

Sex-specific patterns in body condition and testosterone level changes in a territorial migratory bird: the Bluethroat *Luscinia svecica*

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The Bluethroat *Luscinia svecica* is a migratory passerine that exhibits a socially monogamous pair bond and a high level of parental care. Males are territorial both when wintering and breeding whereas females are territorial only in winter. We investigated changes in body condition and testosterone levels during successive life-history stages and determined their relationships. Sex-specific patterns were observed in the variation in body condition and testosterone level. Male body condition varied mainly during the winter. It peaked at the onset of the prenuptial moult and then decreased, whereas it remained stable throughout breeding. In contrast, female body condition varied mainly during the breeding season. It increased during the prelaying stage and then abruptly decreased until fledgling provisioning. As in other monogamous and territorial passerines, testosterone levels in Bluethroat males were low during winter, increased in late winter, peaked during the prelaying stage and then decreased when provisioning young. In wintering females, territorial competition caused testosterone levels to rise. These females were able to produce territorial vocalizations and exhibit aggressive postures. Females showed higher mean testosterone levels than males when wintering whereas the opposite was observed when breeding. Our data from wintering female Bluethroats support the 'challenge hypothesis' under which high testosterone levels are associated with periods of social instability, and testosterone can regulate female territorial behaviour during this period.

The annual cycle can be considered as a series of life-history stages, such as wintering, courtship, incubation and chick rearing, in which birds must cope with different energetic constraints. Changes in body condition may thus reflect changes in energy expenditure. Provisioning strategies and their effects on reproductive success are well documented in long-lived birds (capital breeders). However, some studies have raised the possibility that in passerine birds also (income breeders) conditions in winter and at stopover sites, especially with respect to food availability, have a strong influence on the success of the following breeding season (Nakamura 1995, Sandberg & Moore 1996, Smith & Moore 2003). Moreover, individuals

arriving on breeding grounds with a high fat load may be able to allocate more time to breeding activities, such as territorial defence, mate attraction and nest building, than can lean birds (Sandberg & Moore 1996). The breeding performance of passerine birds is influenced by body condition, i.e. their capacity to store protein and fat (Jones & Ward 1976). Body reserves are a key factor in estimating parental effort (Drent & Daan 1980) and may influence the decision to breed, laying date and clutch size (Ankey & MacInnes 1978, Davies & Lundberg 1985, Chastel *et al.* 1995).

Holding wintering and breeding territories is one of the fundamental ways that provides resources for survival, prebreeding migration and the following breeding season. Androgens are known to be involved in aggression and territorial behaviour, particularly during the breeding season (Balthazart 1983, Harding

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1983). In birds of temperate latitudes, testosterone levels peak when breeding, and testosterone influences a wide array of life history traits, such as social and sexual behaviour in male birds (e.g. Wingfield *et al.* 1990a, Ketterson *et al.* 1992). However, maintaining high testosterone levels imposes a physiological cost and may decrease survival probability (Dufty 1989, Ketterson *et al.* 1996). In male birds that exhibit winter territoriality, high testosterone levels appear to be independent of aggressive behaviour (Burger & Millar 1980, Schwabl & Kriner 1991, Schwabl 1992, Schlinger *et al.* 2001). However, through conversion into 17- β estradiol, this hormone may be involved in the regulation of winter territoriality in Song Sparrows *Melospiza m. morphna* (Soma & Wingfield 1999). The role of this hormone during the non-breeding season has received much less attention; it remains poorly documented in males and even less so in females. Testosterone seems to play a role in territorial song production in wintering female European Robins *Erithacus rubecula* (Kriner & Schwabl 1991).

We studied the Bluethroat *Luscinia svecica*, a migratory species that breeds and winters at temperate latitudes, to investigate (1) the complex relationships between seasonal changes in energy expenditure and life history stages, and (2) the role of testosterone in males and females during wintering and breeding territorial conflicts. This sexually dimorphic passerine exhibits a socially monogamous mating system and territorial behaviours on both its wintering and its breeding grounds (Eybert *et al.* 1989, Geslin 2002). The morphotype *L. s. namnetum* breeds along the French Atlantic coast from March to July and can rear two successive broods. Males arrive on average 12 days earlier than females and establish a breeding territory to which they attract a mate (Geslin 2002, Geslin *et al.* 2004). In this species, females build nests and incubate without assistance but both parents provision the brood. Wintering males and females arrive along the Portuguese coast in late October or early November and both sexes defend winter territories by pursuits and song, until early March, when they migrate back to the breeding grounds after a partial prenuptial moult.

