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Dynamics of phenotypic change: declining wing length despite survival advantage of longer wings in a resident farmland passerine

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Environmental changes, such as climate change and land use change that alter resource availability and energetics, are associated with changes in body size in many taxa. Here, we use wing length as a proxy for overall structural body size to examine a paradoxical trend of declining wing length within a Yellowhammer *Emberiza citrinella caliginosa* population sampled over 21 years, where it has been previously shown that longer wings improve survival. Higher temperatures during the previous winter (prior to the moult determining current wing length) explained 23% of wing length decrease within our population but may also be correlated with non-climatic environmental variation such as changes in farming mechanisms linked to food availability. We found no evidence for within-individual wing lengths shrinking with age, but analysis suggested a progressive decline in the sizes of immature birds recruiting to the population. This trend was weaker, although not significantly, among adults, suggesting that the decline in the sizes of recruits was offset by higher subsequent survival of larger birds post-recruitment. These data support the notion that ecological processes can contribute more than selection to observed phenotypic trends and highlight the importance of long-term studies for providing longitudinal insights into population processes.

Keywords: body size, climate change, longitudinal data, population dynamics

Environmental change, such as changes in temperature, food availability and parasite prevalence, can cause rapid phenotypic responses within populations over relatively few years (Poulin & Thomas, 1999; Ozgul *et al.*, 2009; Yom-Tov & Geffen, 2011). As climate change causes temperatures to rise, individuals within populations across multiple taxa have exhibited decreases in body size (Teplitsky & Millien, 2014). Despite numerous studies demonstrating this, only three have investigated whether body size decreases are adaptive, in terms of positively influencing fitness of individuals within a population monitored through time (Teplitsky & Millien, 2014). A 40-year study of Red-Billed Gulls *Larus scopulinus* found no selection on body mass (Teplitsky *et al.*, 2008), and studies of Great Tits *Parus major* and Soay Sheep *Ovis aries* found positive selection for body size, suggesting that changes in response to climate change may have reduced fitness (Ozgul *et al.*, 2009; Husby *et al.*, 2011). All things being equal we would expect increases in survival to be favoured, and so it poses a paradox if traits linked to survival or fitness, more generally, decrease. However, the Soay Sheep population is growing (Ozgul *et al.*, 2009), and Great Tit populations are generally stable or growing (PECBMS, 2015).

Environmental change, such as climate change, can drive phenotypic change through selection changing gene frequencies (Rausher & Delph, 2015), through the changing environment changing the expression of plastic traits (including epigenetically through parental effects) (Ozgul *et al.*, 2009) or a combination (Pelletier *et al.*, 2007). In order to mitigate the effects of environmental change (e.g. Walther *et al*. 2002; Vasseur *et al*. 2014), we need to understand better how environmental change impacts resource availability and requirements and how this leads to phenotypic change.

Here, we explore data from a long-term (21 year) morphological dataset of a declining, resident farmland bird, the Yellowhammer *Emberiza citrinella caliginosa* (Linnaeus), using wing length as a proxy for body size. Wing length is the best predictor of overall body size within our population (as represented by a composite measure of morphometrics from a subset of our population; see Appendix 1 for a full justification for this rationale) as well as the one for which we have most data. We do not attempt to distinguish between genetic or plastic drivers of phenotypic change, but rather explore a long-term morphological dataset and test associations with potential ecological drivers of change. First, we explore trends in Yellowhammer body size (wing length) at our study site. Finding a long term significant trend towards shorter wings and knowing that longer wings provide a survival advantage in our population (Dunn *et al.*, 2013), we propose three (non-mutually exclusive) hypotheses to explain trends in wing length:

1) Individuals show directional plasticity in wing length, with wing length decreasing over time consistently across individuals;

2) Temporal trends in wing length differ between age classes, and demographic change is driving the overall trend.

3) Temporal trends in wing length are associated with climatic trends at our study site.

