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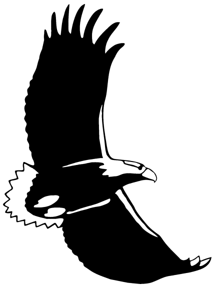

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Temporal increase in migratoriness and increasing male bias among residents in partially migrating Swedish sparrowhawks *Accipiter nisus*

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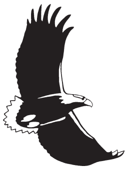

Partial migrants have populations consisting of both migratory and resident individuals. These migrants and residents experience unequal ecological conditions during winter and the underlying factors driving their decision to stay on their breeding grounds or to migrate remain debated—both from the viewpoint of populations and individuals. Here, we studied partial migration in a small raptor, the Eurasian Sparrowhawk (*Accipiter nisus*), from two different but interconnected perspectives: 1) explaining the patterns and variation in the ratio of migrants to residents (migratoriness) at the population level and 2) revealing how age and sex may affect the individual decision to be migratory or resident. We used citizen observation data over four decades to explore the temporal and spatial variation in the age and sex ratio of wintering resident sparrowhawks in Sweden. We found that the migratoriness unexpectedly increased with higher annual temperatures and showed long-term trend across the study period. Also, this migrant-to-resident ratio increased with smaller winter prey abundance. The average winter sex ratio was male-biased and became increasingly so over the years. We suggest that residency benefits territory-establishing males as early presence gives a competitive advantage in obtaining high-quality territories. Moreover, the distribution of overwintering individuals (regardless of sex) moved gradually northwards as the winter progressed, suggesting that smaller-scale migration occurs among the resident fraction of the population. These results provide suggestions for the underlying drivers and regulation of partial migration.

1. Introduction

Climate responses in bird migration have received much attention, with a particular focus on changes in migration phenology (Rubolini *et al.* 2007, Usui *et al.* 2017, Lehikoinen *et al.* 2019) and how insufficient responses lead to temporal mismatches with seasonal resource peaks (Visser

& Gienapp 2019). Migration enables individuals to utilize seasonal resources, but there is a growing interest in why some birds migrate while others do not. In partial migrants, a single population contains both migratory and resident individuals, which is fairly common among short-distance migrants (Lack 1943, 1944, Terrill & Able 1988, Lundberg 1988, Chapman *et al.* 2011). Rising temperatures may tip the balance of whether being migratory is a superior strategy for individual life history, which may alter the composition of migrants and residents within and across partially migratory populations. Such responses have classically received little attention compared to other spatial and temporal aspects of migration, *e.g.*, the timing of arrival in spring (Lundberg 1988, Newton 2008, Chapman *et al.* 2011) despite its potential to cause rapid, large, and unpredictable effects on spatial distribution, population dynamics, and life history.

The average migratoriness has been shown to increase in populations toward areas with harsher winter environments, such as higher latitudes in the northern hemisphere (Main 2002, Newton 2008, Boyle *et al.* 2010, Somveille *et al.* 2013, Ambrosini *et al.* 2016) and altitudes (Boyle *et al.* 2010, Lundblad & Conway 2020). It has been hypothesized that partial migrants may step towards year-round residency, as a way to adapt to climate warming, when the survival prospects of overwintering near breeding latitudes improve (Berthold 1996, 2001, Pulido & Berthold 2010, Chapman *et al.* 2011, Meller *et al.* 2016). While the spatial patterns in migratoriness may result from local adaption over time, and for a few species show temporal responses to annual temperature, there are limited examples showing how migratoriness could directionally divert over time, currently suggesting heterogeneous trends across species (Nilsson *et al.* 2006, Van Vliet *et al.* 2009, Meller *et al.* 2016). While the individual migration decision is binary, the migratory propensity is continuous and heritable (Berthold & Querner 1982, Berthold 1988, 1999, 2001, Biebach 1983, Pulido & Berthold 2010), but to a variable degree plastically modified by environmental components (Able & Belthoff 1998). Besides long-term selection by temperature, the fitness prospects by residency may be additionally affected by factors such as food abundance (Lindén *et al.* 2011, Meller *et al.* 2016), extreme weather (Acker *et al.* 2021) and density dependence (Kokko & Lundberg 2001, Lundberg 1988, Meller *et al.* 2016), potentially at a shorter temporal scale. Thus, the drivers for migratory polymorphism are likely conditional; key individual costs and benefits from either migratory or resident phenotypes remain controversial, and generalizations are yet difficult (Chapman *et al.* 2011).

Heterogeneous responses in migratoriness suggest that the fitness of migrants and residents is individual and conditional in space and time. Within a population, the individual pressure to migrate should be unequal between individuals to maintain both strategies (Pulido & Berthold 2010, but see Pulido 2011, de Zoeten & Pulido 2020). In the temperate region, the migratory and resident fraction may experience very different ecological conditions and life history, and the underlying factors driving this polymorphic trait remain debated both for populations and at an individual level. Recent literature has suggested both scenarios with a fitness benefit for the resident fraction (*i.e.*, Grist *et al.* 2017, Buchan *et al.* 2020) and the migratory fraction of a population (Zúñiga *et al.* 2017, Acker *et al.* 2021), underscoring a lack of uniformity in fitness advantage between the two migratory phenotypes. Also, there is a discrepancy in whether such a benefit is primarily driven by survival (Buchan *et al.* 2020, Zúñiga *et al.* 2017) which would likely affect differently among individuals and areas. Thus, the actual costs and gains an individual faces as a migrant or a resident are likely conditional, depending on pre-existing traits and capabilities, such as migration distance, capability of survival in the cold, and subsequent breeding success.

What phenotypic traits facilitate migration or residency as the superior strategy remains controversial as well, with competing hypotheses having suffered from overlapping predictions (Chapman *et al.* 2011). The most central theories predicting individual migratory propensity concern sex and age, and we here explore three such hypotheses, with predictions for which individuals show higher/lower migratory propensity.

First, the *arrival time hypothesis* states that early spring presence at the breeding grounds gives a competitive advantage for high-quality territories, favouring residency for the territory establishing sex (Ketterson & Nolan 1976), usually males (*e.g.* Schwabl 1983). This, however, assumes that: a) high-quality territories are subject to intra-specific competition, b) resident individuals are best able to acquire such territories by arriving early and c) such acquisition gives a fitness advantage through, *e.g.*, improved fecundity and survival.

Secondly, the *body size hypothesis* is based on the thermoregulatory superiority of larger body size. Reduced surface area to volume ratio decreases heat loss and body size is positively correlated with basal metabolism (Daan *et al.* 1990). This predicts larger residents (Ketterson & Nolan 1976, Belthoff & Gauthreaux 1991, Chapman *et al.* 2011, Lehikoinen 2011) which for most bird species with sexual size dimorphism would be males (Dunning 2008).

Third, the *competitive release hypothesis* (also referred to as *dominance hypothesis*) states that if the available winter habitat for residents is restricted, density-dependent competition may occur. If so, dominant individuals (usually the larger individuals) should gain a competitive advantage forcing subordinates (usually females and juveniles) to migrate (Ketterson & Nolan 1976, Gauthreaux 1982, Lundberg 1985, Smith & Nilsson 1987). These three hypotheses classically overlap in their predictions, suggesting that males are more often resident (Chapman *et al.* 2011) and part of the literature on this topic stems from obligate migrants, using migration distance as the response variable instead of the propensity to migrate at all.

Our aim here is divided into two interconnected parts, focusing on the Eurasian Sparrowhawk (*Accipiter nisus*) as a study system. Firstly, to approximate changes in the migratoriness on a population level, we study the temporal trends and annual variation in the migrant to resident ratio (hereafter 'MRR'), relating it to annual temperature anomalies during the migration period, and food availability, measured as the annual winter prey abundance. We expect that lower temperatures and lower food availability drive more individuals to migrate. We also predict that sparrowhawks have become less migratory as a long-term response to climate warming.

Secondly, we study how sex and age may conditionally affect the costs and benefits of being a resident or migrant, and evaluate the evidence for the three aforementioned hypotheses. Studying the sparrowhawk enables us to untangle overlapping predictions due to the species' reversed sexual size dimorphism. A male-biased sex ratio in winter would support the arrival time hypothesis while more females would suggest the body size hypothesis or the competitive release hypothesis—the latter would be suggested by resident adults. Besides testing the predictions of these hypotheses, we also explore the sex- and age-specific spatio-temporal distribution patterns, such as the latitudinal distribution and long-term temporal change to obtain a more complete picture of their consistency. In all sets, we explore through model selection a possible connection between our study parts 1 and 2; whether the annual variation in the MRR co-varies with the ratio of sex, age or latitude distribution. Such a pattern would further clarify how certain individuals are more likely to migrate when the pressure to migrate increases.

2. Materials and methods

2.1. Study species

We studied the Eurasian Sparrowhawk (*Accipiter nisus*); a small-sized, partially migratory raptor with an extreme reversed size dimorphism, which is also the most common raptor in Fennoscandia (Newton 1986). Females can be more than twice as heavy as males (Dunning 2008), likely providing better thermal resilience in cold winters while leaving males physically subordinate (Newton 1986). The parental effort is skewed; the male establishes the territory and feeds the female, the chicks and himself throughout a significant part of the breeding season (Newton 1986). The quality of territories varies (Newton 1986), and the local prey availability and exploitation can affect breeding productivity (Otterbeck *et al.* 2015). Thus, acquiring high-quality territories is under strong competition among territory-establishing males. Sex separation and age determination (juvenile/adult) are fairly easy in the field for more experienced observers.

2.2. Study area and weather data

Our study area, Sweden, spans over a large latitudinal range and has a long tradition of surveying and reporting both summer and winter bird abundances. Moreover, there is a well-monitored migration hotspot in the south at Falsterbo where a substantial part of migratory sparrowhawks will pass on their journey south. Assuming facultative migration in at least part of the population, partial migrants may adapt their migratory phenotype to prevailing environmental conditions before or during their migration period. To measure such inter-annual variation, we calculated an annual average late autumn temperature (from October 1 to November 30) using temperature data from 7 districts evenly scattered from south to north from 1975 to 2013. The data were obtained from the Swedish Meteorological Institute. This late-autumn period can only affect late migrants, mainly adults, who haven't yet migrated when encountering a relevant drop in temperature. Thus, this period evades the peak of juvenile migration in August–September, during which temperature is not likely to affect the migration decision.

