Breeding Ecology of the Black Redstart Phoenicurus ochruros at a Tibetan Site, with Special Reference to Cooperative Breeding

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Breeding ecology of the Black Redstart *Phoenicurus ochruros* at a Tibetan site, with special reference to cooperative breeding

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This paper provides data on the breeding biology and social system of the Black Redstart *Phoenicurus ochruros* at a Tibetan site (4300 m elevation). Egg-laying occurred between early May and early July during which pairs bred once (10 out of 12 marked pairs) or twice (2). Clutch size varied between 4 and 5 eggs (4.56 ± 0.51 SE), but a seven-egg clutch was recorded. Incubation by the female lasted 12–14 d (13.0 ± 1.0 SE). Nestlings were provisioned by both parents for 13–18 d (16.7 ± 1.6 SE). Nestlings fledged when they were slightly heavier than adult females. Compared to their European counterparts, the high-elevation redstarts had similar clutch size, incubation or nestling periods and tended to produce fewer clutches of larger eggs. This suggests a life history strategy adapted to maximize offspring survival in the harsh highland environments. Most nests were attended by one male and one female, while at several nests the pair was accompanied by a third individual in female-like plumage. One of these helpers was molecularly sexed as a male and its plumage pattern indicated it to be a yearling. Such cooperative groups occurred in two of the 12 closely monitored nests and two additional nests based on opportunistic observations. One of the four trios was confirmed to raise two broods during a single breeding season and another produced the seven-egg clutch. This is the first confirmation of cooperatively breeding among the 11 *Phoenicurus* species.

Key words: cooperative breeding, elevational gradient, life history, nesting parameter, *Phoenicurus ochruros*

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Elevations can generate environmental gradients along which abiotic (ambient temperature, seasonality and oxygen availability) and biotic conditions (predator and food supply) become harsher and less predictable (Potapov 2004). For avian species that occur across different elevations, life-history patterns are expected to vary in response to local selective pressures. Relative to their lowland counterparts, birds nesting at high elevations have shorter breeding seasons, produce fewer broods, smaller clutches of larger eggs, invest more in parental care and enjoy higher annual survival rates (Badyaev 1997, Badyaev & Ghalambor 2001, Lu 2005, Bears *et al.* 2009). However, our knowledge about the evolution of avian life history along elevational gradients is limited compared with the knowledge about latitudinal variation (Lack 1968).

The Black Redstart *Phoenicurus ochruros* is an insectivorous passerine breeding in Europe, Asia and Africa. Originally the species was restricted to rocky mountainous areas where they nested in natural hollows. However, they have successfully colonized human settlements, both rural and urban, where they use building crevices as nest sites (Glutz & Bauer 1988, Cramp 1988). This species now has a wide elevational distribution, ranging from near sea level up to 5000 m in the Tibetan plateau (Zheng *et al.* 1983), being one of the largest elevational distributions of any passerine.

Breeding ecology and social behaviour of the Black Redstart is well-described in Europe (Cramp 1988, Weggler 2000, 2001, 2006, Sedlacek *et al.* 2004, 2007, Draganoiu *et al.* 2005, 2006, Dolenec 2006, Sedlacek & Fuchs 2008, Schwarzová *et al.* 2010), but has rarely

been studied in Asia (Zhang 1982, Mu *et al.* 2008). Here we present such data collected in a Tibetan settlement at 4300 m elevation, where the birds are summer visitors. We compare the data from this high-elevation site with literature data from lower elevations, aiming to identify possible adaptations of life history and social system of this species.

Methods

Our field work was conducted in Dangxiong (30°28'N, 91°05'E; 4300 m elevation), northern Tibet, during the breeding seasons of 2004–2007 and 2010. The study area is a human settlement of about 100 ha surrounded by alpine meadows. Based on the records of a local weather station over the period 1980–2009, the area has an annual average temperature of 1.7°C, mean summer (June–August) temperature of 10.6°C and mean winter (December–February) temperature of –7.4°C. Annual precipitation averages 441 mm, 72% of which falls during summer. Further details of the study area are available elsewhere (Ke & Lu 2009).

