



Relationships of wingtip shape, song-flight and mating success in male black-headed buntings *Emberiza melanocephala*

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Abstract

Wing design in birds is the result of different and potentially opposing natural selection pressures, such as those related to migration, predator avoidance and habitat type. Sexual selection for flight performance may also shape wing design via female preferences for superior performance of flight display. The black-headed bunting *Emberiza melanocephala* is a polygynous species that is sexually dimorphic in both plumage colour and size. Males perform *Towering* song-flight, which is a physically demanding display performed only in the presence of receptive females, potentially affecting male mating success. *Towering* flight features could in turn be influenced by wing morphology. Thus, we studied male wingtip shape in relation to the frequency of *Towering* song-flights and consequently in relation to the mating success of black-headed bunting males. We found that male mating success was not related to the frequency of song-flights even though it was predicted by male wingtip shape, perhaps suggesting that the quality of *Towering* flights, in terms of height, steepness or duration of flight, rather than the quantity, influences male mating success.

Keywords Biometry · *Towering* · Arrival timing · Croatia · PCA

Introduction

Wing design in birds is mainly the result of different and potentially opposing natural selection pressures, among which are those related to migration, particularly of long-distance migrants (Senar et al. 1994; Norberg 1995b; Lockwood et al. 1998; Fiedler 2005; Arizaga et al. 2006), habitat type (Winkler and Leisler 1992) and predator escape behaviour (Swaddle and Lockwood 2003). For example, pointed wings have been identified as beneficial for long flights, allowing greater flight efficiency (Arizaga et al. 2006), and several studies on passerines have confirmed that species that migrate longer distances have longer, more pointed or concave wings (Mönkkönen 1995; Calmaestra and Moreno 2001; Arizaga et al. 2006; Neto et al. 2013). On the other

hand, birds with rounder wingtips can take off at a steeper angle of ascent, which has been demonstrated to be an effective means of predator avoidance (Swaddle and Lockwood 2003). Rounder wings also aid manoeuvrability and are therefore more beneficial in dense vegetation (Vanhooydonck et al. 2009).

Wing design could also be affected by sexual selection (reviewed in Husak and Fox 2008), particularly in species that incorporate flight performance into their display (Völker 2001). For instance, song-flight, a courtship display simultaneously incorporating both flight and song, can play an important role in mate choice, and wing shape could be subjected to intense sexual selection pressure. Courtship displays are physically demanding (Clark 2012), as they can be costly either in terms of high energy expenditure, i.e. the total energy, measured in joules or calories, expended to perform the behaviour (e.g. Vehrencamp et al. 1989; Höglundi et al. 1992) or high power outputs, i.e. energy per unit time that is expended on a behaviour, measured in watts or a correlate such as the oxygen consumption rate (e.g. Usherwood 2008). Courtship flights that are costly can reliably signal male quality and condition (Iwasa et al. 1991; Mather and Robertson 1992). Courtship flights could be regarded as a condition-dependent sexual signal as its cost changes

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depending on the physical condition of the performing male (Halupka and Borowiec 2006), since flight incurred costs in birds increases allometrically with body mass (Pennycuik 1989) and the bird's body mass has strong seasonal and diurnal variation (e.g. Witter and Cuthill 1993). Courtship displays may also increase predation risk (Zuk and Kolluru 1998). Only a few studies have investigated the function of courtship flights in a particular bird species. For example, when selecting social mates blue-black grassquit *Volatinia jacarina* females favour higher-leaping males, an attribute associated with enhanced body condition that could indicate better parenting abilities (Manica et al. 2016). In the common whitethroat *Sylvia communis*, song-flights are used in attracting females (Balsby 2000; Halupka and Borowiec 2006), as opposed to the perch song, which is used in territorial defence (Balsby 2000). Furthermore, common whitethroat males that advertised intensively needed less time to attract a female, and their parental performance was better compared to males that produced cheaper signals (Halupka and Borowiec 2006).

Here, we explore morphometric attributes potentially important for mating success in male black-headed buntings *Emberiza melanocephala*. We predicted pronounced sexual dimorphism in wing morphology. On one hand, black-headed bunting wings are, in comparison to those of other bunting species, rather long and pointed, typical for long-distance migrants (Cramp and Perrins 1994). On the other hand, the song-flight display, which is an integrative part of males' mating behaviour (Barišić et al. 2022), could drive males' wingtips towards a more rounded shape (Lockwood et al. 1998). Thus, in males, as opposed to females, wing morphology could be subjected to additional, possibly opposing, strong selection pressure constraining the wingtip design (Hedenström and Møller 1992). We predicted that male wingtip shape influences flight display and, consequently, male mating success. The variation in male arrival timing was also explored as it is widely accepted that in migratory species the arrival time of birds at their breeding grounds is correlated with their innate quality (reviewed in Kokko 1999).

