult survival, 0.70 (0.27–1.44 95% confidence interval) birds per pair reach sexual maturity, then approximately 35% of the reproductively active population will be replaced each year based on our productivity and nest survival data. This is about the same as the approximate annual loss of 35% of adult Rock Firefinches due to mortality (McGregor *et al.* 2007).

Incubation behaviour

Males and females were both observed to incubate. We obtained radiotracking data of two males and five females while they had an active nest with eggs and were thus able to gather data on their incubation behaviour. Data suggest that females probably attended the nest during the night until the male took over in the early morning at about 06:30–08:30h, freeing the female to forage. The female then seemed to attend the nest during the late morning at 08:30–11:30h until the male again incubated until the early afternoon. Nest attendance seemed to generally be lower during the afternoon and nests were probably unattended for some time during the afternoon until the female started incubating again during the late afternoon and probably stayed on the nest during the night (Fig. 3). The percentage of times that a male was on the nest in relation to total nest attendance at the different times of the day, differed from an equal distribution ($\chi^2 = 80.8$, df = 23, $P < 0.001$). In four radiotracked individuals, where the nest could be observed relatively easily without disturbance (due to an elevation nearby), we observed several occasions when one sex took over incubation from the other. While one bird sat on the nest, the other one approached the nest calling, until the incubating bird left. The other bird was then seen to enter the nest.

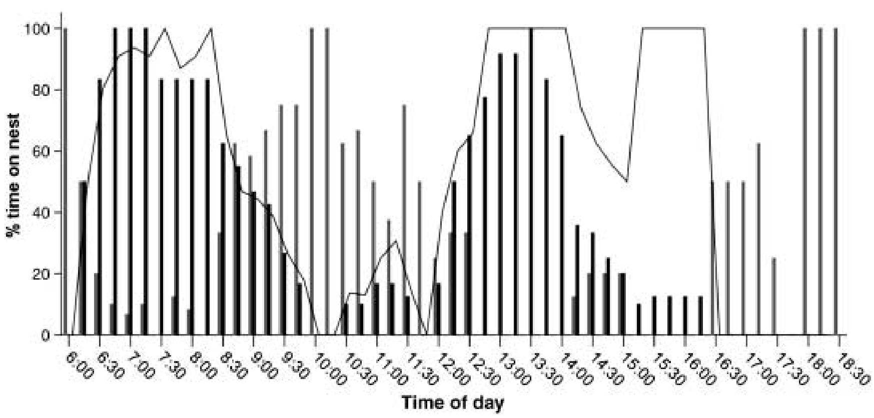

Figure 3. The percentage of 15-min periods that females (light bars) and males (dark bars) spent on the nest incubating in relation to the total number of all 15-min periods radiotracked. Data are pooled over individuals (five females and two males from seven different nests). The line indicates the proportion of each 15-min period that a male incubated in relation to the number of time periods either sex incubated.

DISCUSSION

Site fidelity

Rock Firefinches in this study showed a high degree of site fidelity as evident from radiotracking and from locations of recaptures. The relatively low recapture rate was probably due to birds becoming net shy, as many more individuals were re-sighted (M. Brandt pers. obs.). Only one of the 16 birds tracked left the study area and became resident at a site with similar habitat 2.5 km away. Therefore, Rock Firefinches do not respond to changes in the availability of food and water by moving to different areas like many nomadic birds in desert or in savannah habitats do, where the occurrence of rain and food is less predictable (Davies 1984, Dean 1997). Being a resident and gaining detailed knowledge of a restricted area probably enables animals to locate food resources that are harder to find (Sinclair 1984). Rock Firefinches mainly fed on grass seeds from the ground (M. Brandt pers. obs.), which are probably harder to find but are a resource that is available for longer than seeds on the stem. With a relatively long and slender bill (M. Brandt unpubl. data) Rock Firefinches are well adapted to obtaining seeds buried between sand and vegetation, possibly enabling them to stay in the area throughout the year.

