

Partial migration of birds in a changing climate

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Abstract

Partial migration is a phenomenon where a single population inhabits both migratory and resident individuals. When climate change leads to warmer winter conditions, the pressure for escaping the winter in the non-breeding season get smaller. It has been suggested that warmer climate should lead to more residents, but this hypothesis has not yet been widely tested. Several other factors, such as carry-over effects from previous winter and weather during migration might also affect the proportion of migrants. The purpose of this study is to investigate this long- and short-term variation in partial migration in six avian species using data from Sweden during 1975–2014: two raptors (Red Kite *Milvus milvus* and Sparrowhawk *Accipiter nisus*), two aquatic species (Common Gull *Larus canus* and Mallard *Anas platyrhynchos*) and two passerines (Blue Tit *Cyanistes caeruleus* and Fieldfare *Turdus pilaris*). To reveal what trait poses individuals to be residents, I studied three different hypotheses with respect to predictions on arrival time, body size and dominance. To complete the picture, I explored the temporal and spatial variation in the sex and age composition of wintering Sparrowhawks in Sweden during 1973–2014. In this species, the females are larger and dominant to the territory-establishing males. This reversed situation provides a novel separation of the three hypotheses. In contrast to Red Kite, Common Gull and Mallard which exhibit temporal increasing trends towards residency, Sparrowhawks showed an opposite trend with a clearly increasing proportion migrating. In Fieldfare, I found novel evidence for carry-over effects from last winter's harshness affecting annual variation in the proportion migrating, possibly due to either high mortality of residents, bad experiences of wintering, or both. As a short-term response to prevailing conditions, there was a tendency for Mallard to increase residency with higher temperatures during the autumn migration period. Regarding

gains by residency, I found for Sparrowhawk that the average winter sex ratio was male biased and that the proportion of males has increased over time. This is linked to early presence on breeding sites (due to residency), suggesting males to claim territories with little competition in early spring. Males and females showed latitudinal segregation during winter, with females showing a long-term decrease in mean latitude, opposite of the northward traverse of breeding ranges in birds. Residents moved northwards throughout the winter, suggesting that some resident birds indeed migrate, but at a small scale. My results show largely-species specific responses to past and present climate change; a more complex response than previously suggested.

Preface

Denne oppgaven ble skrevet med hjelp fra mange. Takk til veileder Karl Inne Ugland for de årene vi har kjent hverandre. Du kan være enormt inspirerende, og jeg setter stor pris på de mange samtalene våre om ulike temaer. Du står på for studentene, og det liker jeg! Takk til Andreas Lindén for veiledning og mange års vennskap; jeg kommer snart til Finland så kan vi drikke øl! Videre vil jeg takke alle vennene mine på blindern som gjør det trist å avslutte, ingen nevnt ingen glemt. Takk til Oda Bjærke, Ole Strand og Carina Berentsen for hjelp med referanser og gjennomlesning. Takk til Mamma og Pappa som har støttet meg hver gang jeg har kommet krypende etter matpenger og rene klær. Det har kommet veldig godt med i hektiske perioder.

Table of contents

Abstract	2
Preface	4
Table of contents	5
1 Introduction	7
1.1 Population level responses to weather and climate.....	9
1.2 What promotes residency in some individuals?.....	10
1.3 Aims of this study.....	12
1.3.1 Population responses	13
1.3.2 Individual determinant traits	14
2 Materials and Methods.....	14
2.1 Study species	14
2.1.1 Population level migratory propensity	14
2.1.2 The Sparrowhawk for studying individual migration strategies	15
2.2. Study area	16
2.2.1 Sweden	16
2.2.2 Falsterbo	16
2.2.3 Oslo and Bærum	17
2.3 Data for estimating migratory propensity	18
2.3.1 Swedish summer and wintering indices.....	18
2.3.1.1 Summer period.....	18
2.3.1.2 Winter period	19
2.3.2 Autumn migration counts at Falsterbo.....	19
2.3.2.1 Observer shift bias and correction.....	19
2.3.3 Weather data.....	22
2.3.3.1 Autumn temperature.....	22
2.3.3.2 Previous winter's climate	22
2.4 Data for stidying which individuals overwinter.....	23
2.5 Sparrowhawk breeding data.....	24
2.6 Statistical analysis	25
2.6.1 Migratory propensity model	25
2.6.2 Models for sex ang age specific Sparrowhawk migration	28
2.6.3 Analysis relating productivity to onset of breeding	29

3 Results	30
3.1 Migratory propensity	30
3.2 Sex ratio, age and distribution during winter	33
3.3 Timing of breeding onset and productivity	35
4 Discussion	35
4.1 Migratory propensity	35
4.1.1 Response to previous winter conditions	35
4.1.2 Response to autumn temperatures	37
4.1.3 Long term trends	39
4.2 Why overwinter?	42
4.2.1 Wintering sex ratio	42
4.2.2 Wintering age structure	44
4.2.3 Latitudinal distribution of wintering Sparrowhawks	44
4.3 Future studies	46
5 Conclusions	47
References	48
Appendices	58

1 Introduction

Migratory movements occur across the animal kingdom on a variety of different spatial and temporal scales. Some examples are the daily vertical migration of zooplankton (Lampert 1989, 1993; Hays 2003), the annual journey of many baleen whales from the poles to the tropics (Stone *et al.* 1990) and the bi-annual seasonal transpolar migration of the Arctic Tern (*Sterna paradisaea*) (Egevang *et al.* 2010). The long movements occur between geographical areas which are periodically beneficial for survival and reproduction (Lack 1943; Newton 2008).

Each autumn a large number of birds leave their deteriorating breeding areas towards winter quarters that provide a milder climate with higher food abundance. Migration patterns – such as direction and distance – may differ between different populations of the same species (Ambrosini *et al.* 2016) as well as between individuals (Terrill & Able 1988; Cristol *et al.* 1999).

When a single population possess both migratory and resident individuals, it is considered to be partially migratory (Lack 1943, 1944; Terrill & Able 1988). This phenomenon has been found, for example, in birds (Lundberg 1988), fish (Brodersen *et al.* 2008; Chapman *et al.* 2012), mammals (Myserud *et al.* 2011), amphibians (Grayson & Wilbur 2009) and invertebrates (Hansson & Hyllander 2009). Theoretically, migration is beneficial whenever the net gain of migrating exceeds the gain of residency (Lack 1943). When this gain is low compared to residency, some individuals might benefit from overwintering. While residency typically may imply higher risks in terms of survival, this might be offset by better subsequent reproduction (*e.g.* Schwabl 1983).

In partial migrants, the individuals may be obligate (*i.e.* “hard wired”) migrants or residents, or alternatively, facultative migrants, which means that individuals flexibly choose whether they should migrate or not. Naturally, some individuals are likely to lie somewhere in between these two categories. Individual migratory propensity – or the tendency to migrate – has been demonstrated to be genetically based (Berthold 1978, 1996; Berthold *et al.* 1990), but environmental variation such as weather and food availability is also known to play an important role for many species (*e.g.* Nilsson *et al.* 2006; Lindén *et al.* 2011). Individual migration propensity can be described with a reaction norm (Pulido 1996), *i.e.*, the probability of migrating (y-axis) as a function of one or many environmental variables (x-axis). Whenever the function differs from a horizontal line (has a slope) there is phenotypic plasticity. Both the level and form of the function can be thought to be genetically determined and subject to natural selection.

Partial migration has received relatively little attention compared to other aspects of migration. In the last decades, however, this phenomenon has appeared to be particularly common in birds (Lundberg 1988; Chapman *et al.* 2011). Many bird species formerly thought to be completely migratory have turned out to be partially migratory (Lack 1943; Lundberg 1988). Recent investigations indicate that the percentage of migrating individuals in a population may vary between 1 and 99 % (Chapman *et al.* 2011), but the actual proportion varies geographically (Mueller *et al.* 1977; Ambrosini *et al.* 2016). An overall pattern seems to be that the fraction of migratory individuals increases with climate resistance during winter – such as increasing latitude (Newton & Dale 1996; Newton 2008; Somveille *et al.* 2013); and higher altitude (Newton 2008). For example, the European Robin (*Erithacus rubecula*) is fully migratory near the northern limit of its distribution range, partially migratory in the middle and completely sedentary in the south (Table 1; Ambrosini *et al.* 2016).

Table 1: The proportion of migratory individuals and migration distance among 4 populations of European Robin (*Erithacus rubecula*) across Scandinavia (Main 2002); table modified from Newton 2008).