2.3. Avian abundance data

2.3.1. Migration survey and wintering abundance indices

We used annual total migration counts of sparrowhawks from Falsterbo Bird Observatory. The observatory is situated on a peninsula at the southwestern tip of Sweden (55°23´N, 12°5´E) which acts as a major migration funnel for autumn migration out of Fennoscandia. Although migration occurs along several other pathways, raptors are thought to be especially well represented at this site (Karlsson 2004). Even if not all sparrowhawks are observed, we here suppose that the annual totals at Falsterbo are approximately proportional to the numbers migrating out of Sweden. Here the peak migration of juvenile sparrowhawks occurs in September, and the adults in October. Juveniles comprise the largest demographic group of recorded migrants (Kjellén 1992). The official survey switched observer in 2001, along with some adjusted methodology. To account for possible effects on the time series from this, we modelled the effect of the observer shift in 2001 using a generalized additive model (GAM) to test and correct for any disruption in the counts before and after the switch (Supplementary Material S1, Fig. S1).

The annual winter censuses were part of the organized annual Swedish bird census monitoring scheme (Green & Lindström 2014). The survey was conducted by amateur ornithologists from 1975 to 2016 based on 248–644 point census routes per winter. Every route is observer-chosen and has 20 evenly spread points, each of which is surveyed for 5 minutes. The route is repeated annually whenever possible. The minimum separation between the points was 300 meters in dense forests and 300–400 meters in open landscapes. We used published annual winter abundance indexes from Green & Lindström (2014), which are based on the statistical software TRIM (Pannekoek & van Strien 2005).

2.3.2. Winter abundance of resident prey species

To assess the annual variation in the winter prey abundance for sparrowhawks, we calculated the annual weighted averages of the winter population abundances of the 10 most central prey species for sparrowhawks. The scaled population indices of each species were weighted with the average number of birds observed annually, before averaging. Finally, the annual prey indices ('Win.prey') were scaled by dividing the result by the average over all years, so that the mean of the resulting index is one (Supplementary Material Table S2).

2.3.3. Population structure and latitudinal distribution of wintering individuals

We analysed winter observations of sparrowhawks in Sweden during 1975–2016, extracted from the portal (www.artportalen.se). We extracted observations spanning from day-of-year 305 in late autumn to day 91 the following spring (in non-leap years: November 1 – April 1). This period should fairly well avoid the arrival of spring migrants. Each winter season was named after the year starting in January. We described the day of winter ('Dow') where January 1 is day 1 and the previous year's days get smaller values than that (*e.g.* December 31 is day 0, December 30 is day –1, and so on).

We only included observations where the sex had been determined and reported—reducing the risk of including lower-quality observations. Citizen science data may contain high levels of noise, reflecting both the observer's skills and reporting behaviour, but this subset likely provided at least a notable reduction in the most obvious sources of bias. There is a difference in the difficulty of aging males and females in the field, and the age of females was less frequently determined compared to males in the data (X^2-test: $X^2 = 156.13$, $df = 2$, $P < 0.001$). This is expected, as the adult female plumage is closer to juveniles compared to that of males. The total sample size with known sex was 17,180, dropping to 5,578 when adding the criteria of known age (2 levels: 1 cy and adult) (Table 1).

Another potential confusion is between female sparrowhawks and male goshawks (*Accipiter gentilis*), although the goshawk is approximately twice the weight. Occasional misidentifications would likely add to the number of sparrowhawk females in our data. We assume that long-term changes in the average identification skill/ability of the observers are merely reflected in the sample size, and that the criteria or threshold for identifying the age or sex (or species) have remained constant, and will therefore mainly be reflected in the estimated average (intercept).

2.4. Statistical analyses

All the statistical analyses were conducted in R version 3.5.1 (R Core Team 2018). For fitting GAMs we used packages 'mgcv' (Wood 2017) and 'gamm4' (Wood & Scheipl 2020).

Table 1. Brief explanations of the variables used in this study. The information listed includes the type of variable, the range of values (or factor levels), and usage of the variables in the analysis. Zero-centred variables have been preprocessed by subtracting the average from each observation, so that the new mean is zero.

Variable name	Explanation	Type	Range (unscaled)
Population level analysis			
Migration	Migration count at Falsterbo	numeric	8.32–10.72
Win.pop	Population index winter	numeric	0.33–1.67
ln.MRR	ln(Migration / Win.pop)	numeric (response)	(–2.16)–1.16
Win.prey	Abundance sum of 10 prey species	numeric	0.43–3.99
Temp.c	Zero-centered temperature Oct & Nov	numeric	(–3.34)–3.32
Year.c	Zero-centered year, for temporal trend	numeric	(–20.5)–20.50
Sex and age ratios of residents			
is.male	Individual sex (1 = male, 0 = female)	binary (response)	1 or 0
is.adult	Individual age (1 = older, 0 = first year)	binary (response)	1 or 0
Lat	Latitude of the observation	numeric (response)	55.34–68.36
Dow	Day of the winter centralized on 1.jan	numeric	(–60)–90
Year.f	Year (factor), for annual variation	factor, 39 levels	"1975"–"2013"
ln.MRR.c	Zero-centred ln migrant to resident ratio	numeric	(–2.07)–1.24
Year.c	Zero-centred year, for temporal trend	numeric	(–31.99)–6.01

2.4.1. The ratio of migrants to residents (MRR)

We studied annual variation in migratoriness, by examining the ratio of observed migrants to wintering individuals. To do so, we apply a multiple regression model with the natural logarithm of the migrant to wintering ratio (‘ln.MRR’), denoted as ln(‘Migration’/‘Win.pop’), as the response variable. As the explanatory variables we applied the three zero-centred variables ‘Year.c’, ‘Temp.c’ and ‘Win.prey.c’ (Table 1), to accommodate the long-term trend over 40 years, the effects of late-autumn temperature, and annual index of winter prey availability, respectively. Notice that this approach detects any effects on the number of migrating or wintering individuals, or both simultaneously. To further explore whether the observed results were driven by the migration data, wintering data, or the contribution of both, we also fitted the model to the natural logarithms of ‘Migration’ and ‘Win.pop’ only.

2.4.2. Sex ratio, age ratio and latitude of resident observations

We applied model selection using the Akaike Information Criterion creating sets of generalized additive models (GAM) for studying the 1) sex ratio 2) age ratio and 3) reported latitude (Supplementary Material Table S3). For sex and age (cases 1–2) we apply a logit link function and a binomial error distribution, while for latitude (case 3) we use an identity link and normal error distribution.

For each hypothesis, we set up three groups of model complexity concerning the explanatory variables; a) zero-models with no covariates, b) the covariate ‘Year.c’ coding for a temporal trend, and c) the covariate ‘ln.MRR.c’ which in this case represents the log of the annual migrant to resident ratio. As the ‘Year.c’ and ‘ln.MRR.c’ showed a high positive correlation ($r = 0.7$), these could not co-occur in the same model, but were regarded as alternative explanations in competing models. However, as ‘Year.c’ effectively represents a straight line, we expected the model with ‘ln.MRR.c’ to show a superior negative likelihood for ‘ln.MRR.c’ to be an informative parameter *sensu* Arnold (2010). In all models, we modelled within-seasonal patterns by fitting ‘Dow’ (continuous variable indicating date of the winter season) with a smoothing function, using the default options of the ‘gam’ function in the ‘mgcv’ package (thin-plate spline as smoothing basis, max. $df = 9$). There are two main reasons for doing this; 1) it makes the definition of start and end of the wintering season less critical and 2) helps to safeguard against the pitfalls of the possible biased citizen science data.

Our logic is that if, for instance, adult males are truly more common during the winter, we would likely see a changing sex- and age-ratio with a mid-winter peak. In all models, we included year as a the factor variable of year ‘Year.f’ as a random effect that captures the unexplained of annual variation. The binary variable ‘is.male’ was identified as ‘false’ = female and ‘true’ = male (Table 1) and we assume a 1:1 sex ratio in the population, but acknowledge that we do not know the actual sex ratio. However, an equal sex ratio has been reported for broods (*e.g.* Risch & Brinkhof 2002). We grouped the age of the individuals into the variable ‘is.adult’ with the two categories ‘false’ (*i.e.* juveniles: 1 cy or 2 cy after new year) and ‘true’ (*i.e.* adults: 2 cy before new year, or older than 2 cy) (Table 1). While we applied the results from package ‘mgcv’ for model selection, we re-run the best models of each hypothesis using the ‘gamm4’ package to obtain the estimated standard deviations of the random effect. Also other effects presented and illustrated in figures are based on the refitted best models.

3. Results

3.1. The migrant-to-resident ratio

The migrant-to-resident ratio showed a positive annual relationship with autumn temperature (estimate: 0.065, $SE = 0.031$, $t = 2.10$, $P = 0.042$) and a negative relationship with the annual abundance of the most relevant prey species (estimate: –0.205, $SE = 0.083$, $t = –2.45$, $P = 0.019$). Further, there was a positive partial trend in the migrant-to-resident ratio across the study period (estimate: 0.054, SE = 0.004, t = 13.77, P < 0.001; Fig. 1).

3.2. Population structure and latitudinal distribution of wintering individuals

3.2.1. Sex ratio

The sex ratio was on average male-biased with a 59% proportion of males (logit-scale intercept estimate = 0.376, SE = 0.050, z = 7.68, P < 0.001). The best model included the covariate ‘Year.c’ (Supplementary Material Table S3), which showed a trend in time toward more males among the residents (logit-scale annual change estimate = 0.011, SE = 0.004, z = 3.07, P = 0.002) (Table 2). There was also a pattern within a typical winter, with an increase in the number of males towards new year, dropping towards more females in the spring (Fig. 2a). The model connecting sex ratio to MRR (study part 1) was not supported.

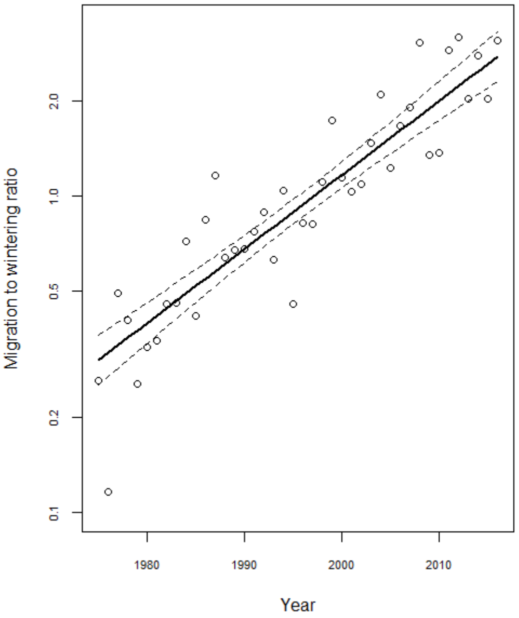

Fig. 1. Long-term trend in the annual migrating to wintering ratio of the Eurasian Sparrowhawk (*Accipiter nisus*). The illustrated regression line and its 95% confidence interval (enclosed by dashed lines), represent the partial effect of (centralized) year from a log-linear multiple regression model. The Y-axis is represented on log-scale.

