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Habitat structure influences the song characteristics within a population of Great Tits *Parus major*

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ABSTRACT

Capsule: The structure of Great Tit *Parus major* songs is shaped by the acoustic properties of the habitat within the breeding territory of individuals.

Aim: To test whether the structure of the habitat influences song structure within a population of Great Tits *P. major*.

Methods: We recorded Great Tit songs from 42 territories on two different days and measured the habitat structure in each territory. We also trapped the males and estimated the breeding density around each territory, so were able to control the analysis by date, breeding density and male characteristics.

Results: Song pause length was positively affected by the ground cover, while the song rate and the minimum frequency were negatively affected by the shrub cover. Male size negatively affected the peak frequency of the songs, whereas the age of the males affected the frequency range; older males sang with a broader bandwidth.

Conclusion: This study suggests that Great Tits are capable of adjusting their vocalizations in each territory, presumably to enhance transmission owing to vocal plasticity.

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Acoustic communication plays an essential role in the lives of many animal species across different taxa, as it is involved in the regulation of social relationships (reviewed in Bradbury & Vehrencamp 1998). This is particularly true in the case of songbirds because many rely on long-range acoustic signals to gather information about each other and resolve conflicts over resources such as food, territories or mates, without the need to engage in more costly interactions, such as fights (McGregor & Dabelsteen 1996, Peake *et al.* 2001, Searcy & Beecher 2009, Maynard *et al.* 2012). Acoustic communication consequently has a direct influence on their survival and reproductive success (Andersson 1994, Slabbekoorn 2013) and it is, therefore, crucial for songbirds to get their message across to potential receivers unaltered in order to fulfil the biological function of communication (Brumm & Naguib 2009). In this respect, bird songs may have evolved in response to the acoustic properties of each habitat to enhance sound transmission, as is proposed in the Acoustic Adaptation Hypothesis (Morton 1975).

The acoustic properties of each habitat are determined by climate conditions, vegetation structure and background noise (Brumm & Naguib 2009), and the three of them condition the degree to which bird songs are attenuated, degraded or masked while propagating across a habitat. These three phenomena diminish the active space of the acoustic signals (Wiley & Richards 1982) and consequently make effective communication more difficult (Slabbekoorn 2013). Attenuation is the loss of the intensity of the acoustic signal with distance owing to the spherical spreading of the sound waves (i.e. the energy per unit surface). However, in natural habitats an excess of attenuation exists owing to vegetation structure and atmospheric absorption (Catchpole & Slater 2008). More specifically, broadleaved foliage poses a serious obstacle to sound transmission as it scatters the sound waves and attenuation increases as foliage becomes denser (Wiley & Richards 1982). The level of attenuation is highly dependent on the frequency of the sound. Higher frequencies tend to have greater attenuation than lower frequencies. This is because they are more easily absorbed by the atmosphere and they do not move around obstacles as easily as low frequencies owing to their shorter wavelength (Catchpole & Slater

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2008). Degradation is the sum of the structural changes that the acoustic signal accumulates at some distance from the source (Morton 1986). It is principally a consequence of the scattering referred to above, and the echoes and reverberations from the ground, foliage and tree trunks which cause alterations in frequency and timing rearrangements in the acoustic signal (Bradbury & Vehrencamp 1998). In closed habitats, such as those with dense vegetation, the sound waves degrade to a greater extent than in more open habitats (Naguib 2003). Background noise is possibly the most limiting acoustic property for bird song transmission (Brumm & Naguib 2009) and involves the acoustic signal being masked in the frequency range in which noise and signal overlap (Brumm & Slabbekoorn 2005). The restrictions that the acoustic properties of habitats impose on signal transmission may explain why the songs of birds belonging to closed habitat species are characterized by having lower frequencies, narrower bandwidths and longer inter-element intervals than those of birds belonging to more open habitat species (Boncoraglio & Saino 2007), as is predicted in the Acoustic Adaptation Hypothesis.

A problem may arise when the acoustic properties in a habitat change, because the acoustic signals may lose transmission efficiency in these new conditions and their active space may be reduced (Brumm & Slabbekoorn 2005). The acoustic properties in many habitats changed in the last century as a result of human activities (Kight *et al.* 2012). A recent example that has attracted the attention of biologists in recent years is the increase in anthropogenic noise (Warren *et al.* 2006, Blickley & Patricelli 2010), which impairs the communication of those species that are unable to modify their acoustic signal so as to make themselves heard in the presence of the background noise (Francis *et al.* 2011, Proppe *et al.* 2013). Besides background noise, the structural modifications that human activity produces in natural habitats (i.e. urbanization, forest clearance or intensive farming) also change the acoustic properties, thus affecting signal transmission, as the vegetation structure and microclimate vary (Kopuchian *et al.* 2004, Nicholls & Goldizen 2006).

