Body mass dynamics of migratory nightjars are explained by individual turnover and fueling

Original Article

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INTRODUCTION

Long-distance migration is energetically expensive and endogenous energy stores in the form of fat and protein are required to sustain the energetic demands of travelling (Odum and Perkinson 1951; Blum 1976; Piersma and Gill 1998; Lindström 2003; Sawyer and Kauffman 2011; Gallagher et al. 2014). Body mass is possibly the simplest and most reliable proxy of endogenous energy stores in animals (Larsson et al. 1990; Molnár et al. 2009; Labocha and Hayes 2012). Many studies across a variety of migratory vertebrates including fish, reptiles, birds, and mammals, stress the significance of the current body mass and its rate of change in determining many different behavioral decisions, such as the propensity to migrate, migratory restlessness,
The Red-necked Nightjar is a crepuscular and nocturnal migratory bird that feeds on aerial insects, mainly moths (Ceballos and Purroy 1977). Food supply in the study area is relatively restricted, granted only for scientific research, small game hunting, and livestock management. The predominant vegetation cover involves sparse Mediterranean scrublands with cattle-grazed grasslands and pine tree plantations for biomass production (see Camacho et al. 2014 for a detailed description of the study site).

The Red-necked Nightjar is a crepuscular and nocturnal migratory bird that feeds on aerial insects, mainly moths (Ceballos and Purroy 1977). Food supply in the study area is relatively abundant from the beginning to the end of the season (i.e., April to October) due to high temperatures during spring, summer, and early autumn (Camacho 2013). Nightjars are “sit-and-wait” foragers and shortly after sunset they travel from their diurnal roosts or nests to open areas, especially roads, where they use the

METHODS

Study system

The data were collected as part of a long-term (2009–2019) study on Red-necked Nightjars in a 2000-ha area of the Doñana Natural Park in southwestern Spain (37°7'N, 6°33'W). Human access to this area is restricted, granted only for scientific research, small game hunting, and livestock management. The predominant vegetation cover involves sparse Mediterranean scrublands with cattle-grazed grasslands and pine tree plantations for biomass production (see Camacho et al. 2014 for a detailed description of the study site).

The Red-necked Nightjar is a crepuscular and nocturnal migratory bird that feeds on aerial insects, mainly moths (Ceballos and Purroy 1977). Food supply in the study area is relatively abundant from the beginning to the end of the season (i.e., April to October) due to high temperatures during spring, summer, and early autumn (Camacho 2013). Nightjars are “sit-and-wait” foragers and shortly after sunset they travel from their diurnal roosts or nests to open areas, especially roads, where they use the

Migratory birds undertake some of the longest migrations in the animal kingdom and are probably the most popular subjects in studies of seasonal body mass dynamics. Generally, the body mass of migratory birds increases at the population level during the post-breeding period (Austin and Fredrickson 1987; Scott et al. 1994; Jenni-Eiermann and Jenni 1996), a pattern that is almost universally interpreted as the result of fuel accumulation (e.g., Holmgren et al. 1993; Lindstrom and Piersma 1993; Piersma and Gill 1998; Morton 2002; Lindstrom 2003; Mazur et al. 2021). Nevertheless, body mass does not only provide a measure of energy stores, it is also often related to structural body size and positively influences competitive ability (Jonart et al. 2007) and predation risk (MacLeod et al. 2005). Hence, demographic and behavioral processes such as the selective appearance and disappearance of small or large individuals due to differential mortality, selective departure, or size-based competitive asymmetries may operate simultaneously—either in the same or opposite directions—to mask or exacerbate the effects of intraindividual changes in body mass (see Figure 1 in van de Pol and Wright 2009 for a schematic example). For instance, smaller, lighter individuals may disperse from the breeding area earlier in the season in search of more profitable foraging sites or, alternatively, they may be excluded by larger, dominant individuals or suffer elevated mortality rates; thus, larger individuals may be selectively retained, causing an apparent change in the relative phenotypic composition of the local population (see e.g., Balbontín et al. 2012 for a lifetime rather than a seasonal approach). Surprisingly, this possibility has been largely ignored in the literature and, as a consequence, the relative contribution of individual (mass gain-loss) and demographic or behavioral (turnover of individuals) processes to the mean body mass dynamics of animal populations is unclear.