Breeding area	% migratory	Median migr. km
Denmark	16	533
Norway	61	894
Sweden	76	1113
Finland	89	1738

1.1 Population level responses to weather and climate

For birds the main hazards posed by overwintering in higher latitudes are related to low food abundance (Jansson *et al.* 1981), low temperatures (*e.g.* Ketterson & Nolan 1982), predation (Jansson *et al.* 1981; Caro 2005) and prolonged snow cover (Hogstad *et al.* 2003). As the daily food demand rapidly increases with lower temperature, even shorter periods without food in winter might be fatal (*e.g.* Vepsäläinen 1968).

During the last decades, the onset of spring has advanced (Schwartz *et al.* 2006) and the global temperature has increased, being particularly noticeable at higher latitudes (IPCC 2013). As a result, various responses are consequently observed in wild birds (reviewed in Visser 2008). As the winter temperatures become gradually milder, the pressure for migration should theoretically be reduced. Berthold (1996, 2001) proposed a hypothesis that partially migratory bird populations should respond to such temperature increase by progressively switching towards residency. As evidence for such a behavioural switch, captive house finches (*Carpodacus mexicanus*) from non-migratory American western populations (southern California) quickly became partially migratory when released in eastern North America, in a clearly colder environment (Able & Belthoff 1998). Moreover, Meller *et al.*

(2016) suggested climate-induced residency in some Finnish bird species, particularly waterfowl, presumed to be due to gradual reduction in ice coverage in the Baltic Sea.

Berthold's theory has been little tested and its generality has been questioned; first, many species show no trend in migratory propensity, while those few responding seems doing so at different rates (Meller *et al.* 2016). Secondly, some evidence from Swedish Blue Tits even suggests the possibility of an opposite response of becoming increasingly migratory (Nilsson *et al.* 2006). Third, the general level of response in migration activity might be veiled if it largely reflects innate species-specific flexibility.

1.2 What promotes residency in some individuals?

Birds have different demands during the breeding and non-breeding seasons. Breeding requires a nesting place, food for parents and their offspring, protection from predators and pressures from competition. Outside the breeding season, survival and condition maintenance are most important. For any individual, the optimal migration strategy depends on whether it would succeed more as either migratory or resident. It is still controversial 1) which traits benefit either residents or migrants, 2) through what ecological advantages those traits are superior and 3) what underlying mechanism(s) regulate such phenotypic expression in wild populations. In this thesis, I will focus on resolving 1 and 2.

Early spring arrival at the breeding grounds might provide an advantage in the competition for the best territories (Ketterson & Nolan 1976) (Table 2). This, however, holds only if 1) high-quality territories are subject to intra- or interspecific competition, 2) resident individuals are better able to acquire such territories than migrants due to their earlier presence, and 3) such acquisition gives a fitness advantage through better reproduction

(perhaps also survival). As a result, the gain of residency could offset the costs for the territory establishing sex, usually the males in birds (*e.g.* Schwabl 1983).

On the other hand, there is a thermoregulatory advantage of increasing body size in environments with low temperatures, because a reduction of surface area to volume ratio reduces loss of body heat. Its generality is illustrated by Bergmann's rule, which predicts endotherm animals to increase in size along climate gradients, such as towards the north and higher altitudes (Bergmann 1847; Meiri & Dayan 2003). When extending this framework to partial migrants in areas where residency includes thermal stress in winter, larger individuals should cope better with the cold, being able to fast for longer periods. Conversely, individuals less well equipped to cope with the thermal costs of extreme temperatures should be more likely to migrate. In most bird species with sexual size dimorphism (*i.e.* one sex is larger than the other) males are larger than females (Dunning 2008) and are therefore likely to have a higher frequency of overwintering (Ketterson & Nolan 1976; Chapman *et al.* 2011) (Table 2).

Besides timing and body size, dominant individuals (often males) might have an advantage in the competition for limited food, so that subordinate individuals (usually females and juveniles) might be forced to migrate (Ketterson & Nolan 1976; Gauthreaux 1982).

All three hypotheses usually predict males as residents, making it difficult to identify the trait upon which the decision to stay or migrate were ultimately made. This might in return be solved by studying species with reversed size dimorphism (RSD), thus controlling for the confounding effects of "Body size" on "Dominance" and "Arrival time" (Table 2). Differential migratory propensity within species might reveal the evolutionary drivers of

migration, and important knowledge for understanding responses to present and future climate change.

Table 2: Overview of three hypotheses for which individuals are more likely migrate or reside. For each hypothesis, I give the general prediction (sensu Chapman et al. 2011), the corresponding predictions for species with reversed size dimorphism (RSD) and possible existing evidence.

Hypothesis	Predictions (general)	Predictions RSD	Evidence
Arrival time			
Ketterson & Nolan (1976)	The territory establishing sex (usually male), and more dominant (competitive) individuals of that sex are more likely to be resident	Males more likely to be residents	Silverin <i>et al.</i> (1989); Grayson & Wilbir (2009); Grayson <i>et al.</i> (2011); Fudickar <i>et al.</i> (2013)
Body size			
(Thermal tolerance) Ketterson & Nolan (1976)	Cold environments: smaller individuals (usually females) migrate	Males (typically) more likely to migrate	Belthoff & Gauthreaux (1991); Able & Belthoff (1998); Gow <i>et al.</i> (2014); Macdonald <i>et al.</i> (2015)
Dominance			
Gauthreaux (1982)	Dominant individuals (usually males) more likely to be resident, subordinates migrate	Females (typically) more likely to be residents, males and juveniles migrate	Smith & Nilsson (1987); Nilsson <i>et al.</i> (2008); Lundberg (1985); Mysterud <i>et al.</i> 2011; Olsson <i>et al.</i> (2006); Näslund <i>et al.</i> (1993); Grayson <i>et al.</i> (2011)

1.3 Aims of this study

This thesis studies two different aspects of partial migration: i) population responses to weather and climate change in six partially migratory bird species, ii) and the individual traits promoting either migration or residency in a partially migratory raptor with strong RSD.

Below the study hypotheses are referred to as bolded numbers.

1.3.1 Population responses

First, I study how the proportion of migrants (migratory propensity) varies in response to short-term weather and long-term climate change in wild bird populations. My aim is to reveal how partially migratory birds might alter their proportions of migrants in response to external conditions, by simultaneously studying six bird species, thus allowing for multiple different responses. Responses to short-term (annual) variation are assumed to reflect facultative partial migration behaviour, and **1)** I predict a larger proportion of individuals to migrate in years with cold temperatures in autumn, prior to and during early migration. In addition to this, **2)** I test how variation in the migratory proportion might be explained by previous winter's harshness and spring earliness, in terms of the winter NAO (December–March). I predict a larger proportion of sedentary individuals following early springs (with positive winter NAO), which may operate through several mechanisms. Early springs often imply an earlier start of breeding, so that offspring have more time to gain experience and sufficient body condition before the migration decision. The previous winter's harshness may also act on the subsequent migratory proportion through the individuals' positive or negative previous wintering experiences (phenotypic plasticity). Finally, higher mortality of individuals with either strategy may alter their proportion in next year (microevolution). This would not only shed light on the flexibility of migration behaviour to present and past weather, but also on future effects of climate change. Finally, as hypothesized by Berthold (2001), **3)** I predict the proportion of resident individuals to show increasing temporal trends in response to climate warming and less harsh winter conditions. My approach is to examine these questions using long-term time series data (30 years) from Swedish summer/winter censuses and autumn migration counts from a bird observatory.

1.3.2 Individual determinant traits

Secondly, my aim is to test, on an individual level, what qualities (traits) might determine either residence or migration. Deeper insights to this issue would shed light on what ecological pressures is implied for individuals from either residency or migration. My approach is to simultaneously test the validity of three hypotheses about who should migrate or stay, related to: **4**) arrival time, **5**) competitive release and **6**) body size (as summarized in Table 2). I allow a novel separation between overlapping predictions by studying a small raptor with RSD, having a particular focus on separating larger body size and dominance from being the territory establishing sex. For this I use a long-term citizen-science data set with winter observations reported by amateur ornithologists, where relevant traits have been identified or could be assumed, along with known age and latitudinal location of the sightings. I also explore spatio-temporal patterns in the data, for a more complete picture of the consistency with the different hypotheses.

