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# Breeding ecology of the Twite *Carduelis flavirostris* in northern Tibet

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The breeding ecology of the Twite was studied during 2004–2007 in a meadow environment at 4,300 m elevation, in northern Tibet. Twite laid eggs between late May and mid-August in response to ripeness of seed food. Nests were located in firewood stacks, trees and marshes, with average inter-nest distances less than 15 m. Pairs formed monogamously and males used both proximity and frequent copulations to guard their paternity. Clutch size averaged 4.2 (± 0.7 SD; 3–7), seasonally increasing or remaining unchanged according to year. Incubation by the female only lasted 12.2 days (± 1.2 SD; 10–15) and provisioning of chicks in the nest was continued by both parents for 14.7 days (± 1.1 SD; 13–17). Males performed courtship feeding when their mates were engaged in egg-laying, incubating and brooding. Breeding success, measured as the percentage of nesting attempts from which at least one nestling fledged, was 64%. Compared to their lowland counterparts, Tibetan Twite produced smaller clutches and larger eggs, suggesting a life history strategy to cope with the harsh high-elevation environment.

## 1. Introduction

The Twite (*Carduelis flavirostris*) is a passerine that weighs on average ca. 16g. It is found in two separate areas, namely northwestern Europe and southwestern Asia (Newton 1972). Phylogeographically, the European Twite, despite isolation from the Asian race by 2,500 km, is considered the only European bird species derived from the Tibetan fauna (Cramp & Perrins 1994). Surveys in the UK have shown that the Twite has experienced a serious population decline during recent decades (Langston *et al*. 2006, Raine *et al*. 2009), and consequently it is listed as a Red Data species (Brown & Grice 2005).

Breeding ecology of the European Twite has been well studied (Nuttall 1972, Marler & Mundinger 1975, Stillman & Brown 1994, Brown *et al*. 1995, Raine 2006, Wilkinson & Wilson 2010). In contrast, information on the breeding ecology for its Asian counterpart is sparse, except for occasional descriptive works (Zhang 1982, Zhao *et al*. 2003).

Here, we describe the breeding ecology of Twite inhabiting meadow habitats at 4,300 m elevation in northern Tibet, a region that represents the elevational extreme of the species' range. Our objectives are to provide baseline data on Twite breeding ecology and examine the covariation between the species' life history and elevation.

## 2. Material and methods

We carried out the field work at Dangxiong, northern Tibet (30°28 N, 91°05 E, 4,300 m a.s.l.) during

the 2004–2007 breeding seasons. The study area is an open and flat landscape with annual mean temperature of 1.7°C (minimum –9.3°C in January and maximum 10.9°C in July) and annual total precipitation of 441 mm, 78% of which falls between May and August (from the records of a weather station situated in the area during 1980–2009). The area accumulates almost no snow cover as a result of low winter precipitation and extensive solar radiation (2,911 hours per year).

The study area comprises a mosaic of steppes, meadows and villages, which account for 60%, 25% and 15% of the landscape, respectively. The wasteland soils are very dry and support sparse vegetation (grass cover <10%, height <15 cm) due to desertification, thereby providing no nesting habitat for Twite. In contrast, the meadows are well vegetated (grass cover >70%, grass height >15 cm), from which a few Twite nests were located. Villages are surrounded by meadows. Data for this study were collected mainly from around the human settlements where firewood stacks next to the walls of courtyards and roadside trees provide the Twite with suitable nesting locations.

Twite nests were sought by inspecting potential nesting sites or by following nest-related behavior of the birds. Each located nest was labelled and the nesting stage was described. Eggs were marked individually with colored waterproof felt-tipped pens, and nestlings were individually marked by clipping specific tufts of down before day 8–10 and thereafter with colored leg rings. Nest dimensions and contents were also recorded. Subsequent nest visits were made at least every 5 days to repeatedly estimate the contents and to monitor nest fate.