Here, we investigated the patterns of body mass variation prior to migration in a population of juvenile Red-necked Nightjars (Caprimulgus ruficollis) and combined longitudinal individual-level data and cross-sectional population-level data collected during 2011–2019 to elucidate putative underlying mechanisms of body mass variation. The Red-necked Nightjar (hereafter “Nightjar”) is a nocturnal migrant that breeds in the Iberian Peninsula and spends the winter in tropical regions southwest of the Sahara desert (Cleere et al. 2013). Nightjars arrive at the breeding grounds from early April to mid-May and migrate south substantially later in the season than other insectivorous migrants breeding and wintering in the same regions (Lessells and Avery 1989; Bechet et al. 1998; Aparicio and Bonal 2002). Departures from the breeding grounds as late as the end of October are common in both adult and juvenile Nightjars, although young birds tend to migrate later than adults (Camacho 2013). Body mass is expected to be particularly severe for inexperienced young of the year because they may not be able to optimally manage the mass-dependent starvation-predation risk trade-off (McLeod et al. 2005) and, also, they may be especially vulnerable during their first migration (Sergio et al. 2014; Cheng et al. 2019). For these reasons, investigating the body mass dynamics of juvenile Nightjars from post-fledging to migration provides an excellent opportunity to analyze the role of individual- and population-level processes in shaping patterns of phenotypic variation in animal populations.

Our study addressed two questions: (1) Did the population mean body mass change throughout the post-fledging period until departure? We expected mean body mass of juvenile Nightjars to increase prior to departure on autumn migration, as observed in most populations of migratory birds. Thus, a positive correlation between mean juvenile mass and time of the season should exist across the population. (2) Did seasonal variation in mean body mass result from (i) fuel deposition, (ii) a change in the phenotypic composition of the population, or (iii) a combination of both processes? Nightjars must prepare for their first migratory flight by accumulating fuel reserves, so an increase in body mass at the individual level is expected (Labocha and Hayes 2012). Besides mass gain, the selective turnover of individuals across the body mass range of the population may contribute to population-level changes in body mass. The selective disappearance of lighter-than-average individuals as the breeding season progresses and/or the gradual appearance of heavier-than-average individuals late in the season could also result in a positive association between mean body mass and time of season in the juvenile population, even in the absence of intraindividual mass increase. Specifically, given a seasonal increase in body mass at the population level (Question 1), positive correlations are expected between individual mass and either date of first appearance (birth or immigration) or date of disappearance (death, departure, or exclusion). We did not consider the potential effect of a selective appearance of migratory Nightjars through immigration from other areas because their passage across the study area is virtually nonexistent (see Figure 3 in Camacho 2013). By investigating these two questions, our study emphasizes the importance of separating inter- from intraindividual sources of variation to detect and understand short-term changes in the body mass composition of populations (Blas et al. 2009).
To analyze body mass variation, we fitted linear mixed models to correct body mass measurements.

Field procedures

From early April to late October we carried out regular car surveys (at 4–7-day intervals) along a 24-km circuit of roads crisscrossing the study area, and captured Nightjars found along roads at night using a flashlight and a butterfly net (Jackson 1984). Capture sessions started 1 h after sunset and continued until we completed the whole circuit driving at a constant speed (30 km/h). Nightjars were marked with numbered metal rings (if not already ringed), sexed according to the size of the white spots on their wing and tail feathers, and classified into one of three age classes based on plumage characteristics described in Gargallo (1994) and Camacho (2013): recently fledged young, self-sufficient and fully-developed fledglings (juveniles), and second year or older birds (adults). Juvenile Nightjars (≥35 days old) are easily distinguishable from recently fledged young because the primaries and rectrices of the latter are still growing from the sheaths (Camacho 2013). Juveniles are no longer fed by their parents, and many of them remain in the natal area for a considerable period after parental independence, typically up to 90 days of age (authors’ unpublished data).