Methods

Study species and site

Black-headed buntings are long-distance protandrous migrants, breeding from the NE Mediterranean to W Iran and from the Caspian to the Arabian Sea, wintering in India and mostly inhabiting scrubland and arable areas (Cramp and Perrins 1994; Ćiković et al. 2021). It is a polygynous species with no or low level (fledging period only) of paternal care (authors' unpublished data). Males arrive at the

study area from the first week of May, and females follow approximately one week later (authors' unpublished data). Males perform two types of song-flight, *Moth* and *Towering* song-flights. *Moth* is performed towards the conspecific male and probably serves as a threat display, while *Towering* is performed only in the presence of the receptive female (Barišić et al. 2022). The *Moth* is simple since a standard song is sung during a level flight, while the *Towering* incorporates a specifically structured song produced during a complex ascending and descending flight. A typical *Towering* song-flight is depicted in Barišić et al. (2022) and involves a male steeply ascending to an estimated 5–10 m above the take-off point, stalling shortly at the peak of the ascent before descending to a nearby perch. While performing the *Towering*, the bird flies with shallow quivering wingbeats, lowered wings, raised tail, ruffled plumage and dangling legs. Here, we focused on *Towering* since it was performed in the presence of the receptive female and since it was a more demanding flight than *Moth* in terms of power or energy requirements.

This study was carried out in Ravni Kotari, a geographic region in Croatia adjacent to the Adriatic Sea (43°50' N, 15°45' E). The climate is Mediterranean, with hot and dry summers and mild and rainy winters. Based on a study of black-headed bunting distribution and abundance carried out by the authors in 2010, we chose a study plot (3 km²) that held a dense population of black-headed bunting and represented the typical habitats of the region: traditional small-scale mosaic agricultural habitats (vineyards, olive groves, orchards, meadows, cereal and vegetable fields) intersected with natural vegetation in different stages of succession (eumediterranean garrigues and maquis and submediterranean deciduous shrubs). In general, the habitat in the study plot was structurally complex, contributing to a high diversity of bird species.

Fieldwork

Catching and measuring birds

Males were caught from 2011 to 2015, at the beginning of the breeding season, mostly in the first half of May. Conspecific song playbacks were broadcast from loudspeakers to lure and catch males into mist nets. Females were caught in 2011, 2012 and 2014, either unintentionally in mist nets while catching males or by intersecting their trajectory from or towards the nests with custom-made nets. Each bird was marked with a unique combination of three colour rings and one engraved metal ring, which allowed individual recognition from a distance. Altogether, 72 individual males and 12 individual females were captured and measured.

Birds were measured by the first author (SB) following the procedure given by Svensson (1992). For each bird,

the following measurements were taken: wing (maximum chord), tarsus and tail lengths; bill dimensions (length, width, depth); the distance of primary feathers P2–P8 (P1 is vestigial) to the tip of the wing (numbered ascendently); and body mass. Bill length was measured from the tip to the skull, while depth and width were measured at the distal corner of the nostrils. Wing, tail and primary feather lengths were measured with a steel wing rule (to the nearest 0.5 mm), tarsus and bill dimensions with a plastic calliper (to the nearest 0.1 mm) and body mass with a digital balance (to the nearest 0.1 g).

Observing the behaviour of birds

From 2011 to 2013, we daily observed the behaviour of birds, usually from dawn (avg. 05:25) to midday and from 17:00 to dusk (avg. 20:30). Each year, the fieldwork started before the arrival of the birds at the breeding grounds (the beginning of May) and lasted until the end of the breeding activity (from the middle to the end of July, depending on the year). In anticipation of the arrival of the birds, we checked all potential territories within the whole study plot daily to record the arrival dates of individual birds. In 2012 and 2013, we recorded the arrival dates of males in the year they were marked. This was achieved by audio recording the song of unmarked territorial males and their arrival dates. Black-headed bunting males sing an individually distinct and stereotyped song, which remains identical throughout the male's lifespan (Barišić et al. 2018). Thus, after a male was caught and marked, his song was again recorded to verify his identity. From 2011 to 2013, we monitored the number of *Towering* song-flights per male per season. Three days were approximately required to survey all males' territories in the study plot, and although we did not record the study effort per male, the time spent in the study plot was equally allocated to all territories. Thus, approximately the same observation effort was given to each male. A male was considered mated if he was following a female and guarding her (leaving the female to chase off or fight intruding males). A female was regarded as mated to the male within whose territory she nested. All territories were searched for nests, even those where no females were observed.

Data analysis

No differences were detected among years in morphometric traits (for all traits: ANOVA, $F < 2.15$, $P > 0.08$), so data were pooled. The Levene test for the equality of group variances was used to compare variability between sexes and among morphometric traits (Jacobs and Podolsky 2010).

