Older is better? Age-related variation in ornamental and breeding traits in bluethroats, Luscinia s. svecica

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Older is better? Age-related variation in ornamental and breeding traits in bluethroats, *Luscinia s. svecica*

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Abstract. Age-related variation in breeding performance is well-known in birds. Similarly, plumage ornamentation as a signal of male quality may affect breeding performance. However, because of inter-correlation between age and plumage ornamentation, it is difficult to estimate the relative contribution of these factors on breeding performance in natural variation. In the current study, we examined the relationship between breeding characteristics, age and throat ornament size of bluethroat males (*Luscinia s. svecica*). The study was conducted on 96 males in the Krkonoše Mountains, Czech Republic, in 2003-2011. The results show that older males had higher reproductive performance: they arrived earlier, were more likely to be territorial, had larger clutches and thus had more hatchlings. On the other hand, ornamentation had a few, inconsistent correlations with breeding performances: well-ornamented males had fewer mates but had more fledglings. Our results suggest that age rather than ornamentation size is the main correlate of variation in breeding performance.

Key words: age, arrival, bluethroat, breeding success, ornament

Introduction

Age-related variation in breeding performance is well documented in birds (e.g. Low et al. 2007, Evans et al. 2011, Kervinen et al. 2016). Several hypotheses have been proposed to explain this age-dependency. First, differential survival explains increased reproductive performances of older birds, because low-quality birds died young, resulting in higher reproductive performance of individuals in older age classes (Curio 1983, Forslund & Pärt 1995, Sanz-Aguilar et al. 2017). Second, residual reproductive value explains increased reproductive investment of older birds, because such birds have lower probability of future reproduction (Pianka & Parker 1975, Curio 1983, Clutton-Brock 1988). However, in long-lived species, aging has a negative effect on physiological conditions and leads to a lower reproductive output and senescence (Hammers et al. 2012, Froy et al. 2013, Nussey et al. 2013). Third, the higher experience of older birds may enable them to have higher reproductive success. With increasing age, individuals improve specific skills (e.g. dominance ability, foraging ability, predator avoidance) and also chick rearing abilities, which positively affect their breeding performance (Saether 1990, Martin 1995, Pärt 1996). These alternative hypotheses are not mutually exclusive but together may explain age-dependent variation in reproductive performances.

Breeding performance could also be related to male plumage ornamentation. By attracting potential mates or by repelling rival males, well-ornamented males have higher mating success and subsequent reproductive performances, because individuals of both sexes use ornament as a signal in their mutual interactions (Møller 1987, Andersson 1994, Andersson & Simmonds 2006). In fact, ornament expression in males can

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be regarded as a sort of reproductive investment, because it indirectly affects reproduction (see above). However, as is the case for reproductive performances, ornament expression is also age-dependent. Age-related variation in plumage ornamentation may be a result of the tradeoff between signaling and survival (Proulx et al. 2002, Lindstrom et al. 2009); a result of life-history dependent development; or a result of within-individual variation originating from correlation between signaling and condition (Freeman-Gallant et al. 2010, Grunst et al. 2014). Although some studies focus on this issue, most studies focus on age class such as second year (SY) versus after second year (ASY) (Delhey & Kempenaers 2006, Bitton & Dawson 2008, Evans et al. 2011), and few studies focused on natural variation of age and ornament expression (e.g. Lifjeld et al. 2011, Potti et al. 2013). Our long lasting study of bluethroats in combination with high fidelity of breeding males gave the opportunity to examine the correlation between the age of males, their ornament expression and breeding performance. Although previous studies of this species focused on plumage colouration and UV reflectance (Johnsen et al. 2001), there is also variation in plumage patch size, which is also functional at least in some other species. Thus, for the current study, we focused on patch size rather than plumage colouration, though patch size and colouration might be functionally integrated in part.

The bluethroat is a dimorphic passerine where males have a distinctive throat patch which is displayed to males in a male-male competition and also to females, which are less colourful than males, during courtship display (Peiponen 1960, Andersson & Amundsen 1997). The feather ornament consists of an ultraviolet-blue throat patch and melanin-based black and chestnut stripes (Andersson & Amundsen 1997, Johnsen et al. 1998). Even though bi-parental care is widely the norm, there are exceptions from the social monogamy system (7-33 % polygyny in a Norwegian population; Johnsen & Lifjeld 2003). In our population, the sex ratio of adult birds was male-biased (three males to two females, Pavel & Chutný 2007), and there are floater males in addition to territorial males (see results).

