Winter body condition in relation to age, sex and plumage ornamentation in a migratory songbird

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Winter body condition may play important roles in the life history of migratory birds, but it is difficult to estimate. We used the growth rate of winter-grown tail feathers of Collared Flycatchers *Ficedula albicollis* as an indicator of winter body condition, comparing this trait between age classes and sexes, and relating it to plumage ornamentation (forehead and wing patch sizes). Adults and males had better nutritional condition during winter as indicated by their faster tail feather growth rate than yearlings and females, respectively, which could indicate differences in individual quality and foraging ability with age, or age- and sex-related winter habitat segregation. However, feather growth rate was related neither to the size of the winter-grown forehead patch, nor the size of the summer-grown wing patch, suggesting weak condition-dependence for the winter-grown ornament, and complex life-history consequences for the summer-grown ornament.

Keywords: Collared Flycatcher, *Ficedula albicollis*, moult, plumage ornaments, ptilochronology, winter habitat quality

In migratory birds, body condition on the wintering grounds could have long-term consequences on spring arrival time, reproductive success in the breeding grounds, annual survival, and lifespan (Takaki *et al.* 2001, Saino *et al.* 2004, Studds & Marra 2005, Reudink *et al.* 2009). Therefore, data on the winter condition of migratory birds may reveal how the non-breeding season affects their life history. Information on winter body condition may also help illuminate the condition-dependence of winter-grown plumage ornaments (Veiga & Puerta 1996, McGlothlin *et al.* 2007), and the condition correlates of ornamental traits grown before winter (Johnstone 1995).

As plumage is important in thermoregulation, social communication, and flight ability, feather regeneration should proceed as rapidly as possible. Feather growth rate has been successfully used to estimate the nutritional condition of birds during moult, a method called ptilochronology (Grubb 2006). Food availability (Grubb & Cimprich 1990, Brown & Sherry 2006), habitat quality (Grubb & Yosef 1994, Carlson 1998), and environmental stress (Carbonell & Tellería 1999, Talloen *et al.* 2008) can all affect feather growth rates. However, ptilochronology has rarely been applied for assessing body condition during the winter moult in migratory birds.

In this study, we used the tail feather growth rate of Collared Flycatchers *Ficedula albicollis* as an index of condition at the wintering quarters in sub-Saharan Africa (Cramp & Perrins 1993), and related it to several phenotypic traits. First, we investigated tail feather growth rate in relation to age. We expected that adult birds would be in better body condition as indicated by their faster tail feather growth rate than yearlings due to experience or better genetic quality (Forslund & Pärt 1995, Hegyi *et al.* 2006). Secondly, we compared feather growth rate between the sexes, predicting faster feather growth, and thus better condition in males than in females due to possible dominance-mediated sexual habitat segregation (Piper 1997, Marra 2000). Finally, we analysed if there was a relationship between tail feather growth rate and plumage ornamentation (forehead and wing patch sizes) of Collared Flycatchers.

In our population, male forehead patch size is used in social mate acquisition (Hegyi *et al.* 2002, 2010). However, it does not indicate spring body condition (Hegyi *et al.* 2002), and seems to be unimportant in male-male competition (Garamszegi *et al.* 2006). Male and female wing patch sizes appear to be important in social mate acquisition (Hegyi *et al.* 2008a, 2010) and intrasexual competition (Garamszegi *et al.* 2006, Hegyi *et al.* 2008b). Wing patch size is highly repeatable and heritable, predicts the viability of adult males, and its within-individual change is related to spring body condition (Török *et al.* 2003, Hegyi *et al.* 2008a). However, a larger wing patch also incurs costs for its bearer (Garamszegi *et al.* 2006, Hegyi *et al.* 2008b). The forehead patch is moulted in the winter in parallel with tail feathers, while the wing patch in the summer (Svensson 1992), so their correlation with winter body condition index would indicate condition-dependence for forehead patch size, but the balance of costs, benefits and individual quality for wing patch size.

METHODS

The study was carried out in a population of Collared Flycatchers in the Pilis Mountains (47° 43′N, 19° 01′E), Hungary, in 2008 and 2009. Birds were captured in the nestbox during the nestling feeding period. The sizes of the white forehead patch of males (Hegyi *et al.* 2002) and the wing patch of both sexes were measured (Török *et al.* 2003). We determined age (yearling or adult) of males from the colour of remiges (Svensson 1992), while age of females was determined from ringing data. We plucked the left and right second outermost rectrices of the birds and stored them in envelopes until analyses.

We measured the growth bars of the tail feathers of 110 and 76 Collared Flycatchers that bred in 2008 and 2009, respectively. One of us (R. H.) marked the length of eight growth bars in the central part of the feather by sticking a pin through a sheet at both ends of the measured section. The distance between the two pin marks was measured using a calliper (to the nearest 0.1 mm). Some feathers could not be measured because the growth bars were too faint. Growth bar width was measured three or four times on each feather, and later averaged (growth bar width repeatability within left and right feathers: $r = 0.88$ and $r = 0.89$, respectively, all $P < 0.001$; Lessells & Boag 1987). The average length of the eight growth bars was divided by eight to obtain the mean daily growth rate (mm/day), then further averaged between the left and right rectrices if data of both feathers were available (correlation between the left and right retrices: $r = 0.54$, $n = 130$, $P < 0.001$).

