MIGRATION STRATEGY IN THE CHAFFINCH, *FRINGILLA COELEBS*

by

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ABSTRACT

Birds have developed morphological and behavioural adaptations as migratory strategies. A comparative study of morphology and demography between the Chaffinches' (*Fringilla coelebs*) sedentary *gengleri* and migratory *coelebs* races was conducted using a ringing dataset collected on Lundy between 1972 and 2017. Migratory individuals were significantly and proportionately longer winged and had greater body weight. The migrant sex and age ratios were skewed towards females and first-year birds and were responsive to annual climatic variations. The results support the species' status as a differential migrant and present the potential of Lundy's extensive ringing efforts in contributing to studies on avian migration.

Keywords: *Chaffinch, differential migration, migration phenology, Lundy, North Atlantic Oscillation*

INTRODUCTION

Avian migration is the result of birds' adaptation to seasonal variations in resource availability and environmental conditions (Alerstam, Hedenström & Åkesson, 2003). The typical pattern of avian autumnal migration in the Northern Hemisphere is from North to South, as birds travel to spend winter in warmer regions; in spring, the birds fly in the reverse direction, returning to their breeding grounds in preparation for the mating season (Jenni & Kéry, 2003).

Morphological adaptations for migration

Migration is energetically demanding and therefore places great metabolic stress on migrating birds (McWilliams *et al.*, 2004). In response, migratory birds gained behavioural and morphological strategies to enhance their capacity for migration. Species that migrate longer distances tend to have longer wing lengths in proportion to body mass to reduce wing-loading (defined as body mass divided by wing area), hence allowing for more powerful and energy-efficient flight (Nowakowski, Szulc & Remisiewicz, 2014). Also, within species, migratory individuals are known to have greater wing lengths and lower wing-loading than sedentary conspecifics, such as in Blackcaps (*Sylvia atricapilla*) (Pérez-Tris & Tellería, 2001) and Yellow-rumped Warblers (*Dendroica coronata*) (Milá *et al.*, 2008).

Additionally, migratory birds that travel southwards from their northern breeding ranges for winter are usually of greater body size and mass than their sedentary conspecifics of southern populations, as an adaptation to reduce heat loss through minimising surface area to body mass ratio (Ashton, 2002). This biogeographical trend in body size and mass is known as Bergmann's rule (Bergmann, 1847) and has been evidenced in avian studies on the intraspecific and interspecific level (Ashton, 2002).

Behavioural adaptations for migration

Classes within migratory bird species have evolved intraspecific variation of migratory behaviour. These classes are defined by categories such as age and sex (Cristol, Baker & Carbone, 1999). Partial migration occurs when only some individuals of a species migrate; in differential migration all individuals in a population migrate, but with differences in timing, duration and distance according to age and sex classes (Ketterson & Nolan, 1983).

Several hypotheses have been developed to explain partial and differential migration:

1) The 'body size' hypothesis predicts that winter conditions force smaller-sized individuals, which face greater relative heat loss and are thus less resilient to the colder and resource-scarce environment, to migrate to more hospitable areas (Ketterson & Nolan, 1976).

2) The 'dominance' hypothesis states that competition for non-breeding resources causes the displacement and redistribution of less dominant individuals (Gauthreaux, 1982).

3) In the 'arrival time' hypothesis, competition for breeding territories and resources mean that individuals of the sex that secures and protects territories for the breeding season will benefit from wintering closer to breeding grounds, so they migrate over shorter distances or depart wintering areas earlier (Myers, 1981).

In most passerines, males and older birds are physically larger, heavier, dominant and territorial (Piper, 1997). Hence, the general trend of differential migration in passerines is that females and younger birds tend to winter further away from breeding grounds than males and older birds. This pattern has been well-evidenced in many species and is especially pronounced in sexually dimorphic species with significant intersexual morphological differences (Ketterson & Nolan, 1976; Cristol, Baker & Carbone, 1999; Catry *et al.*, 2005).

Climate effects on differential migration

Differential migration patterns can also be determined by environmental conditions (Ketterson & Nolan, 1976; Ketterson & Nolan, 1983). Environmental variables such as temperature and precipitation affect habitat quality and food availability in wintering sites, migration stopover points and breeding regions (Barros, Álvarez & Velando, 2013). Due to intraspecific variation such as biological differences caused by sexual dimorphism, individuals of different age and sex classes may respond differently to such environmental stresses (Ketterson & Nolan, 1976; Barros, Álvarez & Velando, 2013). Consequently, winter climates in breeding grounds affect individuals to varying degrees, selecting for stronger individuals while displacing weaker or ill-adapted individuals, ultimately causing intraspecific geographical segregation (Ketterson & Nolan, 1976). As such, in winter, the proportion of individuals in poorer condition increases with decreasing latitude, since only the more resilient ones can afford to remain relatively sedentary at higher latitudes (Ketterson & Nolan, 1976; Catry *et al.*, 2005).

Although studies have established that differential migration is driven by environmental selection, whether these patterns are augmented by climate changes has not been discussed. Current evidence suggests that environmental conditions may amplify intraspecific competition and hence differential migration by limiting the quantity and quality of resources, forcing larger numbers of weaker subordinate individuals to migrate (Ketterson & Nolan, 1976).

In Europe, the large-scale climatic phenomenon known as the North Atlantic Oscillation (NAO) is a major influence on avian migratory behaviour (Hüppop & Hüppop, 2003). Studies have proven the NAO as the most influential factor in yearly variability in European winter temperatures, with a particularly strong effect on northwest Europe (Hurrell, 1995). The NAO index is measured as the sea-level pressure differences between the subpolar and subtropical regions of the North Atlantic, centred on Iceland and Azores respectively. A positive NAO index is indicative of stronger westerly winds blowing across the Atlantic, bringing warmer weather and increased precipitation to northwest Europe; negative NAO indices correspond to colder and drier weather due to weaker warm winds from the west. Therefore, NAO indices from December to March (henceforth 'winter indices') are positively correlated with the corresponding winter temperatures in the North Atlantic region (Hurrell, 1995).

Mean spring passage is advanced in springs following positive winter indices, due to warmer conditions that accelerate plant development and hence food availability (Hüppop & Hüppop, 2003). Existing literature suggests that lower winter indices precede colder winters and springs, which delay the following breeding season and thus the start of autumn migration in the next calendar year (Anthes, 2004). However, NAO effects on autumn migration have not garnered much scientific attention.

Plate 1: Male Chaffinch, ringed on Lundy ©Richard Campey

Avian migration strategy is a complicated phenomenon that is far from being well-studied, especially because such studies demand substantial long-term datasets collected from study sites along migration pathways; these datasets are rarely available and challenging to collect (Hüppop & Hüppop, 2003; Jenni & Kéry, 2003; Payevsky, 2010). The prohibitive cost of precise tracking technology means that many studies still rely heavily on recapture data which are exceedingly rare: recapture rate of the birds ringed in the United Kingdom between 1909 and 2003 stands at a mere 1.90% (Clark *et al.*, 2004).

Given the data collection challenges inherent to avian migration studies, a widespread species with sizeable population and recognised migration pathways is an ideal study target. For these reasons, the Chaffinch (*Fringilla coelebs*) is a highly appropriate model species. It is one of Europe's most abundant bird species (Wernham *et al.*, 2002; Payevsky, 2010). The nominate continental race *coelebs* breeds in north and northeast Europe, migrates in huge numbers to Britain and Ireland in autumn, joining the non-migratory *gengleri* residents for winter (Newton, 1972; Wernham *et al.*, 2002). Within the migratory populations, differential migration where females disperse further from their breeding territories has been observed (Cramp & Perrins, 1994). Linnaeus named the Chaffinch '*Fringilla coelebs*', literally translated as 'bachelor finch', based on his account of highly male-biased wintering populations in Sweden (Wernham *et al.*, 2002).

Yet, there are major knowledge gaps regarding the species' migration tactics. Surprisingly, despite its nomenclature, there are no conclusive studies to ascertain the species' differential migratory patterns (Wernham *et al.*, 2002). Much of the existing literature is focussed on migration speed and timing against climate (Hüppop & Hüppop, 2003; Payevsky, 2010), but none discuss differential migration or the effects of climate on differential migration patterns.