2 Materials and Methods

2.1 Study species

2.1.1 Population level migration propensity

For studying the migratory propensity on a population level, I chose six bird species that are partially migratory in the Nordic, whose migrants overwinter in middle/west Europe: the Eurasian Sparrowhawk (*Accipiter nisus*), Red Kite (*Milvus milvus*), Common Gull (*Larus canus*), Fieldfare (*Turdus pilaris*), Blue Tit (*Cyanistes caeruleus*) and Mallard (*Anas platyrhynchos*). These species represent a wide range of different life histories and wintering

habitat preferences, and only Blue Tit (Nilsson *et al.* 2006) and Fieldfare (Meller *et al.* 2016) have earlier been studied in regard to migratory propensity. Both Sparrowhawk and Red Kite are long-lived predators, with a preference of forests and fields, respectively. While Sparrowhawk is specialised on capturing passerines, Red Kite prey mainly on small to mid-size rodents. Common Gull and Mallard are also long-lived, and as aquatic species, they (Mallard in particular) depend on open water during winter. Both Fieldfare and Blue Tit are relatively short-lived passerines feeding on seed and berries, frequently found close to human settlement. During winter, the Blue Tit makes extensive use of human provided bird feeders while Mallard and Common Gull are frequently fed in urban environments, the latter perhaps more passively. Blue Tit is also known to feed on seeds of European beech (*Fagus sylvatica*), which shows heavy fluctuations. Fieldfare wintering is likely to largely depend on the amount of rowanberries (*Sorbus aucuparia*) available.

2.1.2 The Sparrowhawk for studying individual migration strategies

For studying what individuals tend to overwinter more frequently, with regard to sex, age, size and location, I used citizen observation reports of the Eurasian Sparrowhawk – a small-sized forest-dwelling raptor. It is the most common raptor found across Fennoscandia (Newton 1986). Its RSD is extreme with an average female (325 g) being much larger than an average male (150 g) (Dunning 2008). This size difference also contributes to males being subordinate to females (Newton 1986), and the two sexes being fairly easily identifiable in the field. While size and dominance are reversed compared to most birds, the species have a particularly male-skewed parental effort. In addition to having the sole responsibility for territory establishment, males must alone feed the female, the chicks and himself throughout most of the breeding season (Newton 1986; own observations). The quality of

territories varies (Newton 1986), and local prey availability and exploitation can affect breeding productivity (Otterbeck *et al.* 2015). Thus, I assume there is likely to be strong competition among males for acquiring high quality territories, possibly benefiting resident males who choose territory before the bulk of conspecific competitors arrive in spring.

2.2 Study area

2.2.1 Sweden

To assess migratory propensity I used breeding- and wintering population monitoring data from Sweden on all six species. I also used individual Sparrowhawk data from the whole country, to study which individuals winter more frequently.

Sweden constitutes the middle part of Fennoscandia, and large parts are relatively temperate due to the Gulf Stream. Its type of climate differs across the country and spans from a very mild climate in the southernmost parts barely having sub-zero temperatures in winter, to having harsh winter conditions in the northern part, combined with little or no daylight during mid-winter. The country is categorized into four Köppen–Geiger climate regions, here listed from the South to the North: Cfb (warm temperate, fully humid, warm summers), Dfb (snow, fully humid, warm summer), Dfc (snow, fully humid, cool summers) and ET (polar, tundra) (Kottek *et al.* 2006). The effects of recent climate change have also differed locally, with the northern part currently showing a particularly positive trend in both temperatures and precipitation (Alexandersson & Edquist 2006).

2.2.2 Falsterbo

For the population level analysis of migratory propensity I used autumn migration data from Falsterbo bird observatory. The observatory is situated at the Southwestern tip of Sweden, in

the Scania province (55°23', 12°5'E) (Fig. 1). This peninsula acts as a major migration passage for autumn migration out of Fennoscandia (Karlsson *et al.* 2004), because this tip concentrates migrants following the coast due to hesitation for migrating across open water. Although migrants from several pathways pass this place annually (Fig. 1), these numbers constitute a fraction of the total numbers migrating out of Fennoscandia. However, raptors pose an exception, as their numbers are considered especially well represented at this passage (Karlsson *et al.* 2004).

2.2.3 Oslo and Bærum

For studying the relationship between breeding onset and subsequent productivity I used Sparrowhawk breeding data from a study area in Oslo and Bærum in southeast Norway (60°N, 10°50E, Fig. 1). The area contains both coniferous and deciduous forest, but is dominated by spruce. The climate is a fully humid continental with mild summers (Dfb). All breeding sites were situated at 0–400 m above sea level. The first males arrive at their territories in early March and the female lays eggs in late April to mid-May. The eggs hatch in mid-June, whereas the nestlings fledge in mid-July.

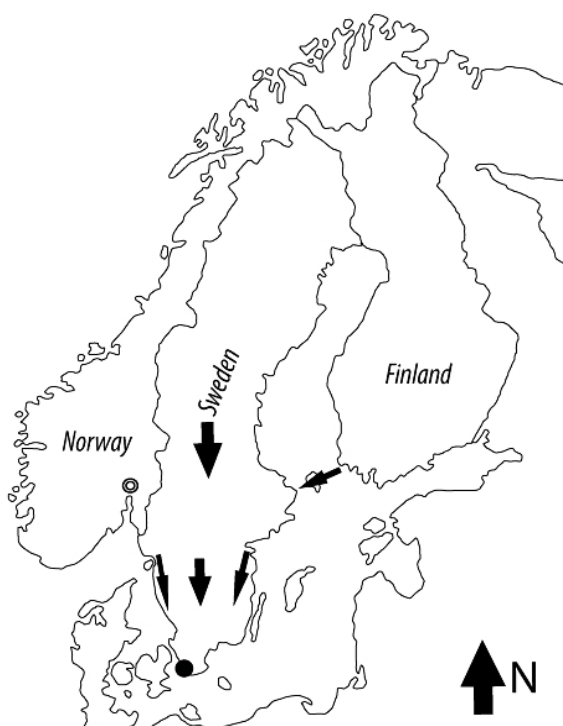


Figure 1: Falsterbo bird station (black bullet) gathers autumn migrants from many parts of Fennoscandia. Arrows indicate important paths of migration. Oslo–Akershus is located at the grey circle.

2.3 Data for estimating migratory propensity

As part of national monitoring programmes, much attention is generally given to collect accurate information on the relative annual population sizes of different bird species. By combining summer and winter censuses with autumn migration counts, it is possible to estimate the annual proportion of migrants for each species, whenever such data exist. In contrast to earlier studies with similar aims, such as Nilsson *et al.* (2006) and Meller *et al.* (2016), The novel model used in this thesis makes simultaneous use of all three data sources in order to produce a better prediction of the resident fraction (Lindén *in prep.*).

2.3.1 Swedish summer and wintering indexes

As size indices of the annual Swedish summer and winter populations, I used census data from the Swedish Bird Survey (1975–2014), which is a part of the national monitoring programme. I obtained these data from the webpage <http://www.zoo.ekol.lu.se/birdmonitoring/res-tretrender.htm>, accessed July 2015. These data are processed prior to publication; survey results for each species are summarized to national abundance indices using the statistical software TRIM (Trends & Indices for Monitoring data; Pannekoek & van Strien 2005). Each annual data point is represented by an index relative to the reference year 1998, which has the index 1 (Green & Lindström 2014). TRIM does regular log-linear Poisson-regression (a generalized linear model), with options for imputation and accounting for overdispersion.

2.3.1.1 Summer period

The summer census data was collected annually by amateur ornithologists from 1975 to 2014 based on 250–300 different point census routes per year. Every route has 20 evenly

spread points surveyed for 5 minutes each. The exact route is chosen by the observers and the same observer typically surveys the same route each year. The minimum distance between each point is 200 m in dense forests, and 300–400 m in open landscapes. As a point of note however, the density distribution of routes reflects the human population density, meaning that the southern parts of Sweden are overrepresented in the data (Green & Lindström 2014).

2.3.1.2 Winter period

Winter censuses are also conducted on routes (20 evenly spread points) chosen by the observers. The distance between each point is minimum 300 m in dense forest, and 400 m in open terrain. The points are surveyed for 5 minutes each. Although there were available census data from the whole winter period, I only used data from the midwinter count 19th December–8th January (Lindström & Svensson 2002), to avoid bias from birds in transit, *i.e.* late autumn or early spring migrants. For the very same reason, the midwinter count is compulsory for the observers, while the other counts are more sporadically counted.

2.3.2 Autumn migration counts at Falsterbo

To measure the annual magnitude of migration, I used daily standardized migration count data from Falsterbo Bird Observatory collected during the autumns in 1975–2014. The data used in this study are annual totals for each species (Table 3). These data are freely available at their website (www.falsterbofagelstation.se).

2.3.2.1 Observer shift bias and correction

The main observer changed once during the 41 year period, accompanied by an adjusted methodology (Kjellén 2002) (Table 3). Up to 2000, Observer 1 (Gunnar Roos) counted from

11th August to 20th November, starting daily 30 minutes before sunrise and counting to 14:00 local time. Observer 2 (Nils Kjellén) later adopted the responsibility of the main counts from 2001 (Kjellén 2002). In contrast to Roos, Kjellen started the count period already on the 1st August. Further Kjellen was accompanied by an assistant counter (i.e., two persons counting).