The lengths of primaries were calculated by subtracting each feather tip distance from the wing length (Evered 1990) and correcting for allometric relationships using the

equation proposed by Senar et al. (1994), $P'_{ji} = P_{ji}(l_0/l_i)^{b_j}$, where P_{ji} is the original measurement of the primary j of an individual i , l_i is the wing length of an individual i , l_0 is a standard wing length (the average wing length of the population) and b_j is the allometric coefficient of primary j according to the growth model $P_{ji} = a_j l_i^{b_j}$. These size-corrected measurements of primary lengths (SP2–SP8) were used in a principal component analysis (PCA) to obtain an assessment of wingtip shape variation in the black-headed bunting. PCA was also performed on the correlation matrix of body measurements (wing, tail and tarsus lengths, and bill dimensions) to acquire an estimate of overall body size (Rising and Somers 1989). The first principal component (PC_{Body1}) had high and positive factor loadings for all traits (see Results) and was thus used as a measure of body size. Body mass was regressed against PC_{body1} scores controlling for sex (GLM, $R^2 = 0.34$, $F_{2, 77} = 24.57$, $P < 0.001$), and residuals (residual body mass) were used as an index of body condition. Residuals from a regression of body mass on a linear measure of body size were shown to be a reliable index of body condition in the sense that it reflects variation in all constituents of body composition, including fat, protein, water and skeletal tissue (Schulte-Hostedde et al. 2005).

For the male arrival date, the first day a male was recorded in his territory was used. In contrast to the conspicuous males, females were discreet and thus hard to spot immediately upon arrival. For that reason, instead of using the female arrival date, we used the breeding onset date, which was identified as the date the first egg was laid. As male arrival dates varied between years, we calculated the “arrival day” for each male as the number of days after the arrival of the first male in that year. Breeding onset dates also varied between years, so the same was done to calculate female “breeding onset day”. Male mating success was expressed in terms of the number of acquired females and in terms of the male mating day, i.e. the female breeding onset day in the male territory. Since the majority of females were not marked, inference on the number of acquired females was based on simultaneously observing more than one female or on the number of simultaneously active nests in the male's territory. Thus, for some males, the number of acquired females could have been underestimated. The majority of females started to breed after males had arrived (90% of females in 2012–2013 started to breed after the last male had arrived, $N_{female} = 30$, $N_{male} = 41$), and breeding onset day was not related to male arrival day (see Results). If a male was mated to more than one female, the breeding onset referred to a first nesting attempt of the first female at the male's territory. The males that disappeared early from the study plot were categorised as nonterritorial males. The nest dataset consisted of 95 nests, of which 22 were used to represent female breeding onset in the male's measurement year.

Male morphometric traits were examined in relation to his arrival, mating success and *Towering* frequency only for the year in which males were measured to avoid potential bias caused by interannual changes in morphometric traits that were recorded in songbirds (Bryant and Jones 1995; Merom et al. 1999), thus narrowing the sample size to 22 males with breeding onset recorded, 24 males with the number of acquired females recorded, 26 males with *Towering* frequency recorded and only 18 males with arrival day recorded.

We separately analysed male mating success and *Towering* frequency in relation to male wing shape and condition with a generalised linear model (GLM) with a Poisson error distribution and a log link function. The dependent variables representing male mating success were either the male mating day (female breeding onset at the male's territory) or the number of acquired females, and the predictor variables were PC_{wing1} , PC_{wing2} (scores for the first two principal component axes of the wing shape analysis) and residual body mass. We repeated the analysis with the *Towering* frequency (number of *Towerings* recorded per season per male) as a dependent variable and PC_{wing1} , PC_{wing2} and residual body mass as predictor variables. Finally, we analysed whether male mating success was related to *Towering* frequency. As *Towering* frequency was expressed per season, we used only the number of females, also expressed per season, as a dependent variable. Each multiple-predictor model was tested for overdispersion, and significant deviance from Poisson dispersion was not detected in any model (for all models: $P > 0.1$). When the deviance analysis suggested overdispersion in the single-predictor model, we adjusted standard errors using negative binomial GLM. Analyses were performed with R version 3.6.3 (R Developing Core Team 2020) using psych, MASS and AER packages.

Results

Males were significantly larger than females in all traits measured (for all traits: Welch's t test, $t > -2.25$, $P < 0.04$) except bill length (Welch's t test, $t = -2.07$, $P = 0.06$). The wing length range did not overlap between sexes, and the mean wing length of a male was approximately 8 mm longer than that of a female (for details, see Appendix 1 in Supplementary material). The percent differences in the wing and tail between sexes were 8–9%, while in the tarsus and bill dimensions, they were 2–4%. The body mass percent difference was 9%.

In males ($N = 64$), the third primary was the longest (61.8%) or the same length as the second (14.7%) or the fourth primary (13.2%), while the second primary was the longest in 7.4% of males and the fourth in 1.5% of males. Similarly, in females ($N = 11$), the third primary was the

longest (41.7%) or the same length as the second (16.7%) or the fourth primary (16.7%), but the second primary was the longest in 25% of females.