Table 2. The estimated fixed effects coefficients from the best candidate models for sex, age and latitude, and the standard deviations (SD) of the annual random effects. The within-year smoothing functions of these models were all statistically significant and are presented in Fig. 2. “s” before parenthesis denotes a smoothing function.

Variable	Estimate	SE	z or t	n	P
Sex, model 1					
Intercept	0.376	0.05	7.68	17152	<0.001
Year.c	0.011	0.004	3.07	17152	0.002
s(Dow)	0.025	0.073	0.34	17152	0.733
Rnd SD (Year.f)	0.177	–	–	17152	–
Age, model 0					
Intercept	1.729	0.06	29	5597	<0.001
s(Dow)	0.164	0.037	4.42	5597	<0.001
Rnd SD (Year.f)	0.175	–	–	5597	–
Latitude, model 3					
Intercept	58.85	0.056	1041.8	17152	<0.001
SexMale	0.162	0.033	4.93	17152	<0.001
s(Dow)	–0.21	0.217	–0.97	17152	<0.001
Rnd SD (Year.f)	0.262	–	–	–	–

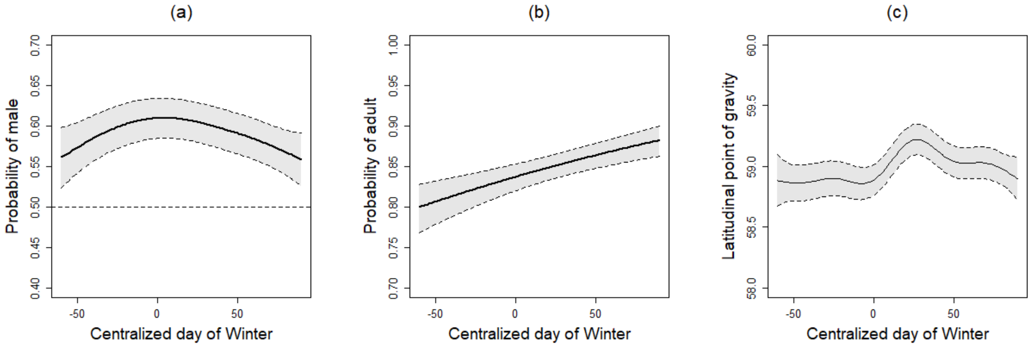

Fig. 2. Within-season effects in sex ratio, age ratio and latitudinal location of overwintering Eurasian Sparrowhawks (*Accipiter nisus*) in Sweden during 1975–2016 (all presented smoothing functions are statistically significant). (a) Males dominated the winter population of residents (horizontal line marks equal probability of male and female) and the probability of a resident being male peaked around new year (December 31 is day 0), while (b) the probability of being adult increased throughout the winter season. (c) The average latitude of males peaked after New Year and gradually became more southerly towards spring. These results are compared to the presented hypotheses of early arrival, body size and competitive release (*i.e.* dominance).

3.2.2. Age ratio

On average 85% of the reported overwintering sparrowhawks were adults (logit-scale intercept estimate = 1.729, SE = 0.060, z = 29.0, P < 0.001). The best candidate model was a model with no covariates included (Supplementary Material Table S3). There was a within-winter seasonal pattern (Table 2), where the age ratio becomes increasingly dominated by adults towards early spring (Fig. 2b). The model connecting age ratio to MRR was not supported.

3.2.3. Latitudinal distribution

The best candidate model was the model with sex included (Supplementary Material Table S3). During winter, males were on average found at higher latitudes compared to females (estimate: 0.162, SE = 0.033, t = 4.93, P < 0.001) (Table 2). Within the winter season, the population weight of residents was found at increasing latitudes, before skewing southward again in early spring (Fig. 2c). The models connecting latitude to MRR were not supported.

4. Discussion

4.1. The migrant-to-resident ratio

Deciding whether to migrate or remain in the breeding areas involves balancing the costs and benefits of each strategy, but the ease with which populations and individuals can switch between these behaviours remains understudied. Additionally, the drivers that regulate this phenotypic variation are not fully understood. On a shorter inter-annual scale, we observed a positive partial effect of late-autumn temperatures on the migrant-to-resident ratio (‘MRR’). This indicates that prevailing temperatures over a small temporal window partly influence the decision to migrate. Moreover, we identified a positive partial trend over the 40-year study period. This response in migration propensity is in a unexpected direction and challenges the hypothesis proposed by Berthold (1996), which suggested that warmer temperatures would reduce the pressure to migrate, thereby lacking a straightforward thermal explanation. Other examples of increased migratoriness include long-term trends in Greenfinches (*Chloris chloris*) in Finland (Meller *et al.* 2016) and Blue Tits (*Cyanistes caeruleus*), in Sweden (Nilsson *et al*. 2006). Berthold’s (1996) hypothesis assumes that all other factors remain relatively unchanged, but this is unlikely over the long term and hence subject to more complex patterns. For example, population trends can lead to density-dependent effects (Kokko & Lundberg 2001, Lundberg 1988), although the sparrowhawk population in Sweden has remained relatively stable during our study period (Green *et al.* 2014). However, in sparrowhawks, the response to annual temperature likely reflects migration intensity alone (Supplementary Material Table S4), suggesting a facultative decision for at least some individuals in early autumn. Yet, the long-term patterns revealed a complementary increase in migrants and a decrease in residents.

In general, food abundance should affect the winter survival of residents and this has earlier been connected with migratoriness in certain terrestrial species (Nilsson *et al.* 2006, Meller *et al.* 2016). We found a connection between annual migratoriness and the winter abundance of key prey species. This correlation reflects annual anomalies since the joint abundance of the 10 selected prey species (Supplementary Materials Table S2) showed no overall temporal trend across 40 years. While sparrowhawks gain from being prey specialists during the breeding season (Otterbeck *et al.* 2015), their dietary niche likely widens and becomes more opportunistic during the winter. The selected prey species may affect the sparrowhawk unequally, and our abundance estimates put more weight on common species, implying that the sparrowhawk responds to wider availability of prey items (in number). The abundance might differ between forest habitats and urban areas—where the latter may facilitate residency (Partecke & Gwinner 2007, Møller *et al.* 2014; but see Deshpande *et al.* 2022). We did not account for such habitat differences, but urban areas may play a particular role during harsh winters and also aggregate prey species around bird feeders (Robb *et al.* 2008a, 2008b; but see Shütz & Schulze 2018).

Recent literature has provided cases both where the resident (Grist *et al.* 2017, Buchan *et al.* 2020) and the migratory fraction of individuals (Zúñiga *et al.* 2017, Acker *et al.* 2021) are suggested to experience a consistent fitness advantage, illustrating how such conditional selection pressures may vary between species, in space and time. There are examples where migratoriness has increased (or even reappeared) in partially migratory species facing marginal environmental conditions. As one, individuals from a resident population of House Finch (*Carpodacus mexicanus*) were relocated to a colder climate, followed by a reappearance of migratoriness within a few generations (Able & Belthoff 1998). Another more naturally occurring example is the northward breeding range shifts of Serin through Europe, eventually creating a pattern of obligate residents in the south, partial migrants in the middle, and obligate migrants in the north (Mayr 1926, Newton 2008). As the climate subsequently warmed in their new northernmost range, many populations switched back to being partially migratory (Bauer & Berthold 1997). Likewise, within Fennoscandia, the European Robin (*Erithacus rubecula*) shows an increasing proportion of migrants from temperate Denmark in the southwest towards the more continental Finland in the northeast, also coinciding with increased migration distances (Newton 2008). The distribution range of sparrowhawk did expand northwards in Sweden within our study period (Ottvall *et al.* 2008) gradually towards harsher climate zones (but within the study area). This is consistent with the general pattern seen among birds in response to climate change (Virkkala & Lehikoinen 2014, Välimäki *et al.* 2016) facilitated by the emergence of areas that were earlier outside of the thermal niche of more southern species. There may still be limits to how well they cope with colder surroundings relative to northern species (Pakanen *et al.* 2016) and thus for year-round residency towards higher latitudes.

Higher latitudes comprise harsher winters and may thus pose a challenge to southern species (*e.g.* Pakanen *et al.* 2016) and affect the overall pressure to migrate (Newton & Dale 1996, Newton 2008, Somveille *et al.* 2013, Ambrosini *et al.* 2016) facilitating increased migratoriness within progressively northern populations. While northerly areas may be suitable for breeding, the winters may entail hostile environmental conditions forcing local breeders to migrate. Northern areas also have fewer urban habitats, which otherwise might to some degree buffer some of the costs of residency during cold, dark and snowy winters. If true, the southern, middle and northern populations may experience opposing selection pressures for migratoriness within larger study areas such as in our study. To validate this as a mechanism, future studies could explore how breeding range shifts affect the average local migratory propensity, ideally across multiple species. Nevertheless, a multi-species approach would likely face the challenge of accounting for a mosaic of species-specific selection pressures which may depend on their morphology, demography, distribution and life history.

The increasing migration numbers at Falsterbo could also partly reflect non-detected long-term population increases (and annual fluctuations) in not only Sweden, but also adjacent areas such as Norway and Finland. However, the reported breeding population in Finland has been suggested to decline (Meller *et al.* 2016) while long-term monitoring lacks from Norway overall. The wintering population in Finland has remained stable compared to the negative Swedish trend in this study, despite that southern Sweden typically provides milder and less continental winter conditions. The opposite trends in migration numbers (increasing) and wintering numbers (decreasing), however, reinforce the result, suggesting that our observed pattern is not solely a result of changes in the breeding population size, nor a methodological artifact in either dataset.

4.2. Demography of migrants and residents

The fitness prospects as a resident or a migrant are likely conditional based on individual capabilities, otherwise the one superior strategy would be fixed in the population (Pulido & Berthold 2010; *cf.* Pulido 2011). In this study, males and adults were over-represented among resident individuals suggesting residency to be a competitive temporal advantage for territory-establishing males in the early spring (Silverin *et al.* 1989, Grayson & Wilbir 2009, Fudickar *et al.* 2013, Lehikoinen *et al.* 2011), while early egg laying increases the clutch size and nestling survival in the species (Otterbeck *et al.* 2019). By studying a species with reversed sexual size dimorphism, we resolved the problem of overlapping predictions from the traits of being male, establishing territory, and having superior body size. Thus, larger body size seems not an overall decisive trait for residency mid-winter (Fudickar *et al.* 2013; but *cf.* Gow & Wiebe 2014, Macdonald *et al.* 2015). It is a relatively common pattern among partial migrants (Newton 2008), including sparrowhawks (Kjéllen 1992), that juveniles are more prone to migrate than adults which implicitly means that it is common to switch between migratory and resident phenotype at least once. During our study period, the proportion of males among the residents also showed a long-term increase, suggesting that the pressure for early arrival has increased over time for males, decreased for females, or possibly both. Early arrival has also gained support in the past, but mainly through studies focussing on intra-specific migration distances in populations where all individuals migrate, *i.e.*, differential migration (*e.g.* Cristol *et al.* 1999, Macdonald *et al.* 2016).