Understanding the effect of habitat change on bird communication and the way in which songbirds cope with new acoustic environments is essential for understanding both the evolution of bird song and the impact on conservation biology (Kight *et al.* 2012). If adaptation to acoustic habitat properties is effectively a strong selective force that acts upon bird song, as the Acoustic Adaptation Hypothesis proposes, then it might be expected that there would also be habitat related variation in song structure within populations (Hunter & Krebs 1979). Although many studies have sought relationships between habitat structure and bird song structure among different species or populations (reviewed in Boncoraglio & Saino 2007), very few have investigated this topic at the population level. The aim of this study was, therefore, to test whether the habitat structure within a territory affects the song characteristics of the owner in a population of Great Tits *Parus major*. Great Tits constitute an ideal species with which to study this topic because they are one of the most frequently studied species in terms of acoustics (Slabbekoorn 2013) and they predominantly use their song as a long-range signal in the context of territorial behaviour (Krebs *et al.* 1981). This species cues on song characteristics such as frequency, song rate or strophe length in order to assess conspecifics by eavesdropping (Peake *et al.* 2001) and distinguish individuals (Weary & Krebs 1992). They also estimate the distance to the sender by song degradation cues (McGregor & Krebs 1984). We hypothesize that the habitat structure within a territory will affect the songs of Great Tits, and predict that those Great Tits that breed in territories with denser vegetation will perform more ‘forest’ songs (i.e. with a relatively lower minimum frequency and longer inter-element intervals) than conspecifics breeding in more open territories.

Material and methods

Study area

The study was conducted in the locality of San Pablo de los Montes (Toledo, central Spain, 39°32′44″N 4°19′41″W). The whole study area has a continental Mediterranean climate, with mean values of annual rainfall of 700–800 mm concentrated in autumn and spring, and pronounced summer droughts with a wide daily thermal oscillation. The study area is made up of deciduous Pyrenean Oak *Quercus pyrenaica* forests accompanied by their typical associated shrubs, mainly formed of Strawberry Tree *Arbutus unedo*, Common Hawthorn *Crataegus monogyna*, Elmleaf Blackberry *Rubus ulmifolius*, Terebinth *Pistacia terebinthus*, Flax-leaved Daphne *Daphne gnidium* and Common Broom *Cytisus scoparius*. These forests are considered to be the most suitable breeding habitats for Great Tits in the area (Atiénzar *et al.* 2012). However, this landscape has been fragmented as the result of human activities, as in other regions of the Mediterranean Basin (Blondel & Aronson 1999), and the remaining forest patches can be considered as ‘habitat islands’ dispersed in a matrix of less suitable pasturelands (García-Navas *et al.* 2014). For this study, we selected ten oak patches separated from each other by a mean distance of 4.2 km, and provided each with a number of nestboxes accordingly to their size. All nestboxes were separated from each other by at least 30 m and were placed at least 50 m from the forest edge. Background noise is homogeneous throughout the study sites because of the reduced urbanization of the area, with a mean (± se) value of 37.41 ± 0.38 dB measured in a previous study (Bueno-Enciso *et al.* 2015).

Field procedure

During the breeding season from 13 March 2012 to 23 May 2012 (day 1 = 1 March) and between 08:00 and 12:00 hours, we recorded Great Tit songs using an EDIROL R-09HR digital recorder equipped with a Sennheiser unidirectional microphone and headphones, pointed directly towards the singing individual. All song recordings were made at a distance of 10–25 m.

We visited each forest patch at least three times, and noted the exact position of the singing male on a map with the aid of a handheld global positioning system (GPS) unit. We identified the individual birds by the territorial behaviour associated with a particular nest box (Doutrelant *et al.* 2000). For the analysis, we included only those males that were recorded on at least two different days, within a radius of 15 m from a nest box occupied by a pair of Great Tits (Rivera-Gutierrez *et al.* 2010). The regular inspection of the nest boxes allowed us to determine the stage of the reproductive cycle of the Great Tit pairs when the recordings were made. As male phenology influences Great Tit songs (Halfwerk *et al.* 2011), only those songs recorded after the nest was built but before the last egg was laid were used in our analyses, as this coincides with the fertile period of the female (Mace 1987). It is in this period that males increase their song activity and mate-guarding behaviour so as to minimize the risk of cuckoldry (Møller 1991, Slagvold *et al.* 1994, Ritschard *et al.* 2011). We captured the males while they were feeding their chicks (8–9 days old), weighed them with a portable digital balance (to the nearest 0.1 g), measured their tarsus length with a digital caliper (0.01 mm) and aged them (yearling or older) according to plumage characteristics. The body condition index of males was obtained from the standardized residuals of a linear regression in which the body mass was the dependent variable and the tarsus length was the predictor. We calculated the density of Great Tits in each breeding territory as the number of Great Tit breeding pairs in a radius of 50 m around each nest box with the aid of Quantum GIS 2.0.1. We used this number of breeding pairs in the neighbourhood of a territory as an index of the intensity of competition among males, as this is an important factor that affects song performance (Martin-Vivaldi *et al.* 2004, Hamao *et al.* 2011).