MATERIALS AND METHODS

Bird survey

Bluethroats were studied from November 1996 to May 2000 at two locations considered as the main

breeding and wintering sites of this species (Eybert *et al.* 1989). Birds were caught using mist-nets or traps and without using playback. Each bird was ringed with metal and colour rings in the Guérande salt-pans (breeding ground in France; 47°20'N, 2°25'W) and in the Tagus estuary (wintering ground in Portugal; 38°50'N, 08°58'W). Depending on the date of capture and field observations, birds were assigned to one of nine stages of the annual cycle (Geslin 2002). These included four winter stages: arrival on wintering ground (late October–early November, $n = 166$), territory establishment (late November, $n = 268$), onset of prebreeding moult (late January–early February, $n = 107$) and prebreeding moult peak of the population (late February, $n = 125$); and five breeding stages (mid-March to late May): arrival on breeding ground ($n = 36$), prelaying ($n = 60$), incubation ($n = 23$), and nestling and fledgling provisioning (respectively $n = 74$, $n = 22$). During the breeding season, unmated males ($n = 18$) were caught during the nestling provisioning period. These males were analysed separately.

Body condition

Body mass (± 0.1 g), wing length (± 0.5 mm) and tarsus length (± 0.5 mm) were recorded. Because in small passerines, body mass may vary in relation to the time of day (Baldwin & Kendeigh 1938, Ullrich 1972), we corrected body mass for the time of day when weighed by using a linear regression ($r^2 = 0.127$, $P < 0.001$, $n = 395$ for females; $r^2 = 0.212$, $P < 0.001$, $n = 517$ for males). An index of body size was calculated using the first factor (PC I) from a principal component analysis (Rising & Somers 1989) on the two body size measurements (wing length, tarsus length). The first factor explained 59.4% of body size variation in males and 61.1% in females. Body mass was correlated positively with PC I in both males (MASS = 0.280 PC I + 14.534, $r^2 = 0.113$, $P < 0.001$) and females (MASS = 0.254 PC I + 14.077, $r^2 = 0.065$, $P < 0.001$). Body condition index was therefore expressed, in grams, as the residual mass from a linear regression relating body mass to body size (Jakob *et al.* 1996, Chastel & Kersten 2002, Lormée *et al.* 2003).

Blood sampling and hormone assays

Blood sampling was only conducted on birds caught between 08:00 and 12:00 h to reduce the possible effect of variation in plasma testosterone levels through

the day. For each bird, a blood sample (150 µL) was collected from the brachial vein into a heparinized microtube. Blood samples were taken within 10 min of capture (Wingfield *et al.* 1982). Blood was immediately centrifuged at 2000 r.p.m. for 8 min in order to separate plasma from blood cells. The plasma samples were stored in a tank of liquid nitrogen until assayed.

Testosterone levels were determined at the CEBC by radio-immunoassay using antibodies specific for testosterone (Chastel *et al.* 2003). Testosterone antiserum was kindly provided by Dr Gérald Picaper (Medecine nucléaire, CHU La Source, Orléans, France). Testosterone was extracted from a 50-µL plasma sample in diethyl-ether and levels determined in duplicate in a single assay. Duplicate aliquots of the extracts, re-dissolved in 0.01 M phosphate-buffered saline (pH 7.4) containing 0.1% bovine albumin (PBS-BSA), were incubated overnight at 4 °C with c. 9000 c.p.m. of the appropriate ³H-steroid and antiserum. Assays ($n = 3$ duplicates) showed 6.2–8.4% intra-assay and 10.5–13.9% interassay variability. The lowest testosterone concentration detectable was 0.039 ng/mL.

Statistical analysis

Data were analysed with Systat 7.0 (Wilkinson 1997) and statistical significance was set at $P < 0.05$. Values are presented as means \pm sem. To avoid pseudo-replication, birds were represented only once in the whole data set. Because of the non-normal distribution of plasma testosterone data, values were \log_{10} transformed. To study the effect of wintering and breeding stages on body condition and testosterone, we used analyses of variance (ANOVA, ANCOVA), followed by *post-hoc* Tukey tests. We used Pearson's correlation to investigate the relationship between body condition and testosterone level.

