

The effect of age and sex on wing morphology and body size of the Bearded Tit *Panurus biarmicus* in relation to complete moult

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In sedentary birds, variation in wing morphology as a result of complete moult during the transition from juvenile to adult plumage is poorly understood. The aim of this study was to characterise sex- and age-related differences in wing morphology resulting from a complete post-juvenile moult in an isolated, sedentary population of the Bearded Tit *Panurus biarmicus* at El Hondo Natural Park reedbeds (SE Spain). Variation in wing morphology was evaluated by means of a Size-Constrained Components Analysis (SCCA) of standardised primary lengths of 66 birds trapped for ringing. Wing traits representing size and shape showed differences among age and sex classes, adults having significantly greater wing sizes than juveniles and males less rounded or convex wings than females. Structural body size also varied significantly among sex classes, females being smaller than males. Sex- and age-specific differences in wing morphology of these Bearded Tits may represent adaptations to the sedentary and colonial behaviour of the local population within constraints imposed by a reedbed microhabitat.

One of the most interesting aspects in the evolution of avian flight is adaptation to environmental constraints, allowing birds to exploit a variety of habitats as a result of subtle changes in different aspects of wing morphology. Although not necessarily adaptive, specific variation in wing morphology as a result of complete moult (ie replacement of flight feathers), can play an important role in the development of flight capacity in passerines (Jenni & Winkler 1994). Feather wear can lead to intraspecific and temporal differences in wing morphology as new feathers replace older, worn ones during moult (eg longer wings in adults and decreased wing roundness: Alatalo *et al* 1984). On the other hand, birds may go through “programmed” ontogenetic changes to optimise wing morphologies at different developmental stages (Hall *et al* 2004) in which moult may not play a determinant role. However, given that, in most passerines, partial post-juvenile moult is the norm, the reasons for a complete post-juvenile moult in some species are interesting, especially in relation to the possible benefits of attaining a more adult-type wing earlier in life.

In sedentary birds, the causes and consequences of variation in wing morphology as a result of complete post-juvenile moult are poorly understood (Nielsen 1993, Pérez-Tris & Tellería 2001). The Bearded Tit *Panurus biarmicus*

can be a good species in which to discuss the possible consequences (and advantages) of complete moult, being a sedentary palustrine bird that inhabits pure stands of reed *Phragmites australis*, and having a distribution in southern Europe restricted to some isolated wetlands (Cramp & Perrins 1993). Its flight morphology (short wing length and long tail) could indicate a bird well adapted to crowded habitats, but not capable of long-distance travel (Winkler & Leisler 1992). Nielsen (1993) points out that changes in its wing morphology after complete moult involve increased pointedness and aspect ratio, and greater wing length.

Although the Bearded Tit has been the subject of studies on its complete post-juvenile moult (Baker *et al* 1975, Pearson 1975, Massi & Spina 1996) and other topics related to flight performance (Romero-Pujante *et al* 2001, 2005), changes in wing morphology involving wing size and shape during moult in wild conditions are not well known.

The aim of this study was to compare the flight-related morphology before and after complete post-juvenile moult in an isolated, sedentary population of the Bearded Tit, on the basis of: (1) characterising the variability in wing shape, wing length and body size of birds caught for ringing, and (2) assessing age and sex differences and time-related variation in the wing traits of birds trapped before or after subsequent complete moult.

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METHODS

Study site

The Bearded Tits in this study belong to an isolated and sedentary population, inhabiting a wetland area of Alicante province (southeastern Spain). The main wetland site of this area is El Hondo Natural Park (38°16'N 00°41'W), 20 km from the Mediterranean Sea. Numbers of Bearded Tits in this wetland, together with other smaller populations in nearby areas (Santa Pola saltpans, 38°12'N 00°32'W), were estimated to be 50 pairs in 1998–2000 (López & Monrós 2003, 2004). This nucleus is geographically separated from other main Spanish populations, with distances of 150 km to one in the east (Albufera de Valencia Natural Park, 39°20'N 00°22'W), 300 km to a northeastern population (Ebro Delta Natural Park, 40°43'N 00°42'E) and about 300–400 km to populations in central Spain, the largest being Tablas de Daimiel National Park (39°25'N 02°56'W). El Hondo is a 2,500 ha reservoir built on the remnants of a natural wetland, in which reed *Phragmites communis* is the dominant emergent plant. Bearded Tits of El Hondo have been trapped for ringing from 1991 (Peiró 1997), and there is no evidence from recapture data for the exchange of individuals with other populations (Peiró & Maciá 2002).