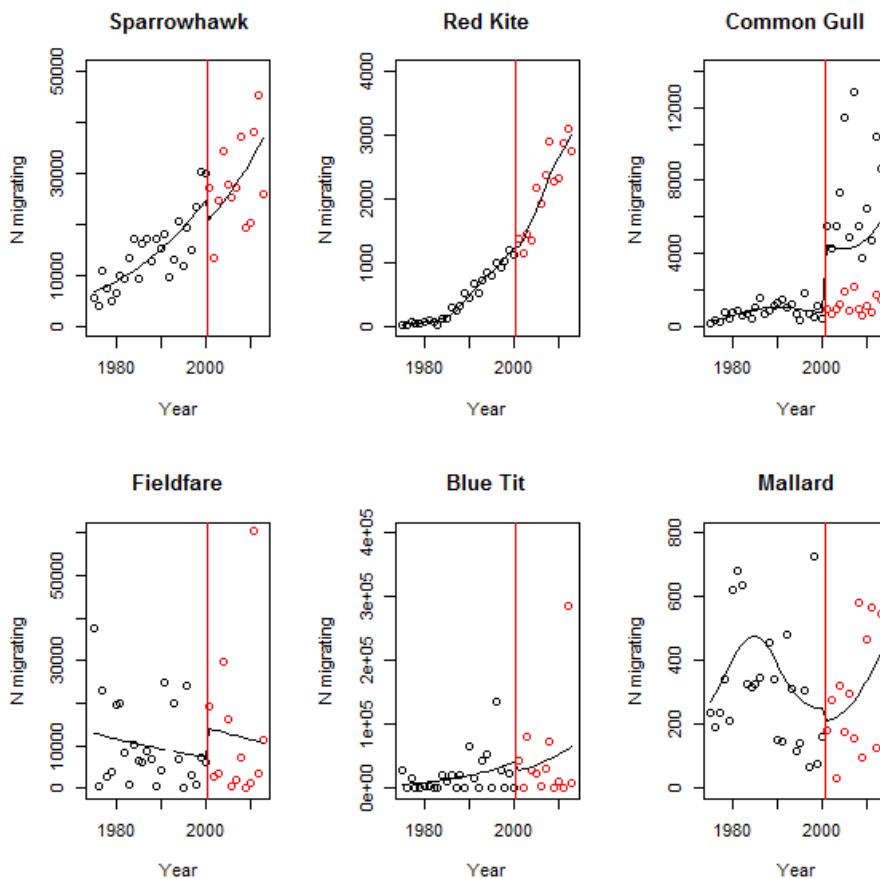
As there were no temporal overlap in counts conducted using the two methods, no direct comparison can be made about their quantitative differences. However, I tested for any discontinuity in the temporal trend in bird numbers caused by the switch in 2001. I applied separately for each species a generalized additive model (GAM) in R (version 3.2.0) (R Core Team 2015), applying a logarithmic link function and negative binomial error distribution. The model was fitted using the package “mgcv” (version 1.8-6) (Wood 2011) and the function “gam”, setting the annual migration total as the response variable. As explanatory variables I used “Observer” (binary factor variable) and “Year” (continuous variable), whose effect was modelled with a smoothing function. Hence, I tested for any effect of “Observer” with the null hypothesis of no difference before and after 2001, adjusting for a flexible trend in time. I used the default smoothing options, *i.e.* thin-plate spline ("tp") as the smoothing basis and a maximum of 9 degrees of freedom.

Although some degree of discontinuity can visually be recognized at 2001 in most species (Fig. 2), the standard errors reveal large levels of uncertainty for all species, which is partially a consequence of no temporal overlap, and partially a consequence of the flexibility of the temporal trend. The discontinuity was statistically significant only for Common Gull ($P \leq 0.05$) (Table 3), hence being the only species on which I applied a correction factor. This was done by multiplying Kjellén’s counts with a correction factor (see Table 4).

Table 3: Estimates of “Observer”, their standard errors (SE) and Z values and statistical significances (P). When the correction factor $1 / \exp(\text{Estimate})$ is multiplied with Kjellén’s data, the data are compatible with that of Roos. Significant results are given in bold font.

Species	Estimate	SE	Z	P	Correction
Sparrowhawk	-0.211	0.188	-1.120	0.263	1.2348
Blue tit	-0.483	0.895	-0.539	0.590	1.6201
Common gull	1.763	0.337	5.229	< 0.001	0.1715
Red kite	-0.059	0.238	-0.245	0.806	1.0603
Fieldfare	0.664	0.698	0.952	0.341	0.5147
Mallard	-0.172	0.567	-0.304	0.761	1.1880

Figure 2: Time series data of the total number of observed migrating birds at Falsterbo bird observatory are illustrated using black circles for the included species. The black line is the fitted GAM, accounting for a switch in counting method and observer during 2001. If Kjellén’s data are multiplied with a correction factor (result illustrated with red circles), the data become compatible with Roos’ data.



2.3.3 Weather data

2.3.2.1 Autumn temperature

Assuming a flexible behavioural decision, partial migrants might choose strategy from prevailing conditions prior to, or during their migration phase. To test this, I used temperatures from a meteorological station situated at Falsterbo (Klein Tank *et al.* 2002). From these, I calculated the mean temperature for August–September annually in 1975–2014. This should well describe the situation prior to migration for most species and partially coincides with the migration of many species. During this period, the mean temperature increased annually on this station (linear regression, 0.047 ± 0.016 , $t = 2.902$, $P = 0.0062$). However, if it is rather the latest migrants who base their decision on prevailing temperatures during migration, a later time span would be relevant (e.g. October–November temperature).

2.3.3.2 Previous winter's climate

Changes in migratory propensity might alternatively be affected by carry-over effects from the harshness of previous winter. As a rough measure of the harshness of previous winter, and annual onset of spring, I used the winter North Atlantic Oscillation (NAO) from the preceding winter (December–March) prior to the breeding and migration period. NAO reflects the oscillating atmospheric masses in the middle between the Arctic and the Subtropic Atlantic (Hurrell *et al.* 2001). This index oscillates between positive and negative phases, describing large-scale pressure centres affecting climate in larger areas of Europe. Positive phases correlate with warmer and wetter winters in northern Europe, with more storms, while negative phases are related to colder and drier periods, with more harsh winters.

2.4 Data for studying which individuals overwinter

To study what traits facilitate residency – being the territory establishing sex, having superior body size or being dominant – the best possible data would be high resolution individual tracking data (satellite or light logger data). However, despite advances in the price and user friendliness of many such devices, there is still a general lack of such data. Yet, few studies on this subject have used individual tracking data, except ringing recoveries count.

In this study, I approached the problem using winter observations of Sparrowhawks from 1973–2014, downloaded from www.artsportalen.se. I grouped all observed individuals into categories that provide qualitative information on their key traits relevant to this study; males are the territory establishing sex, females are of superior body size and hence dominant to males, while juveniles are subordinate adults of the same sex. I grouped observed individuals by sex and age, whenever these pieces of information were identified in the data. I directed my main focus to how 1) sex ratio varied among Sparrowhawks within a typical winter and over the whole study period 1973–2014 (*i.e.* the temporal trend), 2) how the age structure (young vs. > 1st winter birds) varied within and between years, and 3) how the latitudinal point of gravity varied during the winter in both sexes over the 4 decades.

The database “Artsportalen” consists of bird observations from both national monitoring projects and more occasional data reported by amateur ornithologists (“citizen science data”) across Sweden. I extracted all observations based on the following criteria: 1) only observations from the “winter season” spanning from day of year (DOY) 305 in late autumn to day 91 the following spring (in non-leap years: 1th November–1st April), and 2) only observations where the sex has been identified. I redefined DOY as a new variable (DOW

– day of winter) centred at New Year: DOW = 1 equals 1st January, DOW = 0 is 31st December, and DOW = –1 is 30th December.

The resulting subset of data consisted of 17180 observations, with more males than females (Table 4). Such observational and non-standardized “citizen science data” typically contain high levels of noise, and reflect the distribution of volunteers as well as their reporting behaviour. This implies that analyses should always be carefully interpreted. A relevant observer bias with these data was that the age of females was less frequently determined compared to males (chi-squared test: $X^2 = 156.13$, $df = 2$, $P < 0.0001$). This may be because older males have an orange-toned barring on the underparts, being bluish grey on the upperparts. The total sample size with known sex was 17180, dropping to 5578 when adding the criteria of known age (Table 4). I consider this data suitable for the purpose of this study, supposing no temporal trends in the correct identification success of sex and age.

Table 4: Overview of the respective sample sized based on different criteria: “Age 0” represent juvenile individuals in their first winter, “Age 1” represent older than first winter while “Not aged” represent the number of individuals identified to sex but not to age.