RESULTS

Body condition

Body condition was not affected by year (as the covariate) in either males or females (respectively $F_{1,479} = 1.77$, $P > 0.05$; $F_{1,382} = 1.58$, $P > 0.05$). Male and female body condition varied significantly in relation to the annual cycle (ANCOVA: $F_{8,479} = 3.83$, $P < 0.001$ for males; $F_{8,382} = 14.71$, $P < 0.001$ for females). Data for wintering birds revealed a significant effect of both sex and stage on body condition with no significant interaction between these terms (Table 1,

Table 1. Results of two-way analyses of variance (ANOVA) to assess variations in body condition and testosterone levels of wintering and breeding Bluethroats. The effects of stage, sex and interactions are shown as F ratios, degrees of freedom (df) and their P values.

	Winter			Breeding		
	df	F	P	df	F	P
Body condition						
Stage	3,658	6.14	< 0.001	4,205	11.96	< 0.001
Sex	1,658	8.98	< 0.001	1,205	23.81	< 0.001
Stage * Sex	3,658	2.08	ns	4,205	9.99	< 0.001
Testosterone						
Stage	3,466	29.20	< 0.001	4,175	8.05	< 0.001
Sex	1,466	3.73	< 0.05	1,175	37.34	< 0.001
Stage * Sex	3,466	13.95	< 0.001	4,175	0.97	ns

Table 2. Body condition and testosterone levels of wintering and breeding male and female Bluethroats. Results of one-way analyses of variance (ANOVA): F ratios, degrees of freedom (df) and their P values.

	Winter			Breeding		
	df	F	P	df	F	P
Body condition						
Males	3,360	6.85	< 0.001	4,120	2.37	ns
Females	3,298	3.58	< 0.05	4,85	10.03	< 0.001
Testosterone						
Males	3,242	37.21	< 0.001	4,110	9.41	< 0.001
Females	3,224	14.31	< 0.001	4,65	2.53	< 0.05

Fig. 1a). During this period, male and female body condition changed significantly (Table 2). Female body condition increased between the two first stages (Tukey test: $P = 0.029$) when territories were established and then remained unchanged through the rest of the wintering period. In males, body condition peaked in midwinter (Tukey test: $P < 0.001$), at the onset of the prebreeding moult, and then decreased in late February (Tukey test: $P = 0.010$) at the peak moult.

During the breeding season, stage and sex had a significant effect on body condition variations (Table 1, Fig. 2a). However, a significant two-way interaction between breeding stage and sex was observed. Male body condition showed a significant increase from arrival on the breeding ground to nestling provisioning (Tukey test: $P = 0.046$), and then a slight decrease during fledgling provisioning (Table 2). Unmated males were in poorer condition than paired males during