For each juvenile, we measured body mass to the nearest 0.1 g using a digital balance. Body mass upon capture can be strongly influenced by the bird’s previous food consumption due to the large stomach capacity of caprimulgids (Jackson 2003). External palpation of the abdomen provides a simple method to estimate the amount of food contained in the gizzard – the muscular stomach of birds – using an ordinal scale of 0–4 (empty, ¼, ½, ¾, or full) based on the criteria of Jackson (2003). Body mass in this study is subsequently presented as field body mass corrected by stomach fullness (see details in “Statistical analyses”).

Our systematic capture-recapture protocol enabled us to obtain repeated measurements from the same birds during the post-fledging period, but following Braasch et al. (2009), we only used the last recorded mass of the season as an indicator of the physiological state of juveniles prior to migratory departure. Departure dates were estimated as the last observation for each individual (i.e., the date of last capture). Even though we cannot exclude the possibility that some birds departed (or died) later than actually observed, the error is probably small due to our high capture rate of juveniles (the probability of recapturing a marked juvenile within a given season was 0.75 ± 0.27 [SD], N = 225 individuals captured 2–7 times; authors’ unpublished data from years 2009–2019). Hence, we use the terms “last capture date” and “departure date” interchangeably in this article, expressed as day of the year from January 1st.

Statistical analyses

Our analyses only included data from 2011 to 2019, because previous sampling seasons (2009–2010) lacked the information on stomach volume required to correct body mass measurements. To analyze body mass variation, we fitted linear mixed models (LMMs, Gaussian error structure) using the package “glmmTMB” (Magnusson et al. 2019) in the R environment, version 4.0.0 [http://cran.r-project.org]. Before running each model, all continuous covariates were standardized (zero mean and unit variance) to obtain comparable estimates (Schielezh 2010). Model validation was carried out by visually checking the normality of residuals and Q-Q plots (Hartig 2020) and by evaluating goodness-of-fit with the conditional $R^2$, which estimates the fraction of variance in the response variable explained by fixed and random effects combined (Nakagawa and Schielzeth 2013). Conditional $R^2$ was computed using the $r.squaredGLMM$ function of the “MuMIn” package (Barton 2020). To calculate $P$-values for individual predictors, we performed likelihood ratio tests (LRT) comparing full models to those excluding each of the predictors in turn (Forstmeier and Schielzeth 2011).

Body mass measurements included in all analyses correspond to the fitted values (on the natural scale) of a LMM using gizzard fullness (ordinal covariate) and individual identity (random intercept term) to explain variation in body mass upon capture (model statistics: $F_{1,705.95} = 200.59, P < 0.001, R^2 = 0.58$). Exploratory analyses indicated that the body mass of male and female juveniles did not differ significantly (sex effect: $P = 0.93$), nor did the seasonal trends in body mass (sex × day of year interaction: $P = 0.43$). Consequently, sex was not considered further in our analyses.

Cross-sectional pattern of seasonal change in body mass

The LMM used to investigate the relationship between juvenile body mass and time of the season at the population-level included stomach-corrected body mass as the response variable, and day of year, and its squared term as covariates. In addition, we included year of birth and individual identity as random-intercept effects to account for cohort effects and for repeated measures of the same individuals, respectively.