For those nests that were estimated to approach hatching or fledging dates, the frequency of nest inspection was increased to every 1 or 2 days to determine when these events occurred. Breeding behavior, including nest building, egg laying, incubation, mate guarding, copulation, courtship feeding (a male feed his mate), brooding and provisioning, were recorded through observations for selected nests during different breeding stages. Although the birds were not shy and allowed observers to approach within a few meters of the nests, the observations were made at a distance of 20–30 m from the nests to diminish the likelihood for disturbance of nesting activities. The measures of behavior were averaged over all observation bouts, and nest was used as the analysis unit.

In total, 208 Twite nests were located during this study. However, sampling efforts differed among years and individual nests. Investigations were systematically conducted from April through September in 2004 and 2007, but were restricted to the late breeding season (August and September) in 2005 and 2006. Therefore, only the data covering the entire breeding season were used to assess seasonal patterns of egg laying and clutch size. Not all the nests located were regularly revisited so that sample size may differ for different breeding parameters. Only the nests found before hatching were used to establish clutch size. For nests that were located during the incubating or nestling periods, the dates of clutch initiation were determined by backdating from the means of nesting parameters established based on closely monitored nests. All statistical values are given as mean ± SD.

## 3. Results

### 3.1. Social organization and social behavior

Twite were present in the study area year round. Outside the breeding period, they occurred in flocks of several to hundreds of individuals, sometimes mixing with other passerine species, such as Snowfinches (*Montifringilla* spp.). The Twite flocks were also observed to move into alpine habitats around the study area in autumn and stayed there for about 20 days, suggesting non-breeding flexibility of habitat use by Twite populations. Of 187 color-banded, nearly-fledged nestlings, none was located during the subsequent breeding season.

The earliest pair formations were observed in late May. The mating system seemed to be socially monogamous. Before hatching, males spent most of their time mate-guarding, following female-initiated flights, staying close to her and chasing off any conspecific males that approached her. Territoriality was lacking, as in most cases the birds did not chase off conspecific or heterospecific individuals that approached their nest.

Copulations were noted during the nest-building and egg-laying periods only. On average 2.7

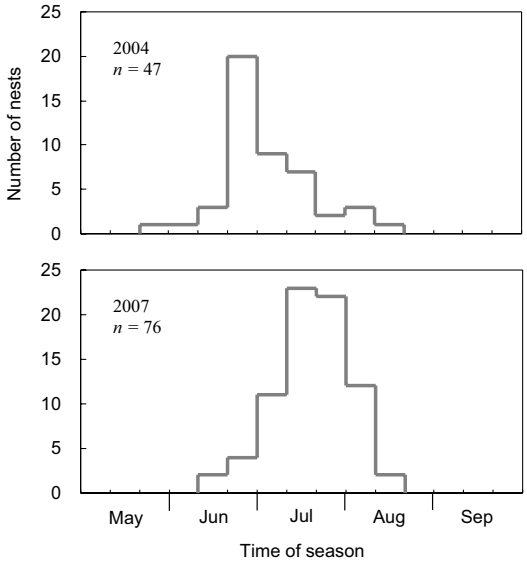


Fig. 1. Distribution of Twite clutches according to the laying date of first egg in 10-day intervals.

copulation events (± 3.0; 0–11.7) were seen per hour during focal observations on 15 nests (78.5 ± 30.5 min for each; 37–135). Fourty-one of the observed 48 copulations (85%) occurred immediately after females had finished lining the nest or egg-laying, and were perching nearby, and copulations took place more often in the morning than in the afternoon (3.6 ± 3.4 per h, 1.0–11.7, $n$ = 9 and 1.5 ± 1.8 per h, 0–5.0, $n$ = 6, respectively; $t$ test, $t$ = 1.36, df = 13, $p$ = 0.20). Copulating attempts were initiated by males in 46 out of 50 cases (92%) or were occasionally rejected by females (4%), but sometimes females solicited through approaching the male with tail erected and wings dangling (8%).

