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Are age and body condition associated with habitat quality around avian song posts? A test with male Bluethroats at a breeding site in Spain

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We explored whether habitat characteristics surrounding the song posts that male Bluethroats (*Luscinia svecica*) use to attract females and defend their territories might be associated with males' quality, in terms of body condition and age (used here as a proxy of their experience). Data were collected at Sierra de Béjar (province of Salamanca, central-western Spain). Overall, we characterized the habitat and captured 44 male Bluethroats at their song posts in 2011 and 2012. The characteristics of male Bluethroats' song posts and their surrounding habitat were associated with both the birds' age and body condition. Second-year Bluethroats were observed to sing in places with higher abundance of spiders as compared to older birds. Moreover, Bluethroats surrounded by a higher proportion of grasslands and with more Opiliones/spiders were found to carry more fuel.

1. Introduction

During the breeding season, most birds are territorial and males often attract females, and defend the territories from conspicuous posts from which they sing and exhibit the signals associated with their individual quality/fitness (Peek 1972, Ketterson 1979, Studd & Robertson 1985, Senar & Quesada 2006). Thus, song posts play an important role during mate-choice and territory defending processes. Previous studies have chiefly addressed the role and characteristics of song posts in relation to vocal interaction in territorial birds (Hultsch & Todt 1981), song degradation during propagation (Mathevon *et al.* 1996) or risk of predation (Møller *et al.* 2006). However, relatively few studies have focused on the characteristics of the song posts and their relationship with habitat quality and birds' condition.

In species with strong social hierarchies, subordinates normally occupy suboptimal habitats compared to dominants (Carpenter *et al.* 1993a, Marra 2000, Figuerola *et al.* 2001). More experienced individuals (Moore *et al.* 2003), or individuals with a better body condition (Lundberg 1985, Ekman & Lilliendahl 1993, Gosler & Carruthers 1999, Lilliendahl 2002) have higher social status. Accordingly, these individuals would be expected to have priority access to optimal habitat, which is often associated with higher food supplies and/or more shelter (Carpenter *et al.* 1993b, Cuadrado 1997, Arizaga *et al.* 2011b).

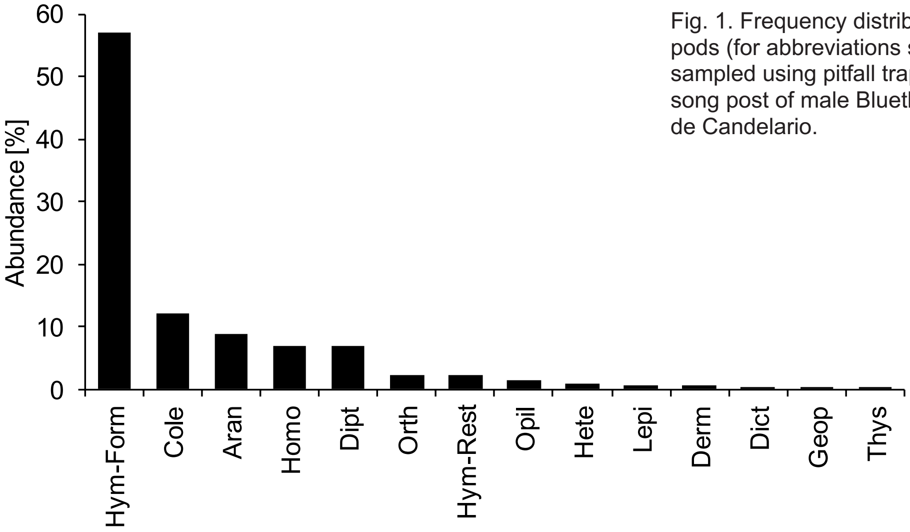

Fig. 1. Frequency distribution of arthropods (for abbreviations see Table 2) sampled using pitfall traps around the song post of male Bluethroats at Sierra de Candelario.