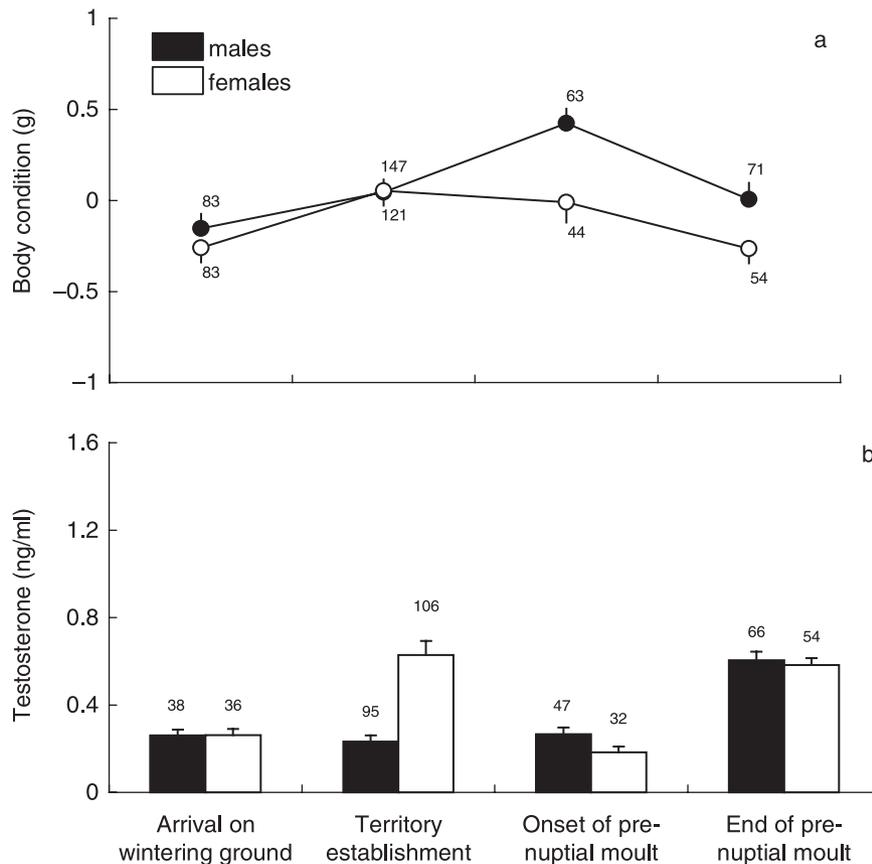


Figure 1. Body condition (a) and plasma testosterone level (b) variation during the wintering period, in male and female Bluethroats (means \pm sem). Sample sizes are given above or below the error bars.

the nestling provisioning stage ($F_{1,41} = 5.18, P = 0.028$). In contrast to breeding males, female body condition peaked during the prelaying stage (Tukey test: $P < 0.001$) and then decreased strongly, reaching a minimum during fledgling provisioning (Tukey test: $P < 0.001$).

Plasma testosterone

Testosterone levels were not affected by year (as the covariate) for either sex (males: $F_{1,351} = 2.49, P > 0.05$; females: $F_{1,288} = 0.60, P > 0.05$). Testosterone concentration varied significantly throughout the annual cycle (ANCOVA: $F_{8,351} = 50.87, P < 0.001$ for males; $F_{8,288} = 6.13, P < 0.001$ for females). In contrast to females, which exhibit similar average levels of testosterone in both wintering and breeding seasons ($F_{1,296} = 0.16, P > 0.05$), breeding males had higher mean values than did wintering males ($F_{1,359} = 231.81, P < 0.001$).

During winter, there was a significant effect of stage and sex on hormone levels and a significant two-way interaction between these terms (Table 1, Fig. 1b).

Wintering males had low testosterone levels, except in late winter (Tukey test: $P < 0.001$; Table 2). In contrast, female testosterone levels peaked significantly twice, once during territory establishment (with higher values than males) and again in late winter (both Tukey tests: $P < 0.001$). The average testosterone level for wintering females was significantly higher than that for males ($F_{1,472} = 15.85, P < 0.001$).

On the breeding grounds, hormone levels varied significantly with life-history stage and sex, but without a significant interaction between these terms (Table 1, Fig. 2b). Males showed significant variation in hormone levels (Table 2), which peaked in the prelaying stage. Compared with this stage, testosterone levels dropped abruptly during the following three stages (Tukey tests: $P = 0.003, P = 0.001, P < 0.001$, respectively). However, while provisioning fledglings, male testosterone levels remained higher than the basal wintering levels (Tukey test: $P < 0.001$). In contrast to mated males, unmated males maintained elevated testosterone levels (similar to testosterone levels found