Aims, hypotheses and predictions

This study aims to contribute to the existing knowledge base on avian migration systems, focussing on the effects of environmental conditions on differential migration. Specifically, the primary objectives of this study were to elucidate the migration strategy in Chaffinches and its responses to climatic variations. These were achieved by assessing the species' status as a differential migrant, investigating the morphological differences between sedentary and migratory individuals, and the responses of the species' migratory strategy associated with climate indices in terms of the winter NAO indices and corresponding winter temperatures.

The following hypotheses were investigated:

1) Differential migration exists in Chaffinches where females and younger birds have a higher propensity to migrate, a pattern driven by and reflected in sexual dimorphism and age-related morphological differences.

2) Migratory individuals have developed morphological adaptations favouring enhanced flight efficiencies for migration and heat conservation for colder weather in their northerly breeding grounds.

3) Differential migration patterns are responsive to environmental conditions. When conditions are harsher, higher numbers of poorly-adapted individuals are displaced from their breeding grounds.

METHODS

Study site

Lundy (51°11'N 4°40'W) is a small island measuring five kilometres long and about one kilometre wide situated 18 kilometres off the northwest coast of Devon. The island is a migration hotspot, serving as important stopover for Chaffinches migrating from mainland Europe. In the autumn migration season spanning late September to early December, *coelebs* individuals arrive in massive flocks from Scandinavia, Finland and Russia (Wernham *et al.*, 2002; Davis & Jones, 2007). Residents on Lundy fall under the British and Irish *gengleri* race and are very sedentary: 90% of *gengleri* individuals do not disperse more than five kilometres from their site of birth (Newton, 1972). Therefore, Lundy's resident Chaffinches rarely venture beyond the island's boundaries (Davis & Jones, 2007). The presence of both resident and migratory subspecies makes Lundy a suitable site to study the species' migration tactics through comparison.

Data collection

For this study, Chaffinch records gathered by bird-ringing efforts on Lundy between 1972 and 2017 were analysed. Relevant information extracted from the records were: each bird's unique ring number, age, sex, date of capture, wing length, weight, brood patch and capture method. A separate dataset comprised individuals controlled on Lundy and abroad between 1958 and 2017 was assessed as supplementary data (see Appendix A).

Bird morphometrics, age and sex

Wing length (maximum chord) and body weight measurements of each capture bird was taken via standard procedures, as per recommendations by the British Trust for Ornithology scheme (A. Taylor, 2018, pers. comm.). Wing area data were not available, so for the purposes of this study, a proxy for wing-loading in grams per centimetre was defined as body weight divided by wing length measurement (henceforth 'wing-load estimate').

 Birds were aged and sexed according to definitions outlined in Svensson's Identification Guide to European Passerines (Svensson, 1992). The Chaffinch is a distinctly sexually dimorphic species: males are distinguished by bluish-grey crown and nape, rusty-red cheeks and breast and a reddish-brown mantle (Svensson, 1992). A wing length of at least 86 millimetres is strongly suggestive of a male, especially for a bird exhibiting the above plumage characteristics (Demongin, 2016). However, sexing was based primarily on plumage due to overlaps between male and female wing length, further confounded by the averagely shorter wing lengths of the *gengleri* race. Only occasionally was it supplemented by wing length measurement. For the same reasons, it was not reliable to correct outlier measurements as misidentifications may occur.

 Age codes were assigned following the European Union for Bird Ringing (EURING) criteria, judging birds based on plumage and moult characteristics (Demongin, 2016; see Appendix B). Chaffinch hatchlings undergo a partial post-juvenile moult in June-October (Demongin, 2016), moulting their greater coverts and tertials, with an observable moult limit that indicates a bird fledged within the current calendar year (EURING age code 3).

This set of feathers is maintained until the birds undergo post-breeding moult in the following year, when a complete moult occurs (Demongin, 2016). Therefore, between January and May, birds seen in the post-juvenile moult plumage were assigned code 5. Throughout the year, individuals in fully moulted plumage were assigned codes 4 or 6. Uncertainties were recorded as code 2. For statistical analyses, all aged birds were categorised as 'first-year birds' (age codes 3 and 5) or 'adults' (age codes 4 and 6).

Residency criteria

Based on past studies, the following criteria were developed to distinguish between migrant and resident Chaffinches:

1. Individuals captured at least once between April and August were regarded as resident birds for the following reasons:

    i) Breeding occurs from April to June (Newton, 1964). Previous studies have established high natal-site breeding fidelity and highly sedentary behaviour in *gengleri* individuals (Newton, 1972; Wernham *et al.*, 2002), and that *coelebs* migrants use Lundy as an autumn stopover or occasional wintering site but adopt a different spring migration pathway and thus rarely appear on Lundy between February and June (Davis & Jones, 2007). It is highly unlikely that an individual caught on Lundy during the breeding season belongs to the migrant *coelebs* race.

    ii) Chaffinches, like many passerines, moult after breeding and prior to their autumnal migration. The species' pre-migration moult period spans June to end September, followed by its autumnal migratory season from end-September to early December (Wernham *et al.*, 2002). It is thus conservative to consider birds captured at least once on Lundy between June and August resident, because during these months the migratory individuals would be moulting in their breeding grounds.

2. Females with brood patches were positively identified as residents, because brood patches indicate breeding activity on the island.

3. Birds in juvenile (age code 3J) plumage were safely considered residents, having fledged on island and therefore belong to the sedentary *gengleri* race (Wernham *et al.*, 2002).

4. Individuals captured and recaptured across at least two non-breeding seasons (September to March) were considered residents. Resident birds may have breeding territories beyond the mist-netting sites, hence they may be missed by mist-netting efforts during the breeding season but caught at other times of the year as they move around the island. Furthermore, it is very improbable that a migrant is captured twice on passage in separate years (A. Taylor, 2018, pers. comm.).

5. Individuals captured and recaptured within one non-breeding season were considered migrants, because the relatively short recapture timeframe suggests that birds were likely intercepted whilst on passage within the same season.

6. Lundy-ringed individuals recovered beyond the island and foreign-ringed birds controlled on Lundy were classified as migrants.

Annual climatic variation

To study the effects of environmental factors on autumnal Chaffinch migration, yearly winter NAO indices and corresponding winter temperatures in the region concerning Lundy were required. We used mean winter NAO indices from year 1972 to 2016 from

Climatedataguide (https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based) and regional mean winter temperatures (December to February) for 1972 to 2016 from the UK Met Office (https://www.metoffice.gov.uk/pub/data/weather/uk/climate/datasets/Tmean/date/England_SW_and_S_Wales.txt). Both the winter NAO and temperature indices were recorded such that each winter mean value was calculated from the mean of December in the year before, and the means from January to February (to March for the NAO indices) of the current year. Thus, to match the autumn ringing data to the climate data, both the winter NAO indices and mean winter temperature measurements were shifted backwards one year, so that the climate data reflected the winter conditions following the autumn in which the migrants were recorded.

Hypotheses testing

All statistical analyses were carried out in RStudio version 1.1.383 (R Core Team, 2017; see Appendix C for packages used).

The first hypothesis was evaluated by testing for evidence of differential migration, using chi-square tests to evaluate if the overall proportions of unique females and first-year birds within the migratory individuals differ from those observed in the resident population. Unsexed and unaged individuals were excluded. Paired t-tests were also conducted between the resident and migrant annual sex and age ratios for greater resolution of analysis by addressing possible temporal fluctuations.

Linear mixed effect models were designed to address the morphological comparisons in the first and second hypotheses. Wing length, weight and wing-load estimate were the response variables, with residency status, age group (first-years and adults) and sex as three-way interaction factors, and ring number as a random effect to address pseudoreplication. Interaction terms were removed when non-significant to ensure proper model specification. Significant interactions were further examined using Tukey's HSD post-hoc tests to evaluate differences between age, sex and residency classes.

To test the third hypothesis, regional winter temperatures were first assessed as the response variable against winter NAO indices in a linear model. This was conducted to evaluate any positive correlation between the two climate indices, which is suggested by existing literature (Hurrell, 1995). A binomial regression model was then built, considering sex as a binomial response variable for each annual cohort of migrants against the winter NAO indices.