The Levene test showed no significant difference in the variability of all morphometric traits between sexes (for all traits: $F < 4.14$, $P > 0.05$). Examining variability in wing and other body measurements for both sexes revealed relatively low coefficients of variation (CV) for wing parameters (wing and primary lengths) but relatively high CV for other body parameters (tail, tarsus, bill lengths and mass) (Appendix 1 in Supplementary material).

The first two principal components (PC_{wing1} and PC_{wing2}) accounted for an accumulated 69.7% of the total variance for standardised primary feather lengths (Table 1, Appendix 2 in Supplementary material). PC_{wing1} represented an axis of increasing proximal primary lengths (SP4–SP8) and could therefore be interpreted as an index of wingtip convexity (sensu Lockwood et al. 1998), where individuals with higher PC_{wing1} scores showed proportionally longer proximal primaries, that is, more convex wingtips. PC_{wing2} represented an axis of decreasing SP2 length and the degree to which it was inversely related to SP3 and, to a lesser extent, SP4, therefore indicating an increase in the tendency to shift the wingtip away from the wing leading edge. Thus, individuals with higher PC_{wing2} scores showed proportionally rounder wingtips. These two axes represented the principal dimensions of wingtip morphology in the black-headed bunting and were used to quantify wingtip shape variation.

There was no significant difference in either PC_{wing} axes scores between sexes (Welch's t test, PC_{wing1} , $t = -1.21$, $df = 23.19$, $P = 0.24$; PC_{wing2} , $t = -0.62$, $df = 15.64$, $P = 0.54$).

A PCA of body measurements extracted two principal components that explained 65.0% of the variation in body size. The first principal component (PC_{body1}) was positively influenced by all body measurements and thus was taken to be a measure of overall size. Contrary to PC_{body1} , the

Table 1 Factor loadings (varimax rotated) of principal component analysis of the standardised primary lengths (SP2–SP8) of the black-headed bunting from Croatia

Primary feather	PC_{wing1}	PC_{wing2}
SP2	– 0.01	– 0.78
SP3	0.15	0.77
SP4	0.48	0.44
SP5	0.85	0.16
SP6	0.92	0.09
SP7	0.94	0.04
SP8	0.80	0.16
Eigenvalue	3.64	1.24
Variance explained	52.1%	17.7%

Table 2 Factor loadings (unrotated) of principal component analysis of the body measurements (wing, tail, tarsus lengths and bill length, width and depth) of the black-headed bunting from Croatia

	PC _{body1}	PC _{body2}
Wing	0.72	− 0.58
Tail	0.71	− 0.63
Tarsus	0.56	0.39
Bill _{length}	0.63	0.01
Bill _{width}	0.58	0.50
Bill _{depth}	0.64	0.53
Eigenvalue	2.49	1.41
Variance explained	41.5%	23.6%

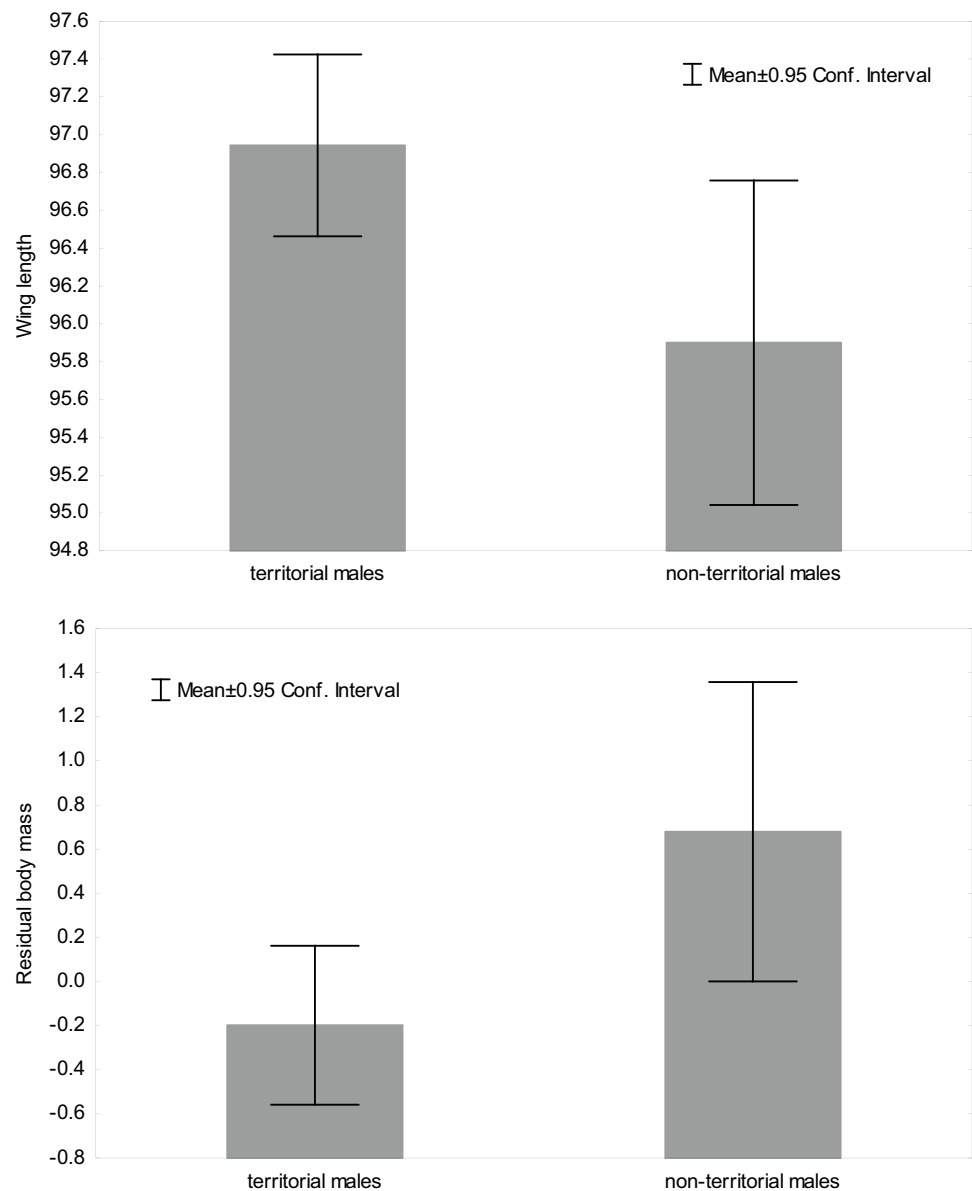
second principal component (PC_{body2}) showed mixed influences of morphological characters (Table 2, Appendix 3 in Supplementary material). Females ($N=10$) differed from