We fitted two general linear models with feather growth rate as the dependent variable, assuming a normal error structure. In the first model, wing patch size measured in the year of feather plucking was included as a continuous variable, and age, sex and year were entered as factors (see Introduction for predictions). The two- and three-way interactions between factors and with the continuous variable were also included to see whether the effect of the ornament varied with age, sex, year or their combinations, and whether the effects of age, sex and year influenced each other. In the second model, forehead patch size was analysed with age and year as factors, as we had data only for males. We used stepwise backward selection with the reintroduction of non-significant ($P > 0.05$) parameters one by one. Wing patch size was significantly affected by age, sex and year, while forehead patch size by year, so they were standardized (mean = 0, sd = ± 1) to remove the confounding effects of factors on the effect of the covariate (Norman and Streiner 2000). Analyses were conducted in STATISTICA, version 5.5 (StatSoft Inc.).

RESULTS

We found a significant effect of age on tail feather growth rate: one-year-old Collared Flycatchers grew their feathers more slowly than adult birds (Table 1; Fig. 1). Moreover, males had faster feather growth rate than females (Table 1; Fig. 1). Tail feather growth rate was not significantly related to the wing patch size of either sex or the forehead patch size of males (Table 1).

DISCUSSION

Adult Collared Flycatchers grew their tail feathers faster than yearlings, as found in previous studies of other passerines (Carbonell & Tellería 1999, Gienapp & Merilä 2010). Adults may have more experience in foraging or higher intrinsic individual quality (Forslund & Pärt 1995, Hegyi *et al.* 2006), which may enable faster feather development during winter moult. Alternatively, there may be a dominance-mediated habitat segregation between age classes in non-breeding areas (Marra 2000, Catry *et al.* 2004). The potentially less suitable areas occupied by young birds may reduce their nutritional condition and increase physiological stress (Marra & Holberton 1998), thereby reducing feather developmental rate (Carbonell & Tellería 1999, Romero *et al.* 2005, Brown & Sherry 2006). In the Collared Flycatcher, one-year-old birds generally arrive later in the breeding area than adults (Mitrus 2004, our pers. obs.), which may reflect their poorer nutritional condition during wintering. However, it is also possible that yearlings arrive later because of their poorer flight performance or lack of experience during migration.

Males and females may compete with one another for access to limiting resources in the non-breeding area. As males are more aggressive and thus probably dominant to females (Piper 1997), they may exclude them from the most suitable areas, a phenomenon known as sexual habitat segregation (Marra 2000, Catry *et al.* 2004). Our results support that male and female Collared Flycatchers were in different nutritional condition during winter moult as feather growth rate, which could indicate the condition during moult (Grubb 2006), was faster in males than in females. In accordance with our results, females of a Swedish Collared Flycatcher population probably winter in more arid, and thus more stressful habitats than males as judged from stable isotope ratios (Hjernquist *et al.* 2009).

Our data showed no relationship between wing patch size and tail feather growth rate, suggesting that this ornament did not influence body condition in the subsequent winter. Wing patch size could indicate individual quality, as it is related to survivorship and spring body condition (Török *et al.* 2003, Hegyi *et al.* 2008a, 2010). However, a larger wing patch elicits enhanced intrasexual aggression (Garamszegi *et al.* 2006, Hegyi *et al.* 2008b), which may limit the time birds can devote to foraging, and the caused stress may also inhibit feather growth (Romero *et al.* 2005). Moreover, a larger white wing patch may facilitate the abrasion of wing feathers (G. Hegyi *et al.* unpubl. data; see also Bonser 1995, Kose & Møller 1999), thereby impairing flight performance and foraging efficiency. It is possible that the higher quality or general condition of birds and the increased wearing costs of the ornament cancelled each other out, thereby leaving no association between wing patch size and winter body condition index. Finally, the non-significant relationship between tail feather growth rate and winter-developed forehead patch size supports the view that forehead patch size in our population provides little information on body condition (Hegyi *et al.* 2002, 2010).

In conclusion, our results illustrate how a relatively simple estimate of winter body condition may shed light on potential causal links in the life cycle of birds that are not easily accessible to researchers. Feather trace element or isotope data from our study population will help outline groups that winter in the same geographical region (Hjernquist *et al.* 2009, Szép *et al.* 2009), potentially explaining the sex and age effects we detected. Our results concerning ornament expression and winter condition, on the other hand, may help interpret links between ornamentation and nutritional state, reproductive success and future ornamentation, thereby placing the ornament into the context of the whole yearly cycle.

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Table 1. Tail feather growth rate of Collared Flycatchers in relation to age, sex, study year and wing patch size (Model 1), and age, study year, and forehead patch size (Model 2). General linear models were applied with stepwise selection. Bold indicates the final model, and normal type indicates *P*-values for other variables when added individually to the final model.

Model 1 (both sexes)	*F*	df	*P*	Model 2 (males only)	*F*	df	*P*
Age	**21.97**	**1, 182**	**< 0.001**	**Age**	**20.87**	**1, 118**	**< 0.001**
Sex	**7.92**	**1, 182**	**0.005**	**Year**	**7.01**	**1, 118**	**0.009**
Year	**7.50**	**1, 182**	**0.007**	Forehead patch size	2.65	1, 117	0.11
Wing patch size	0.58	1, 181	0.45	Age × Year	0.82	1, 117	0.37
Age × Sex	0.52	1, 181	0.47	Forehead patch size × Age	0.12	1, 116	0.73
Age × Year	2.09	1, 181	0.15	Forehead patch size × Year	0.06	1, 116	0.80
Sex × Year	0.11	1, 181	0.74	Forehead patch size × Age × Year	0.35	1, 116	0.55
Wing patch size × Age	0.06	1, 180	0.81				
Wing patch size × Sex	1.40	1, 180	0.24				
Wing patch size × Year	1.42	1, 180	0.24				
Wing patch size × Age × Sex	1.94	1, 180	0.17				
Wing patch size × Age × Year	2.42	1, 180	0.12				
Wing patch size × Sex × Year	0.03	1, 180	0.87				

Figure 1. Tail feather growth rate in relation to age (yearling or adult) of male and female Collared Flycatchers; means ± se.