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Plumage colouration variability of male Bluethroats (*Luscinia svecica cyanecula*) wintering in SE Iberia

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Male colouration has a key role in signalling individual quality during the breeding season. Although winter plumage probably correlates with summer plumage, few studies have focused on the determinants of male colouration during the non-breeding period. If plumage colouration is related to an individual's age or is strongly correlated with body condition during the non-breeding period, this trait could be used by conspecifics to assess quality, origin or status of a given individual. Here, we analysed plumage colouration and body size of male Bluethroats (*Luscinia svecica cyanecula*) wintering in SE Iberia. We found that young individuals had narrower black bands and wider white bands than adult individuals in their throat patch. Also, the width of the chestnut band increased with later capture date. Finally, blue throat colouration was positively correlated with tail length and negatively correlated with tarsus length. We could not find any significant relationship between throat patch colouration and body mass. We concluded that individual's age and capture date were significantly related to black and chestnut throat colouration, respectively. Therefore, these coloured bands could provide reliable cues on individual's age and their geographical origins. The variability of plumage colouration of wintering Bluethroats provides an excellent study system in which to test further hypotheses on the role of the throat patch colouration outside the breeding season.

1. Introduction

In socially monogamous species with bi-parental care, females benefit of being mated with high quality males in two different though complementary ways: (i) directly through male's investment in offspring care (Hoelzer 1989, Price *et al.* 1993), and (ii) indirectly through the transmission to the offspring of high quality genes by high quality males (Hamilton & Zuk 1982, Kodric-Brown & Brown 1984). In the case of birds, male plumage colouration may function as an honest signal of quality, and consequently, it may operate as a sexually selected ornament (Hill & McGraw 2006a).

Plumage colouration may signal the quality of the bearer, enabling females to assess male quality (Hill 1991, Hill & McGraw 2006a). Colourful ornaments also develop a key role for social communication and aggressive interactions among conspecifics, especially in highly territorial species (Senar 2006).

Regardless of the relevance of colourful plumage ornaments during the breeding season, the role of plumage colouration during the non-breeding period has received less attention (Rohwer 1975, Järvi & Bakken 1984, McGraw 2004, Senar 2006). The expression of coloured patches may show marked patterns of seasonal and/or regional variation, due to feather abrasion during the winter (Figuerola & Senar 2006, Delhey *et al.* 2010, Adamík & Vaňáková 2011) or to a complex and highly variable design of these plumage patches among populations (Johnsen *et al.* 2006, Rhijn *et al.* 2014). Moreover, plumage colouration could be the focus of social selective pressures between dominant and subordinate individuals when competing for food resources (Berglund *et al.* 1996, McGraw 2004, Senar 2006, Mercadante & Hill 2014; but see McGraw & Hill 2000). Conversely, juvenile birds of many species display a duller version of the adult colouration (Moreno & Soler 2011). Juvenile individuals suffer stronger temporal constraints to moult than adults, given that they commonly achieve post-breeding moult later than adults (Bojarinova *et al.* 1999, Rohwer 2013). Moreover, juveniles of many species often display smaller ornaments than adults, e.g., shorter tail lengths in Barn Swallows (*Hirundo rustica*; Møller *et al.* 1998) and smaller breast stripes and ties in Siskin (*Carduelis spinus*; Senar *et al.* 1998), Great Tits (*Parus major*; Hegyi *et al.* 2007) and European Robins (*Erithacus rubecula*; Jovani *et al.* 2012). This pattern could be more acute in migratory species, given that they have an additional temporal constraint to moult. In this group, winter events such as moult and pairing are highly relevant and often determine individual performance during the subsequent breeding season (Norris *et al.* 2004). Thus, the assessment of the role and functionality of male colouration outside the breeding season may contribute to a better understanding of the ecology of any given species. We should note however that winter colouration might simply correlate with summer plumage although it has no signalling function. On the other hand, we could state that animals need to communicate year round.