Biometrics

According to Svensson (1992) both adult and juvenile Bearded Tits undergo a complete moult (including flight feathers). Therefore, after the moult it is impossible to discriminate first-year birds from adults. We have observed that juveniles start to moult at the end of July at El Hondo. Given a range of 50–60 days to complete the moult in this species (Pearson 1975, Ginn & Melville 1983), they would finish moult at the end of September. Birds were aged as juveniles (Euring Code 3) according to plumage features before or during post-juvenile moult in spring and summer (Svensson 1992). Any bird with completed moult caught from spring/summer onwards was considered as adult (Euring Codes 4 and 2). Adults and juveniles were sexed by bill coloration according to Svensson (1992). This sexing method has shown to be reliable from shortly before fledging (Cramp & Perrins 1994).

Wing shape was characterised by measuring the wing length and the wing formula for each individual. Wing length (maximum chord method: Svensson 1992) was recorded to the nearest 0.5 mm. The wing formula of the left wing was recorded by measuring the primary distances from the wingtip to the tip of each of the nine primaries (except the first one, vestigial in adults), numbered in ascending order (P2–P10). Measurements were taken to the nearest 0.5 mm on the folded wing, using a transparent ruler. Additionally, bill length (to the skull) and tarsus

length (to the last scale) were measured to the nearest 0.1 mm using dial callipers (Svensson 1992). All measures were taken by the same person in order to ensure repeatability. Primary lengths were calculated by subtracting each primary distance from the wing length (Evered 1990). Prior to statistical analysis, primary lengths were log-transformed to ensure normality and standardised by dividing by the standard deviation for the nine primaries according to the methodology of Lockwood *et al* (1998). Average values are presented \pm standard error (se).

Data analysis

A Size-Constrained Components Analysis (SCCA) method (see Lockwood *et al* 1998), derived from a Principal Components Analysis (PCA) on the correlation matrix of primary lengths, was used to estimate the main sources of variation in the feather-length data and to obtain an independent and objective assessment of wing morphology. This method works well for interspecific comparisons, or when comparing individuals within species with a high sexual dimorphism (Lockwood *et al* 1998) likely to result in sex-specific differences in flight performance (Swaddle & Lockwood 2003). Allometry was tested by means of Pearson correlation coefficients among Principal Components (PC) axes according to Lockwood *et al* (1998).

A PCA on the correlation matrix of tarsus and bill length was used to assess the possibility that any observed relationships between wing morphology and age or sex was affected by daily or seasonal biases in the capture rate of individuals of different body sizes. We used tarsus and bill length as best predictors of the overall body size because they have a strong skeletal component (Pascual & Senar 1996, Senar 1997) and are not influenced by the nutritional status of the bird such as fat or mass (Piersma & Davidson 1991). The first eigenvalue (PC1) is commonly used as an estimator of body size (Rising & Somers 1989). Factor scores obtained from PC1 were normally distributed (Kolmogorov–Smirnov Test; $D = 0.052$; $P > 0.15$). To assess the direction of changes in body size and whether these were consistent with wing morphology, Pearson's correlations between mean structural body size and wing-factor scores were calculated. Correlations between body-size loading factors, hour and month were subsequently used to test trends. Differences in structural body size among age and sex classes were tested by one-way ANOVA.

A mixed univariate Analysis of Variance was used to assess possible differences in wing morphology, as measured by the mean PCA scores, according to age, sex and month (Norusis 1990) taking into account the minimum possible interactions (*eg* age, sex, month, age*sex, and age*sex*month). All analyses were performed using SPSS and MINITAB statistical packages (Norusis 1990, Minitab Inc 1997).

RESULTS

The wing length and wing formula were recorded from 66 individual Bearded Tits, caught from May 2002 to May 2004. Birds were grouped into two age (31 adults; 35 juveniles) and sex classes (46 males; 20 females) to obtain greater sample sizes. The PCA on the standardised primary lengths extracted three components, which accounted for 97.8% of the total variance and were used to evaluate wing morphology (Table 1).