males ($N=71$) in both PC_{body} axes scores, and the difference was much more pronounced in PC_{body1} scores (Welch's t test: PC_{body1}, $t = -9.24$, $df = 12.71$, $P < 0.001$; PC_{body2}, $t = 2.70$, $df = 10.88$, $P = 0.02$).

PC_{body1} scores were higher in territorial ($N=55$) than in nonterritorial males ($N=14$), but the difference was not significant (Welch's t test, $t = 1.78$, $df = 19.71$, $P = 0.09$). However, territorial males had significantly longer wings than nonterritorial males (Welch's t test, wing, $t = 2.23$, $df = 21.91$, $P = 0.04$, Fig. 1). Conversely, residual body mass was significantly lower in territorial ($N=54$) than in nonterritorial ($N=11$) males (Welch's t test, $t = -2.23$, $df = 64$, $P = 0.03$, Fig. 1).

Towering frequency was strongly predicted by residual body mass and, to a lesser extent, by PC_{wing2} (Table 3, Fig. 2). Towering frequency was also significantly negatively

Fig. 1 Wing length and residual body mass comparisons between black-headed bunting territorial ($N=55$ and $N=54$, respectively) and nonterritorial males ($N=15$ and $N=11$, respectively) from Croatia



related to body mass (negative binomial regression, $N = 26$, $\chi^2(1) = 9.12$, $P = 0.003$). Thus, males in poorer conditions and with less rounded wingtips performed more *Towerings* in a season, and *Towering* frequency was not significantly related to the number of acquired females (Poisson regression, $N = 27$, $\chi^2(1) = 0.00$, $P = 0.96$).

Breeding onset was predicted by PC_{wing2} , while PC_{wing1} and residual body mass were not significantly related to breeding onset (Table 4, Fig. 3). None of the predictor variables were significant determinants for the number of acquired females (Table 4, Fig. 4). Thus, males with rounder wingtips started to breed earlier, but the number of acquired females was not related to male wingtip shape or condition.

Male arrival day was not significantly related to measured (wing, tail and tarsus length, bill dimensions and body mass) or calculated male morphometrical traits (body size, wingtip shape or residual body mass) (for all: Poisson regression, $N = 18$, $\chi^2(1) < 2.60$, $P > 0.11$). Male arrival was not significantly related to breeding onset (negative binomial

regression, $N = 29$, $\chi^2(1) = 0.62$, $P = 0.43$) or *Towering* frequency (Poisson regression, $N = 22$, $\chi^2(1) = 1.49$, $P = 0.22$).

