



Autumn migration of Reed Buntings *Emberiza schoeniclus* in Switzerland

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To elucidate the migration strategies of Reed Buntings *Emberiza schoeniclus* migrating through Central Europe, we analysed data from 595 Reed Buntings ringed at La Touvière, Rhône River, Geneva, Switzerland, during the autumn migration from September to November 2004. These data were used to investigate age, sex, biometrics and body condition in relation to timing of migration. The overall sex ratio and the ratio of first-years to adult birds were 1:1 and 3:1, respectively, but there was a chronological sequence of young females, adult females, young males and adult males during the autumn. The mean bill depth varied during the study period with individuals migrating during October having deeper bills. The greater bill depth of males by comparison with other European studies suggests a more northeasterly origin of these birds, compatible with a leap-frog migration.

The Reed Bunting *Emberiza schoeniclus* has a wide Palearctic distribution (Cramp & Perrins 1994) and is ringed in large numbers in Switzerland. In 2004, 4,243 individuals were ringed, representing 4.3% of the ringing totals (Wiprächtiger *et al* 2005). Most Swiss passage migrants breed in Germany, Poland, Austria and the former Czechoslovakia, with a smaller number originating from Scandinavia. The Swiss winter recoveries show a large concentration in southeast France, particularly in the Camargue, although this may be exaggerated by the large-scale ringing in this region. Other birds ringed on passage or in the breeding season in Switzerland have been recovered in southwest France, Spain, and northern Italy (Prys-Jones 1984). In Switzerland, overwintering Reed Buntings are regular but scarce and occur mostly on the Swiss plateau near Lake Léman (Maumary *et al* in prep). The breeding population in Switzerland is estimated at 3,000–5,000 pairs (Schmid *et al* 1998). Because of the loss of adequate breeding sites, particularly reedbeds, in the canton of Geneva, the Reed Bunting has declined there by 63% between 1977 and 2001 (Lugrin *et al* 2003). In the area alongside the River Rhône used for this present study, Reed Buntings occur only as sporadic breeders; however, during autumn migration large flocks converge at dusk to roost in the reedbeds.

The autumn migratory patterns of the Reed Bunting have been described for Europe (Prys-Jones 1984) and component countries such as France (Oliosio 1987), Germany (Tauchnitz 2000, George 2002), and Spain

(Villarán 1999, Villarán & Pascual-Parra 2003). In contrast, published studies from Switzerland refer only to the spring migration (Pedroli & Gogel 1972, Christen 1984). In this paper, we consider the autumn migration of Reed Buntings from September to November 2004 at a study site in the western tip of Switzerland, situated at a junction between the breeding and the wintering grounds in Europe. We have examined the sex ratio, age ratio, and biometric data in relation to timing of migration. We have tested the hypothesis that females depart earlier than males in order to reach their more southerly wintering grounds, and consider the possibility that some of the birds migrating through Switzerland may belong to northeast European populations.

METHODS

Study area

The study was carried out from September to November 2004 at La Touvière (46°10'N 5°59'E), in the Rhône basin, about 13 km W of Geneva, Switzerland. The site is a 1.4 ha, thin stretch of reedbed along the southern bank of the River Rhône, dominated by *Phragmites australis*. The trapping area covered approximately 0.2 ha (14%) of the reedbed. Mist nets were always placed in the same positions during the study (n = 7 nets; 3 m high, total length 54 m). Trapping was carried out from afternoon till dawn twice a week, giving a total of 16 days. Since few birds were present in November we ringed on only one day per week during this month.

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Biometrics

The routine data recorded were sex, age, capture date, wing length (maximum chord, Svensson 1992) and body mass using a 100 g Pesola balance read to the nearest 0.5 g. We also recorded bill depth (at the limit of feathering on the upper and lower mandibles), width (at base) and length (from tip to skull), with a dial calliper to the nearest 0.1 mm (Svensson 1992). Bill measurements are more reliable for comparisons of populations than wing measurements because the latter vary due to feather abrasion and age-related differences between juveniles and adults (Stewart 1963, Collette 1972). All birds were sexed and aged although some individuals were not measured during very busy periods when large numbers of birds were caught at once. Wing and bill measurements were taken by the same ringer (FS) to ensure consistency in measurements. Reed Buntings were aged using flight-feather abrasion (Svensson 1992, De La Puente & Seoane 2001), moult limits of wing and tail (Jenni & Winkler 1994), and iris coloration (Karlsson *et al* 1985) as criteria.