Fuel deposition rates

The change in body mass per unit time calculated from the coefficients of the cross-sectional LMM provided an average population estimate of the mass gain (fuel deposition) rate ($FDR_{population}$) of juvenile nightjars throughout the post-fledging season. For comparison, we also calculated the average fuel deposition rate of juveniles from recaptures of the same individuals ($FDR_{individual}$) as the change in stomach-corrected body mass of birds recaptured at least one day after first capture, divided by the number of days between first and last capture (Åkesson et al. 1995; Schaub et al. 2008). Note that the average $FDR$s presented in this study should not be seen as the maximum $FDR$ of the species, since they are intended to illustrate the influences of individual, demographic processes on the body mass dynamics of juveniles during the entire post-fledging season (4 months), and not only during the peak fueling period.

Distinguishing within- versus between-subjects components of variation

To assess the relative contribution of within-subject and between-subject effects to population-level variation in body mass, we used the within-subject centering approach (van de Pol and Wright 2009). Briefly, this method consists in partitioning the total variance of a phenotypic trait into its between- and within-subject components so that the effect of individual responses can be separated from that of a change in the phenotypic composition of the population (van de Pol and Wright 2009). Despite the broad applicability of the
within-subject centering approach, it is almost exclusively used to explore age effects, although analogous models can be constructed to investigate seasonal rather than annual patterns of variation in the expression of morphological, behavioral and life-history traits (e.g., van de Crommenacker et al. 2011; Zhang et al. 2015).

Our analysis focused on seasonal (capture date) variation in body mass. Therefore, we calculated the between-subject variance component by averaging all capture dates for each individual, and then calculated the within-subject variance component by subtracting the individual’s mean capture date from each capture date (i.e., mean-centering on zero; van de Pol and Wright 2009). Our starting mixed model, based on data from juveniles of the 2011–2019 cohorts, included stomach-corrected body mass as a continuous response variable, the within- and between-subject components of variance as covariates, and year as a random effect to account for interannual variation. The random effects of individual identity, including the intercept and slope, also need to be considered regardless of centering, as they inform the model about the nonindependence of data points, and minimize the probability of obtaining overconfident estimates (Schielezeth and Forstmeier 2009). Nevertheless, the comparison of a full model including the random intercept and the random slope of mass change against a model including only the random intercept showed that the addition of the random slope did not improve model fit (LRT, \( P = 0.99 \)), suggesting that there is no significant between-subject variation in slopes that could substantially inflated type I error rate (Schielezeth and Forstmeier 2009). Consequently, for simplicity, only the random intercept of individual identity was retained in subsequent models to account for repeated measurements of the same individuals.

By splitting up the effect of capture date into statistically independent predictors we could test whether either the within-subject or the between-subject effects are themselves significant (van de Pol and Wright 2009; van de Crommenacker et al. 2011). Moreover, it was necessary to test whether the within-subject and the between-subject effects differed from each other by constructing another model that included again the original predictor (date of capture) and the between-subject component (average capture date), but not the within-subject component. By leaving out the within-subject effect while retaining the original predictors (date of capture as a covariate and individual identity as a random term) the effect of the within-subject variance component on model fit can be explicitly tested. Specifically, the estimated between-subject effect in this model is expected to be nonsignificant when the between- and within-subject effects do not differ from each other (see van de Pol and Wright 2009; van de Crommenacker et al. 2011 for full details).

Because the within-subject centering approach alone does not reveal the population-level mechanism that is operating, to discriminate between the roles of selective appearance and disappearance in driving seasonal changes in the proportion of phenotypes, we used an additional linear mixed-effects model approach originally developed by van de Pol and Verhulst (2006) to analyze age-dependent processes. Briefly, this method specifically tests for within-individual change in the presence of either a selective appearance or a selective disappearance effect, and vice versa, by incorporating the trait value (e.g., date) at first and last measurement. For each individual, we calculated the date of birth (appearance) and date of last capture (disappearance) and then ran a LMM to examine whether there was any covariance between stomach-corrected body mass (response variable) and appearance/disappearance date. Date of birth, date of last capture and their interaction were included as explanatory variables, along with individual identity as a random intercept to account for repeated measurements of the same individuals. This model was based on a smaller subset of individuals (\( N = 24 \) birds, measured one to four times) that had been monitored since the nestling stage and for which date of birth could be reliably estimated based on a regression of age (up to 35 days) on body mass (\( y = 0.30 \times \text{Body Mass} – 1.41; R^2 = 0.97 \)).