The Bluethroat (*Luscinia svecica*) is a small colourful passerine with multiple subspecies and morphs breeding in the Western Paleartic (Cramp 1988, Johnsen *et al.* 2006, Arizaga *et al.* 2011). Male Bluethroats display a combination of blue, chestnut, black and white bands of varying widths and pattern on the throat (Fig. 1) (Cortés *et al.* 2002, Johnsen *et al.* 2006). A white or red central spot, totally or partially concealed by blue feathers, sometimes with some traces of rufous-red shade, is also present (Cramp 1988, Cortés *et al.* 2002, Johnsen *et al.* 2006). Furthermore, a rufous-red coloured band is displayed by both sexes in the basal half of the tail feathers. Blue and white bands are structural colours; chestnut, black bands and the rufous-red tail patch are melanin-based colours (Andersson & Amundsen 1997, Smiseth *et al.* 2001). Bluethroats migrate to their wintering grounds in Mediterranean and Atlantic coastal wetlands of south-western Europe (Peiró 1997, Hernández *et al.* 2003; Arizaga & Tamayo 2013; Correia & Neto 2013). They also undergo a partial pre-breeding moult commonly at early spring involving lores, ear coverts, cheeks, throat and breast (Cramp 1988, Cortés *et al.* 2002).

Previous research of this species suggests that blue- and orange-coloured leg bands were highly likely perceived as more attractive than control bands by the females (Johnsen *et al.* 1997). It has also been shown that male colouration correlated positively with paternity in the own nest (Johnsen *et al.* 2001). Another study found that females may use UV cues to select their mates (Andersson & Amundsen 1997).

Our aim in this study was to assess whether the throat patch would have a role as a cue of individual age and/or social status during the winter. To do this, we characterized throat patch in relation to body morphology in male Bluethroats (*Luscinia svecica cyanecula*) wintering in SE Iberia. We then assessed which extrinsic and intrinsic factors – date, individuals' age or body condition – correlated with throat patch colouration.

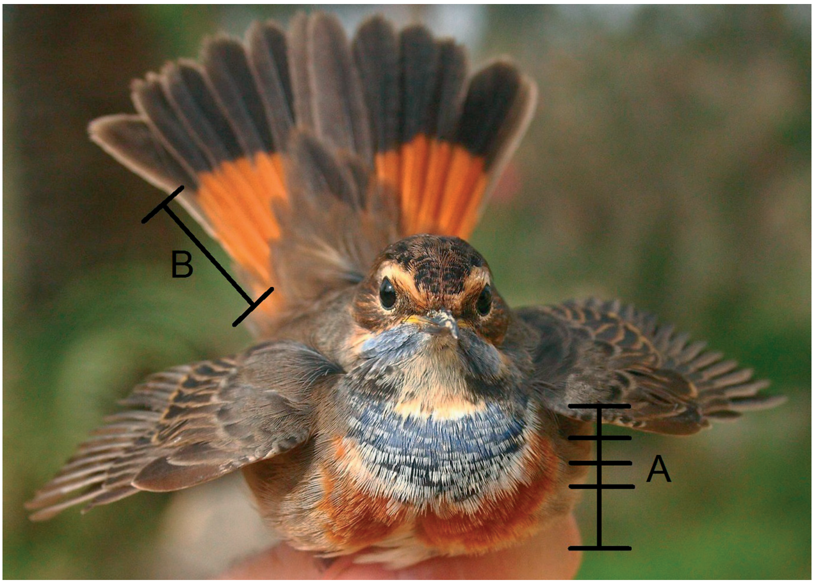

Fig. 1. Picture showing both throat (A: blue, black, white and chestnut bands, from top to bottom) and tail (B: rufous-red band) coloured patches of male Bluehtroats (*Luscinia svecica*).