Statistical analysis

To compare the proportions of different sex and age-classes captured, chi-squared tests with Yates' correction (2x2 contingency tables) were used. Body condition was estimated from the residuals of a regression of body mass on wing length. Biometrics and body condition with respect to date of capture, sex and age-classes were analysed using Analysis of Variance (ANOVA) and Generalised Linear Models (GLM) using the statistical package S-PLUS (MathSoft, Inc). Since Reed Buntings were consistently caught from afternoon until dusk, time of day was not included as a factor in ANOVA and GLM analyses of body mass.

RESULTS

Sex and age ratio and timing of movements

During the study, 595 Reed Buntings were ringed. Two-thirds of this total were captured at dusk and the rest in the afternoon. All birds were sexed and the age was determined for 592 individuals (99.5%) (Table 1). Overall, with 319 females (54%) and 276 males (46%) captured, the sex ratio was not significantly different from 1:1 ($\chi^2_1 = 2.7$; $P > 0.05$). However, sex ($\chi^2_7 = 28.7$; $P < 0.001$) and age ($\chi^2_7 = 45.7$; $P < 0.001$) ratios varied significantly with date of capture. Reed Buntings were first caught in the middle of September, and all were female; females were also more abundant than males during the beginning of the study period (18 September – 8 October). Conversely, the first males were captured

Table 1. Number of Reed Buntings, captured at La Touvière, Switzerland, by sex and age-class.

	Males	Females	Total
First-year birds	197	250	447
Adult birds	78	67	145
Total	275	317	592

$\chi^2_1 = 3.332$; $P = 0.068$

during the start of October, when the number of captures generally increased, and were most abundant at the end of the study period (29 October – 13 November). Capture totals reached a peak during the second half of October (Fig 1) and during this period the sex ratio was not significantly different from 1:1.

With respect to age, first-year birds were most abundant at the beginning and at the end of the study period, and adults were most abundant in the middle (Fig 1). Over the whole of the study period, first-year Reed Buntings ($n = 447$) outnumbered adults ($n = 145$) by 3:1; this age ratio was similar for both sexes (first-year males: $n = 197$ and first-year females: $n = 250$) and significantly different from 1:1 ($\chi^2_1 = 153$; $P < 0.01$).

Wing length, body mass, body condition and bill depth

A summary of biometric data is presented in Table 2. Mean wing lengths differed significantly with respect to sex ($F_{1,544} = 333.51$; $P < 0.001$), age ($F_{1,544} = 15.89$; $P < 0.001$) and date of capture ($F_{7,544} = 15.94$; $P < 0.001$; corrected for sex and age). The mean wing length of adult males was 6.2 mm longer than adult females and 2.0 mm (2.5%) longer than first-year males; similarly, for females the mean wing length of adults was 1.1 mm

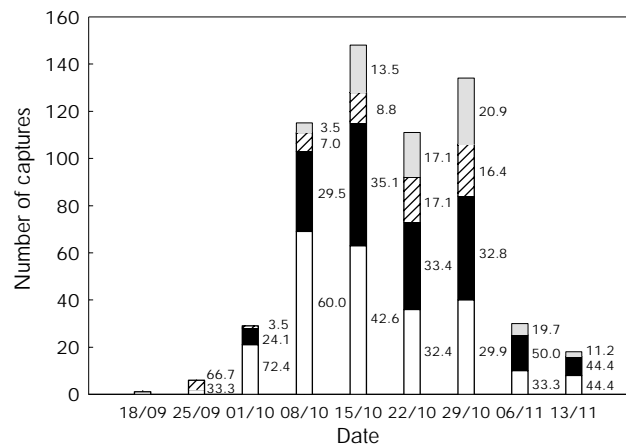


Figure 1. Frequency of captures of adult male (dotted bars), adult female (hatched bars), first-year male (filled bars), and first-year female (open bars) Reed Buntings captured at La Touvière, Switzerland, in relation to date of capture. Percentages adjacent to the bars are shown for each week.