Methods

We analysed wing length data collected from 928 Yellowhammers captured during 17 winters (November - April) over 21 years between 1986/7 and 2008/9 (mean ± SE: 54.61 ± 13.88 captures per winter); details of our study population and capture methods are provided elsewhere (Dunn *et al*., 2013). Birds were ringed using British Trust for Ornithology individually numbered metal leg rings, aged as either first-winter (immature) or older (adult) and sexed using plumage characteristics as described by Svensson (1992) and updated by Dunn and Wright (2009). Maximum wing chord was measured using a stopped metal rule (±0.5 mm). Any birds not sexed or aged at the time of capture were removed from analysis and any birds recaptured in subsequent years were aged, sexed and measured blind to previous capture data.

First, we determined whether a trend existed in wing length over time within our study population. We constructed a general linear model (GLM) with Gaussian error distributions, and designated wing length as the response variable with age, sex (both as two-level factors), and year (as a continuous variable) as predictor variables, along with all two-way interactions. We also included month of sampling (where October = 1) as a fixed covariate to allow for the possibility of wear reducing wing length over the winter. As we had only a small number of between-year recaptures (n = 41), we excluded all but the first measure from each individual from this analysis to ensure independence of data. For all models, we used the ‘dredge’ function in the MuMIn library (Barton, 2012) in R (R Core Team, 2013) to identify the top set of models by comparing all possible models using AIC comparisons, subsequently averaging all models with ΔAIC < 2 (*n* = 6) to create the final model. Age, sex and month were held constant in the model (i.e. they could not be removed from models tested during the dredge process). We determined significance throughout by establishing whether 95% confidence intervals (CIs) in the final averaged model overlapped zero, interpreting a term as influencing the response variable only when there was no overlap. To determine whether any trend might be driven by temperature, we re-ran our model including temperature (defined as the average lowest maximum daily temperature during the winter of capture, for each bird prior to its capture) as a fixed term.

Upon finding a significant decline in wing length over time, we further examined our data to test potential mechanisms. To test hypothesis 1, whether this trend was driven by within-individual decreases in wing length, we examined whether trends in wing lengths of individual birds captured during more than one winter (*n* = 41) declined between captures. We used a linear mixed-effects model with Bird ID as a random effect and Measurement (first or second) as a fixed factor. We also included Month of capture (with October = 1) to allow for any effects of wear reducing wing length within winters. To test hypothesis 2, whether the trend was more marked in first year birds than in adults, and therefore whether there were differences in effect sizes within each age group, we examined whether immatures or adults were driving this trend by re-running our original model with immature (*n* = 563) and adult (*n* = 267) data separately. To test hypothesis 3, whether temporal trends in wing length might be driven by climatic variation at our study site, we first tested our assumption that winter temperature increased at our study site over time. We used a linear model with temperature as the response variable and winter (year, from November – April) as a fixed term. We obtained temperature data (as described in Dunn *et al.*, 2013) and used the average lowest maximum daily temperature prior to capture of each bird, both because this gives a measure of energy intake requirements and because ground that remains frozen during the day locks in seed, thus limiting food availability for granivorous birds (e.g. Alonso *et al*. 1994). Statistics are presented as Estimate ± 1 SE; 95% CIs throughout unless stated otherwise.

Results

We found a significant decline in wing length (Table 1; Figure 1), with the predicted decline from the final model of 1.88 mm, or 2.12%, over 21 years. Forty-one individuals for which wing length was measured in multiple years showed an increase in wing length between captures (Table 2; predicted mean wing lengths during first and second captures: 1^{st} = 88.99 mm; 2^{nd} = 91.35 mm).

The Year × Age interaction term in the original GLM was not statistically significant (Table 1). However, within immatures, wing length declined over time, with CIs not overlapping zero ($z = 4.753$, $p < 0.001$; -0.106 ± 0.022; -0.15 - -0.06 mm per year). The trend within the adult data was slightly weaker but also significant ($z = 1.95$, $p = 0.05$; -0.064 ± 0.025; -0.114 – -0.014 mm per year)..