Overwintering may pose an array of challenges and the gain in breeding success needed to outweigh the higher survival costs can be high (Zúñiga *et al.* 2017). While the subsequent fitness gain by early arrival should outweigh the costs of overwintering to be a superior strategy to year-round residency, the inferior-sized male sparrowhawk may face significant challenges posed by winter conditions. However, we did not find support for a model linking the sex ratio to the annual variation in the proportion of migrants, as these changes were better explained by a mere long-term trend. Within a typical winter, the proportion of males peaked around new year, followed by a drop. It is likely that the left side of this curve partly reflects late female migration in early winter while the decreasing male bias during late winter could even reflect unequal mortality between males and females. Another possibility is an early spring migration of females, which we can not rule out affects the patterns. A more likely factor is that resident males are gradually less observed in agricultural and urban areas as they move closer to their forest breeding territories upon spring. The latter also supports the importance of early arrival due to territory establishment.

While we propose that males gain the most from residency, females were present at all latitudes suggesting that some females benefit from residency as their best option. Early in the breeding season, for instance, conspecific competition among females may be strong as the number of resident males with an acquired territory (a central resource for females) is initially scarcer than the number of territories (a central resource for males) (Kokko *et al.* 2006). Another possibility is that the larger-sized females may have relatively low thermal costs by winter temperatures reducing the pressure to migrate, which means that body size may also have an important role for residency among females and should not be disregarded. It remains a possible condition-dependent factor among resident males as well, as having a larger body size (Hegemann *et al.* 2015) or superior condition (Kokko 1999) should improve the survival prospects of overwintering.

It is a common pattern among partial migrants (Newton 2008), including sparrowhawks (Kjéllen 1992), that juveniles are more prone to migrate than adults, which implicitly means that it is common to switch between migratory and resident phenotype at least once. The resident fraction of sparrowhawks consisted of more adults than juveniles, which coincides with juveniles dominating during autumn migration at Falsterbo (*e.g.* Kjellén 1992, 2019) in line with the part expectations of age in competitive release theory (*i.e.* juveniles). Yet, juveniles regularly do overwinter, and given the species often breed in the second calendar year, this may benefit territory availability in spring. While there were no long-term trends in the adult/juvenile ratio across the study period, adults became increasingly overrepresented as a typical winter progressed. Harsh winter conditions may particularly affect younger and inexperienced individuals, so this could reflect higher mortality of young compared to adults that overwinter.. However, resident males also fit the pattern among juvenile migrants across Falsterbo, where females are overrepresented among the migrating juveniles; while males show a slight overrepresentation among the smaller fraction of migrating adults (Kjellén 1992). In the neighboring country Finland, which has a more continental climate, adults are even more overrepresented in the autumn migration counts compared to Sweden (Lehikoinen *et al.* 2014).

We found clear latitudinal sex segregation during the winter season (Table 2), with the average latitude of resident males being further north than that of females. The overall (*i.e.* both sexes) latitudinal distribution span gradually shifted northwards as the first part of the winter season progressed, possibly reflecting early and mid-winter avoidance of the environmental conditions prevailing at higher latitudes. It therefore seems plausible that some residents migrate but on small latitudinal scales, combining the better of two worlds, move away from most acute winter conditions while remaining positioned for early spring arrival. This result could also appear if the southernmost individuals migrate (disappear from the country) as the winter proceeds. By not passing any major migratory funnels, however, these movements would seldom be counted by bird observatories such as Falsterbo—the primary data source for studies on bird migration. However, latitudinal patterns could potentially also, at least partly, reflect annual latitudinal patterns in overall observer activity if such exists.

5. Conclusions

We studied partial migration from the viewpoint of the small raptor, the Eurasian Sparrowhawk (*Accipiter nisus*), through two different but interconnected perspectives: 1) how the migrant to resident ratio changed over time, responded to short-term autumn temperatures, and food availability, 2) what underlying individual demographic traits may affect the expression of a migratory or a resident phenotype. There was a strong long-term temporal trend towards increased migratoriness across the study period. The migrant to resident ratio unexpectedly increased with higher late-autumn temperatures, and expectedly decreased with higher winter food abundance. The average winter sex ratio of residents was male-biased, which supports the arrival time hypothesis. The sex ratio also became increasingly male-dominated across the study period. However, the vast majority of the overwintering individuals were adults, which fulfils part assumptions from competitive release hypothesis, but showing no trends. The proportion of adults increased throughout the winter, which may reflect asymmetric mortality. The distribution of males was typically more northerly stretched than females and moved gradually towards higher latitudes as the winter progressed. This suggests some form of small-scale migration among individuals typically considered residents. We present a picture of migration being a conditional strategy among partial migrants while small-scale migratory patterns also occur adaptively among residents.

Osittain muuttavan varpushaukan (*Accipiter nisus*) muuttoalttius ja paikalle jäävän osuuden koirasvoittoisuus kasvavat Ruotsissa

Osittaismuuttajien populaatiot koostuvat sekä muuttavista että paikallisista yksilöistä. Muuttavat ja paikalliset kohtaavat talviaikaan erilaisia ekologisia olosuhteita, ja niiden muuttopäätökseen vaikuttavat taustatekijät ovat edelleen kiistanalaisia sekä populaation että yksilön näkökulmasta. Tässä tutkimuksessa tarkastelimme varpushaukan muuttoliikehdintää kahdesta eri, mutta toisiinsa kytkeytyvästä näkökulmasta: 1) selvitimme muttoalttiudessa (muuttajien määrissä suhteessa paikallisten määriin) esiintyviä trendejä ja vaihtelua populaatiotasolla ja 2) tarkastelimme, onko ikä ja sukupuoli yhteydessä yksilön alttiuteen muuttaa tai talvehtia. Aineistona käytimme kansalaishavaintoaineistoa neljän vuosikymmenen ajalta, jonka avulla analysoimme talvehtivien varpushaukkojen ikä- ja sukupuolijakauman ajallista ja alueellista vaihtelua Ruotsissa.

Havaitsimme odotustemme vastaisesti, että vuosittainen muuttoalttius kasvoi ajan myötä ja oli suurempi mitä lämpimämpi syksy oli kyseessä. Lisäksi muuttavien varpushaukkojen osuus kasvoi, kun talvisen saaliseläinten määrä oli pienempi. Keskimääräinen talven sukupuolijakauma oli koiraspainotteinen, ja tämä vinouma kasvoi vuosien varrella. Esitämmekin, että talvehtiminen hyödyttää reviirejä hakevia koiraita, sillä aikainen läsnäolo antaa kilpailuedun korkealaatuisten reviirien hankinnassa. Lisäksi Ruotsissa talvehtivien yksilöiden levinneisyys (sukupuolesta riippumatta) siirtyi asteittain pohjoisemmaksi talven edetessä, mikä viittaa pienimuotoiseen muuttoliikkeeseen paikallisen populaation keskuudessa. Nämä tulokset tarjoavat uusia näkökulmia osittaismuuton taustatekijöihin ja säätelyyn.

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References

Able, K.P. & Belthoff, J.R. 1998: Rapid 'evolution' of migratory behaviour in the introduced house finch of eastern North America. — Proceedings of the Royal Society of London B: Biological Sciences 265: 2063–2071. https://doi.org/10.1098/rspb.1998.0541

Acker, P., Daunt, F., Wanless, S., Burthe, S.J., Newell, M.A., Harris, M.P., Grist, H., Sturgeon, J., Swann, R.L., Gunn, C., Payo-Payo, A. & Reid, J.M. 2021: Strong survival selection on seasonal migration versus residence induced by extreme climatic events. — Journal of Animal Ecology 90: 796–808. https://doi.org/10.1111/1365-2656.13410

Ambrosini, R., Cuervo, J.J., du Feu, C., Fiedler, W., Musitelli, F., Rubolini, D., Sicurella, B., Spina, F., Saino, N. & Møller, A.P. 2016: Migratory connectivity and effects of winter temperatures on migratory behaviour of the European robin Erithacus rubecula: a continent–wide analysis. — Journal of Animal Ecology 85: 749–760. https://doi.org/10.1111/1365-2656.12497

Arnold, T.W. 2010: Uninformative Parameters and Model Selection Using Akaike's Information Criterion. — The Journal of Wildlife Management 74: 1175–1178. https://doi.org/10.1111/j.1937-2817.2010.tb01236.x

Bauer, H.G. & Berthold, P. 1997: Die Brutvogel Mitteleuropas. Bestand und Gefährdung. — Aula-Verlag, Wiesbaden. (In German)

Belthoff, J.R. & Gauthreaux, S.A. 1991: Partial Migration and Differential Winter Distribution of House Finches in the Eastern United States. — The Condor 93: 374–382. https://doi.org/10.2307/1368953

Berthold, P. 1988: Evolutionary aspects of migratory behavior in European warblers. — Journal of Evolutionary Biology 1: 195–209. https://doi.org/10.1046/j.1420-9101.1998.1030195.x

Berthold, P. 1996: Control of Bird Migration. — The Auk 114(3): 534–535. https://doi.org/10.2307/4089262

Berthold, P. 1999. A comprehensive theory for the evolution, control and adaptability of avian migration. — Ostrich

70: 1–11. https://doi.org/10.1080/00306525.1999.9639744

Berthold, P. 2001: Bird migration: a general survey. — Oxford University Press, Oxford

Berthold, P. & Querner, U. 1982: Genetic basis of moult, wing length, and body weight in a migratory bird species, *Sylvia atricapilla*. — Experientia 38: 801–802. https://doi.org/10.1007/BF01972279

Biebach, H. 1983: Genetic determination of partial migration in the European Robin (*Erithacus rubecula*). — The Auk 100: 601–606. https://doi.org/10.1093/auk/100.3.601

Boyle, W.A., Norris, D. R. & Guglielmo, C. G. 2010: Storms drive altitudinal migration in a tropical bird. — Proceedings of the Royal Society of London B: Biological Sciences 277: 2511–2519. https://doi.org/10.1098/rspb.2010.0344

Buchan, C., Gilroy, J.J., Catry, I. & Franco, A.M.A. 2020: Fitness consequences of different migratory strategies in partially migratory populations: a multi-taxa meta-analysis. — Journal of Animal Ecology 89: 678–690. https://doi.org/10.1111/1365-2656.13155

Chapman, B.B., Brönmark, C., Nillson, J.Å. & Hansson, L.A. 2011: The ecology and evolution of partial migration. — Oikos 120: 1764–1775. https://doi.org/10.1111/j.1600-0706.2011.20131.x

Cristol, D.A., Baker, M.B & Carbone, C. 1999: Differential Migration Revisited. — In Current Ornithology vol 15 (ed. Nolan, V., Ketterson, E.D. & Thompson, C.F.). Springer, Boston, MA. https://doi.org/10.1007/978-1-4757-4901-4_2

Daan, S., Masman, D. & Groenewold, A. 1990: Avian basal metabolic rates: their association with body composition and energy expenditure in nature. — The American Journal of Physiology 259: 333–340. https://doi.org/10.1152/ajpregu.1990.259.2.r333

Deshpande, P., Lehikoinen, P., Thorogood, R. & Lehikoinen, A. 2022: Snow depth drives habitat selection by overwintering birds in built-up areas, farmlands and forests. — Journal of Biogeography 49: 630–639. https://doi.org/10.1111/jbi.14326

de Zoeten, T. & Pulido, F. 2020: How migratory populations become resident. — Proceedings of the Royal Society of London B: Biological Sciences B 287: 20193011. https://doi.org/10.1098/rspb.2019.3011

Dunning Jr., J.B. (ed) 2008: CRC handbook of avian body masses. — CRC press, London. https://doi.org/10.1201/9781420064452

Fudickar, A.M., Schmidt, A., Hau, M., Quetting, M. & Partecke, J. 2013: Female-biased obligate strategies in a partially migratory population. — Journal of Animal Ecology 82: 863–871. https://doi.org/10.1111/1365-2656.12052

Gauthreaux, S.A. 1982: The ecology and evolution of avian migration systems. — Avian Biology 6: 93–168.