### 3.2. Nest building and nest-site selection

Only females constructed the nest, followed by their mates during each trip of carrying materials. Observations on eight nests (72 ± 35 min for each; 30–135) showed that hourly trip rates averaged 15 (± 12; 2–40). The nest-building period, from the day on which a few materials were present in a nest site to the day after which no regular material ransporting activities were observed and soft materials inside the nest had well been lined, lasted 3–7 days (5.6 ± 1.7; $n$ = 5).

The nests were bulky, consisting of twigs, and occasionally human-made fibers outside, and fur of yaks and sheep inside. Females continued to bring soft material to the nest during incubation and even during the nestling period. The outer diameter of 14 nests was 92.5 ± 18.8 mm (51.4–115.0), the inside diameter was 62.1 ± 8.3 mm (50.0–80.0), and the depth of the nest cup was 41.8 ± 6.6 mm (34.0–55.0). The dry mass of 29 nests averaged 33.3 ± 22.0 g (10–96), with animal fur accounting for 31.9% (± 11.0, 24.2–47.6).

Twite nested in a variety of locations, including firewood stacks (67% of 208), small conifers (20%) and tall trees (8%) in human settlements, and on the ground (5%) in marshes. As a result, the heights above ground of the nests varied between 0 and 3 m. In continuous nesting habitats, the mean nearest neighbour distance between two nests was 12.6 m (± 9.6, 2–45; $n$ = 49).

### 3.3. Egg laying and breeding season

The time interval between the completion of nest building and the date for the first laid egg was 0–4 days (1.6 ± 1.5; $n$ = 7). One egg was laid daily, in early morning (07:00–08:30), and in this process the time between the female's arrival to and departure from the nest took 21.2 min (± 4.1, 16–27; $n$ = 5 eggs in four different nests). While a female was sitting in the nest to lay the egg, she received food from her mate once ($n$ = 2 nests) or twice ($n$ = 1 nest).

The earliest laying dates differed annually, advanced by May–June rainfall (2004: 23 May and 229 mm; 2005: 3 June and 122 mm; 2006: 16 June and 94 mm; 2007: 27 June and 30 mm). The latest clutch initiation was observed on 17 August in 2007. Clutch-initiation dates exhibited a single peak in late June for 2004 and in mid-July for 2007 (Fig. 1).

### 3.4. Egg and clutch size

The observed Twite eggs were white, marked with brown spots. Fresh eggs weighed 1.6 g (± 0.1, 1.2–2.2; $n$ = 124 eggs from 41 nests), and their average length was 1.8 cm (± 0.1, 1.6–2.1; $n$ = 365 eggs from 116 nests) and average width was 1.3 cm

(± 0.04, 1.2–1.5). Fresh egg mass did not depend on laying order (one-way ANOVA; $F_{4,118} = 0.17$, $p = 0.95$).

The average clutch size was 4.2 (± 0.7, 3–7, $n$ = 170) and did not significantly differ between 2004 and 2007 (4.2 ± 0.6, $n$ = 43 and 4.2 ± 0.8, $n$ = 64, respectively). A seasonal increase in clutch size was observed in 2004 but not in 2007 (Pearson correlation; $r = 0.52$, $n = 43$, $p < 0.001$ and $r = 0.10$, $n = 64$, $p = 0.42$, respectively).

### 3.5. Incubation and care of young

Incubation by females only began with laying of the last egg in 96% of the cases (54 out of 56 closely monitored nests), or in a few cases with the second egg (4%). The incubation period, defined as the time elapsed from the last egg laid to the first egg hatched, was 12.2 days (± 1.2, 10–15; $n = 26$).

During incubation, females received food from their mates at a rate of 0.7 trips/h (± 0.6, 0–2.1; observations on 22 nests, 84 ± 54 min for each; 40–311). Females also left the nest to feed themselves, which occurred 1.1 times/h (± 1.0, 0–3.2; $n = 22$). Nest attendance averaged 82% (± 25, 16–100; $n = 22$).

