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Age-related improvement of reproductive success in Bluethroats *Luscinia svecica*

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Capsule Young birds are less likely to have high reproductive success compared with older ones because of a lack of several skills influencing breeding performance.

Aims To test the 'constraint' hypothesis by investigating the effect of male and female age on reproductive performance of a Bluethroat *Luscinia svecica* population.

Methods We compared two age-classes (yearling versus old), breeding for the first time at Guérande salt-pans, France, by evaluating arrival dates on breeding site, territory quality, laying dates, clutch size and egg size, delay before re-nesting, breeding performance, feeding rate at two different nestling periods (on days 4–5 and 10–11 after hatching) and nestling body condition.

Results Our results clearly demonstrated an age effect on reproductive performance for both males and females: young breeders were less likely to fledge young. In older males, improvement of reproductive success was related to feeding rate during the first nestling period. For females, timing of breeding (laying date) and reproductive investment (such as clutch size, feeding rate in the whole nestling period, brood condition) were the main determinants. The presence of a yearling in a pair strongly decreased the number of young produced per breeding season.

Conclusion Bluethroat supported the 'constraint' hypothesis, i.e. that behavioural and physiological maturation is needed for young breeders to enhance reproductive performance.

Reproductive success of young birds is generally lower than that of old breeders (Curio 1983, Saether 1990, Fowler 1995). Curio (1983) proposed that, because of their heterogeneity in quality, individuals would be selected as time passes, thus leading to a decrease in the proportion of lower quality old individuals. Moreover, Curio (1983) developed two other hypotheses to explain age-related enhancement of reproductive success during a birds' first breeding season. The restraint hypothesis predicts that the poorer performance of first-time breeders is related to the optimization of reproduction in the long-term as investment in the first breeding is minimized. On the contrary, the constraint hypothesis predicts that the poorer breeding success of young compared to old breeders could be due to lack of breeding skill.

The two hypotheses are not mutually exclusive, but currently there is more evidence in support of the constraint hypothesis (Saether 1990). Fowler (1995) defined it as being linked to behavioural and physiological maturation processes necessary to enhance reproductive performance.

The physiological and behavioural parameters commonly studied are breeding dates, clutch size, egg size and nestling-feeding effort. The influence of parental age has been investigated mainly in long-living birds (Coulson 1966, Hamer & Furness 1991, Laaksonen *et al.* 2002) and was not well-known in short-lived species (Green 2001, McGraw *et al.* 2001). The influence of the age of the male remained poorly documented. Forslund & Pärt (1995) suggested further studies to assess factors involved in age-related differences in breeding performance and their relative importance.

We analyse the effect of age in a short-lived bird (Bluethroat *Luscinia svecica*) on the breeding performance of male and female. First breeding attempts occur in the year following hatching and birds can be divided into two age-classes: yearlings (Y) or older birds (O) (Svensson 1992). Two broods (from three to six

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*Correspondence author. Email: Thomas.Geslin@univ-rennes1.fr eggs) are laid between April and July, with a possible replacement brood if failure occurs (Bonnet 1984). Females build their nests on the ground and incubate alone. Males only contribute to provisioning nestlings with their females. Nestlings were fed arthropods (Allano *et al.* 1988) captured inside the territory.

We test the constraint hypothesis by investigating arrival and laying dates, clutch size, egg size, number of young and nestling-feeding effort. We also assess the influence of (1) territory quality, which can improve breeding performance (Högstedt 1980, McCleery & Perrins 1985, Przybylo *et al.* 2001, Geslin *et al.* 2002), (2) delay of re-nesting after brood failure or brood success, which can influence the number of broods per breeding season (Green 2001) and (3) chick body condition, because feeding rates are not always a reliable measure of parental investment (Saetre *et al.* 1995) or quality (Sundberg & Larsson 1994).

The Bluethroat is an appropriate species for such a test because it is a migrating territorial passerine bird with a colourful sexual dimorphism and a socially monogamous mating system with biparental care.