Gow, E.A. & Wiebe, K.L. 2014: Males migrate farther than females in a differential migrant: an examination of the fasting endurance hypothesis. — Royal Society Open Science 1: 140346. https://doi.org/10.1098/rsos.140346

Grayson, K.L. & Wilbur, H.M. 2009: Sex- and context-dependent migration in a pond-breeding amphibian. — Ecology 90: 306–311.

Green, M. & Lindström, Å. 2014: Övervakning av fåglarnas populationsutveckling. Årsrapport för 2013. — Institute of Biology, University of Lund. (In Swedish)

Grist, H., Daunt, F., Wanless, S., Burthe, S.J., Newell, M.A., Harris, M.P. & Reid, J.M. 2017: Reproductive performance of resident and migrant males, females and pairs in a partially migratory bird. — Journal of Animal Ecology 86: 1010–1021. https://doi.org/10.1111/1365-2656.12691

Hegemann, A., Marra, P.P. & Tieleman, B.I. 2015: Causes and consequences of partial migration in a passerine bird. — The American Naturalist 186: 531–546. https://doi.org/10.1086/682667

Karlsson, L. 2004: Wings over Falsterbo. — Falsterbo Bird Observatory, Falsterbo.

Ketterson, E.D. & Nolan Jr, V. 1976: Geographic variation and its climatic correlates in the sex ratio of eastern–wintering Dark–eyed Juncos (*Junco hyemalis hyemalis*). — Ecology 57: 679–693. https://doi.org/10.2307/1936182

Kjellén, N. 1992: Differential timing of autumn migration between sex and age groups in raptors at Falsterbo, Sweden. — Ornis Scandinavica 23: 420–434. https://doi.org/10.2307/3676673

Kjellén, N. 2019: Migration counts at Falsterbo, Sweden. — Bird Census News 32: 27–37. Retrieved from https://www.ebcc.info/wp-content/uploads/2020/06/4-kjellen-32-1-2.pdf

Kokko, H. 1999: Competition for early arrival in migratory birds. — Journal of Animal Ecology 68: 940–950. https://doi.org/10.1046/j.1365-2656.1999.00343.x

Kokko, H. & Lundberg, P. 2001: Dispersal, migration, and offspring retention in saturated habitats. — The American Naturalist 157: 188–202. http://dx.doi.org/10.1086/318632

Kokko, H., Gunnarson, T.G., Morrell, L.J. & Gill, J.A. 2006: Why do female migratory birds arrive later than males? — Journal of Animal Ecology 75: 1293–1303. https://doi.org/10.1111/j.1365-2656.2006.01151.x

Lack, D. 1943: The problem of partial migration. — British Birds 37: 122–130.

Lack, D. 1944: The problem of partial migration. — British Birds 37: 143–150.

Lehikoinen, A. 2011: Advanced autumn migration of sparrowhawk has increased the Predation risk of long-distance migrants in Finland. — PLoS ONE 6: e20001. https://doi.org/10.1371/journal.pone.0020001

Lehikoinen, A., Hokkanen, T. & Lokki, H. 2011: Young and female-biased irruptions in pygmy owls *Glaucidium passerinum* in southern Finland. — Journal of Avian Biology 42: 564–569. https://doi.org/10.1111/j.1600-048X.2011.05461.x

Lehikoinen, A., Ekroos, J., Piha, M., Seimola, T., Tirri, I.S, Velmala, W. & Vähätalo, A. 2014: Muuton ajoittuminen eri ikäluokilla ja sukupuolilla Hangon lintuasemalla rengastuksen perusteella: Osa 1: syksyiset ei-varpuslinnut. — Tringa 41: 30–53. (In Finnish with English summary)

Lehikoinen, A., Lindén, A., Karlsson, M., Andersson, A., Crewe, T.L., Dunn, ... & Tjørnløv, R. S. 2019: Phenology of the avian spring migratory passage in Europe and North America: asymmetric advancement in time and increase in duration. — Ecological Indicators 101: 985–991. https://doi.org/10.1016/j.ecolind.2019.01.083

Lindén, A., Lehikoinen, A., Hokkanen, T. & Väisänen, R.A. 2011: Modelling irruptions and population dynamics of the great spotted woodpecker–joint effects of density and cone crops. — Oikos 120: 1065–1075. http://dx.doi.org/10.1111/j.1600-0706.2010.18970.x

Lundberg, P. 1985: Dominance behaviour, body weight and fat variations, and partial migration in European blackbirds *Turdus merula*. — Behavioral Ecology and Sociobiology 17: 185–189. https://doi.org/10.1007/BF00299250

Lundberg, P. 1988: The evolution of partial migration in birds. — Trends in Ecology & Evolution 3: 172–175. https://doi.org/10.1016/0169-5347(88)90035-3

Lundblad, C.G. & Conway, C.J. 2020: Testing four hypotheses to explain partial migration: balancing reproductive benefits with limits to fasting endurance. — Behavioral Ecology and Sociobiology 74: 1–16. https://doi.org/10.1007/s00265-019-2796-3

Macdonald, C.A., McKinnon, E.A., Gilchrist, H.G. & Love, O.P. 2016: Cold-tolerance, and not earlier arrival on breeding grounds, explains why males winter further north in an Arctic-breeding songbird. — Journal of Avian Biology 47: 7–15. https://doi.org/10.1111/jav.00689

Main, I. G. 2002: Seasonal movements of Fennoscandian Blackbirds *Turdus merula*. — Ringing & Migration 21: 65–74.

Mayr, E. 1926: Die ausbreitung des Girlitz (*Serinus canaria serinus L.*). — Journal für Ornithologie 74: 571–671. (In German)

Meller, K., Vähätalo, A.V., Hokkanen, T., Rintala, J., Piha, M. & Lehikoinen, A. 2016: Interannual variation and long–term trends in proportions of resident individuals in partially migratory birds. — Journal of Animal Ecology 85: 570–580. https://doi.org/10.1111/1365-2656.12486

Møller, A.P., Jokimäki, J., Skorka, P. & Tryjanowski, P. 2014: Loss of migration and urbanization in birds: a case study of the blackbird (*Turdus merula*). — Oecologia 174: 1019–1027. https://doi.org/10.1007/s00442-014-2953-3

Newton, I. 1986: The Sparrowhawk. — T & Poyser, Calton.

Newton, I. 2008: The migration ecology of birds. — Academic Press, Elsevier, London.

Newton, I. & Dale, L. 1996: Relationship between migration and latitude among west European birds. — Journal of Animal Ecology 65: 137–146. https://doi.org/10.2307/5716

Nilsson, A.L., Lindstroem, A., Jonzén, N., Nilsson, S.G. & Karlsson, L. 2006: The effect of climate change on partial migration–the blue tit paradox. — Global Change Biology 12: 2014–2022. https://doi.org/10.1111/j.1365-2486.2006.01237.x

Otterbeck, A., Lindén, A. & Roualet, É. 2015: Advantage of specialism: reproductive output is related to prey choice in a small raptor. — Oecologia 179: 129–137. http://dx.doi.org/10.1007/s00442-015-3320-8

Otterbeck, A., Selås, V., Nielsen, J. T., Roualét, E. & Lindén, A. 2019: The paradox of nest reuse: early breeding benefits reproduction, but nest reuse increases nest predation risk. — Oecologia 190: 559–568. https://doi.org/10.1007/s00442-019-04436-7

Ottvall, R., Edenius, L., Elmberg, J., Engström, H., Green, M., Holmqvist, N., Lindström, Å., Tjernberg, M. & Pärt, T. 2008: Populationstrender för fågelarter som häckar i Sverige. Report 5813. — Naturvårdsverket, Stockholm. (In Swedish)

Pakanen, V.M., Ahonen, E., Hohtola, E. & Rytkönen, S. 2018: Northward expanding resident species benefit from warming winters through increased foraging rates and predator vigilance. — Oecologia 188: 991–999. https://doi.org/10.1007/s00442-018-4271-7

Pannekoek, J. & Van Strien, A. 2005: TRIM 3 manual (Trends &indices for monitoring data). — JM Voorburg, Statistics Netherlands, The Netherlands.

Partecke, J. & Gwinner, E. 2007: Increased sedentariness in European Blackbird following urbanization: a consequence of local adaptation? — Ecology 88: 882–890. https://doi.org/10.1890/06-1105

Pulido, F. 2011: Evolutionary genetics of partial migration – the threshold model of migration revis(it)ed. — Oikos 120: 1776–1783. https://doi.org/10.1111/j.1600-0706.2011.19844.x

Pulido, F. & Berthold, P. 2010: Current selection for lower migratory activity will drive the evolution of residency in a migratory bird population. — Proceedings of the National Academy of Sciences of the United States of America 107: 7341– 7346. https://doi.org/10.1073/pnas.0910361107

R Core Team 2018: R: A language and environment for statistical computing. — R Foundation for Statistical Computing, Vienna, Austria.

Risch, M. & Brinkhof, M. W. G. 2002: Sex ratios of Sparrowhawk (*Accipiter nisus*) broods: the importance of age in males. — Ornis Fennica 79: 49–59.