2. Material and methods

2.1. Field procedures

A total of 41 male Bluethroats were mist-netted in 1998–2002 at "El Hondo" Natural Park (Alicante, SE Spain; 38º12'N 00º45'W), an inland wetland located within the thermo-Mediterranean bioclimatic region (Rivas-Martínez 1983). The sampling period was from September to March, which included both the migration and wintering stages. Three captured individuals had been previously banded with aluminium rings from the Netherlands. All measurements of the birds were taken by the same person (IG) to reduce inter-individual measurement bias. Data from our recaptures events were excluded. Both two white-spotted subspecies of Bluethorat (*L. s. cyanecula* and *L. s. namnetum*) overwinter in our study area (Peiró 1997). Using current criteria to discriminate between these two subspecies (Neto & Correia 2012), a few *L. s. namnetum* individuals were also excluded (n = 4). Based on current knowledge (Cortés *et al.* 2002, Johnsen *et al.* 2006, Campos *et al.* 2011), our sample did not include any *L. s. azuricollis*.

We aged birds, either as adults (birds born before previous summer, n = 14) or as juveniles (birds born in previous summer, n = 27), and sexed the birds according to Svensson (1992). Since some females display bright colouration, we excluded ambiguous individuals (n = 8).

Several morphometric measures were taken (Svensson 1992): (1) tarsus and (2) wing length, from the birds' right side, using a dial calliper (to nearest 0.1 mm) and a metal ruler (to nearest 0.5 mm); (3) tail length using a metal ruler (to nearest 0.5 mm); (4) body mass using a 50 g spring balance (to nearest 0.1 g); and (5) bill length (to the skull), depth and width, using a dial calliper (to nearest 0.1 mm). Additionally, (6) the amount of subcutaneous fat was scored according to Kaiser (1993). We earlier captured an additional sample of 28 individuals during 1992–1993, in the same sampling period as this study (September–March), to verify the presence of winter throat moult and when it occurs in this species. We found that only five individuals (1 of 8 adults and 4 of 20 juveniles) showed active moult at late winter (4 in February, 1 in March). Individuals used in the subsequent analyses did not show active moult of these feathers.

2.2. Measuring colouration

Colour intensity (brightness, chromacity and reflectance) and size of the colour patches have been broadly used to assess male quality (reviewed in Hill & McGraw 2006b). In our case, to

Table 1. Means, standard deviations (SD), minima and maxima of our study variables. All variables have the unit mm, except for body mass, which is given in g.

Variable	*n*	Mean	SD	Min	Max
Chestnut throat colouration	41	8.37	2.39	4.8	15
Black throat colouration	41	3.54	1.51	0	8.3
Blue throat colouration	41	6.07	1.75	1.9	12.5
White throat colouration	41	2.06	1.04	0	4.1
Rufuos-red tail colouration	31	34.39	1.87	30.5	37.5
Wing length	41	75.37	1.47	72.5	79.5
Tarsus length	40	25.76	0.79	23.9	27.7
Tail length	39	55.54	2.26	51	60
Body mass	38	16.74	1.42	14.7	20.8
Bill length	40	14.89	0.6	13.7	16.1
Bill width	40	3.44	0.16	3	3.7
Bill thickness	40	4.06	0.33	3.4	4.6

quantitatively assess the variability of male colouration, the width of each colour band of the throat patch – blue, chestnut, black and white (see Fig. 1 for an image of the throat patch) – was measured using a dial calliper to the nearest 0.1 mm. This procedure is consistent with previous research that has focused on the significance of ornamental displays in this species (Johnsen *et al.* 1997, 2000, Rohde *et al.* 1999). The rufous-red colouration in the basal half of the tail feathers (see Fig. 1) was also measured in a subsample of 36 individuals using a plastic non-stopped ruler to the nearest 0.5 mm. More concretely, we measured the length of rufous-red colouration in the outermost tail feather (until the underpin feather) of the birds' left side. We should note that generally juvenile individuals of this species do not moult tail feathers before first breeding (Jenni & Winkler 1994). Finally, we did not measure the size of the white spot of the throat because feathers in many individuals concealed it. See Table 1 for descriptive statistics of our study variables.