The Bluethroat (*Luscinia svecica*) is a widespread songbird species breeding from Iberia to Alaska and Canada (Cramp 1988). The Iberian population is likely to be a separate subspecies, *L. s. azuricollis* (Johnsen *et al.* 2006), which normally breeds at high altitude in the mountain ranges from north-western and central Iberia, normally between 1,200 and 2,000 m above sea level (García *et al.* 2008, Arizaga *et al.* 2011a). Bluethroats are territorial and have strong social hierarchies (Cramp 1988, Lindström *et al.* 1990). When these Iberian birds reach their breeding sites (from their as yet unknown wintering areas; Arizaga *et al.* 2011a), males rapidly start to look for territories and defend them from visible song posts.

In here, we explored whether the habitat characteristics surrounding the song posts that males use to attract females and defend their territories, might be associated with males' quality in terms of body condition and age (used here as a proxy of their experience).

2. Material and methods

2.1. Sampling area and data collection

Data were obtained near La Covatilla (40°21'N 05°41'W, 1,962 m above sea level), in Sierra de Béjar, situated to the west of Sierra de Gredos, in central-western Spain. This is one of the chief breeding areas for the Bluethroat in Iberia (Gómez-Manzaneque 2003). The density of Bluethroats in Sierra de Candelario is calculated to be 3 birds / 10 ha (Peris 1983), one of the highest across Iberia (Arizaga *et al.* 2011a). The sampling was carried out during the breeding seasons of 2011 and 2012, during the months of May, June and July. The vegetation in this area is made up of shrublands of broom (*Genista* spp.), distributed in patches of varying density among which there are small inundated zones with peat bogs, streams and patches of grassland. The area is used by grazing cattle (cows) during the summer.

Once a bird was detected singing from the same song post for a period of at least 5 min, the bird was caught and the surroundings of this site (post) were characterized. In particular, we measured: altitude (above sea level; of the point where the bird was seen singing; we used a GPS), habitat cover, vegetation height, post height, prey (food) diversity and abundance.

Habitat cover was recorded within a 25 m-radius from the post (± 5% accuracy). The proportion of soil occupied by shrubs (broom cover), grassland or bare soil was measured.

Vegetation height was measured at 8 points, situated 2.5 m from the post, on N, NE, E, SE, S, SW, W, NW axes. After that, the mean vegetation height was calculated for each post. We measured vegetation height at this distance in order to be representative of the vegetation height of the shrub patch where the song post was situated.

Potential food diversity and abundance were measured by sampling soil arthropods, the main prey of the Bluethroat (Cramp 1988). For this, we used pitfalls consisting of plastic glasses (115 mm high, 90 mm for the top diameter, 60 mm for the bottom diameter) filled with a solution of 50% Ethilenglycol. We used two pitfalls per individual post, within a radius of less than 2 m. Traps were systematically located with respect to the song post; one oriented to the north and the other one to the south. The traps were collected after a sampling period of ca. 36 h. Samples were stored in glass pots until they were examined in the laboratory (Aranzadi Sciences Society). We used a magnifying lens to identify (to Order level) and count the arthropods captured. Overall, we considered 14 taxa (Fig. 1). The Hymenoptera were subdivided into two sub-taxa because ants (Family Formicidae) were very abundant (Fig. 1), and likely to be one of the main prey of the Bluethroats (Cramp 1988).

To record individual-associated biometric variables, Bluethroats were captured with a spring trap baited with mealworms (*Tenebrio molitor*). Although we did not measure whether the mealworm was eaten by each individual bird, it can be considered that this possible bias is marginal. Mealworms showed a mean weight of 0.15 g, whilst Bluethroats showed a body mass ranging between 16.0 g and 19.8 g. Thus, a mealworm would represent less than 4% of difference in body mass between the leanest and the heaviest Bluethroats. A tape lure with the breeding song of a male Bluethroat was put near the trap in order to attract the male. Once captured, each bird was ringed and aged (Svensson 1996) either as second calendar year (2Y; EURING code 5; identified by having juvenile feathers in their wings) or adult (>2Y; EURING code 6; older birds, with no juvenile feathers in their wings, thus with more experience as breeders than 2Y). We then recorded wing length (± 0.5 mm; method III by Svensson 1996), tarsus length (± 0.1 mm) and body mass (± 0.1 g, with a digital balance). Overall, we captured 44 Bluethroats, corresponding to 22 2Y and 22 >2Y males.