RESULTS

Overview of ringing data

A total of 9,589 Chaffinch records were collected between 1972 and 2017, of which 143 records were excluded from analyses due to inconsistencies in age and sex. An overview of the remaining 9,446 records revealed that numbers peaked twice annually in April and October, with the latter month accounting for 90.6% of the total dataset analysed (Figure 1). The annual trend in number of records showed a seemingly exponential increase from the year 1972 to 1992 (Figure 2). Thereafter, most years between 1992 to 2011 registered at least 150 records, interspersed by two years with fewer than 150 entries (1998 and 2004).
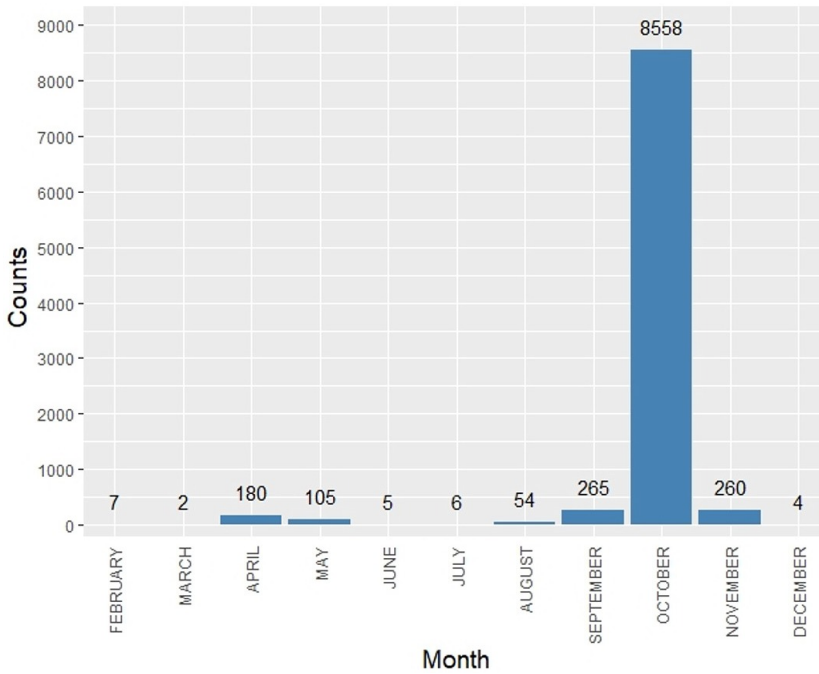
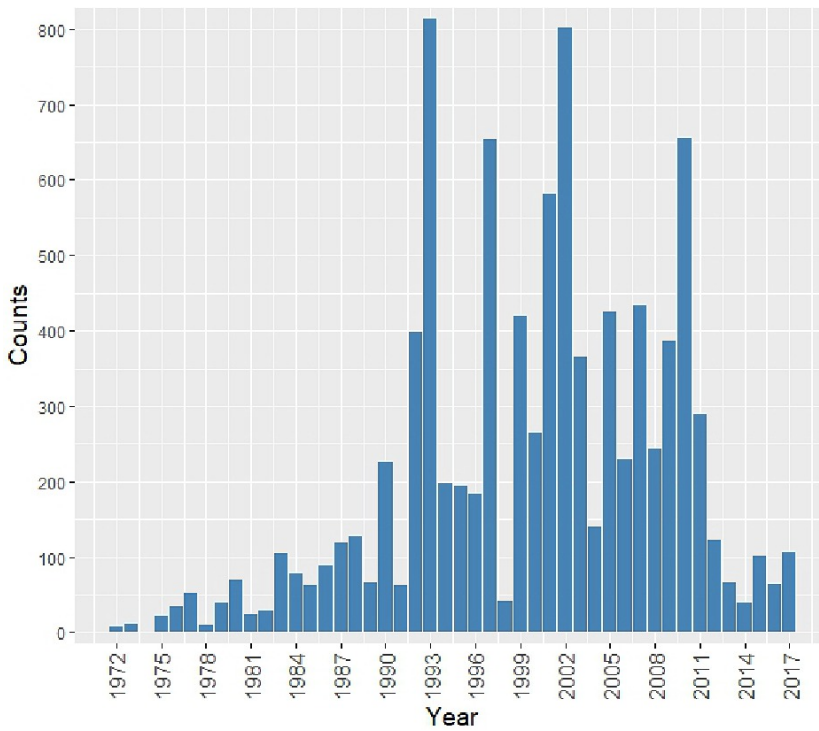**Figure 1**: Overall annual trends in number of records by month (*n*=9,446)

Figure 2: Yearly trends in number of records (*n*=9,446)

Map of recoveries

There were 26 instances of recoveries (Figure 3, see also Appendix A). The geographical pattern in recoveries suggests that migrants to Lundy hailed from Scandinavia or were of north-eastern origin, as shown by recoveries of individuals in Belgium, the Netherlands, Denmark, Norway, Sweden and Russia. Individuals recovered internationally beyond the British mainland were ringed on Lundy during autumn migration season, between September and October. Lundy-ringed individuals recaptured or found on the British mainland were there exclusively between late-November and mid-April, which suggests that they were wintering, or intercepted on spring passage en-route to their breeding grounds. These observations support that *coelebs* individuals use Lundy as an autumn stopover or wintering site as it shows a pattern consistent with the species' known breeding areas, migration season and pathway (Wernham *et al.*, 2002).
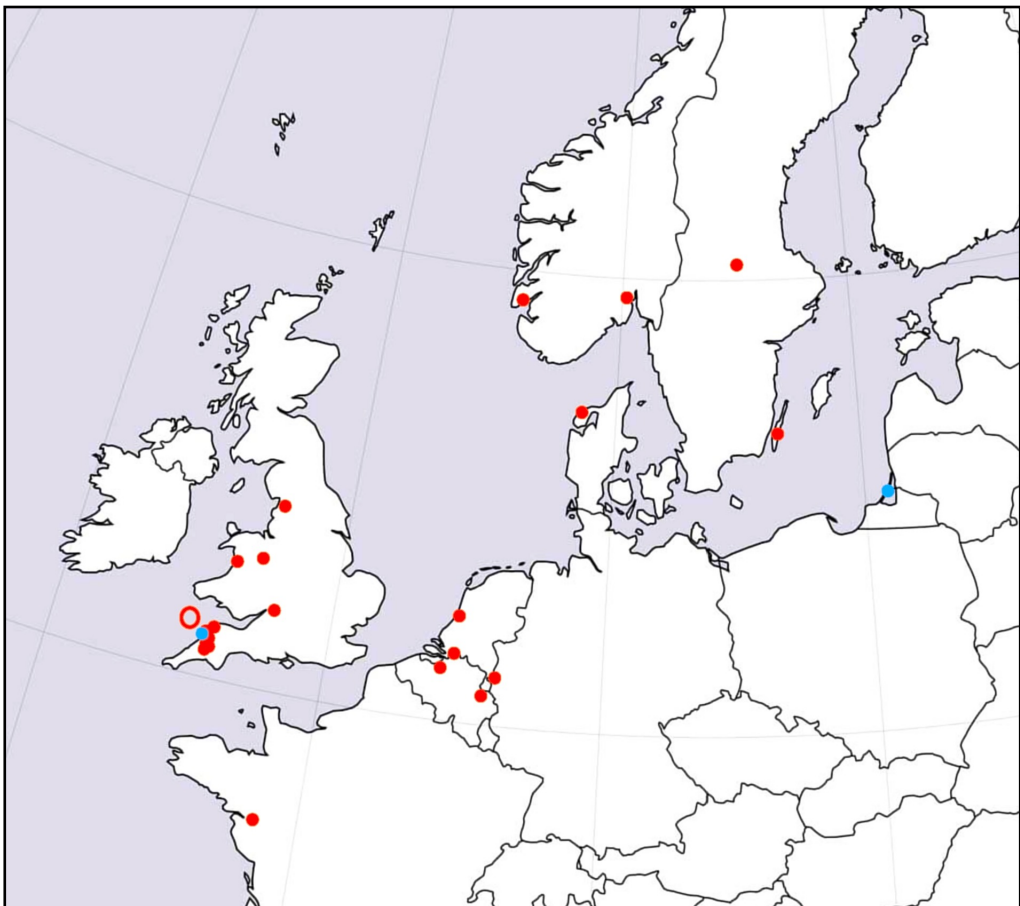