Methods

Bluethroat pairs were individually marked during eight breeding seasons (1994–2001) in the Guérande saltpans (47°20′N, 2°25′W), western France. For three breeding seasons (1995–97), arrival dates were recorded as the first sighting on a territory. The territory quality was determined by the spatial arrangement of the two environmental elements: banks and ponds (Geslin *et al.* 2002). On a raster map (scale: 1/2500, cell size: 2 × 2 m), we used a spatial heterogeneity index (Baudry & Baudry-Burel 1982) that expresses the proportions of each cell-relation type. To avoid pseudoreplication and any effects of pair-bond duration, data were analysed only for the year each individual was ringed.

Nests were regularly monitored (every two days) taking care to reduce predation, the main cause of failure. The first-egg date was directly observed (70% of data) or back-calculated using hatching date and regression of incubation period on clutch initiation date. When re-nesting occurred after failure ($n = 24$) or success ($n = 28$) we calculated the delay required before re-laying. Clutch analysis included data for 125 nests from 1994 to 2001: 90 first and 35 second nesting attempts. Breeding performance was expressed by the total number of young fledged per breeding season, for males and females of both age-classes.

Egg size

Egg size was measured in clutches of four, five and six eggs during two breeding seasons: 14 nests in 1999 and 26 nests in 2000. According to Hoyt (1979), the volume of an egg (V) can be calculated from its length and breadth (± 0.1 mm) using the following equation:

$$V = 0.51 \times \text{length} \times (\text{breadth})^2$$

Egg volume was related to clutch size, since the sizes of eggs within a clutch are not independent.

Parental care

Parental care was estimated by feeding rates (average number of feeding visits per half hour) during a 1 or 2 h observation period between 09:00 hours and 12:00 hours, on days 4–5 and 10–11 after hatching (periods P1 and P2 respectively). We analysed data for the first nesting attempt including three, four or five nestlings, for 1999 ($n = 20$), 2000 ($n = 29$) and 2001 ($n = 17$). The first five minutes of observation data were excluded from the analysis to eliminate any effects the observer. A total of 2128 feeding visits were recorded.

Body condition

We used first-brood data covering five years (1997–2001). Using linear regression, nestling mass (± 0.1 g) was corrected for age and time of day when weighed ($r^2 = 0.47$, $n = 497$, $P < 0.001$, $P = 0.011$ respectively). An index of body size was calculated using the first factor (PC I) from a principal component analysis (Rising & Somers 1989) on the three body size measurements (wing ± 0.5 mm, tarsus ± 0.1 mm and bill ± 0.05 mm). The first factor explained 66.5% of body size variations in nestlings. Nestling body masses were positively correlated with PC I ($\text{MASS} = 0.86\ \text{PC I} + 12.38$, $r^2 = 0.308$, $P < 0.001$, $n = 497$). Body condition was expressed as the residual mass, in grams, from this linear regression (Jakob *et al.* 1996). Mean values of nestling body condition for full broods were analysed.

Data analysis

To account for among-year variation, the original values were standardized. According to the parameter considered, negative standardized values mean lower or earlier values and positive standardized values mean higher or later values than the annual mean performance. Egg size and feeding rates were standardized by brood size.

Data were analysed with SYSTAT (version 9.0, SPSS 1999). Tests were one-way or two-way ANOVAs and ANCOVAs and statistical significance was set at $P < 0.05$. Standardized values are presented as means ± se.

RESULTS

Arrival on breeding site

From 1995 to 1997, arrival dates varied in relation to sex and age (Fig. 1): females arrived later than males. Older birds (O) arrived earlier than yearlings (Y) (ANOVA: $F_{1,90} = 7.49$, $P = 0.007$ for males and $F_{1,60} = 17.01$, $P < 0.001$ for females).