2.2. Data analyses

To obtain an index of individual body condition we regressed body mass on either wing length or tarsus length. We obtained a better fit to the data when using tarsus length ($r^2 = 0.147$, $F_{1,43} = 7.241$, $p = 0.010$) than wing length ($r^2 = 0.070$, $F_{1,43} = 3.171$, $p = 0.082$), and hence the residual values of a regression of body mass on tarsus length were used as an index of body mass in relation to body size (Schulte-Hostedde *et al.* 2005). Such values fitted well to a normal distribution (K–S test: $Z = 0.595$, $p = 0.871$).

Table 1. Factor loadings of the components one and two ($PC1_S$ and $PC2_S$, respectively) obtained from a PCA on the soil cover-associated variables.

Soil covers	$PC1_S$	$PC2_S$
Shrubs (brooms)	–0.994	–0.024
Grassland	+0.569	+0.818
Bare soil	+0.644	–0.760
Eigenvalue	1.728	1.246
Variance [%]	57.593	41.549

Habitat cover and the relative abundances of each prey type were expressed as percentages, so they were highly inter-correlated variables. To avoid these inter-correlations, we performed Principal Component Analyses (PCA). For habitat cover, components one and two ($PC1_S$ and $PC2_S$, respectively) showed eigenvalues >1 (Table 1), thus they were used for the subsequent analyses as a surrogate of habitat cover. The $PC1_S$ was negatively and highly correlated with the broom cover and positively correlated with the other two variables (grassland, bare soil), indicating that positive scores of this $PC1_S$ were associated with zones with lower proportion of broom cover, but with higher proportion of grass or bare soil. The $PC2_S$ was negatively and highly correlated with surfaces rich in bare soil, and positively correlated with grasslands. For the relative abundance of potential prey type, we obtained six components ($PC1_F$ to $PC6_F$) with eigenvalues > 1 (Table 2). The $PC1_F$ to $PC4_F$ accounted for more than 50% of the variance and they were associated (respectively), with relatively more Opiliones and less ants ($PC1_F$), less Coleoptera and more ants ($PC2_F$), less Dermaptera and more Diptera ($PC3_F$), and less Homoptera ($PC4_F$) (Table 2). Two more PCs ($PC5–6_F$) also showed an eigenvalue > 1, so they were also considered in the analyses (Table 2). Moreover, we

Table 2. Factor loadings of the components one to six ($PC1_F$–$PC6_F$) obtained from a PCA on abundance of 14 arthropod taxa potentially preyed by Bluethroats at Sierra de Candelario.

Taxa	$PC1_F$	$PC2_F$	$PC3_F$	$PC4_F$	$PC5_F$	$PC6_F$
Araneae	+0.523	+0.265	+0.259	+0.512	–0.019	+0.077
Opiliones	+0.773	+0.280	+0.045	–0.013	–0.101	+0.302
Geophilomorpha	+0.129	+0.000	+0.452	+0.126	+0.660	+0.222
Dictyoptera	+0.172	+0.184	–0.049	–0.237	+0.072	–0.752
Orthoptera	+0.069	–0.317	+0.387	+0.540	–0.428	–0.145
Dermaptera	+0.504	–0.018	–0.619	+0.202	+0.116	+0.199
Thysanoptera	–0.267	+0.269	–0.039	+0.114	+0.491	+0.096
Homoptera	+0.187	–0.055	+0.241	–0.780	–0.203	+0.270
Heteroptera	–0.247	–0.291	–0.122	–0.072	–0.227	+0.477
Coleoptera	+0.003	–0.795	–0.442	+0.142	+0.072	–0.121
Diptera	+0.281	–0.454	+0.575	–0.179	+0.295	–0.142
Lepidoptera	–0.026	+0.282	+0.289	+0.081	–0.505	–0.037
Hymenoptera–Form*	–0.734	+0.627	–0.046	+0.088	+0.023	+0.040
Hymenoptera–No Form	+0.674	+0.376	–0.307	–0.145	–0.008	–0.151
Eigenvalue	2.415	1.895	1.589	1.381	1.331	1.143
Variance [%]	17.253	13.537	11.348	9.865	9.506	8.161