Discussion

Apart from being highly dimorphic in plumage colour, the black-headed bunting is size dimorphic, with males being significantly larger than females. The size difference was most evident in wing length, the range of which did not overlap between sexes. The difference was less pronounced in the size of the tarsus and bill. Bill size was the most variable morphometric trait in both males and females. Bill length and depth measurements were shown to be highly reliable (Perktaş and Gosler 2010), and variability in the bill length and depth could not be attributed to measurement error. The minimum variability of wing measurements found in the black-headed bunting was expected, as the wing is under the

Table 3 Results of a generalised linear model with a Poisson error distribution of *Towering* frequency (the number of *Towering* song-flights per male per season) of the black-headed bunting males from

Dependent	Predictor	Estimate	SE	IRR	95% CI	<i>P</i>
<i>Towering</i> frequency $N = 26$ $\chi^2(3) = 33.73$ $P < 0.001$	PC_{wing1}	− 0.05	0.13	0.95	0.73, 1.24	0.70
	PC_{wing2}	− 0.36	0.13	0.70	0.55, 0.90	0.005
	Residual body mass	− 0.46	0.10	0.63	0.51, 0.76	< 0.001

Croatia as dependent variables and PC_{wing1} , PC_{wing2} and residual body mass as predictor variables

PC_{wing1} and PC_{wing2} are scores obtained from principal component analysis (PCA) on the standardised primary lengths. Residual body mass refers to scores obtained from the body mass regressed against PCA scores of body measurements

IRR Incidence Rate Ratio, *CI* Confidence Interval

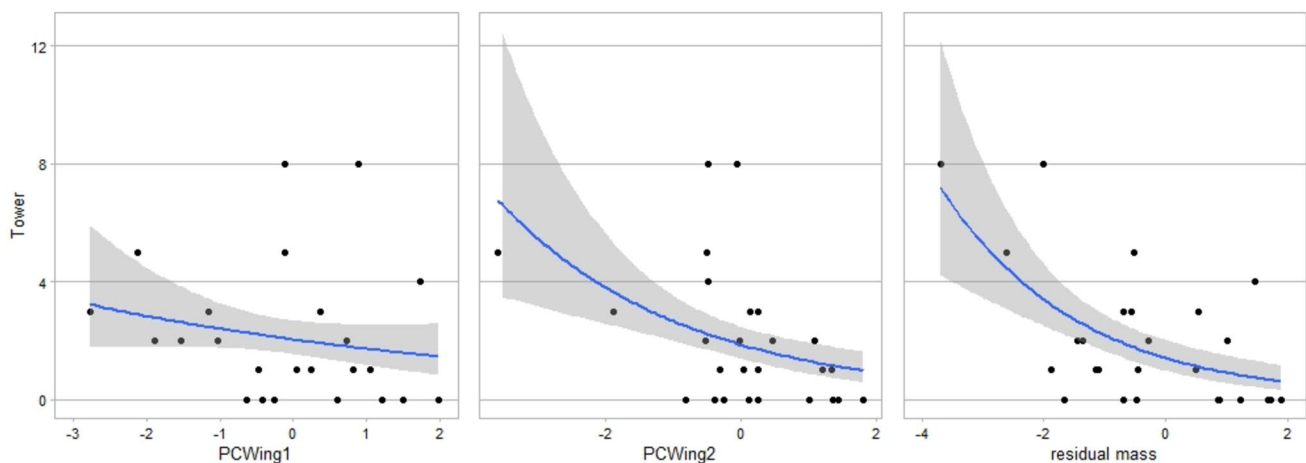


Fig. 2 Scatter plots reporting the relationship between the *Towering* frequency (the number of *Towering* song-flights per male per season) and PC_{wing1} , PC_{wing2} and residual body mass of the black-headed bunting males from Croatia. PC_{wing1} and PC_{wing2} are scores obtained from principal component analysis (PCA) on the standardised pri-

mary lengths. Residual body mass refers to scores obtained from the body mass regressed against PCA scores of body measurements. Regression lines and 95% confidence intervals were derived from a generalised linear model with a Poisson error distribution

Table 4 Results of generalised linear models with a Poisson error distribution of mating success (breeding onset, number of acquired females) of the black-headed bunting males from Croatia as dependent variables and PC_{wing1}, PC_{wing2} and residual body mass as predictor variables

Dependent	Predictor	Estimate	SE	IRR	95% CI	P
Breeding onset N=22 $\chi^2(3)=10.85$ P=0.01	PC _{wing1}	0.06	0.06	1.06	0.95, 1.18	0.32
	PC _{wing2}	-0.25	0.09	0.78	0.66, 0.92	0.004
	Residual body mass	0.04	0.06	1.04	0.94, 1.16	0.45
Number of females N=24 $\chi^2(3)=0.11$ P=0.99	PC _{wing1}	-0.02	0.15	0.98	0.73, 1.31	0.88
	PC _{wing2}	0.05	0.17	1.06	0.77, 1.49	0.75
	Residual body mass	0.00	0.13	1.00	0.78, 1.30	>0.99

PC_{wing1} and PC_{wing2} are scores obtained from principal component analysis (PCA) on the standardised primary lengths. Residual body mass refers to scores obtained from the body mass regressed against PCA scores of body measurements