**RESULTS**

Our analyses are based on a total of 882 measurements of 648 individuals from 9 (2011–2019) different cohorts. Of these, 175 (27%) birds were measured twice or more (range: 2–6 measurements per individual) over the course of the post-fledging period. The first and last juveniles were captured on day 183 (July 1st) and 297 (October 24th), respectively.

**Cross-sectional pattern of seasonal change in body mass**

Body mass of juveniles at the population level ranged from 75 to 112 g and increased throughout the season in a curvilinear manner.

![Figure 1](https://academic.oup.com/beheco/advance-article/doi/10.1093/beheco/arab042/6323567)

**Figure 1**

Relationship between time of the season and body mass of juvenile Nightjars at the population level. The shaded area is the 95% confidence interval of the linear regression model and grey dots denote actual mass measurements after correction for stomach (gizzard) size.

**Table 1**

<table>
<thead>
<tr>
<th>Estimate</th>
<th>SE</th>
<th>z</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>104.300</td>
<td>17.000</td>
<td>6.134</td>
</tr>
<tr>
<td>Day of year</td>
<td>-0.231</td>
<td>0.140</td>
<td>-1.653</td>
</tr>
<tr>
<td>Quadratic day of year</td>
<td>0.001</td>
<td>0.000</td>
<td>2.527</td>
</tr>
</tbody>
</table>

Bold font denotes significance at levels \( P < 0.05 \). The LMM included individual identity and year of birth as random effects to account for repeated measures of the same individuals and for cohort effects, respectively. Sample size: 882 observations from 648 individuals over 9 years. Conditional \( R^2 = 0.688 \).
incorporation of lighter individuals into the population that should operate against the general increase in mean body mass over time, and, on the other hand, a simultaneous disappearance of lighter individuals (or, analogously, a selective retention of heavier individuals) that should reinforce the increasing mass trend. Thus, the turnover of individuals through selective appearance and disappearance appeared to operate in opposite directions to shape the overall phenotypic composition of the population over time.

**DISCUSSION**

By combining longitudinal and cross-sectional data collected during a 9-year study period, we investigated patterns of seasonal change in mean body mass of juvenile Nightjars prior to their first migration and evaluated the role of intraindividual and interindividual variability in such change. Our results are consistent with a predicted seasonal increase in mean body mass, and indicate that this pattern is partially explained by individual mass gain. Our results also revealed that interindividual demographic or behavioral processes contributed to the population-level increase in body mass, playing a more prominent role than intraindividual mass gain. Overall, our findings suggest that the selective disappearance of lighter-than-average juveniles and, to a lesser degree, individual mass gain, are the major processes underlying seasonal change in body mass in this population.

The observed pattern of increase in mean population mass prior to migration agrees with previous findings in other migratory species (e.g., Åkesson et al. 1995; Jenni-Eiermann and Jenni 1996; Fransson 1998; Danhardt and Lindstrom 2001; Schaub et al. 2008). From a functional perspective, this general pattern has been interpreted as reflecting the accumulation of energy stores for migration (Lindstrom and Piersma 1993). However, it has remained unknown to what extent the population pattern is the exclusive result of fuel accumulation, the turnover of individuals, or a combination of both processes. Our approach, involving a combination of cross-sectional and longitudinal data, revealed that the population pattern is not only explained by fueling (within-subject effect), but also by a seasonal turnover of the population (between-subject effect). Moreover, the disparity in slopes of within- and between-subject effects provides compelling evidence that, contrary to the general assumption, the turnover of individuals played a more important role than fueling of stationary individuals.