In this article we ask the following questions: 1) are older males more successful in reproduction? 2) are more ornamented males more successful in reproduction? 3) are older males more ornamented (patch size)?

Material and Methods
Fieldwork
The study was carried out in the Krkonoše Mountains, Czech Republic in 2003-2011. The breeding season starts during the first week of May with the first male's arrival and it ends in the last week of July/first week of August when the last fledglings leave the nests. The accurate arrival date of each male was recorded by searching newly arrived males approximately eight hours each day. For arrival date, we consider the day we observed the male first time. Soon after the observation of un-ringed bird, we trapped the bird using mist nets and playback of a territorial song recorded from the local population. Those males which were ringed in previous seasons were recaptured after they established territory. To avoid nest desertion, we captured females only during the feeding period. After trapping, we noted sex and age category (second year = SY, after second year = ASY) (Svensson 1992). In the already ringed males the actual age could be determined in the case when the already ringed males were first ringed as nestlings or SY birds. In addition we took both morphometric data and a standardized picture of the throat ornament (see below). All captured birds were marked with one aluminum ring and a combination of colour plastic rings. The majority of active nests was found during the nest building period. In several cases, when we failed to find nests during their construction, we found them later during the incubation or feeding period. We documented if the male was territorial (singing, occupying and defending specific territory/female) or floating (silent males, searching for fertile females across the territories), number of mates/nests per male when they are territorial, the clutch size, the number of hatchlings and the number of fledglings. Nestlings were marked with an aluminum ring at the age of nine days.

Body size and condition
The captured males were measured, i.e. wing and tail length to the nearest 0.5 mm, tarsus length to the nearest 0.1 mm, and body weight to the nearest 0.1 g. We used the residuals of linear regression analyses of the body weight on tarsus length to define body condition.

Ornament size
We took a picture of the throat ornament by a digital camera in the raised position of the male's head (Fig. 1). The distance between the bird and camera was fixed to 30 cm. The correct distance was ensured by a special rod attached to the camera. On the distal end of the rod, a standardized label was attached to the scale. Males were photographed next to the label. Pictures were processed in Photoshop version 6.1 software
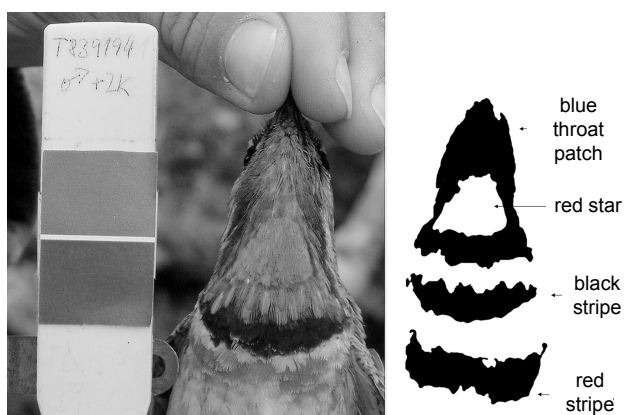
Fig. 1. Picture of the throat ornament of the bluethroat male. Individual spots were processed in Photoshop and measured in Image J graphic software.
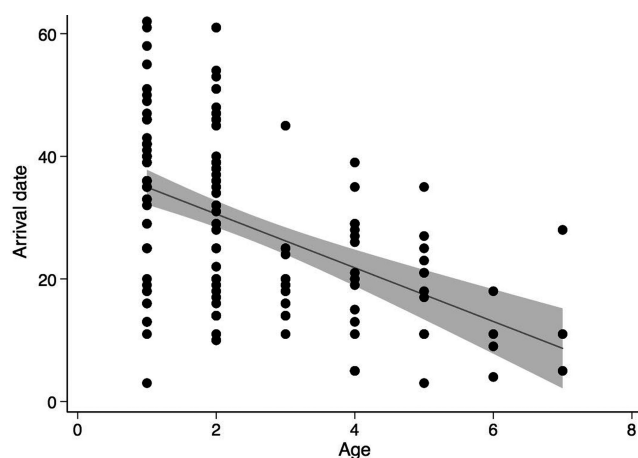