Movement behaviour and habitat choice

Rock Firefinches clearly preferred inselberg habitat, which has also been recorded by Wright and Jones (2005). One reason emerging from this study might be nest-site requirements. Most nests were found within inselberg habitat next to or between boulders, although the birds also used other habitats. Rocky boulders might provide shelter from predators as nests are well hidden from view and serve as shade from sun exposure and high temperatures. However, Rock Firefinches also preferred inselbergs during the non-breeding season, suggesting that they might also be selected for other reasons. Seeds accumulate between rocks and Rock Firefinches seem to prefer feeding between rocks as opposed to the ground of the open savannah (M. Brandt pers. obs.). Higher inter-specific competition in savannah habitat could be a reason for this, but this remains speculative.

During the dry season Rock Firefinches used scrub savannah to a greater extent than during the wet season and this was a consequence of them having to move through these habitats to get to water sources. There was only a tendency for gallery forest to be present within home ranges to a larger extent during the dry season. However, seven of eight birds had gallery forest within their home range during the dry season, while only two of eight birds' home ranges contained gallery forest during the wet season. This was a result of water still being available in the gallery forest when water sources in inselberg and savannah habitat had dried out. Gallery forest grows along deep wet gullies in the reserve, many of them bearing water throughout the year. Only a very small area of gallery forest was contained within home ranges as birds always flew to the same spot to get water, and because of this the seasonal difference was probably only apparent as a tendency. However, it is obvious that linear movements to water sources in the gallery forest only occurred during the dry season and this was the reason for the greater diameter of MCP home ranges during this time. Ideally, we would have tracked the same birds during the dry and the wet season to exclude confounding effects of different bird qualities but unfortunately this was not possible. However, as known from the many re-sightings of colour-ringed birds and some recaptures it is unlikely that there are different individuals in the study area during different seasons and we think that confounding effects of tracking different individuals are minimal. All but one Rock Firefinch tracked during the dry season used gallery forest (the remaining one used a water source in the village) and birds were indeed sometimes observed to fly up from water when we approached them. The straight line the birds flew to the gallery forest, the time of the day when these trips occurred (late morning to early afternoon) and the short time they stayed there, further supports the assumption that these trips served to get water. Gallery forest might therefore be quite important in preserving water for granivorous birds such as the Rock Firefinch, which may depend on fresh water for digestion. Whereas some granivores appear relatively independent of water sources (e.g. the Zebra Finch *Poephila guttata* and the Silverbill Finch *Lonchura malabarcia*), most rely on it, even though metabolic adjustments are likely to exist in most dry habitat species (MacMillen 1990, MacMillen & Baudinette 1993, MacMillen & Hinds 1998). Ward (1978) also noted that Red-billed Quelea *Quelea quelea* had to wet their crop content during the midday heat to aid digestion.

Use of gallery forest as a source of water and possibly shelter, highlights the Rock Firefinch's need not only for inselberg habitat but also for forest habitat.

It probably is important that these two habitats occur in close proximity. Larger home ranges during the dry season were a result of birds having to wander between inselberg and gallery forest habitat. While doing so, they had to cross bush savannah habitat, which was otherwise not extensively used. Besides raising energy expenditure, flying through this more open habitat probably increases predation risk, and this would be even more pronounced if they had to cross more open farmland, which was otherwise avoided. It is also possible that birds inhabiting more isolated inselbergs during the wet seasons (like bird no. 3) cannot do so during the dry season, and Wright and Jones' (2005) finding that Rock Firefinch abundance was high on granite outcrops outside the reserve and therefore away from gallery forest during the wet season, might not hold during the dry season.

Water availability may determine much of the natural history of Rock Firefinches as it might limit time available and timing for breeding. Since Rock Firefinches bred in inselberg habitat, the need to be at the nest-site to provide shade to eggs and chicks during the midday heat may conflict with the need to fly regularly to gallery forest to get water. In addition, provisioning of chicks with fresh water might become increasingly difficult as the dry season continues, temperatures rise and the need for fresh water increases. This might explain why breeding only occurs between the late wet and the very early dry season.