IRR incidence rate ratio, CI confidence interval

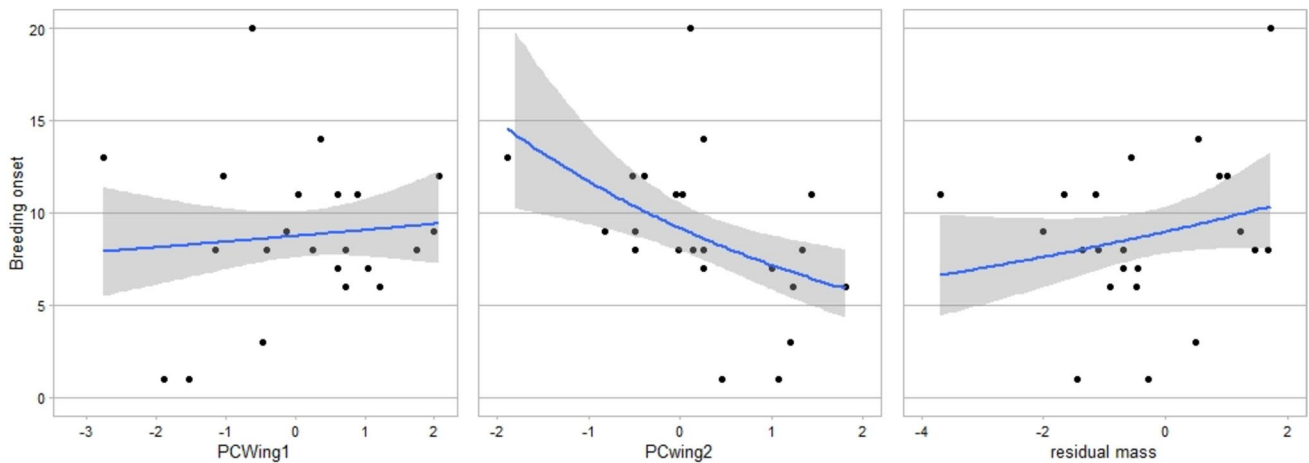


Fig. 3 Scatter plots reporting the relationship between Breeding onset and PC_{wing1}, PC_{wing2} and residual body mass of the black-headed bunting males from Croatia. PC_{wing1} and PC_{wing2} are scores obtained from principal component analysis (PCA) on the standardised pri-

mary lengths. Residual body mass refers to scores obtained from the body mass regressed against PCA scores of body measurements. Regression lines and 95% confidence intervals were derived from a generalised linear model with a Poisson error distribution

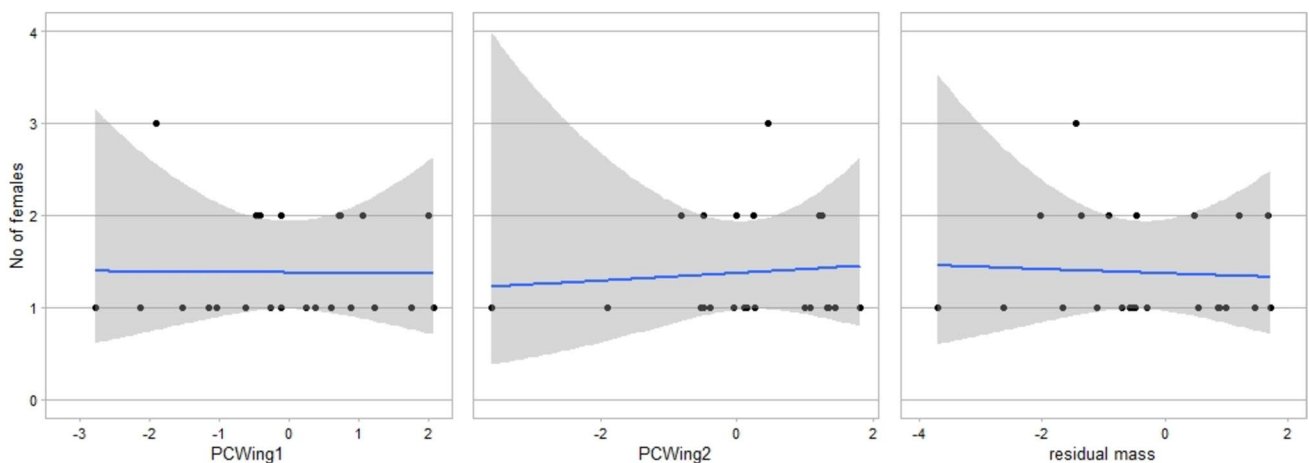


Fig. 4 Scatter plots reporting the relationship between the number of acquired females and PC_{wing1}, PC_{wing2} and residual body mass of the black-headed bunting males from Croatia. PC_{wing1} and PC_{wing2} are scores obtained from principal component analysis (PCA) on the standardised primary lengths. Residual body mass refers to scores

obtained from the body mass regressed against PCA scores of body measurements. Regression lines and 95% confidence intervals were derived from a generalised linear model with a Poisson error distribution

strongest stabilising selection arising from natural selection (Cuervo and Møller 1999).