Fig. 2. Relationship between age and arrival date of bluethroat males. For interpretation of arrival date we used Julian date (1th May = 1). Grey coloured region represents 95 % CI. Circles indicate the male's age of each data point (n = 85).
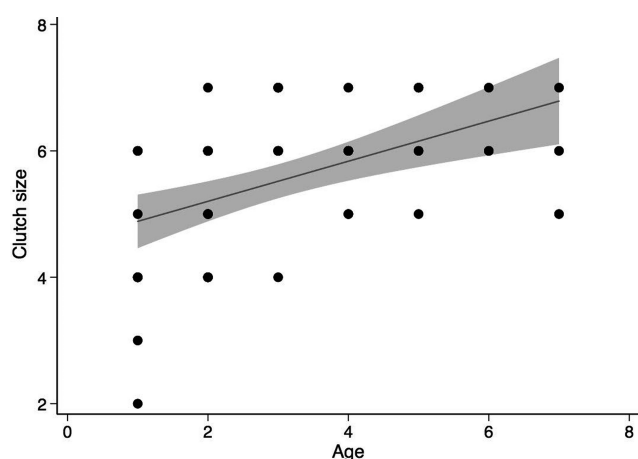

Fig. 3. Relationship between age and clutch size of bluethroat males. Grey coloured region represents 95 % CI. Circles indicate the male's age of each data point (n = 30).

(Adobe systems, U.S.A., Fig. 1). We focused on four sharply bounded areas (blue patch, chestnut star,
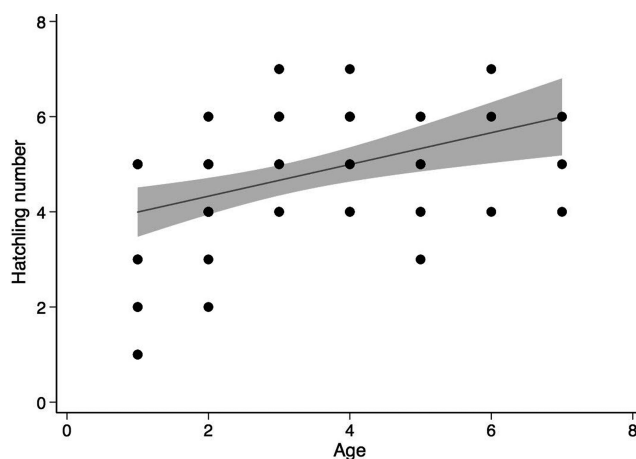

Fig. 4. Relationship between age and hatchling number of bluethroat males. Grey coloured region represents 95 % CI. Circles indicate the male's age of each data point (n = 31).
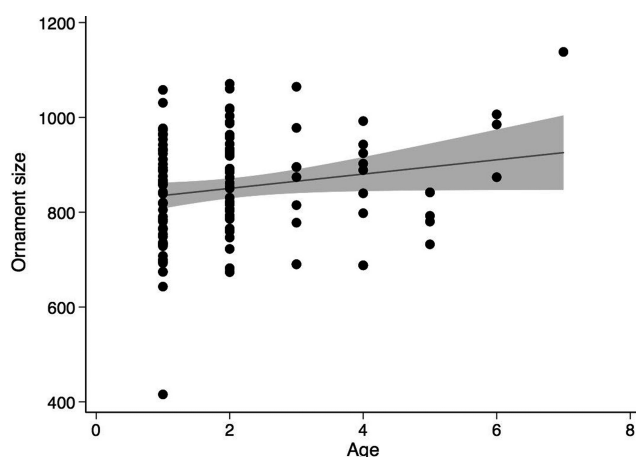
Fig. 5. Relationship between age and ornament size in mm^2 of bluethroat males. Grey coloured region represents 95 % CI. Circles indicate the male's age of each data point (n = 85).

black stripe, chestnut stripe) in the throat ornament. To determine the exact size of these areas we used the magic wand tool which allowed us to select similarly coloured areas. The boundary of each area was precisely marked, cut out from the original picture and its size was subsequently measured in IMAGE J software (http://imagej.net).

As we regarded the dataset including measured sizes of blue, red, black and chestnut patches unacceptable for reduction of dimension with PCA, we used overall ornament size as a single measure in final analyses.