Incubation behaviour

Rock Firefinch parents shared incubation and probably also the feeding of chicks, which has also been reported for the closely related Black-bellied Firefinch (Fry *et al.* 2004). However, only females were observed to develop a visible brood patch (M. Brandt pers. obs.), which might explain why only the female seemed to attend the nest during the night. Cooler overnight temperatures probably require better heat transfer to the eggs and due to the brood patch only the female is able to do this. The sharing of breeding activities might also be necessary for both birds to be able to gain enough food from a resource such as seeds which are usually widely distributed, without the nest being unattended for long periods of time. The sharing of breeding activities might be further favoured by high nest predation in that it enables the female to produce quickly a new clutch should the first one fail. This is because she may need less time to build up enough energy resources necessary for producing eggs than if she had to invest in raising the first brood all by herself, which would inevitably deplete her energy resources to a greater extent. High renesting ability has been shown to be of great importance under high predation (Roper 2005).

Breeding success

We found a relatively high nest predation rate in Rock Firefinches, which supports previously assumed high nest predation rates in tropical birds (Martin 1996, Roper 2005). Roper's (2005) estimate of a nest survival rate of 0.91 per day in the tropical Western Slaty Antshrike *Thamnophilus atrinucha* is close to our estimate of 0.89 per day for Rock Firefinches during the egg stage; however, in the Rock Firefinches causes other than nest predation, such as brood parasitism, also contributed to low breeding output. The average of 35–70% nesting success in north temperate birds (Martin 1996) seems to be well above the 29% of nests succeeding in this study.

From our simple calculations of breeding output it appears that Rock Firefinch populations are stable at present, but this result has to be treated with caution. We assumed Rock Firefinches to start a second breeding attempt should the first one fail, 14 days for incubation, an average of three chicks per clutch and juvenile survival to be the same as adult survival. Slight changes in these assumptions will result in large differences in population trends. We calculated an annual breeding output of 0.36 mature birds per year per pair. Only a few juvenile birds were seen in the field such that this figure does not seem unrealistic. However, we also found a chick survival rate of 1.0, which seems to be overoptimistic and is unfortunately based on a sample size of only four nests. Most likely there can be more than two breeding attempts per year as found in other tropical bird species (Roper 2005), which would increase reproductive output, whereas juvenile survival is likely to be lower than adult survival, which would then lower reproductive output. More data on nest, chick and juvenile survival and number of breeding attempts are needed before firm conclusions about breeding output and population trends can be drawn. In the absence of any other knowledge on Rock Firefinch breeding performance, we believe our data provide valuable information despite being based on a low sample size and several assumptions.

Further work will be constrained by the difficulty in finding nests. Despite extensive searches, only four nests were found by flushing birds, and the majority were found by radiotracking. There might also be a bias for nests found by flushing birds to be more conspicuous and, indeed, all nests found visually were depredated compared to only 30% of those found by radiotracking. This is another reason why our estimates on nest predation have to be treated carefully. For future studies it should be borne in mind that finding nests by radiotracking may be a more promising technique to yield representative results.

Two nests were found to be parasitized by Indigobirds. In one nest, three Indigobird chicks and one Rock Firefinch chick resulted from the initial five eggs. Indigobirds were further developed than the Rock Firefinch chick and it is likely that Indigobird chicks take less time to develop such that they can out-compete Rock Firefinch chicks. This strategy seems sensible given that the parasites' egg might be added some time after the host eggs have been laid and this is well documented in other Indigobird species (Davies 2000). More knowledge on Rock Firefinch breeding success will also provide information on those of its parasite, which might even be of more conservation concern due to its undoubtedly smaller population size and dependence on Rock Firefinches as a host.

Conclusions

Although Rock Firefinches used inselberg habitat for breeding, where almost all nests were located between boulders, they additionally utilized wet gullies within gallery forest when water sources elsewhere had dried out. Close proximity of these water sources to inselberg habitat might be necessary for Rock Firefinches to inhabit inselbergs during the dry season. The necessity to fly long distances to water sources and a greater water demand during the dry season might further limit time available for breeding. Our estimates of nest survival rates suggest that nest predation plays a major role in determining life history traits of Rock Firefinches and might be one factor promoting the sharing of breeding activities. The protection of inselberg habitat and nearby habitats providing water and possibly shade during the dry season like gallery forest might be essential for the long-term survival of the Rock Firefinches and therefore also of the Jos Plateau Indigobirds.

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