All applicable institutional and/or national guidelines for the care and use of animals were followed.

Habitat structure

At the end of the breeding season (day 90), we estimated (by eye) the vegetation structure of the breeding territories in a sampling plot centred on the nest box with a radius of 25 m. This area is hereafter referred to as the territory surrounding the nest box, based on the assumption that it is representative of the habitat structure of the whole territory of breeding pairs (Svensson & Nilsson 1995). The structural variables of the breeding territories included the diameter at breast height (DBH) of oak trees (measured on three random oaks for each territory), and the percentages of tree, shrub and ground cover. Ground cover includes the bare soil and the grass cover in order to simplify the analyses, as Great Tits do not sing from the ground (Marten & Marler 1977).

Song analyses

As stated previously, two song recordings from different days were analysed for each male, as this was the maximum sample size available for all the males recorded. The maximum time gap between two recording days for a male was four days. Following this procedure, 42 different first brood males that held their own territory were selected, which gives a total of 84 Great Tit song recordings used in the analyses. Great Tits have a small discrete repertoire (Lambrechts & Dhont 1986), in which each song type is sung in bouts of the same strophe type, and the separation between adjacent strophes is called a pause. Each strophe is composed of a repetition of the same phrases, which are in turn composed of notes. For song analyses, we selected ten different strophes of each song recording, and exported them to the RavenPro 1.4 programme (Charif *et al.* 2010). After a visual inspection of each audio track, we used a band filter to remove low frequency background noise from the recording without the removing any components of the song (Mockford & Marshall 2009). We focused on the spectral level of the description of the songs (Baker 2006) and measured each strophe separately. We averaged the ten strophes selected from the same song type. The song characteristics measured were: number of notes that comprise each phrase, strophe length (seconds), pause length (seconds), song rate (ratio between the number of phrases and the strophe length), minimum, maximum and peak frequency (Hz) and the bandwidth (difference between the maximum and the minimum frequency, Hz). The average number of phrases was not used in the analyses as it was highly correlated with the strophe length ($r = 0.74$, $n = 84$, $P < 0.001$). Peak frequency was measured automatically, while the remaining variables were measured manually using a Hann window and a fast Fourier transformation with a length of 1024, resulting in a spectral resolution of 43.1 Hz. Minimum and maximum frequencies were measured manually by precisely placing a selection box in the spectrogram view, similar to the method described by Francis *et al.* (2011).

Statistical analyses

In order to test whether the structure of the habitat in each territory affects the song characteristics of Great Tits, we used each habitat variable as an explanatory variable. This enabled us to include all the variations in the habitat structure in each territory, which allowed us to see which specific habitat component influenced each song characteristic. We also included the number of days between the date of each song recording and the date on which the habitat structure was measured as an explanatory variable (relative date). We therefore separated the influence of the date on the singing performance of birds (Lambrechts & Dhont 1986) owing to changes in the motivation and singing practice of the males (Vehrencamp *et al.* 2013) and the phenotypic differences in singing males throughout the breeding season (Perrins 1970). This also allowed us to control for the possible effects that the emergence of leaves in the deciduous forests might have on the singing performance of Great Tits, as it changes the acoustic properties of the habitat (Blumenrath & Dabelsteen 2004). Individuals might consequently change their song characteristics to match these new environmental acoustic properties (Brumm & Naguib 2009). Another factor that may influence the song characteristics of birds is breeding density, as it is an index of the intensity of competition among males (Hamao *et al.* 2011). Relative date and breeding density, together with habitat characteristics and the intrinsic male characteristics can also affect the characteristics of the songs (Derryberry 2009, Slabbekoorn 2013, Read *et al.* 2014), and we therefore included the age, body size and body condition of males as explanatory variables, because of the singing expertise that males acquire with age (Vehrencamp *et al.* 2013, Ota & Soma 2014), the body size constraints in the frequency performance of the songs (Ryan & Brenowitz 1985, Wiley 1991, Price *et al.* 2006) and the body condition constraints owing to the costs of singing (Gil & Gahr 2002, Juola & Searcy 2011). We therefore attempted to explain the variance of each song characteristic with the following nine explanatory variables: relative date, breeding density, mean DBH, tree, shrub and ground cover, male age, tarsus length (as a surrogate of body size) and male condition. We tested whether there was collinearity among these explanatory variables by first obtaining the Variance Inflation Factor (VIF) scores for each one (Table 1). However, all the explanatory variables had a VIF score below 2 and following the recommendations of Zuur *et al.* (2009), we decided to keep all of them in the analyses. For this exploratory analysis we used R (R Core Team 2014) and the 'corvif' function of the Highland Statistics Ltd. R package (Zuur *et al.* 2009).