Figure 3: Geographical representation of ringing recovery data (*n*=26). Lundy is labelled by the hollow red circle. Individuals ringed on Lundy and recaptured elsewhere are given in red (*n*=23) and individuals ringed elsewhere but captured on Lundy are given in blue (*n*=3). GPS coordinates were not available, so locations indicated are approximate, based on localities provided in the recovery dataset. Map used adapted from http://www.freeworldmaps.net/europe/europe-blank-map-hd.jpg

Age and sex ratio comparisons in residents and migrants

The 9,446 records were differentiated following the residency criteria into 8,788 records of 8,238 unique migrants and 658 records of 266 unique residents. The observed sex ratios were female-skewed in both residents and migrants. However, there was a significantly greater proportion of females among migrant individuals (0.69) compared to the resident population (0.60) (χ^2(1,N=8472)=8.75, p=0.0031, see Figure 4). There was a greater discrepancy in age ratio between the two populations: first-year birds vastly outnumbered adults in migrants (0.73) and this proportion was significantly higher than that observed in the resident population (0.48) (χ^2(1,N=8435)=97,1, p<0.001, see Figure 5).
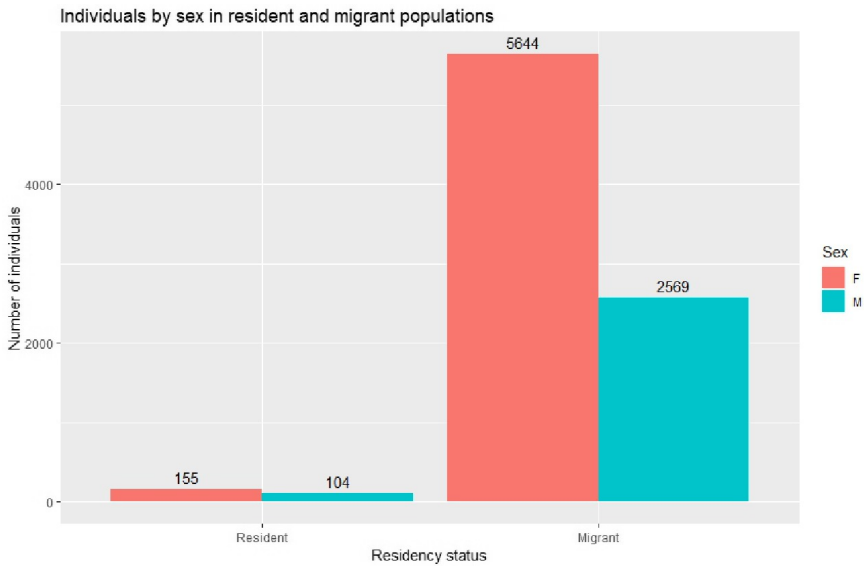

Figure 4: Number of individuals by sex within resident and migrant populations (*n*=8,472)
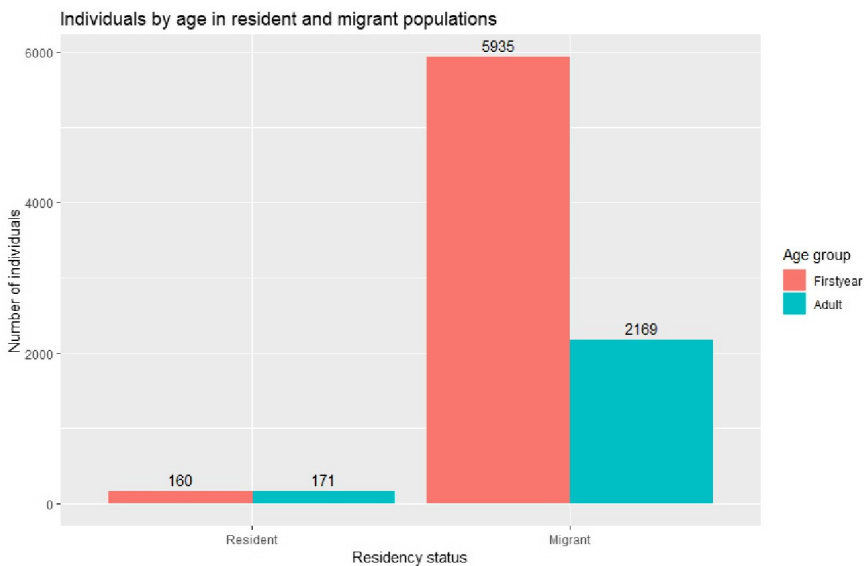

Figure 5: Number of individuals by age within resident and migrant populations (*n*=8,435)

Paired t-tests of annual sex and age ratios supported the chi-squared results. The annual proportion of females within the migrant individuals was on average 0.16 higher than the resident population (paired t-test, t(38)=4.82, P<0.001). Again, the annual age ratio was significantly higher in migrants than residents (paired t-test, mean of difference=0.26, t(37)=7.72, P<0.001).

Sexual dimorphism and age-related morphological differences
There was pronounced sexual dimorphism in terms of wing length, weight and wing-load estimate (Figures 6 to 8 and Table 1). Males had, on average, longer wing length, greater weight and higher wing-load estimate than females.
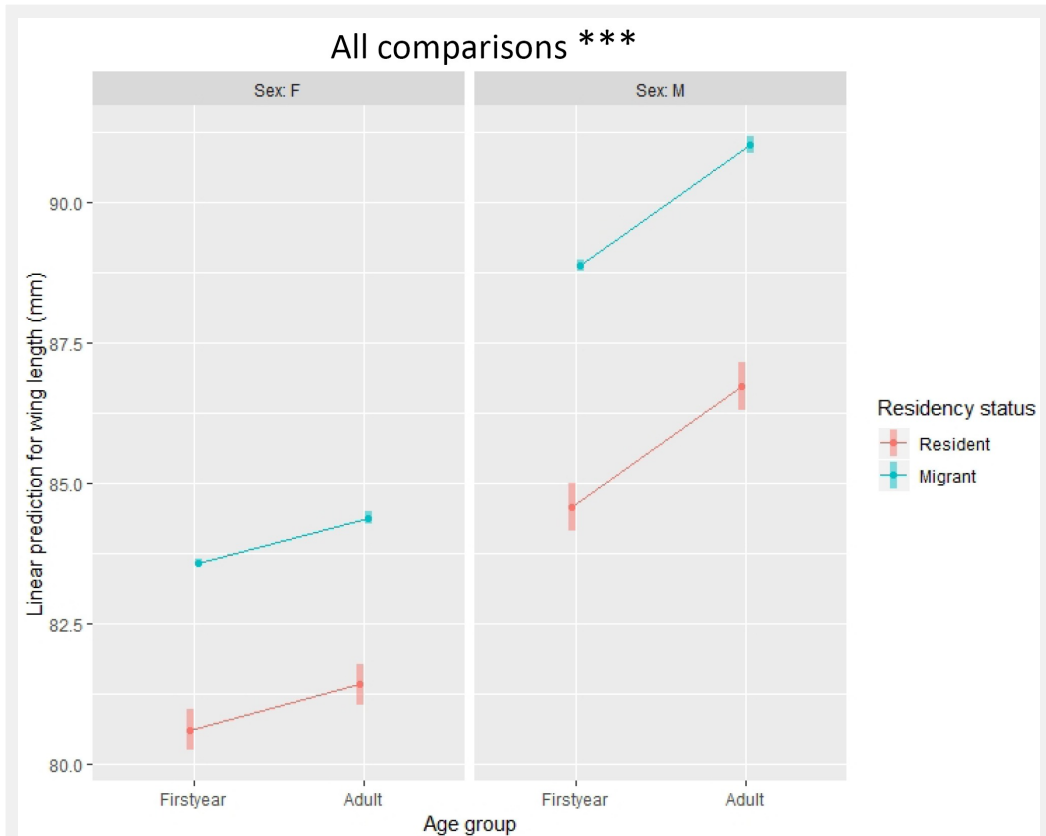