Both parents provisioned the nestlings, and females brooded the nest in the early nestling period. While females were brooding, males fed them. Data for 18 broods with nestlings older than 5 days (duration of a single observation period 82 ± 23 min; 57–149) showed that both sexes visited the nest at similar rates (female: 1.3 ± 0.8 per h; male: 1.5 ± 0.8 per h; $t = 0.61$, df = 17, $p = 0.55$). Direct observations and detection of nestling crops revealed that diets of the birds consisted of Poacea grass seeds.

Hatching was finished within 24 hours in 19 of 22 broods, but was 2–3 days in 3 of 22 broods. Nestlings on the day of hatching weighed 0.6–2.0 g (1.4 ± 0.3; $n = 46$). Nestlings fledged at 14.7 days (± 1.1, 13–17; $n$ = 20). At that moment they weighed 13.7 g (± 0.2, 13.4–13.8, $n$ = 4), which was 87% of the average body weight of a female (15.7 ± 1.4 g, 14.1–17.5; $n$ = 12). The logistic growth equation for body weight was $w = 13.51/(1+e^{2.377-0.389t})$.

### 3.6. Reproductive success

Brood size at hatching averaged 3.5 (± 0.9, 1–5, $n$ = 100), with a marginally significantly higher value in 2004 than in 2007 (3.6 ± 0.9, $n$ = 25 and 3.2 ± 0.9, $n$ = 33, respectively; $t = 1.84$, df = 56, $p = 0.07$). Brood size at fledging was 2.9 (± 0.9, 1–5, $n$ = 76), with no difference between 2004 and 2007 (3.1 ± 1.1, $n$ = 18 and 2.9 ± 0.8, $n$ = 34, respectively; $t = 0.54$, df = 50, $p = 0.59$). Of 118 nests for which the outcome was known, 76 (64%) fledged at least one chick, with no annual difference being detected (2004: 69% of 26; 2007: 52% of 65; Chi-square test, $\chi^2 = 2.17$, df = 1, $p = 0.14$). The total nest survival probability estimated by Mayfield's method (nesting period = 36 days) was 0.34 (2004: 0.43; 2007: 0.24).

Hatching failure occurred in 192 (36.6%) of 525 eggs, due to infertility (9% of the 192 failed eggs), embryo death (14%), breakage (7%), partial egg disappearance (19%) and nest desertion (51%). Sixty-nine (27.6%) out of 250 hatchlings failed to fledge successfully. Death of these nestlings may be attributed to predation (45%, including those in which all nestlings disappeared), brood reduction (some of the nestlings within a brood disappeared, 36%) and desertion (19%). Nestlings that hatched late and had a light body weight were more likely to die (7 of 11 broods).

## 4. Discussion

Twite were present throughout the year in the study area. In autumn, a number of Twite were observed to move up to alpine habitats, coinciding with peaks of plant seed production (Lu *et al.* 2007). However, none of the 187 marked fledglings were relocated in the breeding populations during subsequent years. This may be attributed to high mortality or extensive individual movement among young individuals during the non-breeding periods. In England, Twite migrate to coastal areas in winter, with only small numbers remaining behind on their breeding grounds (Raine *et al*. 2006).

At the present study area, Twite generally did not breed until late May or early June, 3–6 weeks later than other sympatric passerines (Ke & Lu 2009, Lu *et al*. 2009, authors' unpubl. data). Such a delay in breeding time, as observed in many alpine

Table 1. A comparison of the mean values of several reproductive parameters of different Twite populations. Data from Scotland, UK (Cramp & Perrins 1994, Wilkinson & Wilson 2010), South Pennines, UK (Cramp & Perrins 1994, Brown *et al*. 1995, Raine 2006), North Quinghai, China (Zhang 1982), South Tibet (authors' unpubl. data) and North Tibet (present study).