Sex	Age 0	Age 1	Not aged	Total
Male	191	3471	6455	10117
Female	104	1812	5147	7063

2.5 Sparrowhawk breeding data

Arrival time hypothesis states that early arrival implies a reproductive advantage. The reason for this could be 1) higher territory quality for early arriving individuals, and 2) early breeding onset leads to larger clutches in many bird species (ref). Although most of the current literature focuses solely on territory quality, the hypothesized gain in productivity by early arrival might actually result from territory quality and early breeding onset combined.

Having the sole responsibility of nest building, Sparrowhawk males use approximately 100 hours in nest construction before mating (Newton 1986). While resident males acquire territories under little competition, resident females might in turn choose these early males before migratory individuals arrive, resulting in early breeding initiation. To evaluate the local gain of early breeding by “early arrival”, I tested how timing of breeding onset affects breeding output in a representative Nordic Sparrowhawk population. For this, I used data from a long-term monitoring project on Sparrowhawks, in which I have participated during 2008–2016 together with an experienced ornithologist, Eric Roualét. I did however include data only from the last two years, which I considered to be particularly accurate regarding breeding onset. Every nest was inspected twice every season; after egg laying and again when the nestlings were old enough to be ringed (10–25 days). I defined breeding onset as the date when the first egg was laid, which was based on back-calculation of the observed progression of laying (*i.e.* one egg every two days until the clutch is complete). I measured productivity as the number of nestlings present during the last inspection. I chose not to use the number of eggs as a measure of productivity because eggs might not reflect the number of nestlings that are subsequently brought up; some eggs might remain unhatched or a nestling could die early or get predated (Otterbeck *et al. in prep*).

I have no ethical concerns about this fieldwork, which was of a non-invasive nature.

2.6 Statistical analysis

2.6.1 Migratory propensity model

For studying the annual variation in the proportion of wintering partial migrants, I used a statistical model (Lindén *in prep*) which combines three different types of population indices:

breeding population indices (N), autumn migration numbers (M) and wintering population indices (W). This model is neither a pure logistic regression nor a multivariate linear model, but rather borrows ideas from both.

As continuous explanatory variables I used study year “Year” (centred to zero mean), average August–September temperature “Temp” (centred to zero mean) and the winter NAO “NAO” (zero is already the long term average). A logit-linear function of the explanatory variables describes the migratory probability (P_t) in year t , as

$$\text{logit}(P_t) = a_0 + b_1 \text{Year}_t + b_2 \text{Temp}_t + b_3 \text{NAO}_t . \quad (1)$$

As the explanatory variables have zero mean, a_0 describes the average proportion migrating under normal conditions. If the probability of migrating is P_t , the probability of overwintering must be $1 - P_t$. The scaled indices of migration and wintering numbers are then thought to be on average proportional to the breeding population size (N_t) times the probability of migrating/wintering, and the unexplained variation (ε) in the two variables is assumed to be bi-normally distributed on the log-scale.

$$M_t = a_1 N_t P_t \exp(\varepsilon_{t,1}) \quad (2)$$

$$W_t = a_2 N_t (1 - P_t) \exp(\varepsilon_{t,2}) \quad (3)$$

$$\varepsilon_t \sim \text{MN}([0 \ 0], \Sigma) \quad (4)$$

The mean proportion of migrants (the model intercept; α_0) has statistical estimability issues, as it is difficult to separate from the arbitrary scaling on the three indices (M , W , N), or actually from the scaling parameters α_1 and α_2 . As this can affect the results, I include *a priori* information into the model about the average proportion of migrants in the population, similarly to Bayesian analyses (although I use frequentist inference). This was implemented using a maximum likelihood-based frequentist approach, with penalized likelihood. The estimated uncertainties of the parameters were obtained using a parametric bootstrap with 10000 repeated resampling events. The R code for a subroutine fitting the model (written by Andreas Lindén) is given in Appendix 2.

Local quantitative measures on average migratory propensity are seldom available. However, rational guesstimates with appropriately high levels of uncertainty can be made by expert ornithologists based on count numbers and general impression. In addition to the literature and my own impression, I consulted Jan-Åke Nilsson and Nils Kjellén about suitable average levels. The statistical model applied uses a normal distribution as the prior for the parameter α_0 . I determined the normal distribution means and standard deviations (Table 5), by trying out different parameter combinations and plotting the distributions of 50000 pseudorandom normal expit-transformed ($y = 1 / [\exp(-x) + 1]$) numbers using kernel density estimation. I examined visually that the distribution had approximately the correct average/mode and suitable uncertainty (figures of the applied prior distributions in Appendix 1). To account for multiple testing, i.e., six species per hypothesis (explanatory variable), I applied a Šidák correction for multiple testing (6 species and tests per hypothesis) to my analyses, and interpreted all analyses based on these corrected new significance levels ($p_{\text{crit}} = 1 - (1 - 0.05)^{1/6} = 0.00851$) (Šidák 1976).

Table 5: *Approximate average percentage assumed to migrate (Migratory %) for the six study species, and the normal distribution means (μ) and standard deviations (σ) applied as priors for the intercept term (a_0).*

Species	Migratory %	μ	σ
Sparrowhawk	90	2.3	0.5
Blue tit	20	-0.7	1.44
Common Gull	75	0.8	0.6
Red Kite	80	1.4	0.3
Fieldfare	50	0.1	0.7
Mallard	50	0.0	0.8

2.6.2 Models for sex and age specific Sparrowhawk migration

To study which Sparrowhawk individuals are most prone to migrate or overwinter, I set up the three models for studying the temporal (and spatial) trends with regard to sex and age. The response variables of the three analyses are "Sex", "Age" and "Latitude" (analyses summarized in Table 6).

In all three cases, I modelled the effect of "DOW" (continuous variable indicating date) using a smoothing function, again using the default options of the "gam" function in the "mgcv" package (thin-plate spline as smoothing basis, max. df = 9). The binary variable "Sex" was identified to either "1" = male or "0" = female. I grouped the age of the individuals into two categories: "1st winter" (1 cy or 2 cy after New Year) and "adult" (2 cy before New Year, or older than 2 cy). The "quasibinomial" error distribution was used for modelling sex ratio (Model 1) and age (Model 2). It implies a logit link function, binomial error distribution and a correction for over-/underdispersion. The "linear family" used for studying sex specific latitudinal patterns in the centre of gravity (Model 3) implies identity link (no transformation) and normal error distribution.

Table 6: Three generalized additive models (GAMs) are applied to study which individuals of Swedish Sparrowhawks are the most prone to migrate or overwinter. Model 1 studies trends and seasonality in the sex ratio, Model 2 does the same for age structure, while Model 3 studies sex specific patterns in the latitudinal centre of gravity throughout the winter, allowing an interaction between “Sex” and “Year”. Day of winter (DOW) is day of year centered at New Year (1. Jan = 1, 31. Dec = 0).

Model	Response variable	Explanatory variables	Family
1	Sex (factor: "male", "female")	s(DOW) + Year	Quasibinomial
2	Age (factor: "1 st winter", "adult")	s(DOW) + Year	Quasibinomial
3	Latitude (continuous)	s(DOW) + Sex * Year	Linear

Although including age in model 3 might have been informative, I chose not to include this due to 1) significantly different chance of age-determination among males and females, 2) around 68 % of all observations would be dropped if they also have to be aged (illustrated in Table 4). However, in model 2 I used age with the assumption that the bias itself did not change over this long time period, so that any relative change would reflect an actual alteration in sex ratio.

2.6.3. Analysis relating productivity to onset of breeding

To estimate how productivity might reflect the date of breeding onset, as indirect support for the arrival time hypothesis (Table 2), I set up a generalised linear model:

$$\text{ClutchSize} = a_0 + b_1\text{Doy.C} + b_2\text{Year}$$

“ClutchSize” is the number of ringed individuals in each brood, “Doy.C” is the centralized day of year of first egg laid while “Year” is either the study year 2014 or 2015. I applied family "quasipoisson", implying a log link-function, Poisson error distribution and a correction for over- or underdispersion (clutch sizes are more likely underdispersed).

3 Results

3.1 Migratory propensity

The species included in this study varied in their response to altered climatic conditions in terms of the temporal trend over the years (Table 7). A negative trend in migratory propensity was found in Common Gull (-0.040 ± 0.010), Red Kite (-0.049 ± 0.009) and Mallard (-0.036 ± 0.009), and a tendency also in Blue Tits (-0.027 ± 0.013 ; significant only without correction for multiple testing). Conversely, the proportion of migratory Sparrowhawks showed a very prominent annual increase (0.057 ± 0.005). There was no evidence for a long-term trend in the proportion of migrants for Fieldfare (Table 7). The magnitudes of these changes are illustrated in Fig. 3.