Table 1. VIF scores for each independent variable used to explain the variance of the song characteristics within a population of Great Tits *Parus major* in San Pablo de los Montes (Toledo, central Spain).

Explanatory variable	VIF score
Relative date	1.39
Breeding density	1.31
DBH (cm)	1.74
Tree cover (%)	1.19
Shrub cover (%)	1.22
Ground cover (%)	1.23
Male age	1.59
Tarsus length (mm)	1.26
Male condition	1.36

We then created linear mixed-effect models (LMMs) with each spectral song characteristic as a dependent variable and the nine explanatory variables as independent variables. The number of notes was analysed by using generalized linear mixed-effect models (GLMMs) fitted with a Poisson distribution. In all models, the identity of the Great Tit male (Male ID) nested in the identity of the forest patch (Patch ID) was included as a random term. All of the mixed-effect models were created using the function 'lme' in the lme4 package (Bates *et al.* 2014).

Assumptions of homoscedasticity and normality were verified graphically with the residuals in each model (Zuur *et al.* 2009). The initial LMMs and GLMMs were constructed with all independent variables fitted, and final models were selected following a backward procedure by progressively eliminating non-significant variables.

Results

Of all the song characteristics measured, only the number of notes and the maximum frequency were not affected by any of the explanatory variables included in the mixed-effect models (Table 2). With regard to these explanatory variables, the relative date negatively affected the strophe length of the songs. That is, at the beginning of the breeding season Great Tits sang with shorter strophes. Breeding density did not affect any of the song characteristics (Table 2). In relation to the structural habitat characteristics, DBH and tree cover did not affect any of the song characteristics but shrub cover and ground cover did. More specifically, the shrub cover negatively affected the song rate and the minimum frequency of the songs (Figure 1(a) and (b), respectively), whereas ground cover positively affected the pause length (Table 2 and Figure 1(c)). With regard to the male characteristics, the age of the males positively affected the bandwidth of the songs, with older males singing with a broader bandwidth than younger ones (Figure 2(a)), and the tarsus length negatively affected the peak frequency (Figure 2(b)). Finally, male condition positively affected the strophe length (Table 2 and Figure 2(c)).

Discussion

The relative date affected only the strophe length of Great Tit songs. One way in which the date could affect the song structure in deciduous forests, that particularly concerns this study, is indirectly through the emergence of leaves, which change the acoustic properties of the habitat. In their acoustic transmission experiment, Blumenrath & Dabelsteen (2004) showed that the active space of an acoustic signal is reduced by half with budding owing to attenuation and degradation from broadleaved foliage. In our study area, the phenology of oaks is almost synchronized among forest patches because of their similar altitude and orientation, and the reduced geographical extension that they occupy, which imposes homogeneous climate conditions. The emergence of leaves in this area might, therefore, impose some constraints on the song performance that could be detected seasonally. However, the Great Tits' song had a shorter strophe length at the beginning of the breeding season than later on. Singing with short strophes may reduce the degradation of the acoustic signals because it diminishes the risk of the echoes and reverberations of the sound waves intermingling with each other and causing structural changes (Bradbury & Vehrencamp 1998). Nonetheless, the time when the performance of songs with short strophes took place challenges this explanation because it was at this time when the risk of degradation was lower, owing to the absence of leaves on trees (Blumenrath & Dabelsteen 2004). Consequently, it is possible that the effect of the relative date on the strophe length responded to changes in the singing males throughout the breeding season as regards either phenotype, motivation or practice, rather than to changes in the acoustic habitat properties (Vehrencamp *et al.* 2013). Contrary to the relative date, the density of breeding Great Tits in the surroundings of each territory did not significantly affect any song characteristic, despite the fact that the intensity of competition among males in this species has been shown to affect aspects of their songs (Hamao *et al.* 2011). Nonetheless, the aforementioned study was conducted in a city, in which the density of breeding birds is typically higher than in forests (Marzluff 2001). It may, therefore, be that the breeding density in our study area remains low enough to not significantly affect the song characteristics in our population of Great Tits.