Figure 6: Linear mixed effect model predicted values of wing length in mm for females (left panel) and males (right panel) (*n*=8,863 of 8,024 individuals)

Age group, sex and residency status were tested as fixed effects with two-way interactions between age group and sex, and between residency status and sex. Estimated marginal means are plotted with 95% confidence intervals denoted by shaded vertical bars. Results of Tukey's HSD post-hoc tests comparing across all age, sex and residency classes were significant (P<0.001), showing that migrants, adults and males were longer winged than residents, first-years and females correspondingly.
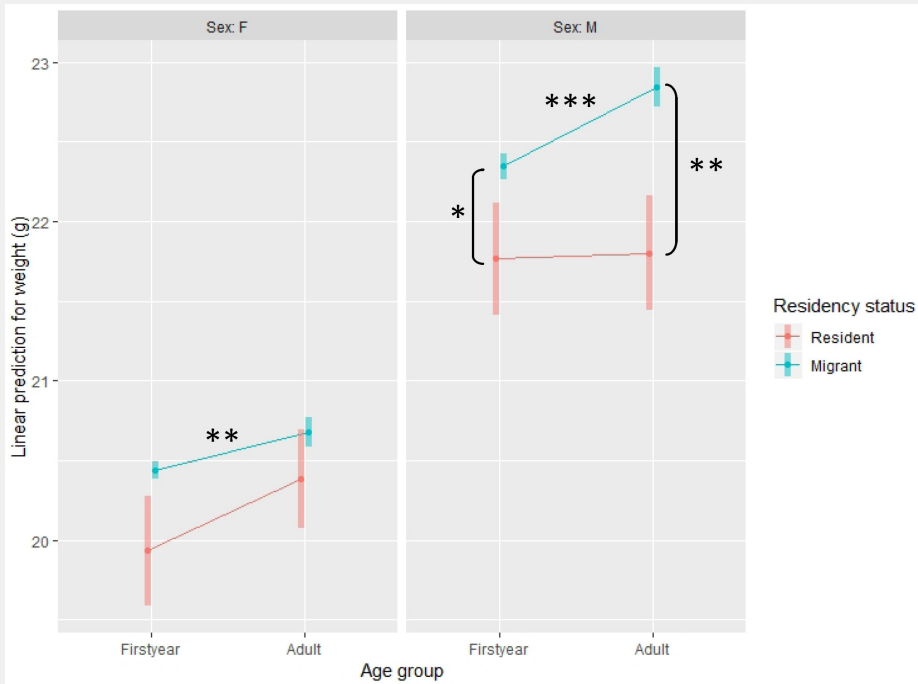
Figure 7: Linear mixed effect model predicted values of weight in g for females (left panel) and males (right panel) (n=8,832 of 7,984 individuals)

Age group, sex and residency status were tested as fixed effects with three-way interaction. Estimated marginal means are plotted with 95% confidence intervals denoted by shaded vertical bars. Significant results of Tukey's HSD post-hoc tests are given across age (horizontal comparisons) and residency classes (vertical comparisons) within each sex (*: P<0.05; **: P<0.01; ***: P<0.001). Not given in the figure: males were consistently significantly heavier than females when age and residency status were controlled for (all P<0.001).

Age-related morphological differences existed: adult individuals had longer wing length and were heavier than first-year birds (Figures 6 to 8). The age-related differences in wing length and wing-load estimates were dependent on sex, denoted by significant two-way interactions (Table 1). Male birds showed a greater increase in wing length with age than female birds (Figure 6). Although there were no overall significant differences in wing-load estimates between the two age groups, male birds exhibited a decrease in wing-load estimate with age, while an increase was seen in females (Figure 8).

Morphological differences between residents and migrants

Migrant birds were significantly longer-winged and heavier but did not differ significantly from resident birds in wing-load estimate (Figures 6 to 8 and Table 1). Additionally, the difference in wing length between migrant and resident birds was significantly greater in males than females, contributing to the significant two-way interaction between residency status and sex (Table 1).
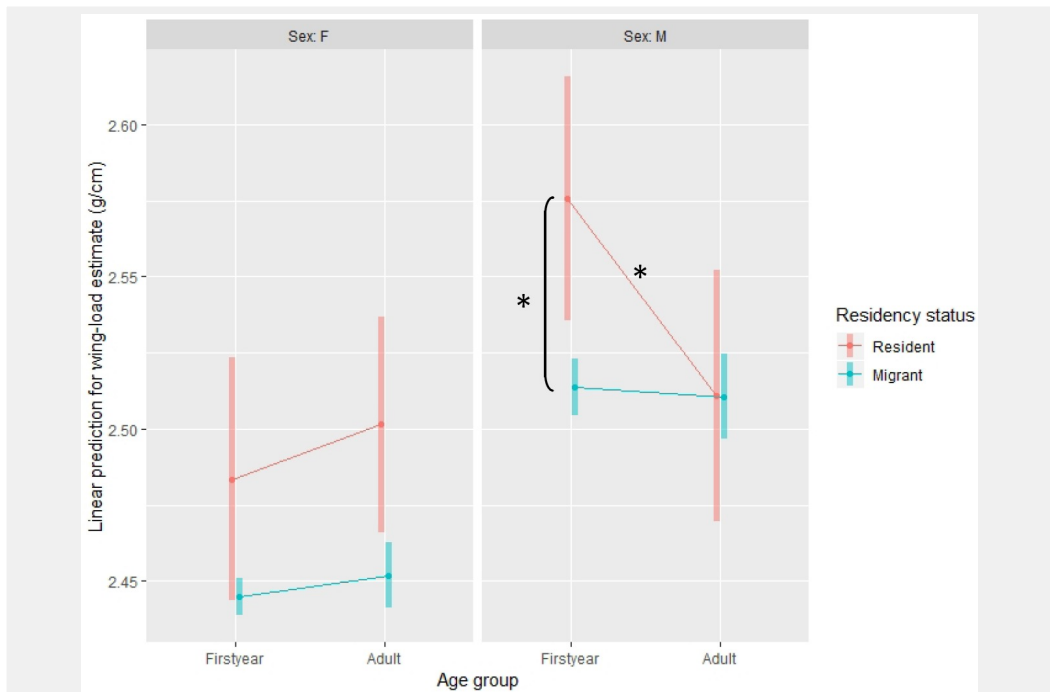
Figure 8: Linear mixed effect model predicted values of wing-load estimate in g per cm for females (left panel) and males (right panel) (*n*=8,776 of 7,956 individuals)

Age group, sex and residency status were tested as fixed effects with three-way interaction. Estimated marginal means are plotted with 95% confidence intervals denoted by shaded vertical bars. Significant results of Tukey's HSD post-hoc tests are given across age (horizontal comparisons) and residency classes (vertical comparisons) within each sex (*: P<0.05). Not given in the figure: sexual dimorphism was significant in all age and residency classes except adult residents (migrant adults and first years: P<0.001; resident first-years: P<0.001; adult residents P>0.05).

There was a significant three-way interaction between sex, age and residency status for weight (Table 1). Post-hoc comparisons of estimated means for weight (given in Figure 7) showed that adult birds of both sexes were significantly heavier than first-years amongst migrants but not amongst residents. Furthermore, migrant birds of both age classes were significantly heavier than their resident conspecifics only within males.

The significant three-way interaction between sex, age and residency status for wing-load estimate was further evaluated via post-hoc comparisons (Figure 8 and Table 1). Females showed an increase in wing-load estimate with age, but this effect was insignificant across both residents and migrants. In contrast, wing-load estimate in males decreased with age but only significantly within the resident population. Overall, wing-load estimate was lower in migrants than residents, but only significantly so within first-year males.

Sexual dimorphism was consistently significant for wing length and weight. However post-hoc comparisons of estimated means for wing-load estimates revealed that females had significantly lower wing-load estimates than males across all age and residency classes, except within adult residents where both sexes shared a similar value (Figure 8).