The weather and climate predictors were not very successful. There was no evidence for altered migratory propensity in response to prevailing weather conditions during autumn migration (August–September) the same year (Table 7). In line with my expectation, previous winter's NAO showed a clear negative effect on the migratory propensity of Fieldfare (-0.442 ± 0.142). However, no other species showed effects of winter NAO (Table 7).

Table 7: The response of 6 partially migratory species to 3 variables. “Year.C” refer to the centralized years (1975–2014), “Temp.C” is the mean annual August–September temperature, while “NAO.W” is the NAO index for previous winter period December–March. Results are bolded whenever significant according to Šidák's correction for multiple testing (6 species and tests per hypothesis; i.e. $p < 0.00851$).

Variable	Estimate	SE	Wald X^2	df	P
(Sparrowhawk)					
Intercept	1.368	0.175	61.33	1	< 0.001
NAO.W	0.016	0.024	0.465	1	0.495
Temp.C	−0.048	0.046	1.095	1	0.295
Year.C	0.057	0.005	126.4	1	< 0.001
(Blue tit)					
Intercept	0.254	0.569	0.199	1	0.656
NAO.W	−0.055	0.036	2.330	1	0.127
Temp.C	0.030	0.051	0.345	1	0.557
Year.C	−0.027	0.013	4.776	1	0.029
(Common Gull)					
Intercept	1.775	0.276	41.46	1	< 0.001
NAO.W	−0.043	0.050	0.766	1	0.381
Temp.C	−0.176	0.093	3.598	1	0.058
Year.C	−0.040	0.010	15.68	1	< 0.001
(Red Kite)					
Intercept	1.578	0.056	797.3	1	< 0.001
NAO.W	−0.039	0.035	1.278	1	0.258
Temp.C	−0.038	0.069	0.294	1	0.588
Year.C	−0.049	0.009	28.38	1	< 0.001
(Fieldfare)					
Intercept	−0.226	0.384	0.347	1	0.556
NAO.W	−0.442	0.166	7.113	1	0.0077
Temp.C	−0.328	0.326	1.015	1	0.314
Year.C	0.000	0.034	0.000	1	0.992
(Mallard)					
Intercept	−0.317	0.404	0.616	1	0.432
NAO.W	−0.008	0.042	0.038	1	0.845
Temp.C	−0.144	0.080	3.228	1	0.072
Year.C	−0.036	0.009	14.62	1	< 0.001

Figure 3: The predicted proportion of migrants in response to "Year" (temporal trend; 1975–2014) in 4 study species with significant trends.

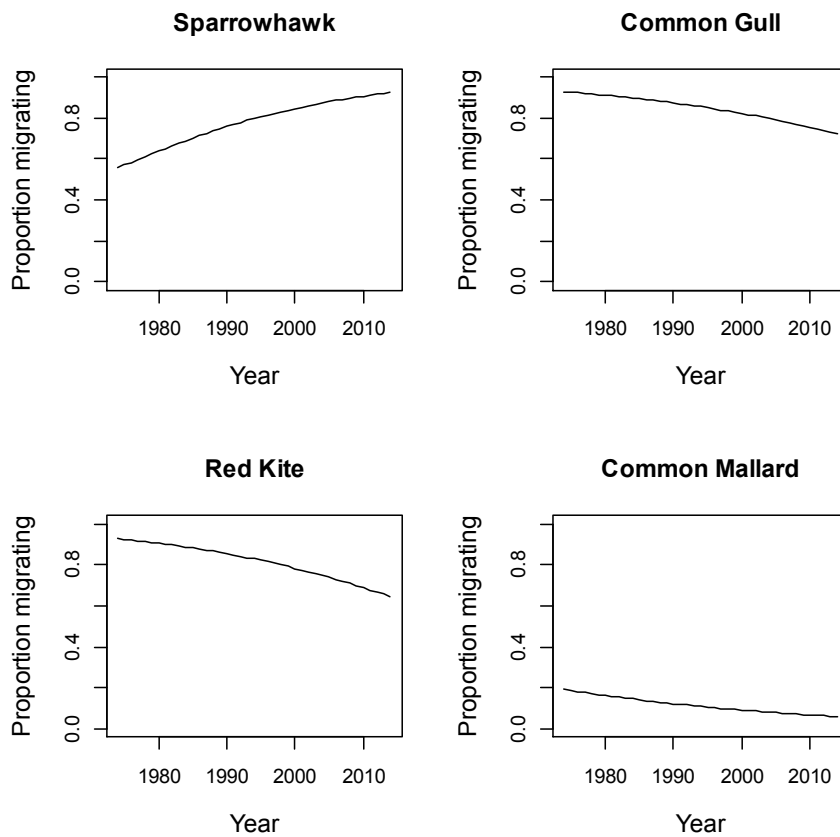
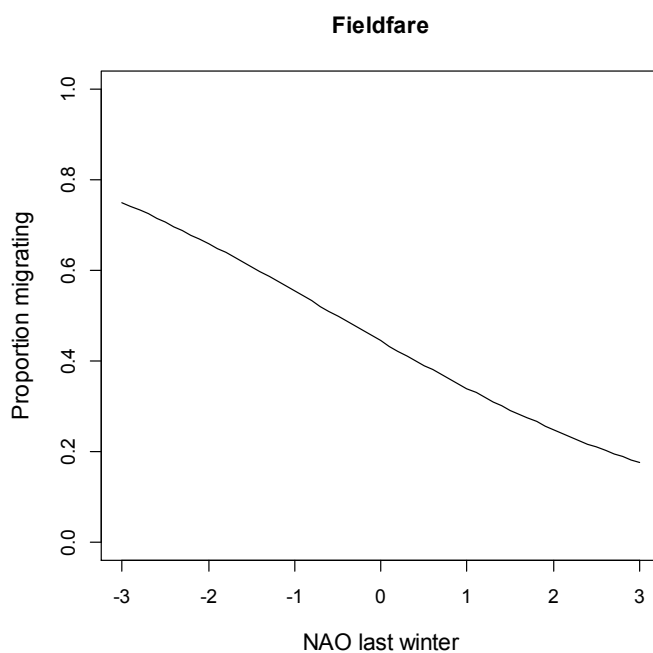


Figure 4: Fieldfares predicted response in the proportion of migrants to NAO (North Atlantic Oscillation last winter). The Y axis represent the proportion between 0 and 1.



3.2 Sex ratio, age and distribution during winter

Males were significantly more common during winter compared to females, with an average proportion of ca 58 % (intercept: 0.318 ± 0.015), and the proportion of males had a clear increasing trend across the whole study period (0.0130 ± 0.0020), with on average 47 % males in 1973 increasing to 61 % in 2014 (coefficients and test statistics in Table 8). The sex ratio also showed a significant humped pattern within a typical winter period, showing a peak of males around New Year (Fig. 5b, Table 8).

Adults wintered significantly more often than young birds, with an average adult proportion of ca 98 % (intercept: 4.054 ± 0.243). The age composition of resident Sparrowhawks showed no temporal trend during the study period 1973–2014, but it showed a significant temporal pattern within a typical winter season, with a clear increase in the proportion of adults after New Year (Fig. 5a; Table 8).

Wintering males were observed on average 15.9 ± 3.3 km further north compared to females (Table 8). Over the study period 1973–2014, the latitudinal point of gravity moved in females ca 0.9 ± 0.3 km / year southwards, while the distribution of males did not change (Table 7). The mean latitudinal location of observed males showed a significant increase within a typical winter period, being fairly stable first (though with a large initial uncertainty), then increasing towards and beyond New Year (Fig. 5c, Table 8).

Figure 5: The variation the ratio of age (a), sex (b) and mean latitude among observed Sparrowhawks during a typical winter season in Sweden, 0 being New Year. Increasing X-axis represents increasing age, more males and higher latitude respectively. The grey area shows the uncertainty based on standard deviation.