2.3. Statistical analyses

We used a generalized linear model (GLM), with log-link and Gaussian error distribution. First, we analysed the correlations among our study variables (see Table 2, *n* = 38, 14 adults and 24 juveniles). Second, we performed a GLM to assess associations between body condition and individuals' age and capture dates in wintering birds. We used body mass as dependent variable, and included age as categorical independent factor, and date and fat scores as continuous independent predictors (*n* = 34, 13 adults and 21 juveniles). Since we expected to find a strong correlation between fat scores and body mass we repeated the analysis excluding fat scores (sample size, *n* = 38, 14 adults and 24 juveniles). Finally, we performed a set of GLMs to assess the effect of date and age on throat patch shape, and its relationships with body mass. This procedure enabled us to detect differences in throat patch colour pattern which could be related to the geographical origins and the age of the individuals. We used the band thickness values for the four different colours as dependent variables. Individual's age (juvenile or adult) was the categorical independent factor. The date (0 = 15 August) and body mass (g) were the continuous independent predictors (*n* = 41 individuals, 14 adults and 27 juveniles). In a subsample (*n* = 31, 10 adults and 21 juveniles), we did the same using rufous-red tail colouration as dependent variable. We used Statistica 6.0 to perform our analyses (StatSoft 2001).

3. Results

3.1. Correlations among studied traits

We found that the width of the blue throat band was negatively correlated with tarsus length and positively correlated with tail length (Table 2, Fig.

Table 2. Spearman's correlations among the most relevant study variables: the different colour bands forming the throat patch (mm) and those variables characterizing body morphology (mm), of 38 males of Bluethroat (*Luscinia svecica*) wintering in SE Iberia. Significant correlations ($p < 0.05$) are highlighted in bold. "T.C." means "throat colouration".

	Chesnut T.C.	Black T.C.	Blue T.C.	White T.C.	Wing length	Tarsus length	Bill length	Tail length
Chesnut T.C.	1.00	–	–	–	–	–	–	–
Black T.C.	**0.35**	1.00	–	–	–	–	–	–
Blue T.C.	0.10	–0.24	1.00	–	–	–	–	–
White T.C.	–0.13	–0.22	0.08	1.00	–	–	–	–
Wing length	0.06	0.13	0.18	–0.24	1.00	–	–	–
Tarsus length	0.03	–0.05	**–0.37**	–0.25	0.02	1.00	–	–
Bill length	0.20	0.09	–0.21	–0.14	–0.05	**0.35**	1.00	–
Tail length	–0.17	0.12	0.32	–0.06	**0.62**	–0.26	–0.22	1.00

2). We could not find any other significant correlations between the different colouration traits forming throat patch and the morphological variables (Table 2). Conversely, we found that the widths of the chestnut and black colour bands were positively correlated with one another. The wing length and tail length were positively correlated with one another. The tarsus length and bill length were positively correlated with one another (Table 2). Adults and juveniles did not differ in their capture dates ($F_{1,39} = 0.65, p = 0.42$).

3.2. Throat patch morphology and body condition

Body mass was only correlated with fat scores, and did not show any significant relationship with individual's age or date of capture (Table 3). After excluding fat scores, the relationships between body mass and individual's age and date of capture were still non-significant (all $p > 0.34$). Body mass did not correlate with the widths of any of the different colour bands forming the throat patch or with the tail patch after controlling for individuals' age and capture date (Table 3).

Different throat patch colours showed different relationships with individual's age and capture date. The chestnut band's width increased in later captured individuals (Table 3, Fig. 3). Although there was considerable overlap between the black and white bands, the black band was wider in adults than in juveniles, whilst in white band there seemed to be opposite tendency in relation to age. In adults ($n = 14$) the black band width was on average 4.34 mm (SD = 1.78 mm, range = 2.20–8.30 mm) and the white band was 1.56 mm (SD = 1.51 mm, range = 0.00–4.10 mm). In juveniles ($n = 27$) the black band was on average 3.12 mm (SD = 1.19 mm, range = 0.00–4.70 mm) and white band 2.32 mm (SD = 0.57 mm, range = 1.50–4.00 mm) (Table 3, Fig. 4). We could not find any significant effect of age or date of capture on the size of the rufous-red patch of the tail (Table 3).