Table 1: Summary of linear mixed effect models

Fixed effects	Wing length			Weight			Wingload estimate		
	Estimates	SE	p	Estimates	SE	p	Estimates	SE	p
(Intercept)	80.61	0.19	**<0.001**	19.93	0.18	**<0.001**	2.48	0.02	**<0.001**
Age_groupAdult	0.80	0.07	**<0.001**	0.45	0.19	**0.016**	0.02	0.02	0.414
SexM	3.97	0.29	**<0.001**	1.83	0.25	**<0.001**	0.09	0.03	**0.001**
Residency_statusMigrant	2.97	0.19	**<0.001**	0.51	0.18	**0.004**	-0.04	0.02	0.062
Age_groupAdult:SexM	1.34	0.11	**<0.001**	-0.42	0.25	0.102	-0.08	0.03	**0.006**
SexM:Residency_statusMigrant	1.33	0.29	**<0.001**	0.07	0.26	0.774	-0.02	0.03	0.429
Age_groupAdult:Residency_statusMigrant				-0.21	0.20	0.275	-0.01	0.02	0.629
Age_groupAdult:SexM:Residency_statusMigrant				0.67	0.27	**0.013**	0.07	0.03	**0.023**
Random Effects									
σ^2	1.08			1.35			0.02		
τ_{00}	3.85 $_{\text{Ring\_number}}$			1.70 $_{\text{Ring\_number}}$			0.02 $_{\text{Ring\_number}}$		
ICC	0.78 $_{\text{Ring\_number}}$			0.56 $_{\text{Ring\_number}}$			0.53 $_{\text{Ring\_number}}$		
Observations	8863			8832			8776		

Key: Linear mixed effect models with wing length, weight and wing-load estimate as response variables. Age group, sex and residency status were tested as fixed effects; interaction terms are denoted by fixed effects punctuated by colons. Standard errors of the predicted estimates are represented by SE. Ring number was added as a random effect to account for pseudoreplication. Within-group and between-group variances and intraclass correlation coefficient are represented by σ^2, τ_{00} and ICC respectively. Estimated marginal means and pairwise contrasts via Tukey's HSD test for each model are given in Figures 6 to 8.

Table 2: Summary of binomial regression models testing climate data against annual sex and age ratios

Fixed Effects	Sex Ratio			Age Ratio		
	Odds Ratios	CI	p	Odds Ratios	CI	p
(Intercept)	2.25	2.14-2.36	**<0.001**	2.83	2.69-2.98	**<0.001**
NAO	0.97	0.95-1.00	**0.017**	0.96	0.93-0.98	**<0.001**
Observations	42			42		

Key: Binomial regression models with winter NAO indices (NAO) as a fixed effect. The response variables were the proportion of females (Sex Ratio) and first-years (Age Ratio) in the migrant population observed in the preceding autumn.

Climate effects on migrant sex and age proportions

Regional winter temperatures were positively correlated to winter NAO indices (R^2=0.42, $F_{(1,40)}$=29.1, p<0.001). Winter temperatures increased by 0.33 degrees Celsius per unit increase in winter NAO index. Binomial regressions results showed that winter NAO indices had a significant effect on both annual migrant sex and age ratios (Table 2). With every unit increase in winter NAO indices, the proportion of females and first-years observed fell by 0.97 times and 0.96 times respectively.

DISCUSSION

Evidence of differential migration

This study presents evidence that the Chaffinch is indeed a differential migrant. The comparisons of sex and age ratios between migratory individuals and the resident population suggest a differential migration pattern in which females and younger birds are the more migratory classes. These results are in support of hypothesis 1 and correspond with Linnaeus' notes and more recent observations on the species (Cramp & Perrins, 1994).

Body size hypothesis

The morphological comparisons conducted in this study have established sexual dimorphism and age-related differences followed by a migration pattern that is consistent with the 'body size' hypothesis (Ketterson & Nolan, 1976). Males and adult birds were found to be longer winged and heavier, which are physical traits that can confer more efficient heat conservation and fasting endurance, resulting in enhanced capacity to cope with colder weathers at higher latitudes (Ketterson & Nolan, 1976). The smaller females and younger birds are less adapted in this regard and thus forced to migrate further south where winters are milder.

This study's findings on sexual morphological differences and resulting trend in differential migration are corroborated by studies on sexually dimorphic avian species (Ketterson & Nolan, 1976; Belthoff & Gauthreaux, 1991). Additionally, improved cold resilience in larger individuals has been evidenced by bioenergetic studies conducted on avian species (Kendeigh, 1970). Thus, it is possible that the energetic constraints imposed by body size can explain the differential migration pattern observed.

However, it remains uncertain if the small, yet significant differences found in wing length and weight (the average differences do not exceed 4mm and 2g, Table 1) are influential to the birds' thermal biology. While there is an abundance of literature on the effect of sexual size dimorphism on thermoregulation (Ketterson & Nolan, 1976), there is limited scientific discourse regarding age-dependent variation in thermal ecology. Most of these studies focussed on older birds' enhanced feeding efficiencies, which translate to more effective harvest and storage of energy for improved heat maintenance (Merila & Wiggins, 1997). Furthermore, even though both intersexual and age-related differences in wing length and weight were significant, the latter was much lower (Table 1). Although this observation warrants additional investigation to be conclusive, it suggests that the body size hypothesis might better account for the species' intersexual distinctions in migratory strategies rather than why its young birds are more migratory than adults.

Dominance hypothesis

Longer wings and greater body mass are typical of dominant social classes in birds, as larger birds tend to win physical encounters against smaller conspecifics and are more efficient in procuring and securing resources (Piper, 1997). Younger individuals tend to be subordinate to older conspecifics, as they are physically less developed and possess comparatively limited experience in resource competition (Piper, 1997). Thus, the results of this study suggest that the 'dominance' hypothesis (Gauthreaux, 1982) for differential migration may be applicable to the Chaffinch.

Although the intraspecific discrepancies in physical characteristics point towards males and adults being the socially dominant classes in Chaffinches, it remains debatable if this is true within the migratory population assessed here. Firstly, there is no relevant commentary from the results of this study because it did not aim to evaluate social hierarchy, so any inferences will have to be extrapolated from existing literature. Secondly, studies on social hierarchy in the Chaffinch and related finch species were conducted within captive populations where social ranks were derived from artificially induced conditions and population densities (Marler, 1955). Given that avian hierarchical structures show some degree of plasticity in response to population density and stochastic environmental conditions (Schradin, 2013), the conclusions of said studies must be interpreted and applied with caution to wild populations. That said, the lack of understanding of social structures in wild migratory bird populations presents a challenging yet important opportunity for future research which will be crucial to our understanding of the social mechanisms underlying avian differential migration.

Arrival time hypothesis

Arguably, the 'arrival time' hypothesis (Myers, 1981) may also be relevant to the results of this study. As aforementioned, the pronounced sexual dimorphism in wing length and weight are suggestive of male-biased social dominance. Past studies have demonstrated Chaffinch males to be the dominant, territorial sex that is responsible for acquiring and defending breeding territories (Marler, 1955). Accordingly, males stand to gain more benefits in terms of reproductive success than females from wintering closer to breeding grounds. Minimising migration distances would mean incurring less cost associated with migration, allowing males to arrive at breeding grounds earlier and channel more resources towards intrasexual territorial competition (Myers, 1981). The resulting advantage in reproductive fitness would select for males to remain as sedentary as possible, which may have contributed to the differential migration trend seen in this study.

However, much like the 'dominance' hypothesis, there is insufficient information to confirm this. Besides the lack of behavioural data to ascertain male territoriality and dominance, proper analysis of this hypothesis demands arrival and departure time of migrants, which were not available. This was largely because bird ringing on Lundy is conducted on a voluntary basis, so seasonal coverage relies heavily on the availability of volunteers. Although capture dates were recorded for every bird, it was not possible to reliably determine migration timings as ringing efforts were non-standardised and intermittent, resulting in irregular coverage of years in their entirety. This issue highlights the value of consistent and standardised ringing in migration studies, and the intensive efforts required in data collection where bird ringing is concerned.

Additional considerations

It is prudent to note that the sex and age ratios calculated in this study are not necessarily representative of the species' migration strategy.