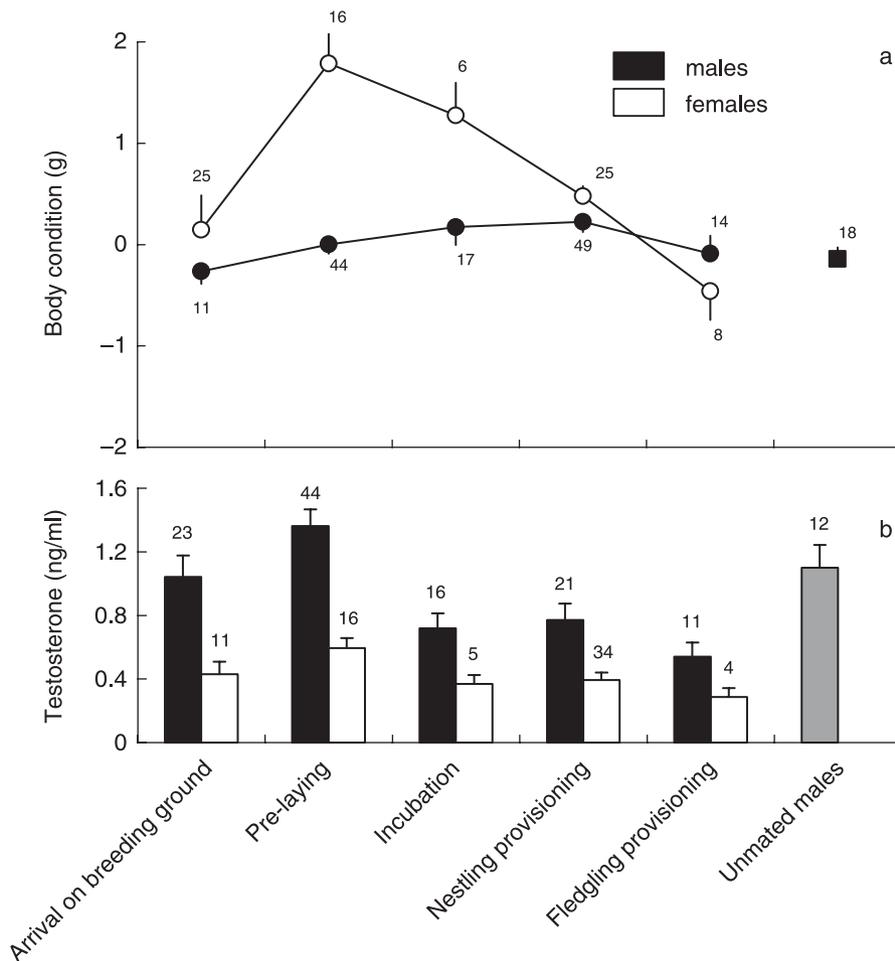


Figure 2. Body condition (a) and plasma testosterone level (b) variation during the breeding season (1st brood from mid-March to late May), in male and female Bluethroats (means \pm sem). Body condition of unmated males is represented by a square and their mean hormonal levels are illustrated by a grey bar. Sample sizes are given above or below the error bars.

in males arriving on the breeding grounds or in 'prelaying' males, $F_{1,31} = 4.44$, $P = 0.043$). Female testosterone levels varied significantly during the breeding cycle, peaking slightly during the prelaying period and then decreasing significantly during the nestling provisioning stage (Tukey test: $P = 0.043$).

Relationship between testosterone and body condition

On average, there was no correlation between testosterone values and body condition in either sex during either the winter (males: $r = -0.03$, $n = 316$; females: $r = 0.07$, $n = 228$) or breeding seasons (males: $r = -0.10$, $n = 115$; females: $r = -0.08$, $n = 228$). We also checked for this relationship at every stage of the wintering and breeding phase. In wintering females,

we detected two significant correlations between testosterone levels and body condition: a positive correlation in the 'territory establishment' stage ($r = 0.25$, $n = 106$, $P = 0.01$) and a negative correlation in the 'end of prenuptial moult' stage ($r = -0.35$, $n = 54$, $P < 0.05$). In breeding males, we detected three negative correlations: in the 'arrival on breeding ground' stage ($r = -0.54$, $n = 23$, $P < 0.01$), in the prelaying stage ($r = -0.36$, $n = 44$, $P < 0.05$) and in unmated males ($r = -0.57$, $n = 12$, $P < 0.05$).

DISCUSSION

Body condition

The body condition of Bluethroat males and females increased significantly while establishing winter