Sample size and statistical analyses

We collected data for 96 males in total. In 70 males we obtained data from a single season; eleven males were sampled in two seasons, ten males in three seasons, one in four seasons, three in five seasons and one in six seasons. It was not always possible to take

all kinds of measurements from each male. Therefore, the sample sizes may differ between analyses and are presented as number of males and total number of observations for those males. In the analyses we used the following parameters of breeding performance as response variables: male status (breeder, floater), arrival date, number of mates, clutch size, number of hatchlings and number of fledglings. As predictors in the generalized linear mixed models (GLMM) we used the following variables: age, year, tarsus length, body condition and ornament size. We performed all possible GLMM (the null model, the full model, and all possible combination of parameters) with suitable error distribution (usually Gaussian) and an identity link function to test the effect of fixed factors (e.g. age, year) and covariates (e.g. ornament size) on dependent variable. Male identity was included as a random factor. The P-values were calculated for Wald statistics. To choose the best models we used a modified version of Akaike's information criterion (AIC_c) for small sample sizes (Burnham & Anderson 2002). To compare the best-fitted model with lowest AIC_c (AIC_{cbest}) to any other model (AIC_{ci}), we calculated ΔAIC_{ci}, where $\Delta AIC_{ci} = AIC_{ci} - AIC_{cbest}$. We only present models which had $\Delta AIC_c < 2$ value (Arnold 2010, Burnham et al. 2011). For these models, we calculated Akaike weights (w_i), which vary between 0 and 1 and can be interpreted as the probability that a given model is the be st at approximating the data. We also present so called evidence ratio (ER), which provides a measure of how much more likely the best model is than model i (Δ_{best} is the Δ value for the best model = 0). For example, if for second best model ER = 2 it means that the first model is approximately two times more likely to be the best approximating model than the second (Symonds & Moussalli 2011). All statistical analyses were calculated in STATA/SE 14.2 (StataCorp, College Station, TX, U.S.A.).

Results

Age, ornament size and breeding success
We found that among 147 observations of 96 males we had 72 cases of breeders in territories and 75 floaters with no territory and no nest found. Six out of 72 breeders gained two mates. We examined the relationship between breeding parameters, male's age, ornament, body condition, tarsus, status (breeder and floater), and year (effect of season) by GLMM models and ranked models by AIC_c value.

Three GLMM models testing the influence of the predictor variables on arrival time, with $\Delta AIC_c < 2$ indicated strong correlation between the male status

and arrival date (Table 1 and 2). Territorial males arrived earlier than floaters. Arrival time was also affected by age and year, however, these effects were weaker and not significant in all models. In general, older males tended to arrive earlier (Fig. 2). When investigating change of arrival date within males, arrival date advanced when males returned to the breeding site compared with their first breeding season at locality (paired t-test, t = 7, 401, n = 27, $P < 0.001$).

Results of GLMM models testing the influence of predictor variables on male status, number of mates, clutch size, number of hatchlings and number of fledglings show that the only significant predictors among the best fitted models were age and ornament size (Table 3 and 4). Male age was the strongest predictor of male status (the probability of holding a territory), clutch size (Fig. 3) and the number of hatchlings (Fig. 4), while ornament size was the significant predictor of number of mates, clutch size and number of fledglings. Unexpectedly, males with smaller ornament attracted more females.

Additionally, we examined the relationship between male age and ornament size. The best two GLMM models included also tarsus and condition, but only age was a significant predictor of ornament size (Table 5 and 6). Ornament size increased with age (Fig. 5).

Discussion

Together with previous studies of bluethroats demonstrating higher reproductive performances of older males, in part due to higher feeding rates of older males (Smiseth et al. 1998, Geslin 2004), the current study shows a positive relationship between male age and reproductive performance. Higher reproductive success of older males might be caused by higher probability of holding a territory. In many other species it has been documented that older males arrive earlier and defend higher quality territories (e.g. Aebischer et al. 1996, Pärt 2001, Smith & Moore 2005) which reflects their individual quality (e.g. Hill 1988, Mitrus et al. 2006) and thus may be responsible for the increased breeding success in terms of higher probability of mating, attracting more females and producing more offspring (e.g. Weatherhead & Robertson 1977, Ens et al. 1992, Vickery et al. 1992). Additionally, territory quality together with previous breeding experience may strongly affect the site fidelity of individual males, which means that those males, which previously bred at the locality, are usually the first to arrive the next spring (e.g. Bollinger & Gavin 1989, Switzer 1997, Catlin et al.