The Black Redstart is the only *Phoenicurus* species breeding in the study area. There are approximately 20 redstart territories per year in our study plot of 100 ha. We searched for their nests mainly using behavioural cues. Nests were visited at least once every 5 days to record clutch size, egg size, hatching success, nestling growth and fledging success. For those nests that were estimated to approach hatching or fledging dates, we increased the frequency of nest inspection to once every 1 or 2 days to determine when these events occurred. At 12 nests, at least one of the two parents was captured near their nests using a mist net. Captured individuals were weighed and measured for body dimensions, and marked with 1–3 colour plastic rings and one aluminium ring to allow individual identification. From each of them, a blood sample of 10–15 μl was taken via brachial venipuncture and saved in pure ethanol for molecular sexing. Nestlings were marked when they were older than 10 days. Mate guarding, incubation and nestling provisioning were recorded through focal observation at selected nests. Focal observations lasted 25–170 min and were made 20–30 m away from the nests to avoid disturbance to nesting activities.

Yearling male Black Redstarts are indistinguishable in plumage from females in the field. For one nest with three attendants, we obtained blood samples of the two nest attendants with female plumage. We established their sex molecularly using the primer-pairs P2/P8 and 2550F/2718R (Du & Lu 2010). This method was valid because the assigned sex of all other 21 adults was in agreement with that assessed from plumage and behaviour in the field.

In total, 56 redstart nests were located during this study. However, sampling efforts differed among years and nests. Only the nests found before hatching were used to calculate clutch size. First-egg dates were either observed directly, or backdated based on egg weight or nestling weight. The relationships between these parameters and incubation time and nestling age, respectively, were established at other nests. Only nestlings that were regularly weighed (once per day) through the complete nestling period were used for estimating growth parameters (logistic model; Ricklefs 1968). Due to small sample size in each year, we pooled the data from the five breeding seasons. Values are presented as means ± SE.

Results

Redstarts arrived in the study area in early April, and left by early November. More males than females were seen during the initial 10 days since the first arrival record (36 males, 10 females). Among the 26 adults that were metal-ringed in 2006 (11 males and 15 females), one male was recaptured in 2007 (as one of the five individuals captured that year) and another in 2010 (one of the four individuals captured). None of the individuals marked as nestlings (2006, 45; 2007, 8) was rediscovered in the subsequent years.

Most nests (53 of 56) were placed in house crevices, and a few in abandoned burrows of the Tibetan Ground Tit *Parus humilis* or the Sand Martin *Riparia riparia*. Egg-laying occurred between early May and early July, with one peak around late May and another around mid-June (Fig. 1). Clutch start date did not differ between years (ANOVA, $F_{4,50} = 2.09$, $P = 0.10$). Thus, the double peak did not result from very late breeding during one year. This interpretation was supported by the fact that out of the 12 closely monitored parents, two (each female was marked) produced two broods during a single breeding season.

BREEDING PARAMETERS

Clutch size usually varied between 4 and 5 eggs (4.56 ± 0.51, $n = 27$), but one nest contained 7 eggs. Excluding the 7 egg clutch, clutches initiated before 1 June (4.71 ± 0.47, $n = 14$) were slightly larger than those initiated after 1 June (4.38 ± 0.51, $n = 13$; $t_{25} = 1.76$, $P = 0.09$). Eggs were pearl blue. The dimensions of 83 eggs were 20.50 ± 0.78 mm (range 16.69–22.33) in length and 14.49 ± 0.42 mm (range 13.54–15.80) in breadth. Brood size at hatching averaged 4.30 ± 0.80 (range 3–5, $n = 20$) and at fledging 3.75 ± 1.08
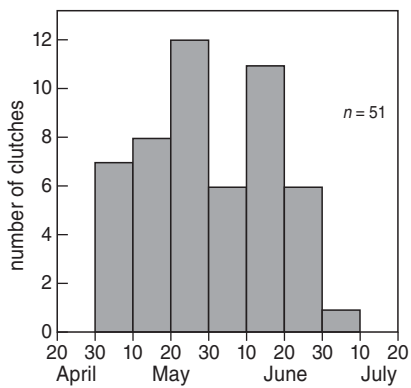
Figure 1. Temporal distribution of the date of laying of the first egg by Black Redstart, southern Tibetan plateau. The time of clutch initiation is arranged in 10-day periods. The data from the five breeding seasons are combined.