To determine differential migration patterns by analysing sex and age ratios, it was important to first consider the population structures in both migrants and residents.

This step was imperative to establishing a valid baseline for comparison by eliminating inherent bias in analyses. Unfortunately, literature surrounding the Chaffinch's population demographics is largely missing, save for a single study conducted in Norfolk, United Kingdom, which substantiated the slightly female-skewed sex ratio found in Lundy's resident population (Browne, 2004).

Age and sex ratios are known to vary across intraspecific populations, mostly due to environmental factors that fluctuate with geography (Ketterson & Nolan, 1976). For instance, given the strong sexual size dimorphism demonstrated in this study, it is likely that offspring sexual size dimorphism exists in Chaffinches. Male chicks are likely energetically costlier to produce, thus colder temperatures in the northern latitudes might select for female-biased offspring sex ratio in the migrants (Trivers & Willard, 1973). Sex or age-based differential mortality due to predation pressures and intraspecific resource competition are sensitive to environmental or ecological factors such as predator abundance, habitat quality and ambient temperature (Székely *et al.*, 2004). Thus, without knowledge on population demographics, the observed differences in migrant and resident age and sex ratios may be merely artefacts of variations in age and/or sex ratio determinants and less due to differential migration.

Moreover, it was neither possible nor relevant to associate Lundy's migrant Chaffinches with their breeding populations. Recaptures were a rarity: only 24 out of 8,504 unique individuals were controlled throughout 46 years' worth of data, giving a recapture rate of 0.28%. Of the 26 records, only 12 were controlled beyond the British Isles and were spread around continental Europe and Fennoscandia. There was an obvious lack of information to pinpoint the breeding populations that Lundy's migrants belong to. However, combining the geographical distribution of Lundy's foreign controlled birds with those from previous studies (Wernham *et al.*, 2002), it is highly likely that Lundy's migrants originate from populations spread throughout northeastern Europe. At best, the migrant sex and age ratios measured in this study were average structures from an assemblage of populations.

A viable solution to the above issues is to evaluate temporal variations in sex and age ratio along latitude (*sensu* Ketterson & Nolan, 1976 and Catry *et al.*, 2005). Although such methodologies typically require large-scale efforts with close international collaboration to execute, they would be more reliable ways to assess differential migration patterns because they control for confounding effects of latitude on demographic parameters.

Morphological adaptations in migratory individuals
The morphological differences revealed between migratory and sedentary individuals were in support of hypothesis 2. Migrants had longer wing lengths, greater body mass and lower wing-load estimates than residents, which suggest that migrant individuals are physically larger and have disproportionately longer wings. These findings are consistent with the predictions of aerodynamic theory and studies that compared the ecomorphology of sedentary and migratory intraspecific populations (Pérez-Tris & Tellería, 2001).

Conflicting selective pressures influencing morphological variations Wing length and body mass have contrasting relationships with avian locomotive efficiency. Shorter and rounded wings give manoeuvrability and are better suited for short-distance flights with frequent take-offs (Pérez-Tris & Tellería, 2001). On the other hand, longer and pointed wings are more energetically costly to develop but are associated with improved flight velocity and efficiency (Nowakowski, Szulc & Remisiewicz, 2014). Body mass is positively related to wing-loading: the heavier the bird, the more weight to be distributed per unit of wing area and thus the more effort expended for flight. Yet, greater body mass is advantageous for heat conservation and improved fasting endurance, which are life-saving traits for cold climates and long-distance travel (Ketterson & Nolan, 1976; Ashton, 2002). Considering the opposing aerodynamic consequences imposed by wing length and body mass, the morphology of migratory individuals would be optimised to reflect a delicate trade-off between the selective pressures of migratory cost and colder climates. Likewise, the discrepancies in age or sex-related variation in morphology between sedentary and migratory individuals may be due to selective forces acting in concert within each population.

Age-related variation of weight
Unlike Lundy's resident birds, migrants showed a significant increase in weight with age. A greater body mass is preferable from a migratory performance standpoint as it suggests a bird in prime physical condition to withstand the caloric and muscular demands of the journey (Guy Morrison, Davison & Wilson, 2007). Yet, increases in body mass can be deleterious as it can impede predator avoidance (Lind *et al.*, 1999), which is an essential survival trait for juvenile birds given their greater susceptibility to predation (Solonen, 1997). Thus, first-year migratory birds might be facing an upper limit constraint on body mass due to predatory pressure. The significant gain in weight with age in migrants is then a consequence of the alleviation of predation risk in adulthood as the birds gain more experience in escaping attacks (Solonen, 1997) and the augmented influence of migratory pressures. There was little biological incentive for the sedentary residents to carry the burden of additional body mass, which may explain why the significant increase in body weight with age was only seen in migrants.

Intrasexual variation in morphological trends
Assuming females were the more migratory sex, it was surprising that differences in morphology between migrant and resident birds were larger in males than females. This finding was in contradiction to hypothesis 2, as it was expected that the more migratory sex would express a greater difference in morphology between residents and migrants. This suggests that selective pressures excluding that exerted by migratory flight were in force. One possibility would be heightened intrasexual competition between migrant males. Colder weather in northern latitudes may limit resource quality and quantity, thus harsher climate could have intensified male-male territorial disputes and hence selected for physically larger, stronger and dominant

males (Marler, 1955). The comparatively lower degree of territoriality expressed by females suggests a reduced selective influence by intrasexual competition in migrant females, which may be reflected by the smaller gap in wing length and weight between female residents and migrants.

The opposite age-related trends in male and female wing-load estimates were also against predictions, since lower wing-loading is typically associated with more migratory classes. Again, additional selective forces were likely responsible for this observation. The species is visually dimorphic in adulthood: juveniles from both sexes share similar appearances, but males develop a distinctly more vivid plumage in their second year (Svensson, 1992). Studies have shown that this predisposes male adults to a higher risk of predation, as their brighter colouration renders them more conspicuous (Götmark & Hohlfält, 1995). Hence, predatory pressures would select for the survival of male adults which are better equipped to avoid predatory attacks, such as those with lower wing-loading. The absence of increased predation threat for female adults may account for the lack of significant age-related variation in wing-load estimate. Furthermore, the steeper gradient of decrease in wing-load estimate with age in resident males may be symptomatic of higher predation pressures on Lundy. Raptors which feed on the Chaffinch are plentiful on the island (pers. obs., November 2017; Davis & Jones, 2007).

Limitations to interpretation

Evidently, it is tricky to disentangle the conflicts and reinforcements to age, sex or residency-related trends in morphology by various forces of natural selection. Thus, the possibility that there were other factors confounding this study's findings cannot be discounted and necessitates additional investigation. Specifically, further studies will greatly enrich our understanding of selective pressures responsible for age and sex-related morphological trends within the sedentary population.

It is important to note that the wing-load estimate used in this study is not a perfect index for wing-load. Wing area data were missing, which limited this study's conclusiveness where wing-load is concerned. The lack of reliable allometric formulas to calculate wing area from wing length meant that the wing-load estimate was the closest approximation to wing-load afforded by available data. Wing length measured via the maximum chord method is far from the standard of deriving wing area from photographs or wing tracings (Yalden, 2012). This presents a future direction for additional research to elucidate the aerodynamic adaptations for migration in Chaffinches.

NAO effects on differential migration

The proportion of females and first-year birds was inversely related to the NAO index, which was congruent to the predictions of hypothesis 3. The results suggest that milder winter climates displaced fewer individuals of the more migratory sex and age classes, likely because less harsh weather conditions meant that more individuals could afford to stay sedentary to avoid incurring costs associated with migration.

An important implication of this observation is sex and age spatial segregation of Chaffinches in winter. If, in colder winters, females and younger birds are more inclined to migrate and overwinter southwards, then in these circumstances they would be more susceptible to environmental threats such as habitat loss in their wintering grounds. This would have profound consequences for the migratory *gengleri* subspecies as this can skew sex and age ratios in affected populations. Where anthropogenic threats are concerned, heterogeneous levels of man-made risks across geographical locations will result in unequal exposure to such threats depending on the birds' seasonal distribution. Although there is no information in this study to comment on this, the pattern of differential migration and its responses to climate suggested in the results can serve as a foundation for further research and hypotheses.