* Form: Formicidae

also considered the standardized number of captures (mean number of individuals per trap and post) of the main arthropod taxa captured during the study (Fig. 1); these taxa were accounted for 91.6% of total abundance and appeared in practically all the samples: ants, Coleoptera, Araneae, Homoptera and Diptera.

Potential prey diversity was estimated by using the Shannon index $H' = -\Sigma p_i \times \ln(p_i)$ (Magurran & McGill 2011), where p_i is the proportion of each prey type around each post.

We conducted Generalized Linear Models (GLMs) to check whether males' condition (age and residual mass) varied in relation with a number of characteristics around the post. In particular, we run two sets of GLMs, each considering one of the following object variables: age (introduced as a binary variable) and residual body mass (introduced as a linear variable). In the former case we used a logistic binary link function and in the second case, a linear link function. The following independent variables were used: altitude, vegetation height, post height, $PC1_S$ and $PC2_S$, $PC1_F$ to $PC6_F$, H' index and total standardized number of captures of the five most frequent taxa (Aranae, Homoptera, Coleoptera, Diptera, ants). For the GLMs on residual body mass, we also included an additional variable, the hour when the bird was captured, since body mass would be expected to change (increase) across the day (Gosler & Carruthers 1999, Polo & Bautista 2002, Lange & Leimar 2004).

Model selection was carried out using the "MuMin" package for R (Barton 2014). Owing to the low sample sizes we added some constraints to the selection procedure: we only considered additive models with a maximum of two parameters and the intercept. We used the small sample sizes-corrected Akaike criterion (AICc) to test for the fit of models to data (Burnham & Anderson 1998). Models differing by less than 2 AICc (ΔAICc <2) values were considered to fit the data equally well (Burnham & Anderson 1998). Because models with additional unsupported parameters will be likely to be within 2 AICc units and these models were non-competitive unless the extra parameter leads to a reduction in AICc (Arnold 2010), we analysed in detail the *B*-parameters from all models having an ΔAICc < 2 from the first parameter to see the parameters with a really significant effect. Parameters with a 95% CI including zero showed a non-significant effect of that variable (Taylor *et al.* 2004). Statistical procedures were run with the software R (R Core Team 2014).

Table 3. Mean (± SE) values and the corresponding *t*-test comparison of individual condition-related variables of male Bluethroats captured as breeders at Sierra de Candelario in 2011 and 2012, in relation to their age class (2Y, second-year Bluethroats, *n* = 22; >2Y, older birds, *n* = 22).

Variable	2Y	>2Y	t_{42}	*P*
Wing length [mm]	77.0 ± 0.3	78.8 ± 0.5	2.879	0.006
Tarsus length [mm]	26.8 ± 0.3	27.5 ± 0.2	1.804	0.078
Body mass [g]	18.3 ± 0.2	18.8 ± 0.2	2.150	0.037
Residual body mass [no unit]	–0.18 ± 0.18	0.18 ± 0.16	1.528	0.134

Table 4. Parameter estimates (*B*), the associated standard errors (SE) *P*-values, of the best two models used to predict age classes or individual body condition in relation to the habitat quality surrounding a song post. All models consider ">2Y" Bluethroats as the reference age. Therefore, a positive effect of a variable (i.e., positive *B*) is associated with higher values of that variable among 2Y birds compared to >2Y.