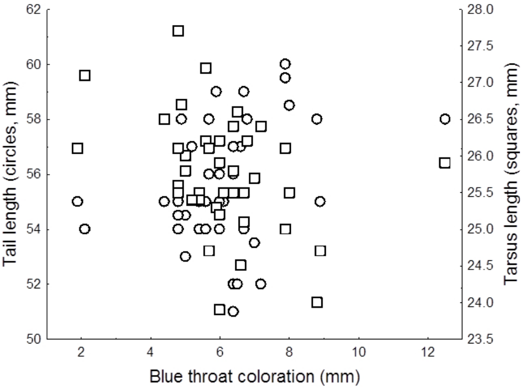

Fig. 2. The relationships between tarsus and tail length (mm) and blue colouration of the throat patch of male Bluethroats (*Luscinia svecica*) wintering in SE Iberia ($n = 38$; tarsus length vs. blue colouration: $r = –0.37$, $p = 0.02$; tail length vs. blue colouration: $r = 0.32$, $p = 0.05$). Circles represent tail length data, whilst squares represent tarsus length data.

4. Discussion

In this study we found that the different colours forming the throat patch of male Bluethroats wintering in SE Iberia were related to individual age

Table 3. Generalized log-linear models using body mass as dependent variable, with date and fat scores as continuous predictors, and individuals' age as a categorical factor. We also show the results of the generalized linear models assessing the relationships between the different colours forming throat and tail patches (a general linear model in the case of tail colouration) and body mass, after controlling for individuals' age and date, in male Bluethroats (*Luscinia svecica*) wintering in SE Iberia (n = 38; 14 adults and 24 juveniles). In relation to the direction of the estimate, negative values correspond to higher values of adults and positive values correspond to higher values of juveniles.

Dependent variable: Body mass

	Estimate	SE	Wald Stat.	*p*
Intercept	2.78	0.02	18022.21	< 0.01
Date	–0.0002	0.0002	1.10	0.29
Fat scores	0.05	0.01	72.75	< 0.01
Age	0.01	0.01	1.18	0.28

Dependent variable: Chestnut throat colouration

	Estimate	SE	Wald Stat.	*p*
Intercept	1.96	0.55	12.94	< 0.01
Date	0.002	0.001	6.80	0.01
Body mass	–0.002	0.03	0.01	0.94
Age	0.01	0.04	0.11	0.74

Dependent variable: Black throat colouration

	Estimate	SE	Wald Stat.	*p*
Intercept	2.10	0.75	7.83	0.01
Date	0.001	0.001	0.58	0.45
Body mass	–0.05	0.04	1.38	0.24
Age	–0.13	0.06	5.60	0.02

Dependent variable: Blue throat colouration

	Estimate	SE	Wald Stat.	*p*
Intercept	1.40	0.52	7.12	0.01
Date	–0.001	0.001	2.41	0.12
Body mass	0.03	0.03	1.30	0.25
Age	–0.03	0.05	0.52	0.47

Dependent variable: White throat colouration

	Estimate	SE	Wald Stat.	*p*
Intercept	1.14	0.99	1.33	0.25
Date	–0.001	0.002	0.30	0.58
Body mass	–0.02	0.06	0.18	0.67
Age	0.18	0.10	3.51	0.06

Dependent variable: Rufuos-red tail colouration

	Estimate	SE	Wald Stat.	*p*
Intercept	3.46	0.12	860.49	< 0.01
Date	–0.00004	0.0002	0.05	0.82
Body mass	0.01	0.007	0.67	0.41
Age	–0.02	0.01	2.80	0.09

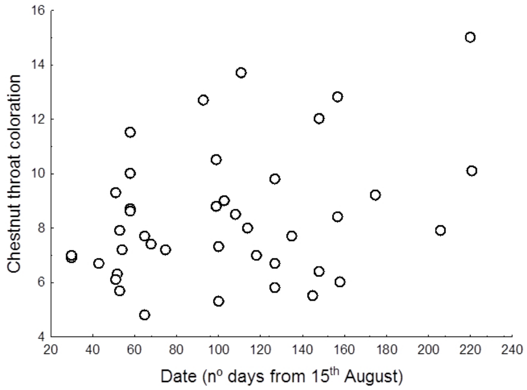

Fig. 3. Scatterplot showing the relationships between chestnut throat colouration (mm) and the date (measured as the number of days from 15st August) of *n* = 41 (14 adults and 27 juveniles) male Bluethroats (*Luscinia svecica*) wintering in SE Iberia.