Robb, G.N., Mcdonald, R.A., Chamberlain, D.E. & Bearhop, S. 2008a: Food for thought: supplementary feeding as a driver of ecological change in avian populations. — Frontiers in Ecology and the Environment 6: 476–484. http://dx.doi.org/10.1890/060152

Robb, G.N., Mcdonald, R.A., Chamberlain, D.E., Reynolds, S.J., Harrison, T.J. & Bearhop, S. 2008b: Winter feeding of birds increases productivity in the subsequent breeding season. — Biology Letters 4: 220–223. https://doi.org/10.1098/rsbl.2007.0622

Rubolini, D., Møller, A.P., Rainio, K. & Lehikoinen, E. 2007: Intraspecific consistency and geographic variability in temporal trends of spring migration phenology among European bird species. — Climate Research 35: 135–146. http://dx.doi.org/10.3354/cr00720

Schütz, C. & Schulze, C.H. 2018: Park size and prey density limit occurrence of Eurasian Sparrowhawks in urban parks during winter. — Avian Research 9: 30. https://doi.org/10.1186/s40657-018-0122-9

Schwabl, H. 1983: Ausprägung und Bedeutung des Teilzugverhaltens einer südwestdeutschen Population der Amsel *Turdus merula*. — Journal für Ornithologie 124: 101–116. (In German)

Silverin, B., Viebke, P.A. & Westin, J. 1989: Hormonal correlates of migration and territorial behavior in juvenile willow tits during autumn. — General and Comparative Endocrinology 75(1): 148–156. https://doi.org/10.1016/0016-6480(89)90020-8

Smith, H.G. & Nilsson, J.Å. 1987: Intraspecific variation in migratory pattern of a partial migrant, the blue tit (*Parus caeruleus*): an evaluation of different hypotheses. — The Auk 104: 109–115. https://doi.org/10.2307/4087239

Somveille, M., Manica, A., Butchart, S.H.M. & Rodrigues, A.S.L. 2013: Mapping global diversity patterns for migratory birds. — PLoS ONE 8: e70907. https://doi.org/10.1371/journal.pone.0070907

Terrill, S.B. & Able, K.P. 1988: Bird Migration Terminology. — The Auk 105: 205–206. https://doi.org/10.1093/auk/105.1.205

Usui, T., Butchart, S.H.M. & Phillimore, A.B. 2017: Temporal shifts and temperature sensitivity of avian spring migratory phenology: a phylogenetic meta-analysis. — Journal of Avian Ecology 86: 250–261. https://doi.org/10.1111/1365-2656.12612

Van Vliet, J., Musters, C.J.M. & Ter Keurs, W.J. 2009: Changes in migration behaviour of Blackbirds *Turdus merula* from the Netherlands. — Bird Study 56: 276–281. https://doi.org/10.1080/00063650902792148

Välimäki, K., Lindén, A. & Lehikoinen, A. 2016: Velocity of density shifts in Finnish land bird species depends on their migration ecology and body mass. — Oecologia 181: 313–321. https://doi.org/10.1007/s00442-015-3525-x

Visser, M.E. & Gienapp, P. 2019: Evolutionary and demographic consequences of phenological mismatches. — Nature Ecology & Evolution 3: 879–885. https://doi.org/10.1038/s41559-019-0880-8

Virkkala, R. & Lehikoinen, A. 2014: North by north-west: climate change and directions of density shifts in birds. — Global Change Biology 22: 1121–1129. https://doi.org/10.1111/gcb.13150

Wood, S.N. 2017: Generalized Additive Models: An Introduction with R (2nd edition). — Chapman and Hall/CRC, New York. https://doi.org/10.1201/9781315370279

Wood, S. & Scheipl, F. 2020: gamm4: Generalized Additive Mixed Models using ‘mgcv’ and ‘lme4’. R package version 0.2-6. Accessed at https://CRAN.R-project.org/package=gamm4/

Zúñiga, D., Gager, Y., Kokko, H., Fudickar, A. M., Schmidt, A., Naef-Daenzer, B., Wikelski, M. & Partecke, J. 2017: Migration confers winter survival benefits in a partially migratory songbird. — eLife 6: e28123. https://doi.org/10.7554/eLife.28123

Online supplementary material

Supplementary material available in the online version of the article (https://doi.org/10.51812/of.122172) includes Figure S1 and Tables S1–S4.

Ornis Fennica 101: 131–137. 2024

The selective consumption of European ivy (*Hedera helix*) berries by the Common Blackbird (*Turdus merula*)

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Seed dispersal of plants affects the spatial structure and population dynamics, contributing to ecosystem functioning. Birds are among the most important seed dispersers. Preferences of birds in fruit and berry consumption are potentially significant selective pressures on the evolution of fruit traits that affect plant fitness. European ivy (*Hedera helix*) is a widespread deciduous species in Europe and the Common Blackbird (*Turdus merula*) is important seed disperser. This study investigates blackbird feeding preferences for specific sizes of ivy seeds. Field data was collected in a small settlement east of Simferopol city in Crimea and included a collection of reference seeds gathered from plants and seeds found in bird excretions. The length of the major axis, minor axis, and aspect ratio were measured, and statistical analysis was performed. The length of the major and minor axes of seeds consumed by blackbirds was higher compared with the reference collection, the aspect ratio was the opposite. Evidence of size differences could suggest weak effect of selective consumption of blackbirds on seed shape. This research extends our knowledge of the ecological relationship between frugivorous birds and plants and the role of birds in directional selection in a particular locality.

1. Introduction

Seed dispersal is a vital process in the life cycle of plants because it influences the spatial structure, population dynamics, gene flow, and tree assembly and consequently, contributes substantially to ecosystem functioning (Levin *et al.* 2003, Flörchinger *et al.* 2010, Harrison *et al.* 2013, Hazell *et al.* 2023). Endozoochory is an example of seed dispersion when the diaspores of plants are eaten by animals and the hard seeds or fruit stones pass through the intestinal canal without damage (Smallwood 1984). Birds are the most important seed dispersers among temperate zone animals (Corlett 2017, Hazell *et al.* 2023). The preferences for fruit and berry consumption could exert selective pressure on the evolution of fruit traits, influencing plant fitness and the mutualistic interactions between fleshy-fruited plants and birds (Flörchinger *et al.* 2010, Eriksson 2016, Hazell *et al.* 2023).

European ivy (*Hedera helix*) has a southerly and westerly distribution in Europe from North Africa, with the nearest islands located in Western and South-Western Asia (Metcalfe 2005). Ivy berries are an important source of energy, containing 47% carbohydrates and 32% lipids relative to the dry weight of the pulp and providing just over 5 kcal per gram of dry pulp (Herrera 1987, Hernandez 2005). The Common Blackbird (*Turdus merula*) has a range that covers all of Europe and North Africa with the nearest islands located in Western and South-Western Asia (Collar & Christie 2020). At the end of twenty century, the species spread to the Steppe Zone of the Northern Black Sea region in response to the emergence of artificial plantings (Tsvelykh 2017, Kucherenko & Ivanovskaya 2020). Blackbirds are well known seed feeders (*i.e.* frugivores) (Williams 2006), making them perfect candidates for dispersing different plant species including ivy seeds (Snow & Snow 1988, Metcalfe 2005). Several researchers have reported that most fruit-eating birds consume only a portion of the diversity of fleshy fruits produced in any habitat (Snow 1981, Wheelwright 1985, Blendinger *et al.* 2016). Selective feeding of birds is one of the types of bird-plant interactions and play an essential role in the maintenance of biodiversity (Blendinger *et al.* 2012). However, the selection of different fruit traits by birds in different environments is poorly known (Hazel *et al.* 2023).

I hypothesized that if the influence of seed dispersers on a plant persists over a long time, the average seed size of the plant will correspond to the average seed size consumed by the primary dispersers. To unravel this hypothesis I assessed seed size selection by blackbirds at a particular ivy hedge site by comparing the size of seeds consumed by the birds to the average seed size on the trees. This may be important for establishing mutualistic interactions between birds and plants, functional diversity, conservation of endangered plant or bird species at the local level.

2. Material and methods

2.1. Study area

The study area is located in a small settlement east of Simferopol city (45°01'N, 34°11'E) in Crimea (the peninsula in the north of the Black Sea). The vegetation is mainly composed of poplar trees (*Populus alba*), sloe brush (*Prunus spinosa*) and dogrose (*Rosa canina*) growing alongside the small river, surrounded by arable fields and steppe patches. European ivy, which is typically found in mountain-forest landscapes 15–20 km south of the research locality, grows in a hedgerow at the study site. Ivy plants were planted in the study area more than 20 years ago from their natural habitat.

2.2. Data collection

In February, when the ivy berries were ripe and consumed by birds, I collected the seeds (n = 65) that had been eaten with berries and excreted by blackbirds near the hedgerow edges. At the same time, the ivy berries which were on plants were gathered to get reference samples of available seeds. In the tree the ivy berries were arranged into umbels thus to ensure random sampling, I collected all berries from 10 umbels taken from various parts of four plants. The selected berries varied in size, and I removed only the very small and damaged ones. Then I collected the seeds (n = 96) from these berries, assuming that they were medium berries and seeds of the plant. The pulp was removed and the seeds were sampled. Each berry contained one or two seeds.

All seeds were measured to obtain the length of the major axis (Fig. 1, see axis A), the length of the minor axis (Fig. 2, see axis a), and the aspect ratio (the ratio A/a). The seeds were flattened on one side, thus the minor axis was measured at the widest part. All measures were carried out by using a caliper. To determine the species of birds that consume ivy berries, I visually inspected plants and recorded all species visited the plants. According to the previous review, 15 bird species were documented as ivy berries consumers (Metcalfe 2005), thus I found out the phenology of their presence in the study area over the past 6 years.

2.3. Statistical analysis

To determine the normality of data Shapiro-Wilk test was used. To evaluate differences in length and aspect ratio of seeds that were eaten by birds, and seeds sampled in trees, the Mann-Whitney

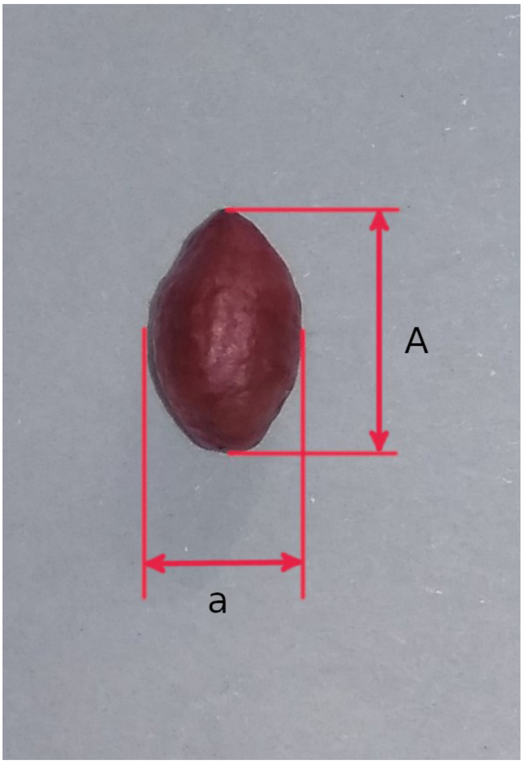

Fig. 1. The seed of European ivy (*Hedera helix*). A – length of major axis, a – length of the minor axis.

test was applied. I used the generalized linear regression model (GLM) with binomial error distribution (Zuur *et al.* 2007, Kabakoff 2014) to obtain the model of the probability of seed consumption by birds as a function of size and shape characteristics.