The first three Principal Components were assumed to be, respectively, isometric wing size (PC1) and shape axes (PC2 and PC3), according to Lockwood *et al* (1998). PC2 is heavily loaded with the outermost part of the wing, particularly P2, depicting basically a pointed wing. PC3 corresponds to an increase in the length of the most distal primary (higher positive loading) and to a decrease in that of feathers towards the wingtip (P3–P4), followed by an increase in the inner primaries (similar positive loadings than P2), rendering a convex wing. Thus, PC2 could be interpreted as a pointedness shape index and PC3 as a convexity or roundness shape index. PC2 and PC3 were not significantly allometric ($r_9 = -0.04$, $P = 0.991$, and $r_9 = 0.264$, $P = 0.493$, respectively).

There was significant variation between ages and sexes in the wing size (PC1) and shape components (PC3) according to the Mixed ANOVA analysis (Table 2). The effect of month was not significant in the mixed comparisons of wing traits (Table 2). In pairwise comparisons, adults and juveniles and males and females differed in mean PC scores, adults having significantly greater wing sizes than juveniles, and males significantly less convex wings than females (negative values of PC1 and PC3, respectively, Table 3).

Table 1. Loading factors of the first three axes of the PCA performed on the correlation matrix of primary feather lengths, numbered in ascending order. Shape variance is the partitioning of variance after the isometric size variance explained by PC1 is removed.

	PC1	PC2	PC3
P2	-0.299	0.817	0.474
P3	-0.336	0.188	-0.399
P4	-0.342	0.085	-0.346
P5	-0.342	0.054	-0.359
P6	-0.340	-0.030	-0.201
P7	-0.341	-0.175	0.004
P8	-0.338	-0.213	0.161
P9	-0.331	-0.357	0.270
P10	-0.328	-0.288	0.479
Eigenvalue	8.3007	0.3321	0.1678
% total variance explained	92.2	3.7	1.9
% shape variance explained	10.6	18.8	

The mean structural body size, measured as the first eigenvector using bill and tarsus length as estimators (eigenvalue = 1.281; variance explained = 64.1%; $n = 65$), did not show a relevant trend with time of day ($r_7 = 0.094$; $P = 0.0824$) although a marginally significant reduction with month, from April to December, was detected ($r_6 = -0.828$; $P = 0.042$). Data analysed by age and sex classes showed a marginally significant reduction in body size with monthly progression in males ($r_6 = -0.818$; $P = 0.046$) and an increase for juveniles ($r_3 = 0.997$; $P = 0.046$). Significant correlations were detected between wing pointedness and convexity loading factors (PC2 and PC3) and structural body size (PC2: $r_{64} = 0.263$; $P = 0.034$; PC3: $r_{64} = 0.274$; $P = 0.027$).

Variations in structural body size were detected among sexes, males having significantly greater body size than females (mean PC1 males: 0.257 ± 0.16 ; mean PC1 females: -0.577 ± 0.22 , ANOVA $F_{1,63} = 8.38$; $P = 0.005$). The variations in wing length between the two main age and sex classes (mean adults = $59.08 \text{ mm} \pm 0.28$, $n = 31$; mean juveniles = $55.19 \pm 0.27 \text{ mm}$, $n = 35$; ANOVA $F_{1,64} = 100.45$; $P = 0.000$; mean males = $57.39 \pm 0.39 \text{ mm}$, $n = 46$; mean females = $55.97 \pm 0.42 \text{ mm}$, $n = 20$; ANOVA $F_{1,64} = 4.74$; $P = 0.033$) were consistent with variations in wing size among ages found from Mixed ANOVA and allometry analyses (Tables 2 and 3).

DISCUSSION

The results of the study indicate that wing morphology of Bearded Tits in this sedentary and isolated Spanish population appears to change as a result of the complete post-juvenile moult, at least in some components of size and shape, since birds attaining adult plumage had a significantly larger wing size compared to pre-moult juveniles. The sexes also differed significantly in wing

Table 2. Mixed univariate model Analysis of Variance, testing for differences in wing size (PC1), wing pointedness (PC2) and wing convexity (PC3) in relation to age, sex and month. Age, sex and month effects were estimated using a Type III sum of squares. Significance level (two tailed): * = $P < 0.05$; *** = $P < 0.01$; NS = not significant.

	Wing size		Wing pointedness		Wing convexity	
	df	F P	F P	F P		
Age	1,48	26.70 ***	1.68	NS	0.03	NS
Sex	1,48	2.28 NS	0.41	NS	5.56	*
Month	6,48	0.57 NS	1.60	NS	1.59	NS
Age*sex	1,48	1.01 NS	0.11	NS	0.98	NS
Age*sex*month	8,48	0.99 NS	1.33	NS	0.51	NS

Table 3. Mean PC scores and standard errors for the age and sex classes. For each pair of values the ANOVA *F* value and probability level is given. Sample sizes: 31 adults and 35 juveniles; 46 males and 20 females. Significance level (two-tailed): * = *P* < 0.05; *** = *P* < 0.01; NS = not significant.