| Parameter | Scotland | South Pennines | North Qinghai | South Tibet | North Tibet |
|---|---|---|---|---|---|
| Latitude (N) | 57.7 | 53.5 | 37.5 | 29.7 | 30.9 |
| Elevation (m) | 0 | <500 | 3,200 | 3,650 | 4,300 |
| Breeding season (Julian date) | 116–212 | 117–207 | 165–230 | 130–? | 155–230 |
| Breeding season length | 96 | 90 | 65 | – | 75 |
| Annual breeding attempts | 2–3 | 1–2 | – | – | – |
| Fresh egg mass (g) | 1.4 | 1.5 | 1.3 | – | 1.6 |
| Egg volume ($mm^3$) | 2,568 | 2,862 | 2,635 | 2,816 | 3,042 |
| Clutch size | 5.2 | 5.5 | 4.5 | 4.0 | 4.2 |
| Brood size at fledging | 4.6 | 4.8 | 2.7 | 2.5 | 1.7 |
| Incubation period (d) | 11.3 | – | 12–15 | – | 12.2 |
| Nestling period (d) | 15.5 | – | 14.0 | – | 14.7 |

seed-eating birds (Potapov 2004), should be a response to the peak ripening of the seeds, which are used as nestling food. The importance of food supply was indicated by the close link between the breeding start date and rainfall level preceding clutch initiation. Moreover, the later onset of clutch initiation by Twite at the present, high-elevation site, compared with other lowland habitats, also suggests the role of food availability in triggering breeding (Table 1).

Nests of Tibetan Twite were located in various habitats and locations, a situation similar to their European counterparts (Cramp & Perrins 1994). Such weak selectivity for nest sites could contribute to the abundance of individuals over most of the species' European and Asian distribution (BirdLife International 2004).

In stressful environments, such as at high elevations, birds tend to have reduced annual reproductive output as a result of producing fewer broods and small clutches, as shown for, e.g., cardueline finches (Badyaev 1997, Badyaev & Ghalambor 2001). Although the realized number of clutches per each Twite pair remained unknown in the present study, the 75-day long breeding season may allow a pair to produce two clutches. Only 12 females had been marked here, and no data on their fate after the first clutch were available. Nevertheless, the observed single peak of nesting phenology suggests that at least not all individuals produce more than one clutch. In contrast, lowland Twite in Europe may raise up to three broods due to the long breeding season (Table 1). As a buffer to harsh conditions, birds may allocate more energy into each offspring in terms of increased egg size along with reduced clutch size, and provide more parental care for their offspring in terms of prolonged incubation and nestling periods (Lu 2005, Lu *et al*. 2008, 2009, 2010a, 2010b). A comparison of breeding parameters for several Twite populations at different elevations suggests a trade-off between clutch size and egg size along elevational gradients, but the life-history shift seems not to occur in the length of incubation and nestling periods (Table 1).

Multi-brooded temperate passerines produce largest clutches in the middle of the breeding season (Perrins 1970), suggesting that selection favors those species that start breeding before the clutch size is largest to maximize seasonal productivity (Crick *et al*. 1993). As a multi-brooded nester, European Twite follows this pattern (Brown *et al*. 1995; Wilkinson & Wilson 2010). However, clutch size of the Tibetan Twite, reported here, tended either to increase seasonally or showed no obvious seasonal variation. A possible explanation is that the food resources of the Tibetan Twite continue to be sufficient as more plant seeds ripen in autumn so that it is unnecessary for late breeders to reduce their production of eggs.

During the presumed fertile period of females (nest building and egg-laying periods), male Twite spent most of their time mate-guarding, and they also frequently copulated with the females. This

behavior suggests that to protect their paternity, male Twite simultaneously adopt both anti-cuckoldry strategies, which are often separately performed by socially monogamous species (Birkhead 1998). As observed in their close relative, the Linnet (*Carduelis cannabina*; Drachmann *et al*. 1997, 2000, Bønløkke-Pedersen *et al*. 2002), the spatial clumping of Twite nests could promote the use of the double paternity protection, because in such cases females are expected to have more chances to find potential extra-pair males (Wagner 1993).