(1.5%) longer than in first-year birds (Fig 2). Body mass also varied with sex ($F_{1,451} = 49.8$; $P < 0.001$) and date of capture ($F_{7,451} = 9.4$; $P < 0.001$; sex corrected), but not with age ($F_{1,451} = 0.009$; non-significant [NS]); males were heavier than females (Fig 3). Maximum mean body mass was recorded in October during the peak of migration, and minimum mean body mass occurred during the start and final stages of autumn migration. Body condition, expressed as the magnitude of the residuals from a linear regression of body mass on wing length, varied significantly with date of capture

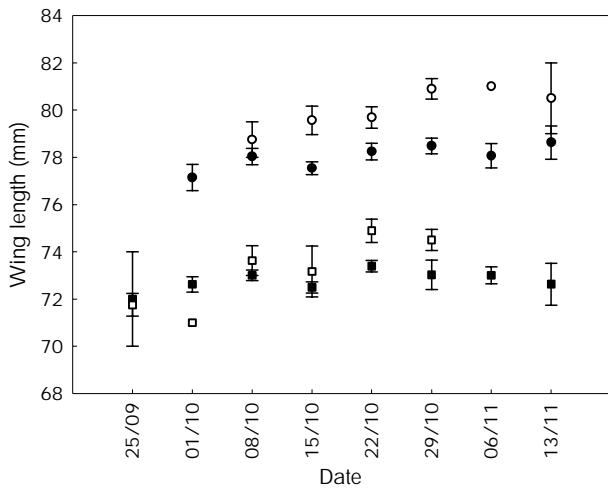


Figure 2. Wing length (mm) of adult male (open circles), first-year male (filled circles), adult female (open squares), and first-year female (filled squares) Reed Buntings captured at La Touvière, Switzerland, in relation to date of capture. Mean and standard error are shown.

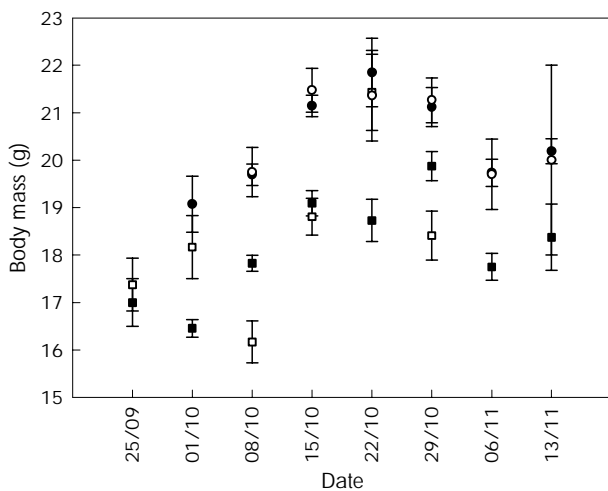


Figure 3. Body mass (g) of adult male (open circles), first-year male (filled circles), adult female (open squares), and first-year female (filled squares) Reed Buntings captured at La Touvière, Switzerland, in relation to date of capture. Mean and standard error are shown.

($F_{1,470} = 3.74$; $P = 0.008$), but not between sexes ($F_{1,470} = 3.04$; NS) or with age ($F_{1,470} = 2.05$; NS; Fig 4).

Bill depth values for the four age and sex categories were normally distributed (Fig 5) and differed significantly between sexes ($F_{1,451} = 13.38$; $P < 0.001$) and with date of capture (Fig 6; $F_{7,451} = 10.83$; $P = 0.002$; sex corrected), but not with age ($F_{1,451} = 2.87$; NS); males had deeper bills than females (Fig 6). Interactions between sex, age, and date of capture on biometric data and body condition were investigated using GLM, and were not significant (all $P > 0.05$), except for the effect of the interaction between sex and age on wing length ($F_{1,544} = 6.56$; $P = 0.01$).