The predictors were major and minor length and aspect ratio (continuous variables), and the response variable was whether seeds were collected in plants or birds' excretions (categorical variable). The best model was chosen by comparing the full model and the model with removed predictors by computing analysis of variance fitted models (Chambers & Hastie 1992) with ANOVA. If the differences were nonsignificant, the model with the lowest AIC (Akaike information criterion) was chosen (Akaike 1998). All assumptions were checked before GLM was applied.

Statistical analyses were carried out in free open source software R version 4.2.3 (R Core Team 2024). To visualize the differences in the size and shape of consumed seeds and seeds gathered from plants the 'ggplot2' package was used (Wickham 2016). The model result was performed with the 'pROC' package (Robin *et al.* 2011). Model residual diagnostics were carried out with the 'DHARMa' package (Hartig 2022).

3. Results

There are four bird species recorded as ivy berry consumers in the study region: Common Woodpigeon (*Columba palumbus*), European Starling (*Sturnus vulgaris*), Eurasian Blackcap (*Sylvia atricapilla*), and Common Blackbird. The first three species were rare visitors, and only a few cases of berry consumption by them were recorded, while the last species was the main ivy berry consumer. During visual observation, a single bird consumed 1–17 berries per feeding visit, in contrast to starling and blackcap, which consumed 1–4 berries per feeding visit.

Based on the measuring of 65 seeds excreted by blackbirds and 96 reference seeds, significant differences were found between the length of the major axis (Mann-Whitney test, $p<0.001$), length of the minor axis ($p<0.001$), and aspect ratio ($p<0.001$) of seeds, found in bird excretions compared to those collected from plants (Table 1, Fig. 2).

Table 1. Mean (± standard deviation, SD) of maximal length, width, and shape index of European ivy seeds.

	N	Length of major axis (mean ± SD), mm	Length of minor axis (mean ± SD), mm	Aspect ratio (mean ± SD)
Seeds excreted by blackbirds	65	6.32 ± 0.584	4.10 ± 0.342	1.55 ± 0.153
Seeds collected from plants	96	5.69 ± 0.514	3.37 ± 0.425	1.71 ± 0.213

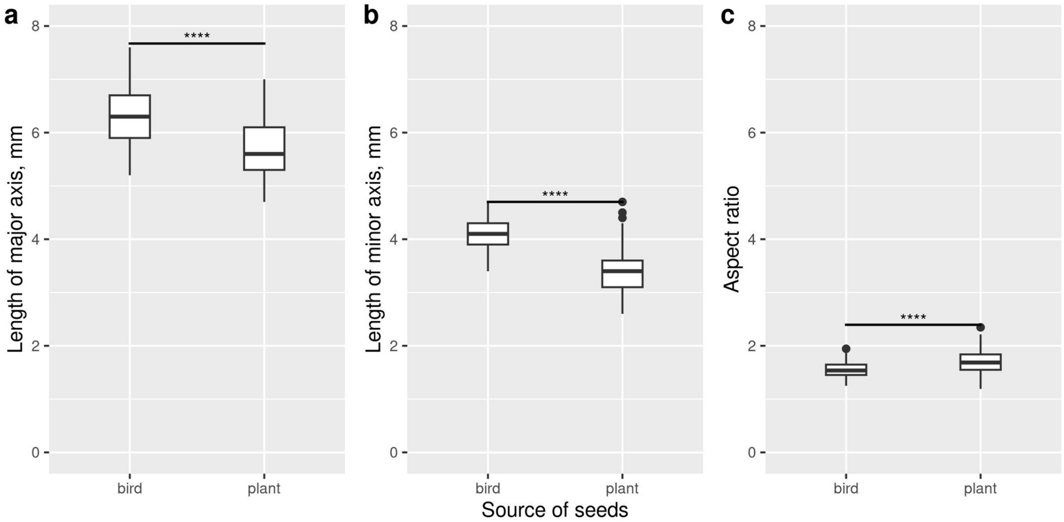

Fig. 2. Box plots representing the differences in length of major axis (a), minor axis (b) and aspect ratio (c) values between seeds found in blackbird excretions (“bird”) and sampled from plants (“plant”). **** – $p < 0.001$.

The GLM results demonstrate that all predictors, except for the length of the minor axis, significantly influence the probability of seeds being consumed by birds (Supplementary Table S1, Supplementary Fig. S1). There was a positive relationship between the length of the major axis and seed consumption, whereas the length of the minor axis had a negative relationship. The model without the length of the minor axis did not differ significantly from the full model but had higher AIC. The model results suggest that blackbirds prefer berries with longer and rounder seeds.

4. Discussion

Previous studies have documented 15 bird species as consumers of ivy berries (Metcalfe 2005), whereas our study recorded only four. Most berries-feeding species are rare (*e.g.* Song Thrush *Turdus philomelos*, Waxwing *Bombycilla garrulus*), or absent (Capercaillie *Tetrao urogallus*) in the study region. Blackcap and Song Thrush are only present in spring, when blackbirds have already consumed most of the berries. Five species—Collared Dove (*Streptopelia decaocto*), Corn Bunting (*Emberiza calandra*), Robin (*Erithacus rubecula*), Fieldfare (*Turdus pilaris*), and Mistle Thrush (*T. viscivorus*)—were relatively abundant in the region to the time ivy are ripening, but I did not record their eating the ivy. It can be assumed that evidence of ivy consumption by other bird species depends on the availability of other food resources and the amount of ivy (Hernandez 2009). Only a few ivy plants grow in the study area, therefore not many birds could have used it.

In earlier research, the number of berries, consumed by blackbirds per feeding visit was 1.3 ± 0.14 (Sorensen 1984), while in this study the observed consumption ranged from 1 to 17 berries per feeding visit. A possible explanation for this result might be fewer disturbance factors in my location compared with Oxford Botanic Garden, where data were collected previously. The crowds of people that are typical of a botanical garden are a strong disturbance factor for birds. The place where my material was collected was sparsely populated and there was little disturbance to the birds. It is well known that some species forage less when people are nearby (Megan 2008).

As mentioned in the literature review, a major challenge in evolutionary ecology is to understand how mutualistic interactions between plants and animals drive the evolution of plant phenotype (Strauss & Irwin 2004, Palacio & Ordano 2018). Although gape width is a known limiting factor for fruit consumption (Wheelwright 1985, Bulgarini & Fraticalli 2023), the size of ivy berries aligns well with the gape size of blackbirds, allowing them to consume these fruits effectively. The current study found predominating long and rounded seeds in blackbirds' excretions compared with the reference seeds. In some plants, a correlation is often observed between berry volume and seed volume (Bulgarini & Fraticelli 2023). Despite this I did not find such information regarding ivy, it is possible that the size of berries eaten by birds was greater than the average size on plants.

One type of behaviour that facilitated selective feeding by tropical birds was based less on choosing fruits with appropriate size than on indiscriminating plucking fruits and being unable to swallow large ones (Wheelwright 1985). In contrast to these observations, data of feeding blackbirds by European Laurel (*Laurus nobilis*) suggests that birds search for berries on specific specimens or carefully select among the available berries on the branches, prioritizing those with rare shapes and sizes for consumption (Bulgarini & Fraticalli 2023). During the observation, there were many berries on the ground under the ivy, but I did not record any instances of small berries being picked or dropped.

The difference in seed size may be result of weak effect of selective consumption of blackbirds on seed shape, or indicate a additional factors whose action is stronger than the action of selection by the blackbirds. It is also possible that in the natural habitat of ivy, a different selective process occurs than the one we have observed. Some authors have emphasized the food specialization of individual birds in natural conditions (Grant 1981, Price 1987, Jung 1992). It is possible, that the preference for feeding by certain berry sizes by the local population of blackbirds differs from the sizes consumed by birds in the natural ivy habitats. From this point of view, future studies should explore seed dispersal in natural ivy populations to compare selection criteria for seed dispersal across different environments.

Mustarastaan (*Turdus merula*) valikoiva muratin (*Hedera helix*) marjojen syönti

Kasvien siementen leviäminen vaikuttaa merkittävästi ympäristön rakenteeseen, kasvipopulaatioiden dynamiikkaan ja ekosysteemien toimintaan. Linnut ovat keskeisiä siementen levittäjiä, ja niiden mieltymykset hedelmien ja marjojen suhteen voivat luoda valintapaineita hedelmien ominaisuuksille, mikä puolestaan vaikuttaa kasvien kelpoisuuteen ja ominaisuuksien evoluutioon.

Euroopan muratti (*Hedera helix*) on laajalle levinnyt kasvilaji Euroopassa, ja mustarastas (*Turdus merula*) toimii sen tärkeänä siementen levittäjänä. Tässä tutkimuksessa tarkasteltiin mustarastaan ravintomieltymyksiä erityisesti muratin siementen kokoon liittyen. Aineisto kerättiin Simferopolin kaupungin itäpuolella Krimillä sijaitsevasta pienestä asutuksesta, ja siihen sisältyi sekä kasveista kerättyjä vertailusiemeniä että lintujen ulosteista löydettyjä siemeniä. Siementen pää- ja sivuakselin pituudet sekä muotosuhteet mitattiin, ja tulokset analysoitiin tilastollisesti.

Tulokset osoittivat, että mustarastaan syömien siementen pää- ja sivuakselin pituudet olivat suurempia kuin vertailusiementen, mutta niiden muotosuhde oli päinvastainen. Havaittujen kokoerojen perusteella voidaan päätellä, että mustarastaan valikoivalla syönnillä on vain vähäinen vaikutus siementen muotoon. Tämä tutkimus syventää ymmärrystä hedelmiä syövien lintujen ja kasvien välisestä ekologisesta vuorovaikutuksesta sekä lintujen roolista kasvien ominaisuuksien evoluutiossa tietyssä ympäristössä.

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References

Akaike, H. 1998: Information theory as an extension of the maximum likelihood principle. — In Selected papers of Hirotugu Akaike (eds. Parzen, E., Tanabe, K. & Kitagawa, G.): 199–213. Springer, New York, USA.