Table 1. Generalized Mixed Models with the highest probability ($\Delta AIC_c <$ 2) assessing variation in arrival date (Gaussian distribution) as predicted by male's age, size (tarsus), condition, status (breeder *vs.* floater) and season effect (year). All models include random effect (male ID). Sample sizes; arrival date: 85 males and 112 observations. The Akaike weight (w_i) and evidence ratio (ER) were calculated on the basis of Akaike's Information Criterion corrected for small sample size (see Methods for details). ΔAIC_c shows the difference in AIC_c value between the given model and the model with the lowest AIC_c value. The weight indicates the support for each model relative to other models.

Model	AIC_c	ΔAIC_c	w_i	ER
Arrival date				
(1) Age + Year + Tarsus + Status	904.76	0.00	0.44	
(2) Age + Year + Condition + Status	905.54	0.78	0.29	1.48
(3) Age + Year + Tarsus + Condition + Status	905.75	0.99	0.27	1.64

Table 2. Estimates with standard errors and significance for predictor variables used in models with highest probability ($\Delta AIC_c <$ 2) assessing variation in arrival date. Models are explained in Table 1. Significant test results are in bold.

Model	Predictors	Estimate	SE	*P*
Arrival date				
(1)	Age	−1.92	0.961	**0.045**
	Year	−0.87	0.469	0.063
	Tarsus	1.81	1.285	0.159
	Status	−12.20	2.448	**< 0.001**
(2)	Age	−1.48	0.997	0.137
	Year	−1.01	0.462	**0.029**
	Condition	−1.04	0.972	0.282
	Status	−12.86	2.47	**< 0.001**
(3)	Age	−1.63	0.989	0.100
	Year	−0.85	0.469	0.070
	Tarsus	1.863	1.292	0.149
	Condition	−1.09	0.966	0.260
	Status	−12.62	2.461	**< 0.001**

2005). We can expect such scenario in bluethroats with observed breeding site philopatry 53 % (own obs.), as arrival date of philopatric males advanced when they returned to the breeding site compared with their first breeding season at locality.

Worthy of consideration is a positive relationship between male age and clutch size in comparison of previous works where neither male effect on clutch size nor differential allocation have been found (Rohde et al. 1999, Geslin et al. 2004). If only the phenomenon of differential allocation would be present so that the pattern actually could indicate the possibility that females invest more in clutches when they have an older mate having better territory or being of superior quality (differential allocation hypothesis, Burley 1988). As the differences in environmental quality of territory between young and old males have not been

Table 3. Generalized Mixed Models with the highest probability ($\Delta AIC_c <$ 2) assessing variation in breeding success of territorial males as predicted by male's age, size (tarsus), condition, ornament size and season effect (year). In all models except those for male status and number of mates (binomial distribution) the Gausian distribution was used. All models include random effect (male ID). Sample size; male status: 89 males and 117 observations; number of mates: 34 males and 50 observations; clutch size: 30 males and 40 observations; hatchling number: 31 males and 44 observations; fledgling number: 31 males and 44 observations. The Akaike weight (w_i) and evidence ratio (ER) were calculated on the basis of Akaike's Information Criterion corrected for small sample size (see Methods for details). ΔAIC_c shows the difference in AIC_c value between the given model and the model with the lowest AIC_c value. The weight indicates the support for each model relative to other models.

Model	AIC_c	ΔAIC_c	w_i	ER
Male status (breeder *vs.* floater)				
(1) Age + Year + Tarsus + Condition	135.14	0.00	0.52	
(2) Age + Year + Tarsus	135.30	0.16	0.48	1.08
Number of mates				
(1) Age + Ornament	42.89	0	0.71	
(2) Age + Year + Ornament	44.68	1.78	0.29	2.44
Clutch size				
(1) Age + Year + Tarsus + Ornament	122.85	0.00	0.51	
Hatchling number				
(1) Age + Year + Tarsus + Ornament	156.01	0.00	0.23	
Fledgling number				
(1) Age + Ornament	181.69	0	0.90	

Table 4. Estimates with standard errors and significance for predictor variables used in models with highest probability ($\Delta AIC_c < 2$) assessing variation in breeding success of territorial males. Models are explained in Table 3. Significant test results are in bold.