Models	*B*	SE	*P*
Object variable: age			
(Intercept)	+1.21	0.57	0.033
$\mathrm{PC2_S}$	+0.90	0.47	0.054
Araneae	–0.95	0.39	0.014
Object variable: residual mass			
(Intercept)	–0.44	0.51	0.395
Hour	+0.06	0.03	0.037
$\mathrm{PC2_S}$	+0.28	0.12	0.025
$\mathrm{PC1_F}$	+0.30	0.13	0.395
$\mathrm{PC6_F}$	–0.23	0.12	0.060
Homoptera	–0.19	0.10	0.078

Table 5. Ranking of the best models predicting residual body mass (i.e., body condition) in Bluethroats. Variables: for $\mathrm{PC1_F}$, $\mathrm{PC6_F}$ and $\mathrm{PC2_S}$, see Tables 1 and 2; Hour: hour when the bird was captured; Homo, standardized number (abundance) of Homoptera. Abbreviations: AICc – Akaike information criterion corrected for small sample sizes; Weight – Akaike weights based on AICc.

Models	AICc	Weight
$\mathrm{PC1_F}$ + Hour	107.54	0.10
$\mathrm{PC2_S}$ + Hour	108.31	0.07
$\mathrm{PC2_S}$ + $\mathrm{PC6_F}$	108.58	0.06
$\mathrm{PC1_F}$ + Homo	109.31	0.04

3. Results

We studied 44 song posts, corresponding to 22 2Y and 22 >2Y males. Wing length and body mass, but not tarsus length and residual body mass, varied between age classes (Table 3). Overall, >2Y males showed longer wings and tarsi, and higher body mass.

Overall (mean values for the entire sample), male Bluethroats were captured at 1,910 ± 9 (SE) m a.s.l., within a song post of 83.8 ± 3.5 cm height, surrounded by vegetation of 52.8 ± 3.2 cm height, with habitat cover of 78.0% ± 2.6% broom, 11.0% ± 2.0% grassland, and 10.0 ± 2.0% bare soil. The mean *H*' index was found to be 1.28 ± 0.06. With almost 60% of total abundance, ants were by far the most abundant available prey (Fig. 2).

Regarding bird age, the model which best fitted our data was that which included an additive effect of $\mathrm{PC2_S}$ and the amount of spiders (Aranae) (AICc = 55.54, AICc weight = 0.16). This model was 2.10 units above the second one, which was shown to have an AICc = 57.64 (AICc weight = 0.06). A look at the *B*-parameters of model one showed a positive, although marginal effect of $\mathrm{PC2_S}$ on age, but a negative significant effect of the amount of spiders on age (Table 4). Therefore, overall, >2Y Bluethroats tended to occupy posts with lower abundances of spiders as compared to 2Y Bluethroats.

Regarding residual body mass, the model which best fitted our data was one including an effect of the hour and $\mathrm{PC1_F}$ (the model had an AICc = 107.54, AICc weight = 0.10). However, we detected 3 additional models with AICc values at a difference < 2 in relation to the top model (Table 5). Averaged coefficients revealed a positive, significant effect of the hour and $\mathrm{PC1_F}$ and $\mathrm{PC2_S}$ on residual body mass. Thus, birds caught in places with proportionally greater cover of grasslands and with more Opiliones tended to be heavier.

4. Discussion

Potential food availability and habitat had significant effects on both age and body condition of male Bluethroats captured at song posts in their breeding areas at high altitude in central Iberia.