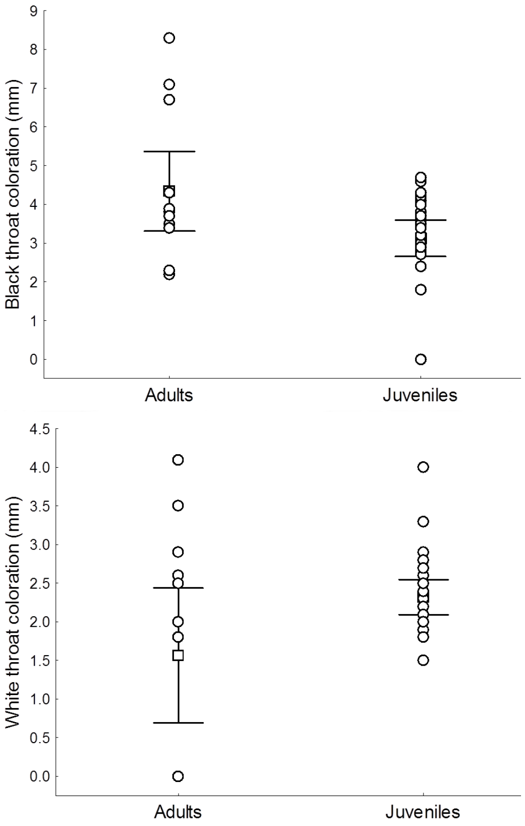

Fig. 4. The differences in black and white throat bands (mm) between juvenile and adult individuals of 41 (14 adults and 27 juveniles) male Bluethroats (*Luscinia svecica*) wintering in SE Iberia. The middle point (the empty square) represents the mean value, the whisker lines are the 95% confidence intervals, whilst the circle points represent the raw data.

and to capture dates. The chestnut throat band was positively correlated with capture date. Moreover, adults displayed wider black throat bands and a tendency to show narrower white throat bands than juveniles. Populations at different latitudes show different throat colouration patterns and different timing of migration (Cortés *et al.* 2002, Markovets & Yosef 2005, Correia & Neto 2013). However, in this study we recorded these significant differences in throat colouration between age classes. Hence, throat ornaments could provide information about the social status of the individuals during aggressive interactions during the wintering period (Geslin *et al.* 2004a). Irrespective of this, our data suggest that there was significant variation in the colours of the various bands in the throat patches of wintering Bluethroats, which was linked to different age classes and capture dates of the birds.

In contrast to the delayed plumage maturation scenario (in which juveniles retain the plumage corresponding to the fledging stage (Berggren *et al.* 2004), plumage colouration of adult and juvenile individuals greatly overlapped. Our findings are consistent with previous research on age-related changes of carotenoid-based plumage colouration, which show that juveniles usually display a duller version of adult plumage (Delhey & Kempenaers 2006, del Val *et al.* 2010, Pagani-Núñez & Senar 2012). In this case, probably as a consequence of the lower migratory efficiency of juveniles (Ellegren 1991), our data suggests a relevant role of temporal and/or physiological constraints on the expression of throat patch colours of juvenile Bluethroats (Deviche *et al.* 2008, Moreno & Soler 2011, del Val *et al.* 2014). Additionally, we should note that we do not have any clear evidence of a relevant role of the throat patch as a signal of quality during the winter, as there is a lack of relationships between throat patch colouration and body mass (see also Geslin *et al.* 2004b). It is also possible that the condition of the birds could have changed between the phases of moult and capture. Therefore, these age-related differences might be a consequence of their life-history stage rather than a difference in quality between age classes.