Blendinger, P.G., Ruggera, R.A., Núñez Montellano, M.G., Macchi, L., Zelaya, P.V., Álvarez, M.E., Martín, E., Acosta, O.O., Sánchez, R. & Haedo, J. 2012: Fine-tuning the fruit-tracking hypothesis: spatio-temporal links between fruit availability and fruit consumption by birds in Andean mountain forests. — Journal of Animal Ecology 81: 1298–1310. https://doi.org/10.1111/j.1365-2656.2012.02011.x

Blendinger, P.G., Martin, E., Acosta, O.O., Ruggera, R.A. & Araoz, E. 2016: Fruit selection by Andean forest birds: influence of fruit functional traits and their temporal variation. — Biotropica 48(5): 677–686. https://doi.org/10.1111/btp.12329

Bulgarini, F. & Fraticelli, F. 2023: The European laurel *Laurus nobilis* berries in the diet of the blackbird *Turdus merula*. — Rivista Italiana di Ornitologia – Research in Ornithology 93(2): 23–26. https://doi.org/10.4081/rio.2023.693

Chambers, J.M. & Hastie, T. 1992: Statistical models in S. — Wadsworth & Brooks/Cole Advanced Books & Software, Pacific Grove. 608 p.

Collar, N. & Christie, D.A. 2020: Eurasian Blackbird (*Turdus merula*), version 1.0. — In Birds of the World (eds. del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E.). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.eurbla.01

Corlett, R.T. 2017: Frugivory and seed dispersal by vertebrates in tropical and subtropical Asia: An update. — Global Ecology and Conservation 11: 1–22. https://doi.org/10.1016/j.gecco.2017.04.007

Eriksson, O. 2016: Evolution of angiosperm seed disperser mutualisms: The timing of origins and their consequences for coevolutionary interactions between angiosperms and frugivores. — Biological Reviews 91(1): 168–186. https://doi.org/10.1111/brv.12164

Flörchinger, M., Braun, J., Böhning-Gaese, K. & Schaefer, H.M. 2010: Fruit size, crop mass, and plant height explain differential fruit choice of primates and birds. — Oecologia 164: 151–161. https://doi.org/10.1007/s00442-010-1655-8

Harrison, R.D., Tan, S., Plotkin, J.B., Slik, F., Detto, M., Brenes, T., Itoh, A. & Davies, S.J. 2013: Consequences of defaunation for a tropical tree community. — Ecology Letters 16(5): 687–694. https://doi.org/10.1111/ele.12102

Grant, P.R. 1981: The feeding of Darwin's finches on *Tribus cistoides* (L.) seeds. — Animal Behaviour 29: 785–793.

Hartig, F. 2022: DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. — R package version 0.4.6. Retrieved from https://CRAN.R-project.org/package=DHARMa

Hazell, R.J., Sam, K., Sreekar, R., Yama, S., Koagouw, W., Stewart, A.J.A. & Peck, M.R. 2023: Bird preferences for fruit size, but not color, vary in accordance with fruit traits along a tropical elevational gradient. — Ecology and Evolution 13: e9835. https://doi.org/10.1002/ece3.9835

Hernandez, A. 2005: Blackcaps, *Sylvia atricapilla* and blackbirds, *Turdus merula* feeding their nestlings on fleshy fruits. — Folia Zoologica 54(4): 379–388.

Hernandez, A. 2009: Birds and guelder *Viburum opulus*: selective consumption and dispersal via regurgitation of small-sized fruits and seeds. — Plant Ecology 203: 111–122. https://doi.org/10.1007/s11258-008-9514-y

Herrera, C.M. 1987: Vertebrate-dispersed plants of the Iberian Peninsula: a study of fruit characteristics. — Ecological Monographs 57: 305–331.

Jung, R.E. 1992: Individual variation in fruit choice by American robins (*Turdus migratorius*). — The Auk 109(1): 98–111.

Kabakoff, R.I. 2014: R in Action. Data analysis and graphics with R. — Manning Publications Co., New York. 451 p.

Kucherenko, V.M. & Ivanovskaya, A.V. 2020: Variation in common blackbird, *Turdus merula* (Passeriformes, Turdidae), nest characteristics in urban and suburban localities in Crimea. — Zoodiversity 54(2): 157–162. https://doi.org/10.15407/zoo2020.02.157

Levin, S. A., Muller-L andau, H. C., Nathan, R. & Chave, J. 2003: The ecology and evolution of seed dispersal. — Annual Review of Ecology, Evolution, and Systematics 34(1): 575–604. https://doi.org/10.1146/annurev.ecolsys.34.011802.132428

Megan, P. 2008: The impact of human disturbance on birds: a selective review. — In Too close for comfort: Contentious issues in human-wildlife encounters (eds. Lunney, D., Munn, A. & Meikle, W.): 63–71. Royal Zoological Society of New South Wales. https://doi.org/10.7882/FS.2008.023

Metcalfe, D.J. 2005. *Hedera helix* L. — Journal of Ecology 93: 632–648.

Palacio, F.X & Ordano, M. 2018: The Strength and Drivers of Bird-Mediated Selection on Fruit Crop Size: A Meta-Analysis. — Frontiers in Ecology and Evolution 6: 1–13. https://doi.org/10.3389/fevo.2018.00018

Price, T.D. 1987: Diet variation in a population of Darwin's finches. — Ecology 68: 1015–1028.

R Core Team 2024: R: A Language and Environment for Statistical Computing. — R Foundation for Statistical Computing, Vienna, Austria. Retrieved from https://www.R-project.org/

Robin, X., Turck, N., Hainard, A., Tiberti, N., Lisacek, F., Sanchez, J.-C. & Müller M. 2011: pROC: an open-source package for R and S+ to analyze and compare ROC curves. — BMC Bioinformatics 12: 77. https://doi.org/10.1186/1471-2105-12-77

Snow, D.W. 1981: Tropical frugivorous birds and their food plants: a world survey. — Biotropica 13: 1–14.

Snow, B.K. & Snow, D.W. 1988: Birds and Berries: a study of an ecological interaction. — Poyser, Calton, England. 268 p.

Sorensen, A.E. 1984: Nutrition, energy and passage time: experiments with fruit preference in European blackbirds (*Turdus merula*). — Journal of Animal Ecology 53: 545–557.

Smallwood, J. 1984: Ecology of seed dispersal. — Annual

Review of Ecology, Evolution, and Systematics 13: 201–228.

Strauss, S.Y. & Irwin, R.E. 2004: Ecological and evolutionary consequences of multispecies plant-animal interactions. — Annual Review of Ecology, Evolution, and Systematics 35: 435–466. https://doi.org/10.1146/annurev.ecolsys.35.112202.130215

Tsvelykh, A.N. 2017: The expansion of the Blackbird, *Turdus merula* (Passeriformes, Muscicapidae), in the Steppe Zone of Ukraine. — Vestnik Zoologii 51(5): 413–420. https://doi.org/10.1515/vzoo-2017-0049

Wheelwright, N.T. 1985: Fruit size, gape width, and the diets of fruit-eating birds. — Ecology 66(3): 808–818.

Wickham, H. 2016: ggplot2: Elegant Graphics for Data Analysis. — Springer-Verlag, New York. ISBN 978-3-319-24277-4. Retrieved from https://ggplot2.tidyverse.org

Williams, P.A. 2006: The role of blackbirds (*Turdus merula*) in weed invasion in New Zealand. — New Zealand Journal of Ecology 30(2): 285–291.

Zuur, A.F., Leno, E.N. & Smith, G.M. 2007: Analysing Ecological Data. — Springer, USA.

Online supplementary material

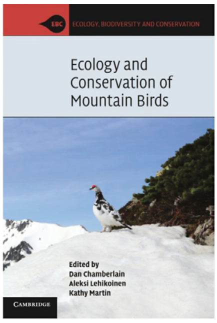
Supplementary material available in the online version of the article (https://doi.org/10.51812/of.148001) includes Figure S1 and Table S1.

Ornis Fennica 101: 138–139. 2024

Book review

A helpful and long-overdue resource for work with mountain birds

Chamberlain, D., Lehikoinen, A. & Martin, K. (eds.): Ecology and conservation of mountain birds. Cambridge University Press. 2023. 450 pp. https://doi.org/10.1017/9781108938570



As an early-career researcher working in ptarmigan conservation, being asked to review a new textbook relevant to my investigations was a welcome opportunity that paid dividends. The newly published *Ecology and Conservation of Mountain Birds* compiled by Dan Chamberlain, Aleksi Lehikoinen, and Kathy Martin, brings together the collective skill and experience of over 50 subject experts to give a clear roadmap for the future of alpine avian conservation and provide an understanding of what we still need to learn about this understudied niche. In less than 400 pages of text the authors have provided primary literature to methodically show the extent of our knowledge. Ten rationally divided chapters tackle a wide range of topics from avian adaptations and ecology to modelling and conservation priorities. The chapter on anthropogenic activities includes subsections like “The Impact of Skiing on Birds” and “Renewable Energy Development”. In this way the textbook can serve as a comprehensive educational tool for students or a quick reference guide for discerning wildlife scientists.

The first four chapters begin with a formal review of definitions so readers can appropriately frame non-trivial concepts like “‘high’ mountain birds” and “alpine habitats”. This builds a strong foundation for the latter chapters to explore more robust introductions that preface the considered topics. All sections move through deep and balanced discussions ranging from the effects of grazing on alpine ecosystems to the impacts of climate change on avian breeding phenology. While more general statistical information can be found in the “Population Trends” chapter, detailed discussions of theory and physiology can be found in the chapter on “Avian Adaptions to High Mountain Habitats”. Each chapter then ends with acknowledgements and a full list of references.

Praise is warranted for the appearance of the front cover and spine which are lighter and brighter than many other recent biology works and should be easily recognizable on a shelf. The cover photo of a Rock Ptarmigan (*Lagopus muta*) shown on a snowy mountainside serves as an apt representative of the book’s contents. The binding was well done for the paperback version which is in-line with other core textbooks from Cambridge University Press. Crisp images of landscapes and birds along with figures throughout the book are rendered in black-and-white with several included in every chapter. Additionally, sandwiched in the center there are eight full-color plates showing descriptive maps, research results, and artistic illustrations of alpine species.

Of particular interest to Finnish readers, a coauthor of the textbook Aleksi Lehikoinen is a senior curator of the University of Helsinki’s zoological collections. Many of his contributions include references to Fennoscandia and Finland proper. This includes points in both chapter four and five where the text discusses local distributions for “Birds of Treeline Ecotones” and the “Population Trends of Mountain Birds in Europe and North America”. In general, however, the contents should be praised for providing generality and specificity that can allow researchers to apply ideas and concepts to any system at any scale.

The authors note that due to expected ecosystem and range shifts in the future, high altitude habitats may become more important to the maintenance of avian biodiversity than they are today. Thinking in advance about the ramifications of such a shift becomes imperative to conservation success and puts readers of this text ahead of the curve. I was personally most impressed that the textbook managed to provide extensive resources for Africa while also acknowledging that the Global South is severely underrepresented in knowledge and literature. This book serves as a modern tool that belongs in the collection of any serious ornithologist looking to continue work into the coming decades. For those of us focusing on avian alpine specialists, this textbook should be recognized as a groundbreaking and indispensable new resource summarizing the state of our field.

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