With regard to the effects that the habitat structure has on Great Tit songs, the only habitat variables that significantly affected their songs were the shrub and ground cover. The fact that the tree cover and the relative date did not affect the song characteristics in our population of Great Tits suggests that the emergence of leaves had no effect on Great Tit songs in our study area, as shrub and ground cover were almost invariable throughout the breeding season. The way in which songbirds can counteract the effects of broadleaved foliage on sound transmission is by diminishing the height of their singing perch and singing beneath the canopy, because of a sound 'channel' between the canopy and the undergrowth (Blumenrath & Dabelsteen 2004). This change in the sender position would prevent changes in the song structure resulting from the inevitable emergence of leaves, which would be adaptive if changes in the song characteristics entailed changes in the message (Patricelli & Blickley 2006, Slabbekoorn & Ripmeester 2008, Halfwerk *et al.* 2011, Luther & Magnotti 2014, McMullen *et al.* 2014). This behavioural response could be occurring in our population, although we were unable to confirm this as we did not measure the singing height of the individuals. Great Tits therefore confront the impediments that habitat structure imposes on sound transmission beneath the tree canopy from the beginning of the breeding season and may therefore adjust their vocalizations to match these invariable acoustic habitat properties shortly after settling into their territories. Great Tits specifically sang with a slower song rate and a lower minimum frequency in territories with high shrub cover, similar to the result obtained by Derryberry (2009). Singing fast may be disadvantageous in this type of territory, since rapid and consecutive sound waves can easily intermingle with each other owing to the echoes and

Table 2. Results of the mixed-effect models analysing the effects of the date, breeding density, habitat structure and male characteristics on the song characteristics of Great Tits *P. major* in San Pablo de los Montes (Toledo), central Spain. The ID male nested in ID patch is included in all models as the random term. Significant results are highlighted in bold.

	Number of notes			Song rate			Strophe length (s)			Pause length (s)		
	Estimate ± se	*z* value	*P*	Estimate ± se	*t* value	*P*	Estimate ± se	*t* value	*P*	Estimate ± se	*t* value	*P*
Intercept			n.s.			n.s.	10.08 ± 3.86		0.01			n.s.
Relative date	1.57e^{-6} ± 0.01	0.00	1.00	0.35 ± 0.36	0.42	0.52	−0.02 ± 0.01	−2.21	**0.03**	0.01 ± 0.03	−1.16	0.84
Breeding density	0.01 ± 0.07	0.06	0.95	−0.04 ± 0.1	−0.42	0.68	−0.08 ± 0.09	−0.88	0.39	0.16 ± 0.37	0.45	0.66
DBH (cm)	0.01 ± 0.01	0.85	0.40	0.003 ± 0.01	0.04	0.83	−0.02 ± 0.02	−1.21	0.23	−0.04 ± 0.06	−0.80	0.43
Tree cover (%)	0.001 ± 0.004	0.40	0.69	−0.01 ± 0.01	−1.53	0.13	−0.003 ± 0.01	−0.54	0.59	−0.02 ± 0.02	−1.20	0.24
Shrub cover (%)	0.002 ± 0.003	0.67	0.50	−0.01 ± 0.004	−2.13	**0.03**	−0.01 ± 0.004	−1.99	0.06	−0.001 ± 0.02	−0.28	0.78
Ground cover (%)	0.001 ± 0.003	0.34	0.74	−0.01 ± 0.01	−1.64	0.11	−0.001 ± 0.01	−0.03	0.98	0.03 ± 0.01	2.35	**0.02**
Male age	0.04 ± 0.09	0.41	0.68	0.14 ± 0.10	1.34	0.18	−0.20 ± 0.11	−1.88	0.07	0.07 ± 0.45	0.16	0.87
Tarsus length (mm)	−0.04 ± 0.12	−0.32	0.75	0.19 ± 0.15	1.21	0.23	−0.24 ± 0.17	−1.41	0.17	1.05 ± 0.60	1.75	0.09
Male condition	−0.01 ± 0.08	−0.16	0.88	−0.01 ± 0.12	−0.1	0.92	0.20 ± 0.09	2.19	**0.03**	0.44 ± 0.40	1.11	0.27