Territory quality

Territories of O and Y males had the same environmental quality (ANOVA: $F_{1,96} = 0.31$, $P = 0.58$; standardized means: –0.24 ± 0.23 versus –0.41 ± 0.31 respectively).

Laying date and delay before re-nesting

Yearling females started their first clutch later than O females (one-way ANCOVA: $F_{1,104} = 6.86$, $P = 0.01$; Fig. 2). Age of partner had no effect on laying date (covariate: $F_{1,104} = 0.07$, $P = 0.79$). Delays before re-nesting after nest failure or nest success were similar for Y and O females (two-way ANCOVA: $F_{1,47} = 1.07$, $P = 0.31$; $F_{1,47} = 1.39$, $P = 0.25$ respectively; Fig. 2). Moreover, age of male did not influence the interval between re-nesting (covariate: $F_{1,47} = 0.04$, $P = 0.85$).

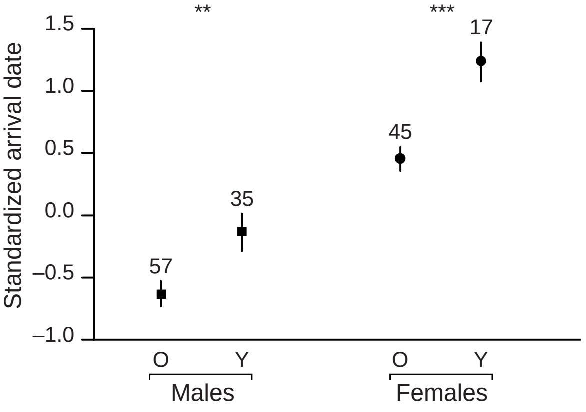

Figure 1. Standardized mean (± se) arrival dates of old (O) and yearling (Y) males and females. Sample sizes are given above the error bars. $^{**}P < 0.01$; $^{***}P < 0.001$.

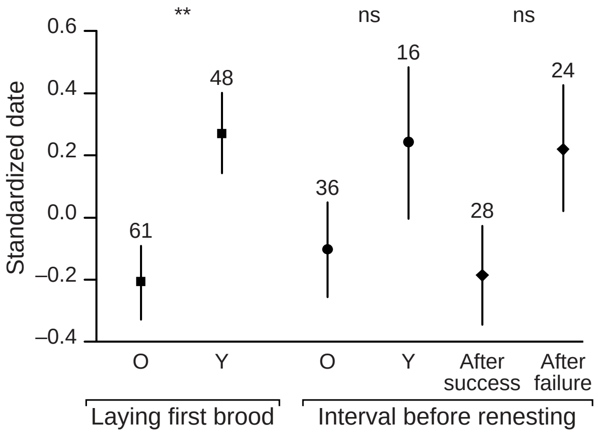

Figure 2. Standardized mean (± se) laying dates and postponements for re-nesting of old (O) and yearling (Y) females. Postponements for re-nesting after failure or success are also given. Sample sizes are given above the error bars. $^{**}P < 0.01$; ns, not significant.

Clutch and egg sizes

Clutch sizes differed in relation to age of female and between first and second nesting attempts, but no interaction was observed between these two factors (two-way ANCOVA: $F_{1,118} = 7.16$, $P = 0.008$; $F_{1,118} = 14.12$, $P < 0.001$; $F_{1,118} = 1.40$, $P = 0.24$ respectively; Fig. 3). Age of male had no influence on clutch size (covariate: $F_{1,118} = 0.07$, $P = 0.79$).

Egg volume was not affected by age of female, year (two-way ANCOVA: $F_{1,31} = 2.40$, $P = 0.13$; $F_{1,31} = 0.01$, $P = 0.94$ respectively; Fig. 3) or age of male (covariable: $F_{1,31} = 0.09$, $P = 0.77$).

