

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

Andreas Otterbeck* & Andreas Lindén

A. Otterbeck, The Helsinki Lab of Ornithology, Finnish Museum of Natural History, University of Helsinki, Finland & Novia University of Applied Sciences, Raseborgsvägen 9, FI-10600, Ekenäs, Finland

A. Lindén, Natural Resources Institute Finland (Luke), P.O. Box 2, FI-00791, Helsinki, Finland

** Corresponding author's e-mail: andreas.otterbeck@helsinki.fi*

Received 10 October 2022, accepted 11 November 2024

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, Lehtikoinen *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 adaptation 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 pre-processed 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 $\ln(\text{'Migration'}/\text{'Win.pop'})$, 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.

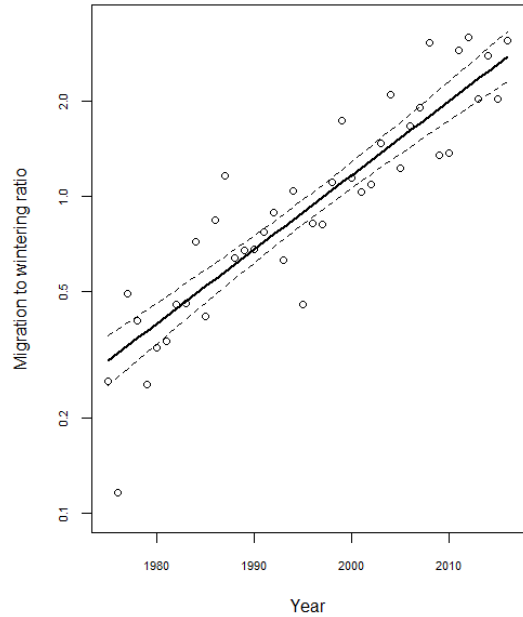


Fig. 1. Long-term trend in the annual migrating to wintering ratio of the Eurasian Sparrowhawk (*Accipiter nisus*). The illustrated regression line and its 95% confidence interval (enclosed by dashed lines), represent the partial effect of (centralized) year from a log-linear multiple regression model.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

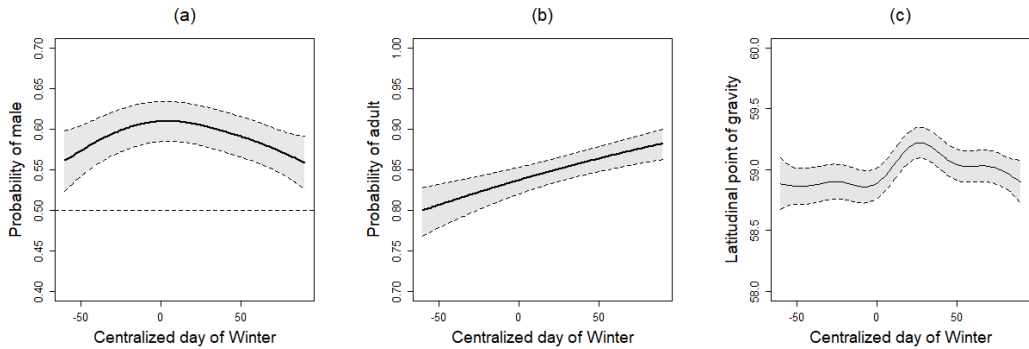


Fig. 2. Within-season effects in sex ratio, age ratio and latitudinal location of overwintering Eurasian Sparrowhawks (*Accipiter nisus*) in Sweden during 1975–2016 (all presented smoothing functions are statistically significant). (a) Males dominated the winter population of residents (horizontal line 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 an 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, Møller *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 (Kjällén 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 (Kjellén 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 muuttoliikkeitä kahdesta eri, mutta toisiinsa kytkeytyvästä näkökulmasta: 1) selvitimme muuttoalttiudessa (muuttajien määrissä suhteessa paikallisten määriin) esiintyviä trendejä ja vaihtelua populaatiossa 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. Esitämme, että talvehtiminen hyödyttää reviiirejä hakevia koiraita, sillä aikainen läsnäolo antaa kilpailuedun korkealaatuisten reviiirien hankinnassa. Lisäksi Ruotsissa talvehtivien yksilöiden levinneisyys (sukupuolesta riippumatta) siirtyi asteittain pohjoisemmaksi talven edetessä, mikä viittaa pienimuotoiseen muuttoliikkeeseen pai-

kallisen populaation keskuudessa. Nämä tulokset tarjoavat uusia näkökulmia osittaismuuton taustatekijöihin ja säätelyyn.

Acknowledgements. We want to thank two anonymous referees and Anssi Vähätalo for their valuable comments on the manuscript. A big thanks to Aleks Lehikoinen for helpful input during the process. We are grateful for the many volunteers who contributed to the Swedish Bird Survey. Andreas Otterbeck was funded by Societas pro Fauna et Flora Fennica and Novia University of Applied Sciences. We want to thank Lennart Carlsson for help with extracting the Swedish dataset from the Swedish 'Artportalen'.

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., Nilsson, 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* 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 eivarpuslinnut. — *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](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](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/](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.