The greater relative role of individual turnover is unlikely to be an artifact of sampling caused by the underestimation of mass gain rates due post-capture stress responses, since the average time between captures in this study (18.3 ± 13.9 [SD] days, N = 268 captures) is much longer than the minimum time required for captured birds to re-establish normal foraging behavior (<24 h, data from radiotagged nightjars in the study population, see Camacho et al. 2014). The fueling period of nightjars may be shorter than the maximum time interval between some captures (up to 63 days), and also they may fatten up more quickly during the bright nights around full moon (Norevik et al. 2019), potentially resulting in an underestimation of the maximum FDR in these birds. Nevertheless, it is important to note that we are primarily interested in body mass dynamics during the entire post-fledging season (four months) and not during the first fueling period only; therefore, the comparison of the influences of individual vs. demographic processes over this time frame is meaningful.

Our analysis examining the roles of selective appearance and disappearance of individuals suggested that juveniles that fledged
Table 2
Results of the LMMs examining (a) within- and between-subject effects of day of year on body mass of juveniles, (b) the effect of between-individual variation of day of year alone and day of year on body mass of juveniles, and (c) the effect of birth date, last capture date, and their interaction on body mass of juveniles.

<table>
<thead>
<tr>
<th>Model (a)</th>
<th>Estimate</th>
<th>SE</th>
<th>z</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>91.766</td>
<td>0.535</td>
<td>171.65</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Within-subject effect</td>
<td>0.736</td>
<td>0.109</td>
<td>6.73</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Between-subject effect</td>
<td>2.540</td>
<td>0.188</td>
<td>13.55</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Model (b)</th>
<th>Estimate</th>
<th>SE</th>
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<th>P</th>
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<tbody>
<tr>
<td>Intercept</td>
<td>91.766</td>
<td>0.535</td>
<td>171.76</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Day of year</td>
<td>2.022</td>
<td>0.300</td>
<td>6.730</td>
<td>&lt;0.001</td>
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<tr>
<td>Between-subject effect</td>
<td>0.657</td>
<td>0.337</td>
<td>1.95</td>
<td>0.051</td>
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</table>

<table>
<thead>
<tr>
<th>Model (c)</th>
<th>Estimate</th>
<th>SE</th>
<th>z</th>
<th>P</th>
</tr>
</thead>
<tbody>
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<td>1.111</td>
<td>78.02</td>
<td>&lt;0.001</td>
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<tr>
<td>Day of Birth</td>
<td>−6.416</td>
<td>1.377</td>
<td>−4.66</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Last capture date</td>
<td>6.187</td>
<td>1.441</td>
<td>4.29</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Day of birth × Last capture date</td>
<td>0.523</td>
<td>0.901</td>
<td>0.58</td>
<td>0.579</td>
</tr>
</tbody>
</table>

Bold font denotes significance at levels $P < 0.05$.

LMMs included individual identity and year of birth as random intercept effects to account for repeated measures of the same individuals (models a–c) and for cohort effects (models a–b), respectively. Sample size: 882 observations from 648 individuals over 9 years (models a–b); 34 observations from 24 individuals (model c). Conditional $R^2$ ranged from 0.698 (model a) to 0.736 (model c), supporting that all models provided a good fit to the data.

Figure 3
Individual slopes of change in body mass of juvenile Nightjars. For illustrative purposes, only data for individuals captured three times or more ($N = 157$) are presented. The mixed-model does incorporate all data, and therefore takes differences in sample size into account. Differently colored slopes correspond to different individuals and make overlapping lines more easily visible.

later in the season tended to be lighter than earlier fledged ones, a process that would alone cause a seasonal decrease in mean body mass. This trend is common to most temperate-zone bird populations (Lessells and Avery 1989; Monró et al. 2002), supporting the reliability of the results despite the relatively small sample size. On the other hand, lighter-than-average juveniles progressively disappeared from the study area, promoting a turnover of phenotypes in the expected direction. Taken together, the opposing concurrent processes of selective appearance and disappearance of phenotypes suggest that the selective retention of individuals of high body mass until the end of the season is strong enough to counteract the effects of the progressive appearance of lighter individuals and thus account for the observed temporal change in the phenotypic composition of the population.