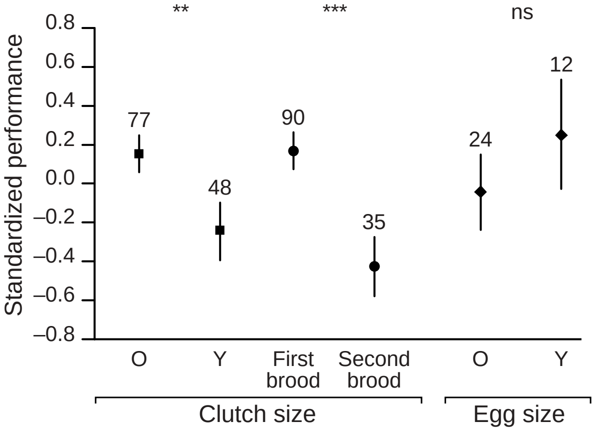

Figure 3. Standardized mean (± se) clutch size and egg size of different-aged females: O, old; Y, yearling. The clutch sizes are shown for first and second broods. Values of egg size were standardized by clutch size. Sample sizes are given above the error bars. $^{**}P < 0.01$; $^{***}P < 0.001$; ns, not significant.

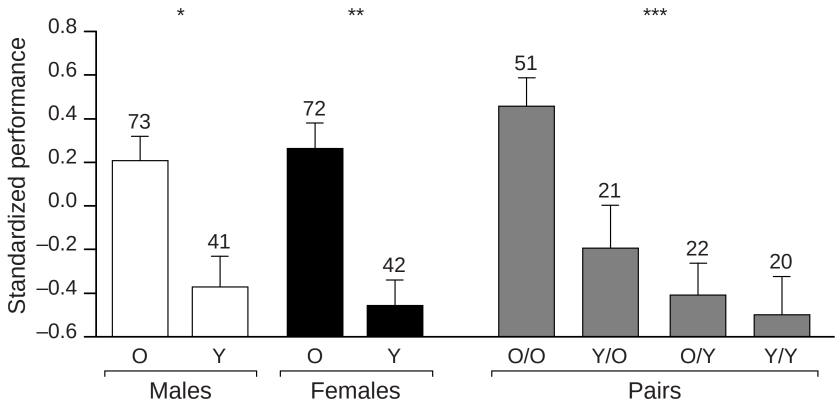

Figure 4. Standardized mean (± se) number of fledglings produced per breeding season for different age-classes of individuals: males, females and pairs (e.g. O/O = O male paired with O female). O, old; Y, yearling. Sample sizes are given above the error bars. $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

Breeding performance

The mean number of young produced per breeding season increased with age of males and females (two-way ANOVA: $F_{1,110} = 4.66$, $P = 0.034$; $F_{1,110} = 10.08$, $P = 0.002$ respectively; Fig. 4), but no interaction between age of males or females was found ($F_{1,110} = 3.29$, $P = 0.07$). The presence of a yearling breeder in a pair induced a decrease in the number of fledglings produced per breeding season (one-way ANOVA: $F_{1,110} = 8.71$, $P < 0.001$; Fig. 4).

Feeding rate

There was an effect of age of breeder on feeding rates in males and females. O males fed more young than Y males and during the 10–11-day-old nestling period, feeding rates were higher than during the 4–5-day-old nestling period (two-way ANCOVA: $F_{1,59} = 4.21$, $P = 0.045$; $F_{1,59} = 4.71$, $P = 0.034$ respectively) (Fig. 5). The two-way interaction term was not significant ($F_{1,59} = 1.19$ $P = 0.28$). Age of mate had no effect on the feeding rate of males (covariate: $F_{1,59} = 2.06$ $P = 0.16$). Similarly, O females fed more young than Y females and increased their feeding rate as the nestlings grew older, but no effect could be found of either the interaction term (female age × nestling period) or partner age (as covariate) ($F_{1,59} = 16.46$, $P < 0.001$; $F_{1,59} = 7.60$, $P = 0.008$; $F_{1,59} = 3.74$, $P = 0.06$ and $F_{1,59} = 2.38$, $P = 0.13$ respectively; Fig. 5).