Temperature increased significantly over the 21-year study period ($F_{1,15} = 6.67$, $p = 0.02$; 0.098 ± 0.038; 0.017 – 0.178°C per year). Further supporting this finding, we also found a significant negative relationship between temperature during the previous winter and wing length ($z_{8,822} = 2.69$, $p = 0.007$; -0.22 ± 0.08;

-0.38 - -0.06 mm per °C) with a corresponding decrease in AIC (model with temperature: AIC = 3503.5; model without temperature AIC = 3510.1).

Discussion

Wing length within our population declined by 2.07% over a 21-year period. When examining data from 321 birds sampled over four years, we found longer wings confer a survival advantage within our population (Dunn *et al.*, 2013), possibly due to an increased ability of larger birds to withstand cold winters. Whilst we are unaware of data on heritability of wing length within our study species, there is evidence from other species that wing length can be heritable and is likely influenced by a combination of genetic and environmental factors (e.g. Lessells & Ovenden, 1989). Therefore, this trend of decreasing wing length presents an apparent paradox, with three possible (non-mutually exclusive) explanations, all of them leading from the observation that ecological processes can contribute more than selection to phenotypic trends (Ozgul *et al.* 2009). These are: 1) Wing lengths of individual birds have decreased between years; 2) Immature recruits to the population are getting ever smaller, leading to a larger effect size in immatures than in adults and; 3) Body size changes are driven by climatic or environmental impacts resulting from changing resources during development. Additionally, the relationship between wing length and survival is likely not constant. For example, smaller individuals may survive as food becomes less limiting on survival (but not growth and size) (Ozgul *et al.*, 2009) but then they may be more prone to the impacts of extreme weather. Thus, a declining body size may be selected against only periodically although we do not have sufficient data to test this within our population.

Recapture data show that within-individual wing lengths within our population increase over time, suggesting that within-individual variation is not responsible for the observed decline in wing length at the population level, and so failing to support Hypothesis 1. We found weak support for Hypothesis 2: there was a progressive decline in the wing lengths of immature birds recruiting into the population, but the effect size among immatures was larger, although not significantly, than that among adults (effect sizes -0.106 in immatures vs. 0.064 in adults), suggesting that the decline in the wing lengths of immature birds recruiting into the population may have been offset by higher subsequent survival of larger birds post-recruitment. It is possible this population-level decline in size may result from genetic changes, even if selection is in the opposite direction: for example, wing length may be genetically linked to another trait under selection (Merilä *et al*., 2001; Merila, 2012). This decline in the wing length of immature birds may have been driven by adverse environmental conditions such as low food availability during the nestling period (Hart *et al*., 2006): our population is known to be resident year-round, with no ringing evidence for a winter influx of birds from other populations (Robinson *et al.* 2015a) and immature birds do not moult flight feathers in their first winter.

We also found support for Hypothesis 3. Temperature increased over the 21 years of the study and was strongly linked to wing length. Despite 23% of variation in wing length being explained by temperature variation in our study population, this does not negate the influence of other factors. Loss of habitat, loss of prime sources of food, higher temperatures leading to more parasites and reduced weather-related mortality potentially all create grounds for more severe competition and immune challenges (Yom-Tov & Geffen, 2011; Goodman *et al*., 2012).Yellowhammer populations within the UK, including our study population are declining (Robinson, *et al.* 2015b), due to removal of breeding habitat and a reduction in the availability of both summer and winter food (e.g. Cornulier *et al.* 2011), likely leading to increased competition with both conspecifics and heterospecific granivorous birds. Eglington and Pearce-Higgins (2012) found a tighter link between Yellowhammer population trends and land use than with climate. We recently found a high prevalence of haemoparasites within this same Yellowhammer population during the non-breeding season: a time of year where levels of circulating haemoparasites were previously thought to be negligible (Dunn *et al*., 2014): we also found associations between parasite infection and wing length, where infected birds had shorter wings than uninfected birds during one, mild, year (Dunn *et al*., 2013). Parasite infection may potentially contribute to wing length variation within our population, especially because haemoparasite prevalence is predicted to increase with increasing temperatures (Møller, 2010); however we currently have no longitudinal parasite prevalence data to test this hypothesis directly.