DISCUSSION

During migration, Reed Buntings of the *schoeniclus* subspecies are present at La Touvière between September and November. The timing of autumn migration at this site, in the western part of Switzerland, is consistent with other observations for Switzerland as a whole (Winkler 1999). In spring, adult males depart from their wintering grounds in Spain (Villarán & Pascual-Parra 2003) and arrive in Switzerland earlier than adult females (Pedroli & Gogel 1972, Christen 1984), followed by young birds (Christen 1984). A similar sequence is observed during the prenuptial migration along the North Sea coast in Belgium (Collette 1972). Although the autumn migration data from La Touvière reported here refer to one year only, the chronological sequence was the opposite to that during spring migration in Europe, with females migrating through the site approximately two weeks before males and a

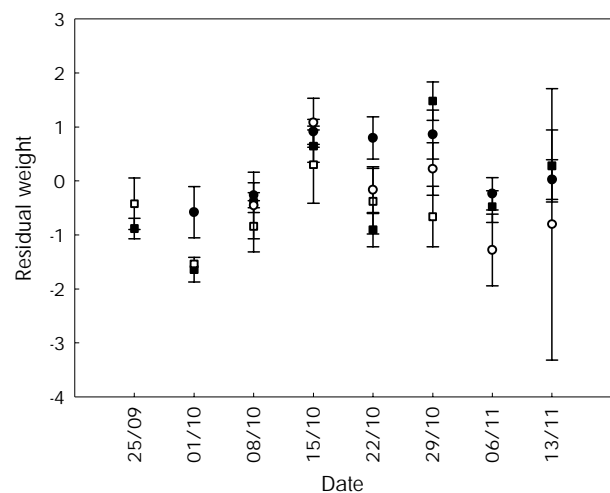


Figure 4. Body condition of adult male (open circles), first-year male (filled circles), adult female (open squares), and first-year female (filled squares) Reed Buntings captured at La Touvière, Switzerland. Mean and standard error are shown.

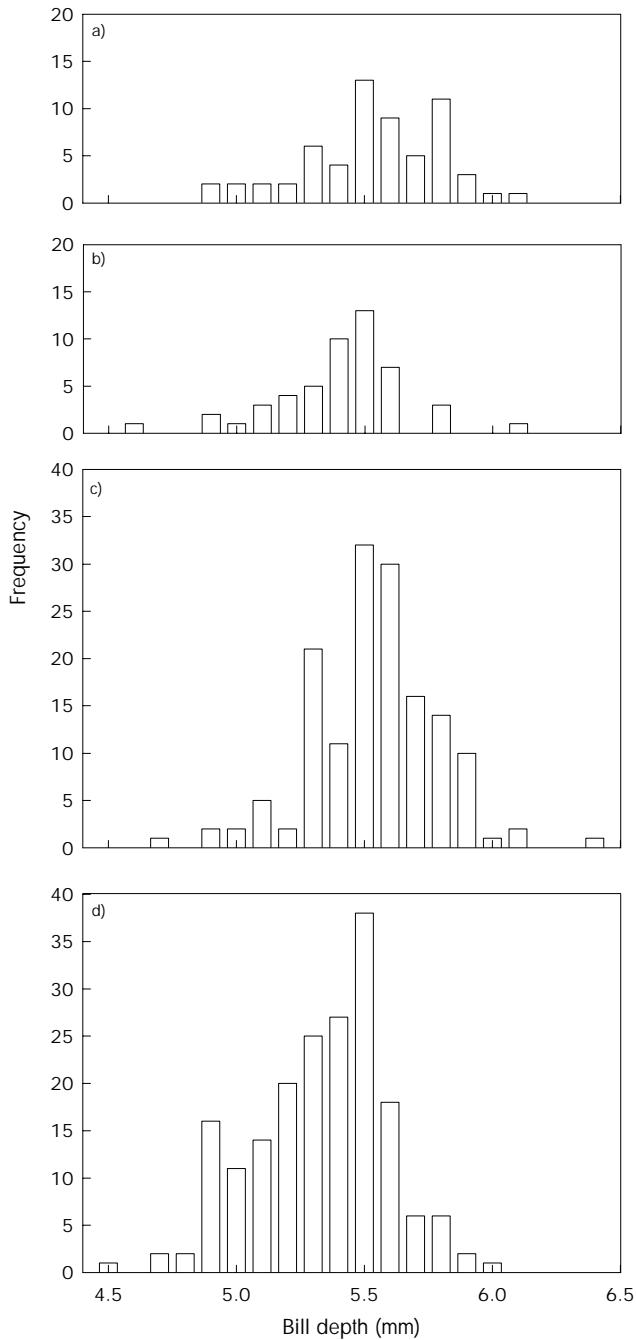


Figure 5. Frequency of bill depth (mm) of (a) adult male, (b) adult female, (c) first-year male, and (d) first-year female Reed Buntings captured at La Touvière, Switzerland.