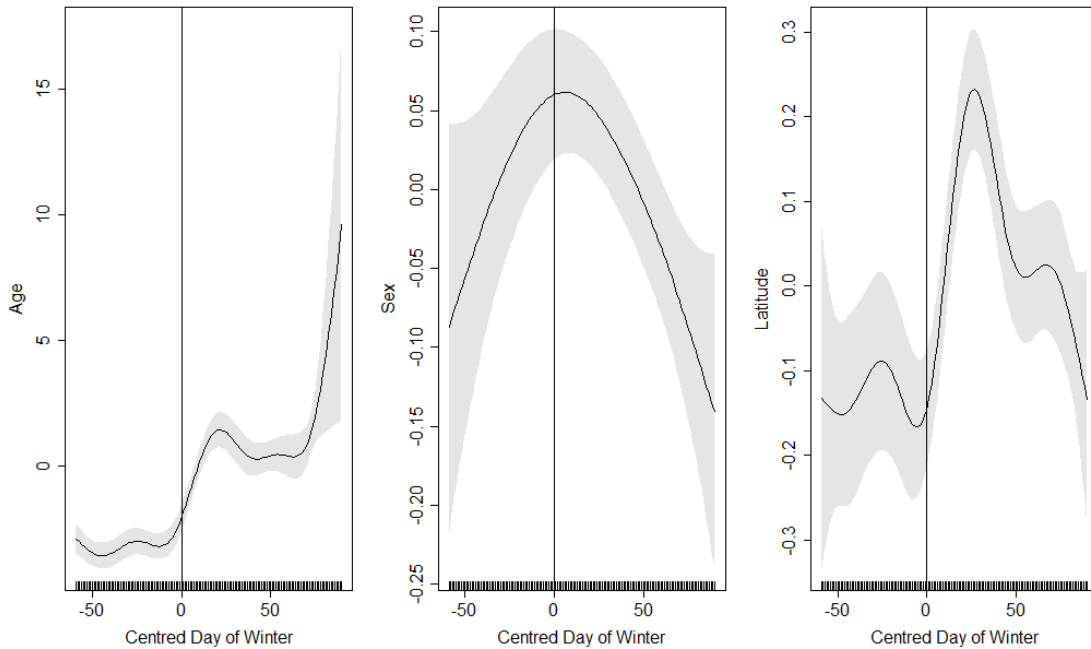


Table 8: Overview of the three models: The Sex and Age model intercepts reflect on average more adult birds and more males, respectively. The centered variable “Year” represent the time period 1973–2014. “s(DOW)” represents Day of Winter, with 0 being New Year. A smoothing function was applied for explaining effects of this variable.

Variable	Estimate	SE	<i>t</i>	<i>F</i>	<i>df</i>	<i>P</i>
Sex (Female = 0, Male = 1)						
Intercept	0.318	0.015	21.72	–	19330	< 0.001
Year	0.013	0.002	6.604	–	19330	< 0.001
s(DOW)	–	–	–	18.75	19330	< 0.001
Age (Young = 0, Adult = 1)						
Intercept	4.054	0.243	17.29	–	6293	< 0.001
Year	0.114	0.009	1.212	–	6293	0.225
s(DOW)	–	–	–	26.29	6293	< 0.001
Latitude						
Intercept	–0.228	0.025	–9.082	–	17180	< 0.001
Sex (Male)	0.159	0.033	–2.864	–	17180	< 0.01
Year	–0.009	0.003	–1.874	–	17180	0.004
Male:Year	0.010	0.005	2.172	–	17180	0.023
s(DOW)	–	–	–	7.521	17180	< 0.001

3.3 Timing of breeding onset and productivity

The number of chicks on the nest increased significantly with earlier laying date (quasi-Poisson regression: -0.0351 ± 0.0159 , $t = -2.204$, $P = 0.044$, $n = 19$). This corresponds to a ca 22 % decrease in productivity, when laying is delayed with one week. Productivity was not significantly different between the two study years 2014 and 2015 (estimated log-difference: -0.0668 ± 0.2567 , $t = -0.260$, $P = 0.798$, $n = 19$).

4 Discussion

4.1. Migratory propensity

As the climate is under constant change, animals must adapt to their new environments. While many aspects of bird migration have been adjusted (Newton 2008), partial migrants might switch from being migratory to resident. Among the six partially migratory bird species in my study, there was no clear-cut common response on the population level to either long-term or short term climate. Here I discuss these results separately, although their implications may overlap in some aspects.

4.1.1 Response to previous winter conditions

The proportion of migrants might be mediated by carry-over effects of past climatic conditions, either as an experience-based choice after a bad winter or strong unequal mortality between resident and migrants. The possibility for such effects was revealed by studying how migratory proportion is influenced by the harshness (*i.e.* winter NAO) the preceding winter. Fieldfare was the only of the studied species that showed such response, with increasingly fewer residents following harsher winter conditions almost a year ahead

(Table 7; Fig. 4). This is the first case where such a relationship is found in a partially migratory bird (*cf.* Meller *et al.* 2016).

Such relationship suggests the two hypothesized causes that unfortunately are not directly distinguishable with the type of data used in this study. Fieldfare seems sensitive to snow covering the food on the ground, seen by reduced body condition among survivors the following spring (Hogstad *et al.* 2003). Therefore, it is plausible that Fieldfare suffers under combination of low food availability and low temperatures. If this leads to entering the breeding season with a sub-optimal body condition, this is generally known to negatively affect breeding success (*e.g.* Chastel 1995). If individuals change migration strategy based on such negative experience, this would present a plastic response to past climate.

The not mutually exclusive alternative is that the fraction of residents which dies is so large that the ratio of residents to migrants is lowered next winter. This is under the assumptions that 1) being migratory or not is partly heritable (Berthold & Querner 1982; Berthold 1990), and that 2) a large enough fraction dies. Assuming that 50 % of the individuals migrate on average, this provides a case in which selection might quickly have visible effects. Winter mortality is well documented, and particularly affects younger individuals (Robinson *et al.* 2007) and birds residing at higher latitudes (Wiklund 1985). Therefore, the lack of evidence until now, even in cold-sensitive species (*cf.* Meller *et al.* 2016) seems somewhat surprising. However, there are several possible sources that could bias my results. Winter NAO used in this study pose a sensible proxy for general winter harshness, but does not reveal shorter periods of extreme weather; events which negatively affect body condition and could result in mortality (Newton 2008). Additionally, the rising numbers of bird feeders, along with hand feeding in parks etc. ensures food supply through

even the harshest winters (Robb *et al.* 2008a,b), which could dampen the sensibility in local residents (Partecke & Gwinner 2007). Moreover, if high resident mortality reduces density, migrants might compensate by opportunistically switch to residency the next autumn. None of the species included in my analyses are known to experience mass mortality during winter, and including particularly sensible species such as Treecreeper (*Certhia familiaris*) (Peach *et al.* 1995), Goldcrest (*Regulus regulus*) (Hogstad 1984) and Wren (*Troglodytes troglodytes*) (Peach *et al.* 1995) would seem as a particular opportunity for studying effects of winter mortality.

Which mechanism (mortality, plasticity or both combined) ultimately affected Fieldfare migratory propensity through preceding winter NAO cannot be concluded from my analysis using unmarked individuals. Whatever the mechanism, my results reveal that carry-over effects are relevant for migratory propensity, and could possibly affect population dynamics as the winter climate keeps warming.

4.1.2 Response to autumn temperatures

If proportion of autumn migrants correlates with the autumn temperature, this suggests that migration or residency is a conditional decision based on the prevailing temperature conditions right before and during the migration period. I found no such responses in any of the six species included in this study (Table 7). This shows that temperature alone is not an important factor for the migratory propensity on a population level. Other factors such as food availability (Nilsson *et al.* 2006; Meller *et al.* 2016) and conspecific density (Nilsson *et al.* 2006) seems more relevant, although their effect is highly species-specific. Food availability and density dependence is known to highly affect the nomadic movement patterns of facultative irruptive migratory species (Lindén *et al.* 2011); specialised on food resources with

highly variable supply, such as seeds, berries, cones and rodents (Newton 2012). The lack of response in the other four terrestrial species probably reflects that their food abundance is not strictly temperature related, at least so early in autumn. While accounting for the annual food abundance for each species would refine the actual effect of temperature, Meller *et al.* (2016) only found migratory propensity in waterfowls to be related to temperature alone. This is not entirely true however, as this was linked to the ice cover in the Baltic Sea correlating with temperature; Ice cover effectively removes both habitat and food availability for such species (Lehikoinen *et al.* 2013). The reason why the aquatic Common Gull and Mallard showed no such response in my study could be due to their more southern location than their Finnish counterparts. If so, this suggests that aquatic species' sensitivity to climatic inter-annual variation increases with latitude.

However, this could also be explained by my usage of the mean August–September temperature; a period which is earlier than when water actually start freezing. This period describes the situation just before migration and in the beginning or peak migration of some of the species, but most continue their migration much later on, sometimes even in fairly large numbers. For example, Blue Tit migration peak clearly in October (Karlsson *et al.* 2004). The mean temperature clearly later, *e.g.* in October–November, could have been a better predictor, if only the later migrants make their migration decision using temperature as a cue, or for waterfowl the freezing of water. Indeed, the first migrants might be individuals intending to migrate anyway, while those considering staying could possibly postpone migration. Including population density as an explanatory variable as such in my model would cause a spurious effect, as any noise in the estimate of population density will occur on both the left and right hand side of the equation. By developing statistical methods

accounting for observation error, such models could produce sensible and interesting additional results.