Nestling body condition

A two-way ANCOVA on parental age revealed no differences between O and Y males on nestling body condition ($F_{1,92} = 0.39$, $P = 0.54$; (Table 1). In contrast, nestlings of O females tended to be in better condition than those of Y females ($F_{1,92} = 4.69$, $P = 0.033$), but no interaction between ages of partners was found (age of male × age of female) ($F_{1,92} = 0.56$, $P = 0.46$). However brood size (used as covariate) significantly influenced

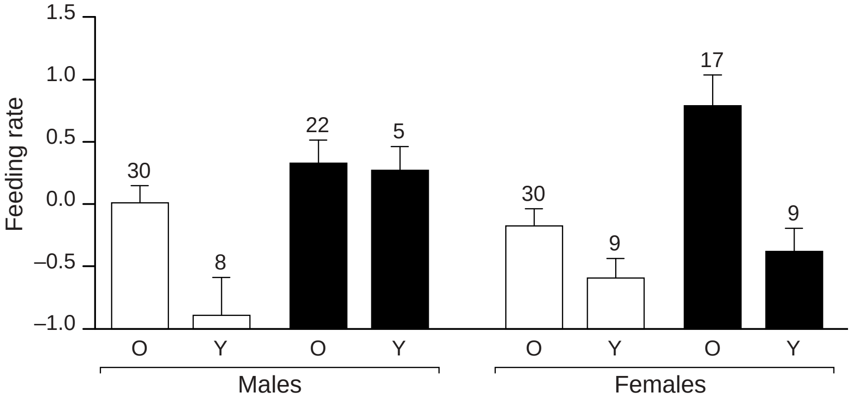

Figure 5. Standardized mean (± se) feeding rate for different age-classes of males and females at two nestling periods: 4–5 days-old (□) and 10–11-days-old (■). O, old; Y, yearling. Sample sizes are given above the error bars.

Table 1. Standardized mean (± se) body condition of nestlings fed by yearling (Y) or older (O) males and females on day 7 after hatching in different brood sizes (three, fours and five nestlings). Sample sizes are given into parentheses.

	Brood size			
Nestlings	3 nestlings (13)	4 nestlings (33)	5 nestlings (53)	*P*
All	0.39 ± 0.24	0.24 ± 0.15	–0.21 ± 0.14	**
Fed by O males	0.27 ± 0.37	0.34 ± 0.17	–0.29 ± 0.17	ns
Fed by Y males	0.57 ± 0.27	–0.21 ± 0.38	–0.02 ± 0.25	
Fed by O females	0.34 ± 0.34	0.29 ± 0.18	–0.03 ± 0.16	*
Fed by Y females	0.49 ± 0.31	–0.03 ± 0.30	–0.81 ± 0.32	

Results of a two-way ANCOVA (factors: ages of males and females; covariate: brood size): **P* < 0.05; ns, not significant.

body condition of nestlings ($F_{1,92} = 7.14$, $P = 0.009$). Nestling body condition declined as brood size increased.

DISCUSSION

Based on within-two-cohort data, our results clearly demonstrate, in Bluethroat, an effect of parental age on breeding performance and are summarized in Table 2. Y breeders were less likely to fledge young. Fertility did not seem to be the reason for this difference as the same proportions of unhatched eggs were observed for both age-classes (7.5%, Geslin 2002). Conversely, physiological conditions may explain the difference in arrival dates on breeding sites, where Y birds were later than O birds. Arrival dates on breeding sites and commencement of breeding depend on date of departure from wintering site in accordance with prebreeding moult that begins earlier in O than Y birds and earlier in males than females (Geslin 2002).