territories because body mass was recovering after the autumn migration. In late winter, body condition showed distinct changes, which differed between sexes, probably because the prebreeding moult began earlier in males than in females (Geslin 2002). This partial moult occurs between February and March and includes lores, ear-coverts, cheeks, throat and breast (Cramp 1988). Only males then develop the metallic blue throat, among other characteristics, that give the species its name. Moult involves a high energy expenditure and imposes costs through the biosynthesis of feather material and heat loss due to decreased insulation (King 1981, Lindström *et al.* 1993). Moreover, the full development of structurally based ornaments such as these requires unrestricted access to nutrients at the time of moult (Hill & Montgomerie 1994, Keyser & Hill 1999, Hill 2000). To meet their energetic needs, Bluethroat males thus expand their territories in late winter, compelling females to forage in feeding areas outside of their own territories (Geslin 2002). At the onset of the prenuptial moult (early February), male body condition, in contrast to that of females, increased significantly, as has been observed in prenuptial moult of other small passerines (Newton 1968, Peters *et al.* 2000). Proportionately more males than females completed their prenuptial moult in late February (Geslin 2002). Male body condition then dropped back to the mean value observed before moult. In contrast, female body condition did not increase but remained stable. There are three non-mutually exclusive explanations for the discrepancy found between sexes in late February: (1) females reached the peak of moult later than males; (2) because of their less-colourful plumage, females required less energy for feather synthesis than males; and (3) social dominance of males (Gauthreaux 1978, Piper 1997) induced more aggressive behaviour in females. In fact, from early to late winter, the proportion of conflicts on feeding areas where a female was implicated (female–female and female–male) increased significantly (Geslin 2002).

Males were in poorer body condition early in the breeding season than when feeding nestlings. At the beginning of the breeding season, males fed less and spent more time in territory defence with pursuits, song and conflicts. Territorial males may spend 60% of their time singing (Bonnet 1984) and this may be energetically costly (Chandler *et al.* 1994, Thomas *et al.* 2003). Male body condition increased slightly between their arrival and the nestling-feeding period because of the decrease in territorial activity while

females incubated. Although equal bi-parental investment in brood provisioning has been shown in Bluethroats (Geslin *et al.* 2004), male body condition remained stable through the nestling stage.

Unlike the situation in males, female body mass peaked sharply during the prelaying period, in relation to the storage of reserves used for laying (egg and ovary development) and incubation (Moreno 1989a), and declined gradually after hatching until the chicks fledged. Female mass change is not necessarily a consequence of feeding effort because female feeding rate is similar to that of males (Geslin 2002), in which we did not observe a mass decrease through the nestling period. This mass loss might represent either a cost of incubation (Moreno 1989b, Chastel & Kersten 2002) or an adaptive response by females to breeding effort and a compromise between different selective factors (Moreno 1989b). For example, mass loss may increase flight efficiency (Freed 1981, Jones 1987, Cavitt & Thompson 1997, Kullberg *et al.* 2002).

Testosterone levels

From arrival on the wintering grounds to the onset of prenuptial moult, male testosterone levels remained around the basal level, as has been recorded in species in the closely related Muscicapidae (Schwabl 1992, Gwinner *et al.* 1994). Nevertheless, wintering males exhibited territorial behaviour with vocalizations (Eybert *et al.* 1989). As in other bird species winter territoriality appeared therefore to be independent of testosterone levels (Burger & Millar 1980, Schwabl 1992, Soma *et al.* 2002). In late winter, male Bluethroats exhibited slightly higher testosterone levels, although this was not associated with development of the cloacal protuberance (Geslin 2002), and so indicated that males were not sexually active. At this stage, the male population had almost completed prenuptial moult (Geslin 2002). Our results showed that high testosterone levels were not necessary to induce prenuptial moult but seemed to be linked to the completion of nuptial plumage, as observed by Peters *et al.* (2000) in the Superb Fairy-Wren *Malurus cyaneus*. Moreover, in both sexes testosterone production is associated with hyperphagia prior to the spring migration (Schwabl & Farner 1989, Wingfield *et al.* 1990b; Boswell *et al.* 1995, Deviche 1995). However, at the end of February, we rarely observed significant fat deposition, presumably because migration must not overlap with the prenuptial moult (Payne 1972, Lindström *et al.* 1994). Fat deposition presumably takes place later, in early March.