Yellowhammer population declines have been linked to a reduction in over-winter survival (Siriwardena *et al*., 2008), but reduced reproductive success has also been linked to a reduction in the availability of invertebrate food for chicks during the breeding season (Hart *et al*., 2006); thus a reduction in food availability and/or habitat quality may be behind the wing length decline in immature birds within our declining study population (Robinson *et al.* 2015b).

Either immature birds do not, on average, reach the same body size as they did previously, or larger fledglings now have reduced survival; additional data from young fledglings would be required to distinguish between these two hypotheses. Elsewhere, we suggest that behavioural changes induced by increased nest predation risk and reduced chick food availability may lead to a reduction in fledgling body condition (Dunn *et al*., 2010), potentially concurring with our reduction in first-year wing length.

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Appendix 1. Rationale for using wing length as a surrogate for body size.

For a subset of our population ($n = 126$) we obtained a range of morphometric measurements. These were wing length, measured as the maximum wing chord using a stopped metal rule (± 0.5 mm); head and bill length, measured from the tip of the bill to the centre of the back of the skull (Redfern and Clark, 2001); mass (measured using a digital electronic balance ± 0.1 g; Satrue, Taiwan), tarsus length, measured as the minimum tarsus length from the foot to the inside of the tarso-metatarsal joint; tail length, measured from the tail base to the tip of the longest outer rectrix; bill length, measured from the the feathering to the tip of the bill; and bill depth, measured at the point of feathering (Svensson, 1992); as detailed in Dunn & Wright (2009). All measurements apart from wing length and mass were taken using Vernier digital callipers (± 0.1 mm; Draper Tools, UK). Where we had duplicate measurements for the same bird ($n = 6$) we removed the second measurement to avoid pseudoreplication.

We carried out a principal components analysis (PCA) based on a covariance matrix using the *pcal* command in R. Factor loadings and the proportion of variance explained by each PCA are given in Table A1.

Table A1. Factor loadings from the PCA analyses performed to identify the strongest predictor of overall body size in Yellowhammers in West Yorkshire, UK

	PCA1	**PCA2**	**PCA3**	**PCA4**	**PCA5**	**PCA6**	**PCA7**

Head bill length		-0.140			-0.793	0.567	-0.151
Wing length	-0.719		0.688				
Mass	-0.147	-0.968	-0.147		0.128		
Bill length				-0.122	-0.572	-0.809	
Bill depth					-0.104	0.111	0.987
Tail length	-0.678	0.201	-0.704				
Tarsus length				0.991			
% variance explained	0.797	0.082	0.061	0.039	0.014	0.004	0.002

Table 1. Model estimates, adjusted standard errors and 95% CIs from the final averaged model predicting wing length of Yellowhammers in north-east England between 1986 and 2008 inclusive (prior to the addition of temperature to the model). The final averaged model predicted 64% of variation in wing length (R^2 = 0.64). Terms in bold denote significant terms where 95% CIs do not overlap zero.

	Estimate	SE	Lower CI	Upper CI
Intercept	87.01	0.68	85.68	88.34
Age (Immature)	**-2.26**	**0.62**	**-3.48**	**-1.04**
Sex (Male)	**4.56**	**0.60**	**3.39**	**5.72**
Year	**-0.08**	**0.03**	**-0.14**	**-0.02**
Month	-0.07	0.05	-0.17	0.02
Age × Sex	**-0.63**	**0.30**	**-1.22**	**-0.04**
Age × Year	-0.02	0.03	-0.11	0.02
Sex × Year	0.02	0.03	-0.01	0.10

Table 2. Model estimates, adjusted standard errors and 95% CIs from the linear mixed-effects model determining whether individual Yellowhammer wing lengths decrease over time from birds caught in more than one winter. Terms in bold denote significant terms where 95% CIs do not overlap zero.

	Estimate	**SE**	**Lower CI**	**Upper CI**
Intercept	82.98	1.04	80.95	85.02
Measurement	**2.36**	**0.30**	**1.77**	**2.94**
Month	0.11	0.14	-0.18	0.39

Figure 1: Declining mean wing length (± 1 SE) over time in a population of Yellowhammers. Lines are predicted mean ± 95% CI from the averaged model (Table 1) for adult females.