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**Vuorihempon pesimäbiologia Pohjois-Tiibetissä**

Työssä tutkittiin vuorihempon (*Carduelis flavirostris*) pesimäbiologiaa niitty-ympäristössä Pohjois-Tiibetissä 4 300 m korkeudella merenpinnasta vuosina 2004–2007. Muninta tapahtui toukokuun lopun ja elokuun puolivälin välillä samanaikaisesti siemenravinnon kypsymisen kanssa. Pesiä löytyi polttopuupinoista, puista ja kosteikoilta, ja ne olivat usein alle 15 m päässä toisistaan. Parit olivat monogamisia, ja koiraat varmistivat isyyttään oleskelemalla naaraan läheisyydessä ja parittelemalla tämän kanssa usein. Keskimääräinen pesyekoko oli 4,2 (± 0,7 keskihajontayksikköä; vaihtelu 3–7), mikä kesän edistyessä joko nousi tai pysyi samana, vuodesta riippuen. Naaras hautoi vain 12,2 päivää (± 1,2; 10–15), ja molemmat vanhemmat ruokkivat pesäpoikasia 14,7 päivää (± 1,1; 13–17). Koiraat kosioruokkivat naaraita näiden muniessa, hautoessa ja hoitaessa poikasia. Pesimämenestys, mitattuna niillä pesimäyrityksillä, jotka tuottivat vähintään yhden lentopoikasen, oli 64 %. Alavampien alueiden vuorihemppoihin verrattuna Tiibetin yksilöt tuottivat pienempiä pesyeitä ja suurempia munia, mitkä lienevät sopeumia ankaraan vuoristoilmastoon.

## References

Badyaev, A.V. & Ghalambor, C.K. 2001: Evolutional gradients: trade-off between parental care and fecundity. — Ecology 82: 2948–2960.

Badyaev, A.V. 1997: Avian life history variation along altitudinal gradients: An example with cardueline finches. — Oecologia 111: 365–374.

BirdLife International 2004: Birds in Europe: population estimates, trends and conservation status. — BirdLife Conservation Series, no. 12. BirdLife International, Cambridge.

Birkhead, T. 1998: Sperm competition in birds: mechanisms and function. — In Sperm Competition and Sexual Selection (eds. Birkhead, T. &, Møller, A.P.): 579–622. Academic Press, London.

Bønløkke-Pedersen, J., Drachmann, J., Frydenberg, J. & Boomsma, J.J. 2002: Rare extra-pair fertilizations in the semi-colonially breeding linnet *Carduelis cannabina*. — Journal of Avian Biology 33: 203–206.

Brown, A. & Grice, P. 2005: Birds in England. — T. & A.D. Poyser, London.

Brown, A.F., Crick H.Q.P. & Stillman, R.A. 1995: The distribution, numbers and breeding ecology of twite *Acanthis flavirostris* in the south Pennines of England. — Bird Study 42: 107–121.

Cramp, S. & Perrins C.M. 1994: Handbook of the birds of Europe, the Middle East and North Africa birds of the western Palaearctic. Handbook of the Birds of Europe, the Middle East, and North Africa: The Birds of the Western Palearctic, Vol 8. Crows to Finches. — Oxford University Press, Oxford.

Crick, H.Q.P., Gibbons, D.W. & McGrath, R.D. 1993: Seasonal changes in clutch size in British birds. — Journal of Animal Ecology, 62: 263–273.

Drachmann, J., Komdeur, J. and& Boomsma, J. J. 2000: Mate guarding in the linnet *Carduelis cannabina*. — Bird Study 47: 238–241.

Drachmann, J., Komdeur, J. and& Boomsma, J. J. 1997: Copulation behaviour in the linnet *Carduelis cannabina* and the insemination window hypothesis. — Journal of Avian Biology 28: 191–196.