More generally, we could argue that plumage colouration variability is a matter of size for Bluethroats. Previous research has highlighted substantial geographical variation in plumage colouration among populations and subspecies (Questiau *et al.* 1998, Cortés *et al.* 2002, Johnsen *et al.* 2006). Divergent wing morphologies have also been reported among different European Bluethroat populations (Arizaga *et al.* 2006). These plumage and morphological differences among populations could help to explain our results. The arrival of new individuals from different populations throughout the winter could result in the differences in throat colouration with date of capture that we observed. Moreover, we recorded contrasting relationships between the blue throat colouration, which is displayed in a central position in the throat patch, and tarsus and tail length. These findings might be related to these differences in throat colouration and body morphology among the different European populations. Since males have colourful and larger throat patches compared to females, we may suggest accordingly that throat patches may provide cues to other individuals on the age and the status (e.g., geographical origin) of their conspecifics.

In conclusion, our work contributes to the topic of honest signalling of colourful ornaments (Hill & McGraw 2006a). Throat patch might be a reliable signal of social status, geographical origin, of age, or of individual quality. However, in absence of active moult, feather abrasion may have contributed to shape the date-related changes in colouration that we found in this study (Figuerola & Senar 2006). The absence of significant relationships between age, date, and tail colouration suggests that this coloured patch does no develop any role as a signal, as would be expected in juvenile individuals (which generate these feathers in the nest). Conversely, our data suggest that the throat patches may have multiple pieces of information that might inform other individuals about age, origin and perhaps social status (Johnstone & Grafen 1993, Kokko 1997, Senar 1999). Juvenile individuals had narrower black throat bands when compared to adult individuals and the chestnut band increased in width with later capture date. Therefore, we suggest that the multi-coloured throat patch could have a role as social and/or sexual signal outside the breeding season and we encourage further research to test this hypothesis.

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Höyhenpuvun vaihtelu talvehtivilla valkotäpläsinirintakoirailla

Pesimäaikainen koiraan väritys välittää tärkeää tietoa yksilön laadusta. Myös talvehtimispuvun väritys voi olla merkityksellinen yksilöiden välisessä viestinnässä, mutta harvat tutkimukset ovat perehtyneet koiraiden väritykseen tai siihen vaikuttaviin tekijöihin pesimisajan ulkopuolella. Jos jokin tietty höyhenpuvun piirre on yhteydessä yksilön ikään tai kuntoon, sillä voi olla merkitystä lajitovereiden arvioidessa yksilön laatua, alkuperää tai statusta.

Me pyydystimme Kaakkois-Espanjassa talvehtivia valkotäpläsinirintoja (*Luscinia svecica cyanecula*) syyskuun ja maaliskuun välisenä aikana. Tutkimme koiraiden kurkkulapun värityksen vaihtelua suhteessa lintujen ikään ja ruumiin kokoon.

Nuorten koiraiden kurkkulapun musta vyö oli kapeampi ja valkoinen vyö oli leveämpi kuin aikuisten koiraiden. Punaruskean värinen vyö oli puolestaan sitä leveämpi mitä myöhemmin talvella lintu oli pyydystetty. Valkotäpläsinirintojen kurkkulapun väritys oli yhteydessä myös lintujen kokoon. Kurkkulapun sininen alue leveni pyrstön pituuden mukaan, mutta kapeni nilkan pituuden mukaan. Kurkkulapun väritys ei ollut yhteydessä linnun massaan. Kurkkulapun väritystä voidaan siis käyttää apuna talvehtivien koiraiden iän määrityksessä, ja sen väritys saattaa kertoa myös linnun synnyinseudun sijainnista. Talvehtivien sinirintojen höyhenpeitteen vaihtelu on erinomainen tutkimuskohde, mikäli halutaan selvittää erinäisiä hypoteeseja liittyen kurkkulapun värityksen merkitykseen pesimäajan ulkopuolella.

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