Model	Predictors	Estimate	SE	P
Male status				
(1)	Age	0.21	0.030	**< 0.001**
	Year	0.02	0.017	0.151
	Tarsus	−0.04	0.046	0.369
	Condition	−0.06	0.036	0.117
(2)	Age	0.20	0.030	**< 0.001**
	Year	0.02	0.017	0.162
	Tarsus	−0.04	0.046	0.323
Number of mates				
(1)	Age	0.05	0.034	0.170
	Ornament	−0.001	0.0004	**0.022**
(2)	Age	0.05	0.034	0.154
	Year	0.01	0.021	0.482
	Ornament	−0.001	0.0004	**0.023**
Clutch size				
(1)	Age	0.49	0.097	**< 0.001**
	Year	−0.10	0.066	0.134
	Tarsus	0.04	0.151	0.809
	Ornament	−0.003	0.0013	**0.047**
Hatchling number				
(1)	Age	0.36	0.118	**0.002**
	Year	−0.08	0.082	0.348
	Tarsus	−0.11	0.199	0.596
	Ornament	−0.007	0.0016	0.675
Fledgling number				
(1)	Age	0.13	0.183	0.48
	Ornament	0.005	0.002	**0.043**

found in the previous study (Geslin et al. 2004), we consider possible fact that females are sensitive to

the male age. If the assortative mating with respect to age would be present, so that our result could reflect also female age, but no such phenomenon has been

Table 5. Generalized Mixed Models with the highest probability ($\Delta AIC_c < 2$) assessing variation in ornament size (Gaussian distribution) as predicted by male's age, size (tarsus) and condition. All models include random effect (male ID). Sample sizes; ornament size: 85 males and 112 observations. The Akaike weight (w_i) and evidence ratio (ER) were calculated on the basis of Akaike's Information Criterion corrected for small sample size (see Methods for details). ΔAIC_c shows the difference in AIC_c value between the given model and the model with the lowest AIC_c value. The weight indicates the support for each model relative to other models.

Model	AIC_c	ΔAIC_c	w_i	ER
Ornament size				
(1) Age + Tarsus	1380.40	0.00	0.89	
(2) Age + Tarsus + Condition	1381.60	1.20	0.27	2.67

Table 6. Estimates with standard errors and significance for predictor variables used in models with highest probability ($\Delta AIC_c < 2$) assessing variation in ornament size. Models are explained in Table 5. Significant test results are in bold.

Model	Predictors	Estimate	SE	P
Ornament size				
(1)	Age	20.64	8.400	**0.014**
	Tarsus	4.38	12.727	0.731
(2)	Age	19.13	8.464	**0.023**
	Tarsus	3.63	12.665	0.774
	Condition	9.84	10.028	0.326

documented so far (Geslin et al. 2004). Our result provides a possibility of re-evaluating the issue of assortative mating and differential allocation in bluethroats.

On the other hand, male ornamentation size showed less pronounced relationship with reproductive performance. Our results indicate a positive relationship between ornament size and number of fledglings but a negative relationship with the number of mates. These seemingly contradictory results may indicate that age rather than ornamentation size is the main correlate of reproductive performance, which is consistent with results of the previous study (Lifjeld et al. 2011). An alternative explanation is that throat patch size is not the target of sexual selection, while other aspects of the male ornament can be related to reproductive performance. Indeed, throat patch colouration, which could be functionally linked to throat patch size in part, was found to be sexually selected in this species (e.g. Johnsen et al. 1998, 2001). Moreover, we found that throat patch size is linked to the male age, and thus may indicate aspects of quality to potential signal receivers. Such inter-correlation of age and sexual trait may cause problems for determining the relative importance of these factors in the breeding process (Lifjeld et al. 2011).

In conclusion, our results shows that age affects breeding performance in bluethroats. Older males arrive earlier, have higher probability of being a territory holder, have larger clutches, and more hatchlings. Throat patch size of males has few detectable relationships with reproductive performance. Less ornamented males produce less fledglings, seem to mate with more females. It is unlikely that throat patch size has no function in sexual selection, though this remains to be clarified in the future.

Acknowledgements

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