Bluethroats show a strong site attachment (Constant & Eybert 1995) with very high territory fidelity of both sexes (Geslin 2002); early arrival dates of O birds favoured the settlement and exploitation of territories they defended previously. Knowledge of territory features helped old birds forage more efficiently than young birds (O'Connor 1985). Based on our study where there was a better production by O males, the same qualities Y and O male territories suggested that the knowledge of territory was a factor of prime importance to enhance breeding success. Differences in feeding rates in both age-classes revealed that Y Bluethroats were poorer foragers, as found in Blackbirds *Turdus merula* (Desrochers 1992a).

In Bluethroat, egg and nestling predation rates were 15% and 39.8%, respectively, of eggs laid (Geslin 2002). These rates were higher for Y breeders than O ones. Several positive effects of age accounted for a decreased predation effect: good nest-site location directly influenced nest predation (Ludvig *et al.* 1995, Cresswell 1997) and secretive feeding enabled birds to rear their young without attracting predators (Green 2001, Pärt 2001).

Mate age has an effect on reproductive success. The presence of a yearling in a pair strongly decreased the number of young produced per breeding season. Differences were observed in each sex.

Male age influence

Age-related differences in paternal care were greatest during the first few days after hatching when nestlings had to be brooded by females. The same pattern was observed in House Wrens *Troglodytes aedon* (Johnson *et al*. 1992). This suggests that O provisioning males may compensate for the females' inability to increase their feeding rates at this stage.

Table 2. Summary of results of age-related influence on Bluethroat reproductive traits by comparing two age-classes: young breeders (Y) versus older ones (O). The effects of mate age are reported.

Factor	Males	Females	Mate age effect
Territory quality	No male age effect		
Arrival date	Earlier for O	Earlier for O	
Laying date		Earlier for O	No male age effect
Clutch size		Higher for O	No male age effect
Egg size		No age effect	No male age effect
Delay of re-nesting		No age effect	No male age effect
Breeding performance	Higher for O	Higher for O	Effect of mate age
Feeding rate	Higher for O	Higher for O	No mate age effect
Chick body condition	No age effect	Higher for O	No mate age effect

Female age influence

The age-related difference in laying dates in Bluethroat has been observed in other passerines (Harvey *et al*. 1985, Dhondt 1989, Wheelwright & Schultz 1994). Discrepancies in laying dates are supposed to be related to protein deposition during egg formation, which is better in old females (Hipfner *et al*. 1997) or influenced by age-related resource acquisition (Nakamura 1995). Moreover, foraging tactics may also influence laying dates because young birds are less capable foragers (Desrochers 1992b). Although laying dates differed with Bluethroat female age, no effect was noticed on the mean delay before a new clutch was laid (after either a success or a failure) as observed in Brown Thornbills *Acanthiza pusilla* (Green 2001).

In Bluethroat, O females laid larger clutches than Y females. Conversely, female age had no effect on egg size as in other passerines (Nager & Zandt 1994). Generally, egg size decreases with increasing clutch size (Perrins 1996, Geslin 2002). The contradictory result observed in O females suggested that they were more likely to invest in egg production than were Y females.

During the naked-nestling period, female brooding activity interfered with feeding activity, and O females fed their young more than Y females. Because time spent brooding decreased with brood size (Dunn 1976), O Bluethroat females may forage more than Y ones. Moreover, when nestlings were older, O females also fed their young more than Y females, indicating that they were more able to invest in feeding activities. In contrast to males, nestlings of O females were in better condition than those of Y females, particularly in large broods. This suggested that O females adapted their feeding effort to chick number more efficiently.

These observations indicated an age-related improvement of breeding success in Bluethroat. Our results revealed some physiological and behavioural differences with age that favoured O birds. The physiological constraints affected the prebreeding moult that induced the onset of reproduction: arriving on breeding site and laying date of first-egg. The behavioural constraints concerned nest-site selection in relation to egg and nestling predation and the foraging skill required for nestling feeding. In agreement with Saether (1990), the better success of experienced Bluethroats compared with inexperienced ones gave strong support for the constraint hypothesis.

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