To our knowledge, no specific information exists regarding the effect of turnover of individuals on the short-term (intra-annual) mean body mass dynamics of migratory birds. However, the relative contribution of plasticity and selective disappearance in explaining cross-sectional patterns of variation in body condition has been previously noted over longer (inter-annual) scales in other long-distance migrants (Balbontín et al. 2012), suggesting that the combined operation of individual- and population-level processes may be more common than previously recognized. Hence, an incomplete understanding of the role of inter- and intra-individual variability in body mass over short time scales may have important implications for behavioral ecology and particularly the study of migration. First, disparity in the slopes derived from longitudinal and cross-sectional data may result in the misestimation of basic migration parameters, such as the duration of the first fueling period and the rate of fuel accumulation (cf. Lindström and Piersma 1993). Second, despite their potential ecological and evolutionary importance, cryptic patterns of covariance between phenotype and time of season, as well as temporal population structure, may pass undetected.

Nonrandom appearance and disappearance of body mass phenotypes contributed to the pattern of phenotype-time covariance in this population, but the ultimate demographic or behavioral mechanisms underlying the turnover of phenotypes are unclear. On the one hand, recently fledged juveniles of poorer quality could progressively appear as the breeding season progresses due to the seasonal deterioration of environmental (raising) conditions (Monró et al. 2002; Prop et al. 2003). On the other hand, lean, smaller individuals could be competitively excluded from the study area soon after independence by larger, dominant individuals (Greenberg 1986; Stahl et al. 2001) or, perhaps, they choose to evaluate neighboring areas in search of better foraging opportunities (Wilson et al. 2012). Nonetheless, the contribution of post-fledging movements at the regional level is probably small, since no ringed juvenile has been detected in extensive searches outside the study area ($N = 291$ captures in a 20-km radius; Camacho 2014).
Migration decisions could also contribute to the early disappearance of lighter juveniles, although it is unlikely that all individuals last seen around midsummer disappeared as a result of early departure (Camacho 2013). Finally, some of these birds may have died prematurely because of decreased starvation or thermal resistance in lean individuals. However, the important fraction of juveniles last recorded early in the season that recruited in subsequent years (27.6%, N = 185 juveniles last seen before 31 August 2009–2016) suggests that death is not the only cause of early disappearance. More exhaustive tests of differential mortality and departure/exclusion based on GPS and accelerometer data are in progress to clarify the reasons for the greater preponderance of individuals of large body mass at the end of the season.

To conclude, the use of longitudinal data and an individual-based statistical approach allowed us to uncover a population pattern indicating an increase in body mass during the post-fledging period, and to disentangle the relative contribution of individual mass gain and turnover of individuals to the population pattern. For vertebrates in general and migratory birds in particular, the post-fledging period remains a largely overlooked life stage, despite the fact that early life events may carry over to influence key demographic parameters in later stages, such as first-year survival, age at first breeding, and recruitment probability (Clutton-Brock 1988; Newton 1989). Our study shows that the contribution of demographic and/or behavioral factors to cross-sectional patterns of variation in body mass should be carefully considered to confirm the validity of estimates of migration parameters in the absence of longitudinal data. More generally, this study suggests that patterns of phenotype-time covariance, as opposed to phenotype–environment covariance, may be often overlooked in natural populations, because of our tendency to ignore patterns not expected in the first place.

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Conflict of interest: The authors declare that they have no conflict of interest.

Data availability: Analyses reported in this article can be reproduced using the data provided by Hidalgo-Rodríguez et al. (2020).

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REFERENCES