Female Bluethroats defended territories throughout winter with the same intensity as males, using intra- and intersexual aggression, vocalization and territorial postures (Geslin 2002). Nevertheless, females exhibited higher mean testosterone levels than males with two distinct peaks. These two peaks were associated with periods of highly aggressive behaviour. The first peak was observed during the period of territory establishment. This probably benefited their foraging because it was correlated positively with body condition. The second peak, which was comparable with the peak for males, occurred during late winter and testosterone levels were, at that time, correlated negatively with body condition. In fact, in late winter, unlike the females, most males had completed their moult. Because of competition with males, which were socially dominant, females were constrained to increase feeding to meet their nutritional requirements. Moreover, in females, testosterone may depress foraging efficiency (see Nagy 1987, Bednekoff & Houston 1994), which might cause females to devote more time than males to foraging without increasing their net energy intake. It is also possible that high testosterone levels depressed energy assimilation efficiency, as was suggested by Lynn *et al.* (2000) with regard to the Dark-eyed Junco *Junco hyemalis*.

Few studies have investigated the function of testosterone in wintering females. In closely related species (e.g. European Robin, Stonechat *Saxicola torquata*), female territorial behaviour appears to be independent of testosterone levels in winter (Kriner & Schwabl 1991, Schwabl 1992, Gwinner *et al.* 1994). However, several studies have stressed the relationships between testosterone and female territorial vocalizations during the wintering season (Kriner & Schwabl 1991) as well as during the breeding season (Kern & King 1972, Hausberger *et al.* 1995). Testosterone contributed to enhancing female territorial behaviour, but once territories have been established (midwinter), testosterone levels decreased to basal values. This pattern could be interpreted in terms of the 'challenge hypothesis' applied to breeding males (Wingfield *et al.* 1990a) and breeding females (Langmore *et al.* 2002). This predicts that high testosterone levels are only associated with periods of social instability and decrease later to avoid the potential costs of sustaining elevated testosterone levels.

As in many other monogamous birds in temperate regions (Beletsky *et al.* 1989, Wingfield 1990), testosterone levels in male Bluethroats increased in spring,

reaching a maximum when males established territories and attracted a mate. The presence of sexually active females increases and maintains high testosterone levels in males (Runfeldt & Wingfield 1985, Silverin 1993). After the females had laid, male Bluethroat testosterone levels decreased gradually until the broods fledged. In other species, this has often been interpreted as a mechanism initiating parental care. Elevated testosterone levels maintain aggression and courtship behaviour, favouring territorial activity (Ketterson *et al.* 1996), but reducing parental care (Hegner & Wingfield 1987, Ketterson *et al.* 1992, Schoech *et al.* 1998). After the first brood had fledged, male testosterone levels decreased but remained slightly above the basal winter levels. Intermediate testosterone levels were probably required for re-nesting (Wingfield & Farner 1993) or investing in extra-pair fertilizations. The presence of two broods and a high extra-pair fertilization rate (Questiau *et al.* 1999) in the studied Bluethroat population may confirm this hormonal operating cycle. In males, two negative correlations between testosterone levels and body condition were observed in the breeding season, first at their arrival on the breeding grounds and then during the prelaying stage when males were defending territories. Increasing testosterone levels induce a corresponding depletion of energy reserves and thus a reduction in body condition (Reid 1987, Dufty 1989). Unmated Bluethroat males also exhibited a corresponding decrease in body condition induced by the high testosterone levels that were maintained well beyond early spring. Compared with mated males that were provisioning nestlings, these unmated males, with full-size cloacal protuberances (Geslin 2002), were still engaged in territorial defence and courtship. As observed in the Pied Flycatcher *Ficedula hypoleuca* (Silverin & Wingfield 1982), plasma levels of testosterone in unpaired males were similar to those in males sampled during the prelaying period. The testosterone pattern of mated males, with a short and distinct peak corresponding to when females were fertile, is typical of a socially monogamous species with high levels of paternal care. The converse pattern of testosterone in unmated males was similar to that observed in polygynous males that provide little or no parental care (Wingfield 1990).

In breeding Bluethroat females, the highest testosterone levels were measured during the prelaying stage. During this stage, some females were observed singing and chasing other females. Vocalizations may be used by females to compete for males (Langmore

& Davies 1997, Langmore *et al.* 2002). Moreover, according to Silverin and Wingfield (1982), three main functions can be attributed to testosterone in breeding females: (1) aggressive behaviour, especially in relation to territory and nest defence; (2) nest-building; and (3) egg-laying. After laying, and until the end of the provisioning period, female testosterone levels decreased, as has been observed in other passerine species (Hegner & Wingfield 1986, Wingfield & Farner 1993, Cristol & Johnsen 1994).

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