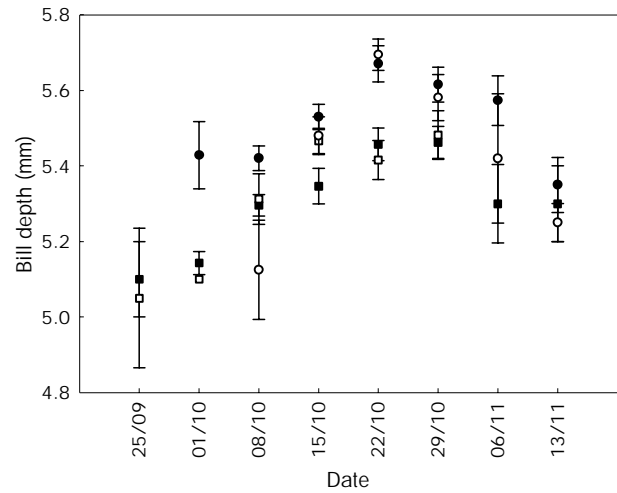


Figure 6. Bill depth (mm) of adult male (open circles), first-year male (filled circles), adult female (open squares), and first-year female (filled squares) Reed Buntings captured at La Touvière, Switzerland, in relation to date of capture. Mean and standard error are shown.

high proportion of first-year birds passing through earlier than the adults, although there was considerable overlap (Fig 1). A similar pattern was observed for Chaffinches *Fringilla coelebs* in Switzerland (Schifferli 1963) and may be a general trend within passerines for short-distance migrants.

The phenology of the sex ratio observed on the study site suggests that females leave their breeding grounds first, disperse earlier and possibly migrate longer distances than males to reach their wintering grounds in southern Europe. For males, a shorter spring migration distance would allow them to return to their breeding sites earlier, where they can occupy better territories and so increase their chances of obtaining a mate (George 2002). However, the relationship between the Reed Buntings passing through the study site and wintering populations further south is not clear. During the winter in Europe a skewed sex ratio according to latitude is observed with three females to each male present from October to February in Spain (Villarán 1999, Villarán & Pascual-Parra 2003), whereas a higher percentage of males is present in Switzerland (Pedroli & Gogel 1972), and Germany (Tauchnitz 2000). In contrast, although slightly more females than males were caught at the study site in autumn, the sex ratio was not significantly different from 1:1. Furthermore, the first-year:adult ratio of 1:1 observed in Spain during winter (De La Puente & Seoane 2001) contrasts with the large age ratio difference of three first-year birds for each adult during migration through the Swiss study site. One interpretation of this is that young birds might disperse without migrating further southwest as females

Table 2. Biometrics of Reed Buntings in migration from September to November 2004 at La Touvière, Geneva, Switzerland.

	Wing length, mm mean \pm SD (N); range	Body mass, g mean \pm SD (N); range	Bill depth, mm mean \pm SD (N); range	Bill width, mm mean \pm SD (N); range	Bill length, mm mean \pm SD (N); range
First-year males	78.3 \pm 1.9 (181); 72.0 – 83.0	20.6 \pm 1.8 (150); 16.0 – 27.0	5.5 \pm 0.3 (150); 4.7 – 6.4	5.3 \pm 0.3 (150); 4.6 – 5.9	12.0 \pm 0.4 (150); 11.2 – 13.2
First-year females	73.0 \pm 1.7 (226); 69.0 – 79.0	18.3 \pm 1.8 (200); 15.0 – 25.0	5.3 \pm 0.3 (189); 4.5 – 6.0	5.2 \pm 0.3 (189); 4.0 – 5.9	1.7 \pm 0.4 (189); 10.4 – 12.8
Adult males	80.3 \pm 2.3 (74); 74.0 – 86.0	21.0 \pm 2.0 (54); 17.5 – 26.5	5.5 \pm 0.3 (61); 4.9 – 6.1	5.4 \pm 0.3 (61); 4.7 – 5.9	12.1 \pm 0.5 (61); 10.5 – 13.6
Adult females	74.1 \pm 2.2 (60); 70.0 – 79.0	18.7 \pm 2.0 (44); 15.5 – 24.5	5.4 \pm 0.3 (50); 4.6 – 6.1	5.3 \pm 0.2 (50); 4.9 – 5.9	11.8 \pm 0.5 (50); 10.8 – 12.8