	Maximum frequency (Hz)			Peak frequency (Hz)			Minimum frequency (Hz)			Bandwidth (Hz)		
	Estimate ± se	*t* value	*P*	Estimate ± se	*t* value	*P*	Estimate ± se	*t* value	*P*	Estimate ± se	*t* value	*P*
Intercept			n.s.	9955.06 ± 1985.09		<0.001	4635.76 ± 2254.98		0.04			n.s.
Relative date	−0.62 ± 10.45	−0.06	0.95	−9.19 ± 4.63	−1.99	0.06	−6.61 ± 5.32	−1.24	0.22	4.10 ± 9.32	0.44	0.66
Breeding density	−13.68 ± 121.60	−0.11	0.91	−77.01 ± 53.98	−1.43	0.16	−34.54 ± 62.00	−0.56	0.58	40.98 ± 108.35	0.38	0.71
DBH (cm)	12.28 ± 16.97	0.72	0.48	−6.82 ± 7.09	−0.96	0.37	8.94 ± 7.85	1.14	0.26	8.97 ± 16.39	0.55	0.59
Tree cover (%)	0.26 ± 6.26	0.04	0.97	0.87 ± 2.72	0.32	0.75	0.91 ± 3.09	0.29	0.77	0.75 ± 5.69	0.13	0.90
Shrub cover (%)	−2.18 ± 5.52	−0.40	0.69	−2.32 ± 2.48	−0.93	0.36	−8.14 ± 2.87	−2.83	**0.01**	4.21 ± 4.85	0.87	0.39
Ground cover (%)	0.94 ± 5.04	0.19	0.85	0.02 ± 2.24	0.01	0.99	1.99 ± 2.56	0.78	0.44	0.34 ± 4.45	0.08	0.94
Male age	272.83 ± 145.19	1.88	0.06	7.39 ± 64.44	0.12	0.91	−4.64 ± 72.29	−0.06	0.95	324.8 ± 128.68	2.52	**0.01**
Tarsus length (mm)	−2.57 ± 201.86	−0.01	0.99	−247.52 ± 88.14	−2.81	**0.01**	−44.86 ± 100.40	−0.45	0.66	7.44 ± 183.91	0.04	0.97
Male condition	46.54 ± 132.503	0.35	0.73	49.92 ± 59.62	0.84	0.41	117.21 ± 68.99	1.70	0.10	−68.11 ± 116.41	−0.59	0.56