We found no relationship between male body size and arrival. In contrast, in Asian protandrous buntings, larger males arrived at the studied spring stopover sites earlier (Nam et al. 2011). Furthermore, as opposed to some other studies (Bowlin and Lank 2007; Matyjasiak et al. 2013), we found no correlation between any wing characteristics and the arrival of males. However, the statistical power of our analysis was low and limited in detecting the true effect of male arrival timing since our sample size of males with recorded arrival day in the measurement year was only 16.

In many passerines, adult males have longer wings and tails than other age and sex classes (Alatalo et al. 1984; Arizaga et al. 2007). In this study, body size, mostly reflected in wing length, differed between territorial and nonterritorial males, which perhaps reflects different age classes. Nonterritorial males appeared in the study site throughout the breeding season. These males were present only for a short time and generally provoked weak reactions from territorial males. Some of these males were paler in colouration and had plastic song consistent with second-year males (Barišić et al. 2018). However, since first-year black-headed buntings undergo complete moult at their nonbreeding quarters (Jenni and Winkler 2011), we were unable to decisively differentiate between second-year and older birds. Furthermore, there was a significant difference in residual body mass between territorial and nonterritorial males, and perhaps territorial males in familiar territory with known food resources could afford fewer energy reserves than nonterritorial males.

In this study, males with rounder wingtips tended to acquire a female earlier in the season. Wing shape influences the ascending abilities of a flying bird, and more rounded wings can generate more thrust from flapping, especially at low flight speeds (Lockwood et al. 1998). For example, starling *Sturnus vulgaris* with rounder wingtips can take off from the ground at a steeper angle of ascent (Swaddle and Lockwood 2003). If it is presumed that the optimisation of take-off in birds is similar to the optimisation of ascending during the display, more rounded wingtips would be expected to aid *Towering* displays and could explain the tendency of black-headed bunting males with rounder wingtips to mate earlier in the season. As opposed to take-off flight, where velocity is prioritised (Williams and Swaddle 2003), the ascending flight of the *Towering* display is performed at low speed, thus emphasising the potential positive effect of rounder wingtips.

Voelker (2001) found that contrary to his expectation, pipit *Anthus* males of migratory species are more likely to use flight displays of the “parachuting” type than males of sedentary species. The species of the *Emberiza* genus (45 species) range from resident/nomadic (33%), partly migratory (22%), short-distance migrants (9%) to long-distance

migrants (36%), and only 4 species, all of which are long-distance migrants, have a song-flight display (Billerman et al. 2022). The *Towering* song-flight of the black-headed bunting, a long-distance migrant, is rather similar to the “parachuting” display of pipits. One possible explanation for why long-distance migrants are more likely to use flight displays is that flight displays in species with more pointed and concave wings could be more costly and therefore could reliably signal male quality.

Lighter males and males in lower conditions performed more *Towerings* in a season, which was not surprising given that flight costs in birds increase with body mass (e.g. Pennycuik 1989; Hedenström and Møller 1992; Norberg 1995a; Nudds and Bryant 2000). Even though *Towerings* are performed only when receptive females are in the vicinity (Barišić et al. 2022), we found no relationship between the *Towering* frequency and male mating success in terms of the number of acquired females. We offer two possible explanations for this discrepancy. The power of our analysis could be limited due to several confounding factors that influence *Towering* frequency. A particular male could by chance perform more *Towerings* simply because a female nesting on his (or even a neighbour’s) territory lost her clutch and is reneesting. Additionally, males could engage in *Towering* displays to gain extrapair copulations. We were not able to control for the effects of female receptiveness due to the small sample size. Another plausible explanation is that male mating success is affected by the *Towering* flight quality (power output) rather than the frequency. Moreover, given the relative infrequency of *Towerings* (Barišić et al. 2022), it is highly unlikely that the performing males are limited by energetic cost (Clark 2012). For example, Usherwood (2008) demonstrated that Collared Doves *Streptopelia decaocto* display with maximum muscle capacity and that their display flights represent an honest signal of male flying abilities. Similarly, rather than by energetic demands, black-headed bunting flight displays could be constrained by physical abilities. Interestingly, the male wingtip shape influenced breeding onset and *Towering* frequency in different directions. Males with rounder wingtips tended to acquire females earlier and perform *Towering* fewer times in a season. Thus, later mated males perhaps perform more song-flight displays simply because they spend a longer time courting females.

Although this study showed a relationship between male wingtip shape and mating success, it is highly unlikely that females directly choose males based on their wingtip shape. Rather, females could choose males on flight performance as a function of wing morphology, which in turn reflects the male quality that can be selected by females (Arnold 1983). However, it remains unclear what aspect of flight performance females could base their choice on. Females could perhaps pay attention to height, steepness or duration of

flight. Direct measurements of *Towering* quality and quantity, mating success, including extrapair fertilisations, and whole wing morphology would allow a re-evaluation of the relationships between wing shape, song-flight display and mating success in the black-headed bunting.

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Data availability statement The datasets generated during and analysed during the current study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflicts of interest.

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

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