Limitations to interpretation
Data collection was limited to Lundy; thus information was inadequate for constructing a complete representation of differential migration in the Chaffinch and its sensitivities to climate. The current dataset relied on intercepting migrants en route. Since the migrants are known to use Lundy as a stopover, the birds could have bypassed the island in weather conditions favourable for onward migration and were thus not captured and reflected in subsequent analyses. This could have resulted in an underestimation of sex and age ratio variation in response to winter NAO indices. To overcome this limitation, it is pertinent to expand the geographical coverage of data, preferably in a latitudinal way parallel to studies by Ketterson & Nolan (1976) and Catry *et al.* (2005).

Another major assumption in the interpretation of winter NAO effects on annual migrant demography was that the indices were representative of relevant winter conditions that affected differential migration. Differential migration is known to be affected by the phenology and resource quality of breeding and wintering sites plus areas along the associated flyway (Anthes, 2004). The NAO is a large-scale climatic phenomenon; thus, its indices do not necessarily reflect local weather conditions that were influential to the extent of differential migration. Consequently, even though regional winter temperatures did show the expected positive relationship with winter NAO indices, this was only indicative of winter temperatures at a stopover site and was not fully representative of the weather conditions of interest.

Unfortunately, due to data deficiency, it was not possible to ascertain the breeding and wintering areas utilised by Lundy's migrant Chaffinches. This hindered the derivation of appropriate local weather indices for sufficient geographical coverage in this study. The inclusion of regional climate indices across continental Europe and other weather indices with recognised impact on site phenology (e.g. rainfall: Gordo, 2007 and references therein) in further analyses is a plausible solution to this challenge. Another consideration is to employ remote sensing technology to identify and monitor environmental conditions at sites of interest, to directly establish the relationship between climatic variations and migratory patterns (Gordo, 2007).

CONCLUSION

This study presents morphological and population demographical evidence supporting the notion that the Chaffinch *Fringilla coelebs* is a differential migrant, and that its females and younger individuals are the more migratory classes. While there are many hypotheses for differential migration, the 'body size' hypothesis may be the closest in explaining the phenomenon in this species. However, because these hypotheses share similar predictions, and data inadequacies in this study impaired conclusive judgement, further research is required to disentangle the underlying mechanisms.

In general, migratory individuals showed morphological traits that agree with aerodynamic theory, but discrepancies exist across age and sex classes. A bird's morphological characteristics are the reflection of selective pressures acting simultaneously and are optimised for individual fitness and survival. Due to the multifaceted and interconnected character of natural selection, teasing apart the cause and effects of each force of selection is no trivial task, and should be a challenge tackled in future studies.

The value of understanding climatic effects on differential migration should not be underestimated. Given impending climate change, seasonal segregation and distribution of intraspecific classes in migratory avian species are likely to shift spatially and temporally in the future. Improving our comprehension of the climatic mechanisms behind differential migration can be key to predicting seasonal population distribution when individuals are highly vulnerable. This will better inform conservation policies, especially those concerned with the protection of sites of migratory importance.

ACKNOWLEDGEMENTS

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APPENDIX A: Chaffinch recovery data (*continued on next page*)

Scheme	Ring	Age	Sex	Date	Place	Date	Place	Circumstances	Notes
GBT		4	F	30/10/1958	Lundy	15/10/1961	Kohlscheid, nr Aachen, Germany		
GBT		3	F	13/10/1959	Lundy	14/10/1960	Liege, Belgium		
GBT		3	M	26/10/1969	Lundy	24/3/1973	Googstraten, Antwerp, Belgium		
GBT	B580928	3	M	16/9/1984	Lundy	15/3/1985	Bideford, Devon	Hit window. Flew off unharmed	Later retrapped twice on Lundy
GBT	D184049	3	F	20/10/2012	Lundy	4/4/2014	Mulvika, Re, Vestfold, Norway	Controlled by ringer	
GBT	D184209	5	M	26/4/2013	Lundy	1/5/2016	Ynys Hir, Ceredigion	Freshly dead (Trichomonosis)	
GBT	E186791	4	F	4/4/1988	Hartland Point, Devon	8/10/1989	Lundy	Controlled by ringer	
GBT	F969110	4	M	23/4/1991	Hartland Point, Devon	28/10/1991	Lundy	Controlled by ringer	
GBT	J477793	3	M	26/10/1993	Lundy	15/1/1995	Alston Hall, Lancashire	Controlled by ringer	
GBT	J477809	3	F	26/10/1993	Lundy	8/4/1998	Ottenby, Oland, Sweden	Controlled by ringer	
GBT	J509136	3	M	29/10/1993	Lundy	16/5/1997	Vester Vandet So Thisted, Jylland, Denmark	Controlled by ringer	
GBT	J509136	3	M	29/10/1993	Lundy	9/5/1998	Vester Vandet So Thisted, Jylland, Denmark	Controlled by ringer	
GBT	K923322	4	F	30/10/1997	Lundy	6/11/1998	Zele Heikant, Oost-Vlanderen, Belgium	Controlled by ringer	

APPENDIX A: Chaffinch recovery data *(continued from previous*

Scheme	Ring	Age	Sex	Date	Place	Date	Place	Circumstances	Notes
GBT	L026586	3	F	14/10/2009	Lundy	23/4/2012	Bomyra,Randaberg, Rogaland, Norway	Controlled by ringer	
GBT	L026586	3	F	14/10/2009	Lundy	6/4/2015	Bomyra,Randaberg, Rogaland, Norway	Controlled by ringer	
GBT	N407155	3	M	26/10/1997	Lundy	19/10/2004	Wassenaar Meijendel Sparregat, Zuid-Holland, Netherlands	Controlled by ringer	
GBT	N879249	3	F	24/10/1999	Lundy	22/12/2001	Uley Bury, Gloucestershire	Controlled by ringer	
GBT	P660612	4	F	29/10/2001	Lundy	16/12/2001	Nr Venusbank, Cound, Shropshire	Controlled by ringer	
GBT	P660754	3	F	1/11/2001	Lundy	4/1/2002	Muddiford, Barnstaple, Devon	Killed by cat	
GBT	R009392	3	M	21/10/2002	Lundy	13/3/2004	Tavistock, Devon	Found freshly dead	
GBT	R009559	3	F	22/10/2002	Lundy	7/8/2003	Borlange, Kopparberg, Sweden	Found dead; hit window	
GBT	R009700	3	M	22/10/2002	Lundy	15/3/2003	West Town, Bideford, Devon	Found dead	
GBT	T949551	3	F	7/9/2007	Lundy	20/4/2008	Okehampton, Devon	Killed by cat	Retrapped on Lundy x3 in Oct '07
GBT	V935134	3	F	26/10/2007	Lundy	17/2/2008	Le Chene, Saint-Colomban, Loire-Atlantique, France	Found dead; hit window	
RUM	XY20913	3	F	26/9/2005	Rybachiy, Kaliningrad, Russia	27/10/2005	Lundy	Controlled by ringer	
GBT	Z981660	3	F	25/10/2017	Lundy	12/11/2017	Lifton, Devon	Found dead; hit window	

APPENDIX B: EURING age classification

EURING age code	Age of bird
2	Non-juvenile, exact year uncertain
3J	Hatched in current calendar year, still in juvenile plumage
3	Hatched in current calendar year
4	Hatched before current calendar year, exact year unknown
5	Hatched in previous calendar year
6	Hatched at least two calendar years prior, exact year unknown

APPENDIX C: Statistical analyses

Packages used were lme4 for linear mixed effect models (Bates *et al.*, 2015), lmerTest for processing p-values for fixed effects in linear mixed effect models, using Satterthwaite approximation to degrees of freedom (Kuznetsova, Brockhoff & Christensen, 2017), emmeans to obtain estimated marginal means and conduct Tukey's Honest Significant Difference (HSD) post-hoc tests (Lenth, 2018), and car for verifying homoscedasticity assumptions (Fox & Weisberg, 2011). Data were visualised with ggplot2 (Wickham, 2016), sjPlot (Lüdecke, 2018) and native packages.

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