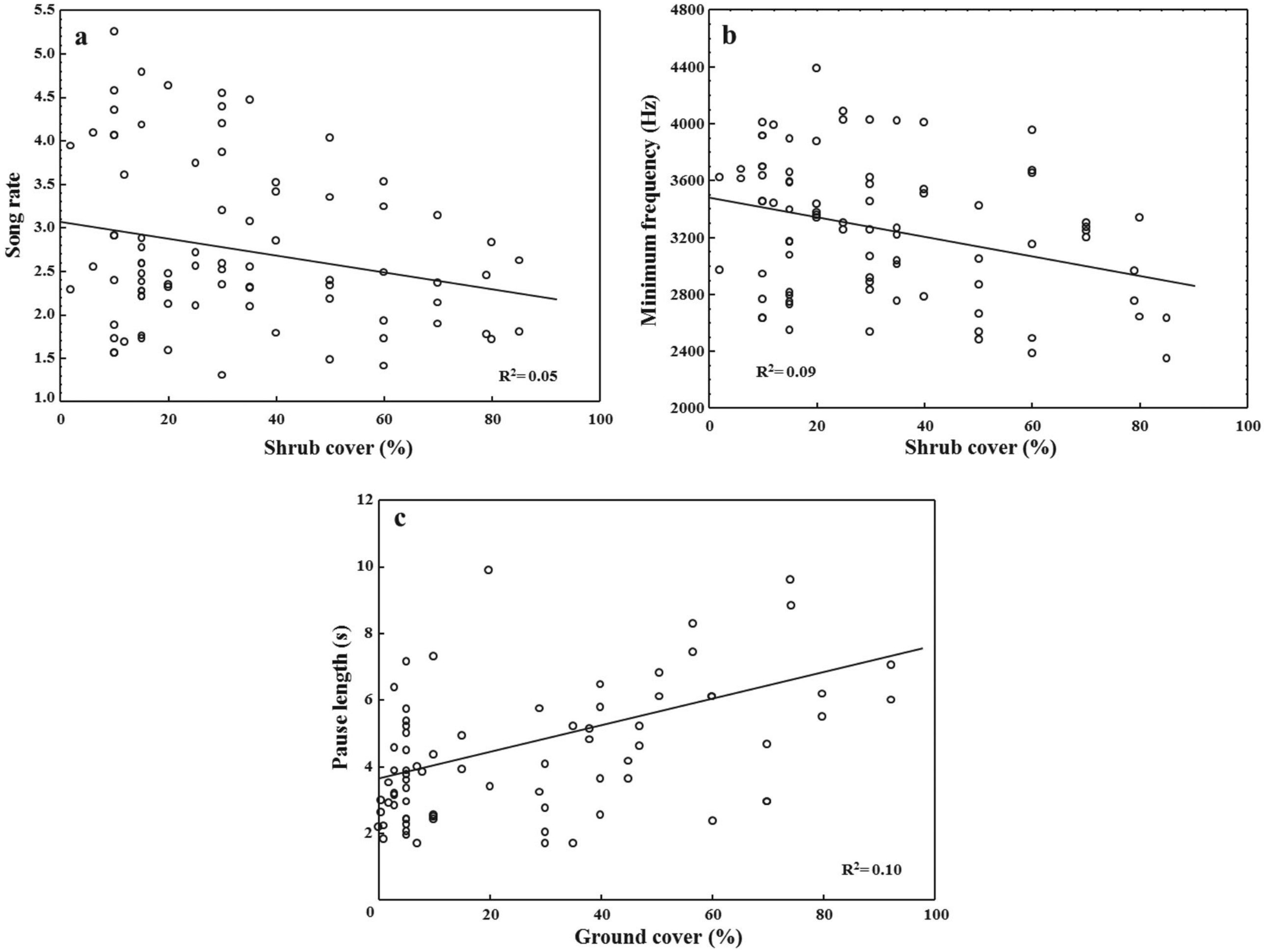

Figure 1. Relationships between the habitat structure and Great Tit *Parus major* song characteristics. The scatterplots show the correlations between (a) the shrub cover and song rate, (b) the shrub cover and the minimum frequency and (c) the ground cover and the pause length in a population breeding in San Pablo de los Montes (Toledo, central Spain). Two measures from each individual are represented.

reflections off tree trunks and shrub vegetation, causing a rapid degradation and a drastic decrease in the active space of the signal (Wiley & Richards 1982, Naguib 2003). Singing high-frequency songs in these territories may similarly entail transmission problems in terms of frequency-dependent attenuation (Wiley & Richards 1982); higher frequencies have a higher degree of attenuation from vegetation than do lower frequencies (Aylor 1972, Marten & Marler 1977). In denser habitats it is, therefore, advantageous to diminish the song frequency in order to avoid attenuation, especially in the lower frequencies of the song, which carry more energy (Boncoraglio & Saino 2007). However, in more open territories Great Tits sang with a longer pause length, which goes against predictions from the Acoustic Adaptation Hypothesis, as the transmission problems associated with degradation are lower in these territories.

With regard to the effects of the male characteristics on the song performance, the tarsus length negatively affected the peak frequency. As occurs with the minimum frequency of bird song (Wiley 1991, Price *et al.* 2006), low-peak frequency songs could be constrained by body size if they are performed near the physiological limit (Gil & Gahr 2002, Searcy & Beecher 2009). Peak frequency contains the maximum power of the song (Charif *et al.* 2010) and it is therefore expected to reach greater distances without attenuation. Encoding an honest message of body size in it would thus be advantageous (Gil & Gahr 2002, Boncoraglio & Saino 2007). For example, in Great Frigatebirds *Fregata minor* the peak frequency is negatively related to the size of their gular pouch (Juola & Searcy 2011). The bandwidth of the song was also affected by the age of Great Tits, with older males singing with a broader bandwidth than younger ones. These age-related changes in song characteristics have been seen in other close-ended learning species and are related to an enhancement of singing skills with age (Vehrencamp *et al.* 2013). More