Ke, D.H. & Lu, X. 2009: Burrow use by Tibetan ground tits *Pseudopodoces humilis*: coping with life at high altitudes. — Ibis 151: 321–331.

Langston, R.H.W., Smith,T., Brown, A.F. & Gregory, R.D. 2006: Status of breeding twite *Carduelis flavirostris* in the UK. — Bird Study 53: 55–63.

Lu, X. & Ke, D.H., Zeng, X.H., & Yu, T.L. 2009: Reproductive ecology of two sympatric Tibetan snowfinch species at the edge of their altitudinal range: response to more stressful environments. — Journal of Arid Environments 73: 1103–1108.

Lu, X. 2005: Reproductive ecology of blackbirds (*Turdus merula maximus*) in a high-altitude location, Tibet. Journal of Ornithology 146: 72–78.

Lu, X., Gong, G.H. & Zeng, X.H. 2008: Reproductive eco-

logy of brown-cheeked laughing thrushes (*Garrulax henrici*) in Tibet. — Journal of Field Ornithology 79: 152–158.

Lu, X., Yu, T.L., Liang, W. & Yang, C.C. 2010a: Comparative breeding ecology of two white-bellied redstart populations at different altitudes. — Journal of Field Ornithology 81: 167–175.

Lu, X., Wang, C. & Yu, T.L. 2010b: Nesting ecology of the grey-backed shrike (*Lanius tephronotus*) in South Tibet. — Wilson Journal of Ornithology 122: 395–398.

Lu, X., Zhang, L.Y. & Zeng X.H. 2007: Comparisons of the alpine bird communities across habitats and between autumn and winter in the mid-Yalong Zangbo River valley, Tibet. — Journal of Natural History 41: 2511–2527.

Marler, P. & Mundinger, P.C. 1975: Vocalisations, social organisation and breeding biology of the twite *Acanthus flavirostris*. — Ibis 117: 1–17.

Newton, I. 1972: Finches. — Collins, London.

Nuttall, J. 1972: The status and distribution of the twite (*Carduelis flavirostris*) in east Lancashire, with some notes on breeding biology. — Naturalist 23: 140–141.

Perrins, C.M. 1970: The timing of birds' breeding seasons. — Ibis 112: 242–255.

Potapov, R.L. 2004: Adaptation of birds to life in high mountains in Eurasia. — Acta Zoologica Sinica 50: 970–977.

Raine, A.F. 2006: The breeding ecology of twite *Carduelis flavirostris* and the effects of upland agricultural intensification. — PhD Thesis, University of East Anglia.

Raine, A.F., Brown, A.F., Amano, T. & Sutherland W.J. 2009: Assessing population changes from disparate data sources: the decline of the twite *Carduelis flavirostris* in England. — Bird Conservation International 19: 401–416.

Raine, A.F., Sowter, D.J., Brown, A.F. & Sutherland, W.J. 2006: Migration patterns of two populations of twite *Carduelis flavirostris* in Britain. — Ringing & Migration 23: 45–52.

Stillman, R.A. & Brown, A.F.1994: Population sizes and habitat associations of upland breeding birds in the south Pennines, England. — Biological Conservation 69: 307–314.

Wagner, R.H. 1993: The pursuit of extra-pair copulations by female birds: a new hypothesis of colony formation. — Journal of Theoretical Biology 163: 333 46.

Wilkinson, N.I. & Wilson. J.D. 2010: Breeding ecology of twite *Carduelis flavirostris* in a crofting landscape. — Bird Study 57: 142–155.

Zhang, X.A. 1982: Studies on breeding biology of 10 species of passerine birds in alpine meadow, northern Qinghai. — Acta Zoologica Sinica 28: 190–199. (In Chinese with English summary)

Zhao, L., Liu, Z.H., Zhang, X.A., Yi, X.F.& Li, M.C. 2003: Feeding of nestling in the twite *Carduelis flavirostris* in an alpine meadow, north Qinghai. — Zoological Research 24: 137–139. (In Chinese with English summary)