	PC1		PC2		PC3	
Adults	-2.29 ± 0.32	85.75	-2.29 ± 0.32	0.49	-0.09 ± 0.08	2.93
Juveniles	2.04 ± 0.34	***	2.04 ± 0.34	NS	0.08 ± 0.06	NS
Males	-0.30 ± 0.44	1.70	-0.02 ± 0.09	0.24	-0.08 ± 0.06	5.60
Females	0.69 ± 0.56	NS	0.05 ± 0.11	NS	0.17 ± 0.07	*

shape, because females attained significantly more convex wings than males after the moult. Month had no effect on these differences, showing that the gradual abrasion of plumage was not a significant factor in wing-shape variation between the sexes.

Our results also indicate that some components of wing shape, such as the wing pointedness explained by PC2, were not age- or sex-related after complete moult. These conclusions differ from the results reported by Nielsen (1993), who observed that adults after moult had attained more pointed wings than juveniles.

Alatalo *et al* (1984) point out that differences in wing measurements with respect to age in species with complete moult should be smaller than in species with partial moult. Our observations are in accordance with this and indicate that both adults and juveniles do not differ in some components of wing morphology, such as wing pointedness. Alatalo *et al* (1984) also suggest that the optimal compromise between manoeuvrability and speed must differ between resident and migratory birds, and between species living in dense and open habitats.

Intraspecific differences in wing morphology are also found in other passerines of different migratory status (Mulvihill & Chandler 1990, Monkkonen 1995, Copete *et al* 1999, Pérez-Tris & Tellería 2001, Peiró 2003). Pérez-Tris & Tellería (2001) found that juvenile Blackcaps *Sylvia atricapilla* had shorter wings than adults in migratory populations but not in sedentary ones. They find support for the hypothesis that, in sedentary populations, the costs of migration are absent and hence morphological adaptations to long-distance flights lack importance, providing an explanation for the absence of differences in wing shape between ages.

The sedentary and colonial behaviour of Bearded Tit in the El Hondo study area may have resulted in subtle differences in wing morphology among ages and sexes. Adults and males with larger and less convex wings may perform better on long trips in crowded habitats, behaving as transients, while juveniles and females with smaller and more convex wings may be better adapted for short trips, behaving, in the context of reedbed microhabitat structure and a colonial behaviour system, as residents.

In this respect, this population of Bearded Tits may be similar to flocking Siskins *Carduelis spinus*, in which Senar *et al* (1994) found intraspecific differences in wing shape between winter residents and transients.

Wing-size differences between adult and juvenile Bearded Tits could be due to an overall increase in winglength after completing the moult (Nielsen 1993), as also exhibited by other species in relation to complete moults (Svensson 1992).

Wing-shape differences between sexes in favour of more convex (or rounded) wings in females could enhance their manoeuvrability. Although this wing shape could reduce the ability of females to take off in dense habitats (such as reeds) (Williams & Swaddle 2003), they may be adept at moving around these crowded habitats (Swaddle & Witter 1998). Males could be at a relative disadvantage since their more pointed wings perform worse in such habitats, although in other respects they may be somewhat more mobile than females in long-distance flights. These different aspects of male and female wing morphology may be adapted to the typical colonial breeding behaviour of Bearded Tits (Hoi & Hoi-Leitner 1997).

Differences in body size were seasonally dependent and consistent with morphometric differences. A reduced body size was more pronounced in winter (November–December), which can indicate the selective capture of low size classes as time progresses, but may also result from selection operating against larger individuals in the population, particularly in harsh periods. Given that short flights and hanging foraging positions are energetically very costly for small passerines (Norberg 1977, Tatner & Bryant 1986, Carlsson & Moreno 1992), under environmental stress, food or habitat constraints, selection should favour reduced size because foraging efficiency is higher in smaller individuals as a result of reduced energetic costs of maintenance, increased manoeuvrability and less expensive foraging (Andersson & Norberg 1981, Norberg 1981, Merilä & Wiggins 1997, Merilä *et al* 1997). Further research is needed in other European populations of Bearded Tit to ascertain how the complete post-juvenile moult affects flight performance in relation to ecomorphological constraints.

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