do, combined with a greater mortality rate of first-year birds during migration.

One possible bias which might affect the proportion of the sex and age-classes is the turnover rate of the birds captured at the study site. If for example, there is a greater chance of females moving on to winter further southwest than males, then it may be that females spend on average less time in the reedbed. The same applies to the high proportion of first-year birds caught, which may be due to the fact that they tend towards spending more time at the study site. This could affect our interpretation of the relative numbers of different classes trapped.

Our biometric data (Table 2) confirm other data on sexual size dimorphism within Reed Buntings (Svensson 1992, Cramp & Perrins 1994, Villarán & Pascual-Parra 2003) and show that adults are longer-winged than first-year birds. At the study site, mean wing length increased progressively over the migration period (Fig 2). The lowest values for body mass during the autumn migration were recorded at the beginning of October when the birds were starting to disperse, and at the end of November when the birds started to remain on the study site as their wintering quarters. Maximum values for mean body mass corresponded to the peak of the migration in October (Fig 3) and may have been

due to fat accumulation and flight-muscle hypertrophy (Kaiser 1992). Body condition values were slightly lower than those reported by Villarán & Pascual-Parra (2003) and did not vary between the sexes (Fig 4).

Mean bill depth (corrected for sex) increased progressively during the migration period until the middle of October when the highest bill depths were recorded, and then decreased (Fig 6). A continuous cline of increasing bill depth exists towards the northeast of the Western Palearctic (Cramp & Perrins 1994). A comparison of the bill depth of males in Geneva with those of birds from other European studies (Table 3) suggests that, at the peak of migration, the passage migrants included birds from large-billed populations with a more northeasterly origin, although these birds were not bigger overall on the basis of wing length. For example, an individual with a 6.4 mm bill depth is likely to have originated from northeastern Europe (Fig 6). Bill depth is a highly heritable trait (Grant 1983) and, in contrast to wing length, does not vary greatly with age or season (Boag 1984), and can be therefore considered as a reliable and repeatable measurement for comparisons between distinct geographical populations. As proposed by Prŷs-Jones (1984) and Villarán (1999), the fact that birds with deeper bills are present during the peak of migration

Table 3. Bill depth of male Reed Buntings from European studies, according to Cramp & Perrins (1994).

Location	Bill depth (mm)	subspecies
S Sweden, Finland	5.3 \pm 0.2 (17); 5.0 – 5.6	<i>schoeniclus</i>
S Sweden, E Germany, Poland, SW Belarus	5.3 \pm 0.18 (16); 5.1 – 5.6	<i>schoeniclus</i>
Lapland	5.3 \pm 0.2 (32); 4.7 – 5.8	<i>schoeniclus</i>
Russia, St Petersburg	5.4 \pm 0.3 (25); 5.1 – 6.0	<i>schoeniclus</i>
Switzerland*	5.5 \pm 0.3 (212); 4.7 – 6.4	<i>schoeniclus</i> + ?
N Ukraine	5.7 \pm 0.3 (37); 5.2 – 6.5	<i>ukrainae</i>
E Austria, Hungary, N former Yugoslavia	6.0 \pm 0.25 (23); 5.7 – 6.4	<i>stresemanni</i>
NE Bulgaria, NE Romania, S Ukraine	6.9 \pm 0.35 (8); 6.4 – 7.4	<i>tschusii</i>

may indicate leap-frog migration, with northeastern migratory populations tending to overwinter further to the southwest of Europe, overtaking the more sedentary populations of Reed Buntings from Central Europe.

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