(range 2–5, $n = 32$). Out of the 36 known-fate nests, 32 (89%) fledged at least one nestling.

Only the female built the nest. Incubation was undertaken solely by the female for 12–14 d (3.0 ± 1.0, $n = 3$). Observations at one nest showed that the female spent 48.8% of her daily time (total observation time 678 min) attending the nest , with on-nest bouts lasting 15.8 ± 7.3 min (range 7–32, $n = 21$) and off-nest bouts 9.0 ± 4.6 (range 2–22, $n = 26$). Nestlings were provisioned by both parents for 13–18 d (16.7 ± 1.6, $n = 12$ nestlings from four nests, day 0 = hatching date). Provisioning rates (observations of 279 min at four pairs) did not differ statistically between the male (25.4 ± 18.9 trips/h) and the female parent (18.5 ± 6.9 trips/h; Wilcoxon test, $z = 0.73$, $P = 0.47$). Growth rate constants of the logistic model for the 8 nestlings from 3 broods averaged 0.44 ± 0.04 g/day (range 0.38–0.50). Shortly before fledging, nestlings weighed 18.2 ± 1.1 g (range 15.3–21.2, $n = 62$), corresponding to 104% of the adult females (17.5 ± 0.4 g, range 14.6–21.6, $n = 19$).

BREEDING SYSTEM
Of the 12 closely monitored breeding units where at least one adult was marked, ten bred as pairs, and two had three attendants. The latter two consisted of one breeding male, one breeding female and one individual with female-like plumage. We captured the breeding female and the female-like attendant from one of the cooperative groups. We found that only the former had a brood patch and was responsible for incubation (twice we observed the female entering the nest cavity and remaining there during the incubation period). The other bird was determined to be a male using molecu-

lar sexing. All three individuals in each cooperative group delivered food to the nestlings. In two other nests where we failed to mark any attendants, we observed trios consisting of the pair members and one additional nest attendant with female-like plumage, which all carried food to the nest. We confirmed that one of the two cooperative groups in which one adult male and one adult female were marked produced two broods during a single breeding season. The first nest contained 5 eggs and fledged 5 nestlings on 22 June; the second nest had 5 eggs hatched on 7 July but the nestlings died at day 5. Nests of the three other cooperative groups were located on 8 June (with 5 nestlings), 6 July (7 eggs) and 17 July (3 newly hatched nestlings and 1 egg), respectively. Brood size at fledging was 4.33 ± 0.37 (range 3–5) for three cooperative nests.

Discussion
Birds breeding at high elevations have evolved life histories that favour relatively few offspring of high quality in response to the harsh, unpredictable environments (Bears *et al.* 2009). The prediction is supported by comparisons of breeding parameters of birds nesting on the Tibetan plateau with their lowland conspecifics or congeners (Lu 2005, 2006, 2008, 2011, Lu *et al.* 2008, 2009, 2010a, b). Here we compare breeding parameters of two Black Redstart populations on the Tibetan plateau with those reported for their European counterparts at lower elevation (Table 1). We find that the Tibetan redstarts are similar to the European ones in clutch size and length of incubation and nestling periods. However, the higher-elevation redstarts raise fewer broods per season, and lay larger eggs than lower-elevation ones, in particular when taking body size (measured with wing length) into account. The large eggs observed on the northeastern Tibetan plateau may be attributed to potentially higher food availability due to more annual precipitation (782 mm) compared with the drier southern Tibetan plateau (441 mm). The number of annual nesting attempts of birds is mainly limited by the length of the season available for reproduction (Lack 1968). Therefore, given a lower annual reproductive output, higher-elevation redstarts should put more energy into individual offspring to increase their chances of survival. Such a life history strategy is adopted by many organisms breeding in stressful environments (Roff 2002).

An interesting finding of this study was that some redstart nests (16.7%) were cooperatively cared for by both parents and one helper. The helpers were all in female-like plumage, but one individual that was molecularly sexed proved to be a male. Unfortunately, the

Table 1. Breeding parameters of Black Redstart in different regions.