Regarding ages, we observed that second-year (2Y) Bluethroats tended to be captured at places with greater abundance of spiders. Although the number of traps was small (two traps per song post), this result is consistent with the rest of the analyses of this study suggesting that variations in prey abundance were only possibly due to habitat specific variations in prey densities. Causes underlying this association remain unknown, but we may propose some plausible hypotheses. Out of all captured potential prey (Fig. 1), the spiders may be preyed upon preferentially owing to their abundance, palatability (they have a softer body than other arthropods) and higher energy reward compared to other prey groups (Norberg 1978).

Thus, spiders were likely to be an easily detectable prey also rich in energy, an aspect which might be very relevant for those individuals which may need to settle in places rich with particular food resources, in this case spiders. Younger Bluethroats, such as those undertaking their first breeding attempt, may give priority to this requirement. In contrast, older birds (>2Y), with more experience, could prioritize other parameters (e.g., places with more shelter, better places to nest), even if this could entail lower availability of accessible prey with a high energy reward.

In this possible scenario, our results may support the idea that either first-breeding birds prioritize food access at their breeding sites, whilst older birds might not give priority to this factor, or that older birds could prioritize food access to chicks, which might be abundant at different times or in certain habitats. Also, second-year birds could be excluded from the best breeding habitats, rather than selecting different habitats than older birds. Furthermore, all else being equal, 2Y songbirds are less likely to secure a mate and establish a territory than >2Y, allowing them greater flexibility in their use of areas and habitats with more abundant, perhaps changing, food resources (e.g., Holt *et al.* 2012). These hypotheses should be tested in future studies of Bluethroats.

Residual body mass (i.e., body condition) did not vary between age classes, and tended to be higher in zones where Bluethroats were surrounded by proportionally larger areas of grassland and with more Opiliones/spiders. A positive relationship between these factors supports the idea stated above: that spiders probably provide more energy reward than other prey types, hence birds settling in places with more arachnids have a better body condition.

Alternatively, it is possible that Bluethroats settling in suboptimal habitats might regulate their body mass at higher levels than dominant Bluethroats, which might reduce predation risk by maintaining a lower body mass (Kullberg *et al.* 1996). The status of those birds having higher residual mass remains unknown to us. Our models indicate that residual body mass did not vary between ages, hence other factors may explain why some birds were more fuel loaded than others. Maybe Bluethroats with a higher residual body mass, which also occupied habitats richer in grasslands (considered suboptimal to breed), could be impaired males or birds that still did not have a well-established, definite territory.

This result also suggests that these grasslands could have an important role for the entire breeding population, including the fledglings, due to the availability of prey that might allow rapid mass gain, or at least lower foraging effort, compared to other habitat types. In this study area, the mosaic comprising broom areas and grasslands may be of great conservation value for the population.

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Onko espanjalaisten sinirintakoiraiden ikä ja kunto yhteydessä laulupaikkoja ympäröivään habitaattiin?

Sinirintakoiraat laulavat vakiintuneissa paikoissa houkutellakseen naaraita ja puolustaakseen reviiriään. Selvitimme, onko laulupaikkojen ympäröivän habitaatin laatu yhteydessä koiraan laatuun – linnun kuntoon (rasvan määrään) tai ikään, olettaen että ikä kuvaa kokemusta. Keräsimme aineistoa Keski–Länsi-Espanjassa sijaitsevassa Sierra de Béjarissa (Salamancan maakunnassa) vuosina 2011 ja 2012. Pyydystimme yhteensä 44 koirasta laulupaikoiltaan ja arvioimme niiden ympäröivän habitaatin laatua, mm. ravinnon määrää.

Sinirintakoiraiden laulupaikkojen- ja ympäröivän habitaatin laatu olivat yhteydessä sekä lintujen ikään että kuntoon. Verrattuna vanhempiin lintuihin, toisen kalenterivuoden koiraat lauloivat paikoissa joissa oli enemmän hämähäkkejä. Lisäksi, hyväkuntoisten lintujen laulupaikkojen ympärillä oli enemmän ruohomaata, lukkeja ja hämähäkkejä.

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