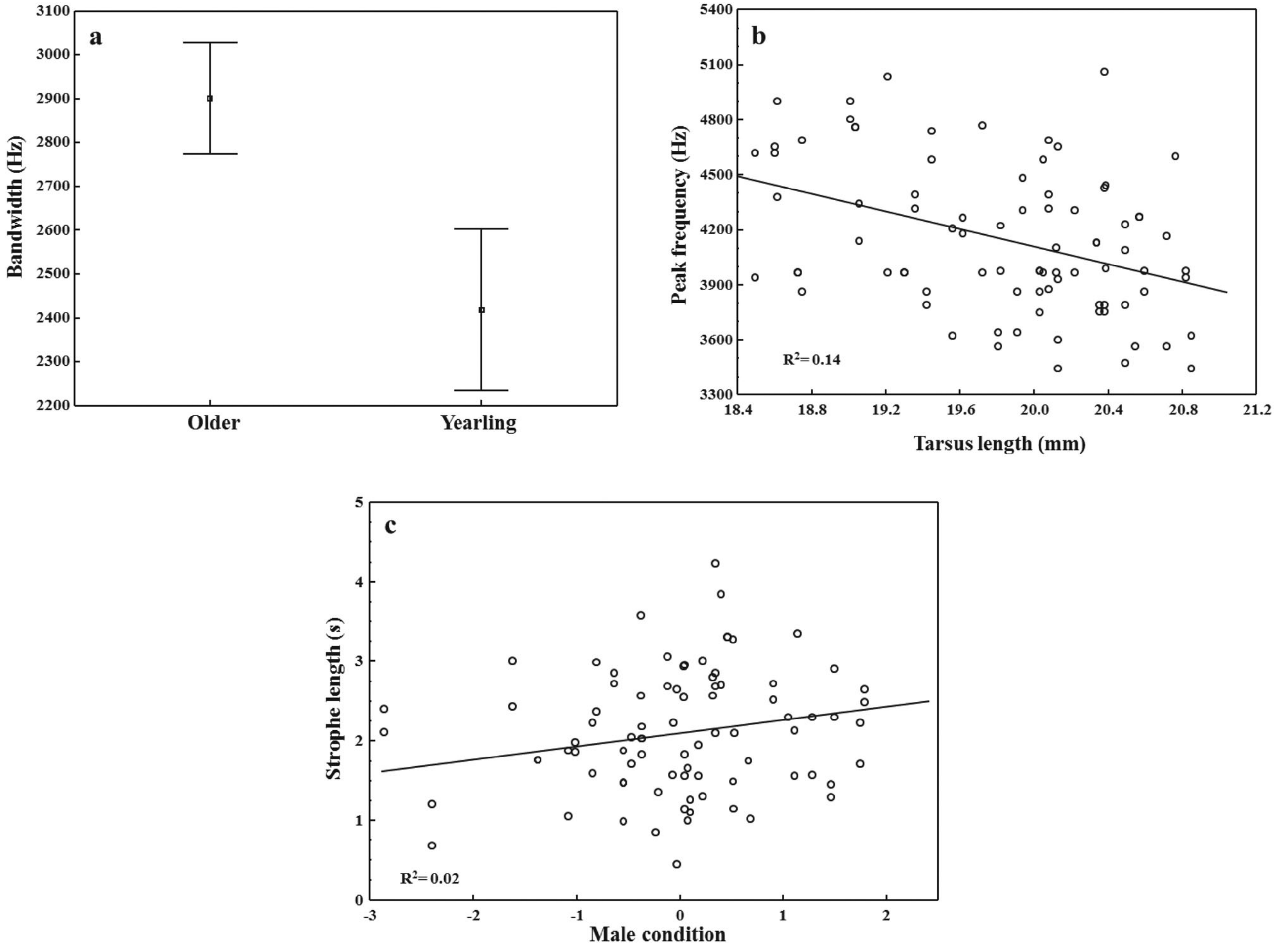

Figure 2. Relationships between the male characteristics and Great Tit *P. major* song characteristics. The scatterplots show the correlations between (a) male age and the bandwidth, (b) tarsus length and the peak frequency and (c) male condition and the strophe length in a population breeding in San Pablo de los Montes (Toledo, central Spain). Two measures from each individual are represented.

specifically, Ota & Soma (2014) also observed an increase in the bandwidth of Java Sparrows *Lonchura oryzivora* with age, which was only achieved by an increase in the coordination between the syringeal muscles and the air flow (Podos 1997). Nonetheless, as Ota & Soma (2014) pointed out, this increase in the bandwidth with age could be a side effect of singing louder, as the bandwidth is dependent on sound pressure (Zollinger *et al.* 2012). Finally, those males with a better body condition sang with longer strophes, so the length of the strophes in our population could be encoding an honest message of quality, owing to the costs of singing (Gil & Gahr 2002, Catchpole & Slater 2008).

Despite being unable to confirm the mechanism by which Great Tits shape their songs to the acoustic habitat properties in each territory this study suggests that habitat structure has an effect on the song of Great Tits, despite the fact that background noise is often seen as a more important driver of song structure (Brumm & Naguib 2009, Proppe *et al.* 2012). Indeed, a variation in song characteristics within a population owing to the acoustic properties of the habitat has only been assessed with different levels of background noise (Slabbekoorn & Peet 2003, Salaberria & Gil 2010). This study reinforces the idea that changes in habitat resulting from human activities, such as habitat fragmentation or degradation, can affect wildlife in several ways, and even the performance of bird songs. These vocal adjustments, although they might appear to improve transmission, could entail fitness costs in the sender and receiver if the message is compromised (Patricelli & Blickley 2006, Warren *et al.* 2006, Halfwerk *et al.* 2011, Read *et al.* 2014).

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