	S Tibetan plateau	NE Tibetan plateau	W Europe
Latitude (°N)	30.9	34.1	50
Altitude (m)	4300	3470	<500
Female wing length (mm)	83.4 (78–90)		85.4 (83–90)
Breeding season	Early May – early July	Early May – mid-July	Early April – late July
Duration of breeding season (d)	67	75	110
No. of clutches	1–2	1–2	2–3
Clutch size	4.6 (4–5)	4.8 (3–6)	4–6
No. of eggs/female/season[a]	5–9	5–10	10–15
Fresh egg mass (g)	2.34	2.51	2.16
Egg volume (cm^3)[b]	2195	2659	2052
Incubation period (d)	13 (12–14)	13–14	13–17
Nestling period (d)	16.7 (13–18)	16.9 (15–18)	12–19
Reproductive success[c]	89%	83%	
Reference	This study	Mu *et al.* 2008	Cramp 1988

[a]Average clutch size multiplied by the minimum and maximum numbers of clutches/female/season.
[b]Calculated as Egg volume = $0.51 \times$ length $\times$ breadth^2 (Hoyt 1979).
[c]Percentage of nests from which at least one young fledged.

relatedness of the helpers with the helped breeders remained unknown. Three of the four cooperative nests we observed had a normal brood size. The seven eggs present in a single nest cared for by a cooperative group (an uncommon clutch size for the study population) had probably been laid by more than one female through intraspecific brood parasitism.

Cooperative breeding has been found in a few hundred bird species world-wide (Ligon & Burt 2004). However, the behaviour is unevenly distributed across taxa, with species of cooperative lineages usually being poor migrants and inhabiting tropical and subtropical regions (Cockburn 2003). However, a few cooperative species in the Tibetan plateau have recently been reported (Lu 2004, Lu *et al.* 2007, Du & Lu 2009, Johannessen *et al.* 2011). None of the 11 members of the genus *Phoenicurus* has been listed as cooperative breeders (Ligon & Burt 2004), although some of them have been extensively studied. Trios associated with the same nest have occasionally been recorded in two European Black Redstart populations out of at least 15 populations studied (Cramp 1988). Our results indicated that cooperative breeding occurred at a relatively high frequency on the Tibetan population. The presence of helpers may improve reproductive success of the nest by preventing brood reduction (Hatchwell 1999). For the Tibetan Black Redstart population, it appeared that more nestlings on average fledged from group-fed nests (4.3 fledglings per nest) than from pair-fed ones (3.6 fledglings per nest). Moreover, parents with helpers may benefit from workload lightening so that they are able to produce more broods during a single breeding season (Brown *et al.* 1978; Russell & Rowley 1988). This seems to be applicable to our study species where the double-brooded case occurred in a cooperative group. We acknowledge that conclusions about social system of the birds based on the current results should be viewed with caution because of limited field samples.

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Samenvatting

Broeden in het hooggebergte vergt andere aanpassingen dan broeden in het laagland. De Zwarte Roodstaart *Phoenicurus ochruros* broedt van zeeniveau in Nederland tot op 5000 meter hoogte in Tibet. Het is daarmee een ideale soort om aanpassingen aan het leven langs een hoogtegradiënt te bestuderen. In dit onderzoek maten de onderzoekers verschillende broedbiologische parameters in een populatie op de Tibetaanse hoogvlakte. De Tibetaanse Zwarte Roodstaarten legden minder broedsels per seizoen en grotere eieren dan hun Europese soortgenoten. Ook werden er enkele gevallen van coöperatief broeden en een mogelijk geval van broedparasitisme vastgesteld. Dit is het eerste bevestigde geval van coöperatief broeden onder de 11 soorten van het slacht *Phoenicurus*. Broedparasitisme treedt uiterst zeldzaam op in Europese Zwarte Roodstaarten. Het lijkt erop dat Tibetaanse Zwarte Roodstaarten inzetten op minder jongen, maar meer investeren per jong dan hun soortgenoten dichter bij zeeniveau. (KK)