4.1.3 Long term trends

Climate change alters the environment to which birds must adapt. Over time, warmer winters reduce the hazards posed by winter conditions and improve food availability. It has therefore been hypothesized that partially migratory birds should respond by becoming less migratory (Berthold 2001). Of all the six species studied, I found that Common Gull, Red Kite and Mallard became less migratory during the period 1975–2014 (Table 7; Fig. 3). While this could be linked to improved winter conditions, the crucial factors involved could be unequal between the species. For instance, the both Common Gull and Mallard are aquatic species that is dependent on open water throughout the winter, while this is not important for neither Sparrowhawk, Blue Tit, Red Kite nor Fieldfare. Sweden has a long coastline to the low saline Baltic Sea which has a variable ice cover depending on winter temperatures. During the study period, the mean ice coverage the Baltic Sea decreased (Luomaranta *et al.* 2014) which support that changes in ice cover is of great importance aquatic species. Additionally, similar effects could be expected in freshwater ponds and lakes, but which would typically melt to climate change at a later stage than seawater due to zero salinity.

The increase in residency found in the terrestrial Red Kite was strong (Table 7; Fig. 3), and must be explained by other factors than sea cover. Warmer winters generally provide more frost-free fields which improve rodent hunting (Newton 2010), which is the main prey for Red Kite (Carter 2007). Also, the reduced winter harshness ultimately leads to lower metabolic stress, which poses a large challenge on residents. While the two obvious winter stressors have indeed improved; food availability and thermal stress, there are other factors

concerning Red Kite that should be addressed. The species has been subject to long-term restoration projects with the aim to prevent extinction in Sweden. During the study period of this study, the Swedish population increased from 50 to 2000 (Evans & Pienkowski 1991). This is a significant increase would likely not occur naturally. The projects involved winter feeding by providing carcasses throughout the winter, and the nesting areas have been protected from forestry. However, despite the large increase in population size, the main abundance of Swedish Red Kite seems to have remained located in Southern Sweden (Carter 2007). Here the climate was governed by mild winters even before the study period (Alexandersson & Edquist 2006), which questions the direct benefits from the rising temperatures on both metabolism and hunting. I suggest it to be likely that climate change has to some degree facilitated winter conditions for Red Kite, but likely in combination with a larger effect by restoration; both have improved winter conditions which have been positive for the size and robustness of the Swedish Red Kite population. In fact, the magnitude of the project effort could in light of this thesis be seen as an experiment showing that the proportion of residents does increase when winter conditions are artificially improved. However, such interpretations of my results are done without concluding that this effect is due to temperature alone (*cf.* Berthold 2001).

Sparrowhawk unexpectedly became drastically more migratory throughout the study period (Table 7; Fig. 3). This response is in the opposite direction than I found for Common Gull, Mallard and Red Kite. The ecological explanation for such opposite effect seems not straight forward, by a response contrary the hypothesized increase in residency. Responses in the same direction have earlier only been found in Finnish Greenfinchs (Meller *et al.* 2016) and indicated for Swedish Blue Tits (Nilsson *et al.* 2006). There were likely not any drastic changes in the winter food abundance for Swedish Sparrowhawks along the study period, as

this raptor prey on a broad selection of small birds. If anything, the food abundance have increased due to the increasing number of bird feeders which attracts larger number of easy prey (Robb *et al.* 2008a,b). However, the population size of Sparrowhawks has increased in Sweden during the study period (Green & Lindström 2014; Birdlife International 2015). This could possibly introduce effects from density dependence, which could possibly force relatively more individuals to migrate (Kokko & Lundberg 2001; Lundberg 1988). However, such population increase in elevated density if their breeding range has remained constant, then inhabiting more birds. This is not the case as the Sparrowhawks in Sweden have shifted their breeding ranges northwards (Ottvall *et al.* 2008).

While Berthold (2001) hypothesize a response when local habitats get warmer, he does not visualize a scenario when the population itself moves into different climate zones. In both cases the experienced climate is changed, but the way this change did arise differs. Given that improved winter habitats promote residency, as seen in this study by Common Gull, Mallard and Red Kite, worsening might provide an opposite response. Although being somewhat speculative and not directly testable with my data, I suggest the possibility that Sparrowhawks in their novel northern habitats is responding to their local winter harshness by becoming more migratory. In this way, an evolving tendency to migrate away could re-appear in the population. The ability to adapt to new distribution areas has been previously seen in House Sparrows in America, in which individuals originating from sedentary populations quickly became migratory when introduced to areas with harsher climate (Able & Berthoff 1998). Also, a northward expansion of Serin in Europe resulted in the northern populations being fully migratory, partially migratory in the middle and fully resident along the south end of their distribution range (Mayr 1926). This illustrates the presence of reaction norms by expressing different phenotypes in different conditions.

4.2 Why overwinter?

Differential behaviour among partial migrants raises questions on the asymmetric selection pressures among individuals within a species; why do some individuals migrate significant distances while others are year-round residents?

By studying resident Sparrowhawks, I found clear temporal patterns in 1) sex ratio, 2) winter age segregation, and 3) latitudinal point of gravity, both as long-term (sex specific) temporal trends and within-season patterns.

As expected, males and adults overwintered significantly more often than females and young, respectively, an asymmetry which increased over the study period for the proportion of males. Within a winter season, the proportion of adults increased while the proportion of males peaked around New Year. The latitudinal point of gravity moved for females southwards throughout the study period, while it remained unchanged in males. These results are compared to the presented hypotheses (Table 2).

4.2.1 Wintering sex ratio

I found that more males overwintered than females during an average winter (Table 8). This clearly shows that the winter season is dominated by the sex with smallest body size. This alone gives firm support to the Arrival Time hypothesis (Ketterson & Nolan 1976) by displaying that superior body size does not facilitate residency. This theory assumes that early presence on breeding sites gives a competitive advantage over migratory, later arriving individuals. Residency might therefore result in acquiring territories of better quality than if being migratory (Kokko *et al.* 2006). Furthermore, early onset is often associated with

increased productivity (*e.g.* Klomp 1970) – a general pattern which based on my own data seems to be the case also for Nordic Sparrowhawks (see section 3.3.).

Additionally, this proportion of males increased throughout the study period 1973–2014 (Table 8). This might reflect a conditional strategy; a warming climate promotes residency as the optimal strategy for an increasing number of males. One reason for this could possibly be explained by combination of elements from both Arrival time hypotheses and body size hypothesis; as the inferior sized male benefit from successful residency, a warming climate would gradually reduce winter mortality. This result suggests that the predictions of Arrival Time pose a gradually stronger selection on males to reside due to climate change.

Besides the gains by early arrival, males seem to risk mortality from residency. Within a typical winter, the male proportion increased until a peak around New Year, and then declined towards the end of the winter (Fig. 5b). While the initial increase might reflect late migration of females, the increase of males after New Year could reflect ongoing winter mortality in males.

First, the Body Size hypothesis (Ketterson & Nolan 1976) states that larger individuals should be more likely to overwinter due to their superior thermal capacity. However, the fact that more males overwintered, which is half the size of females (Newton 1986; Dunning 2008) does not support the Body Size Theory.

Second, the Dominance hypothesis (Gauthreaux 1982) predicts dominant individuals to reside while expelling subordinates. Since females are subordinate to males, the larger fraction of resident males does not suggest dominance to be the determining trait for residency.

However, that early onset benefits males alone might not be entirely true; the “mate opportunity hypothesis”, regarding fully migratory birds, states that competition between females is stronger than that between males early in the season, since males with territory (resource for females) are initially scarcer than the number of territories (resource for males) (Kokko *et al.* 2006). This would explain why females are present at all latitudes. Being the first study on the topic using on a species with strong RSD, this novel result provide the first firm evidence that superior body size might indeed not be the trait currently facilitating residency.

4.2.2 Wintering age structure

There was on average more adults than juveniles during an average winter (Table 8). While this, when looked upon separately, could add support to Dominance theory (juveniles expelled), the age ratio followed a within-seasonal pattern of gradually more adults (Table 8; Fig. 5). This probably instead reflects a high juvenile mortality which indicates residency being a poor strategy for unexperienced individuals. Fitting to this picture, juvenile Sparrowhawks of both sexes dominate the annual autumn migration (70–80 %) over Falsterbo (Nils Kjellén unpubl. data). As a possible bias, the age ratio might theoretically be explained by that males reside more in winter combined with the lower chance of an arbitrary female to be age determined.

4.2.3 Latitudinal distribution of wintering Sparrowhawks

I found a clear latitudinal segregation of sex during winter (Table 8; Fig 5 c); males generally wintered further north compared to females. Such segregation would not be expected from a survival perspective based on body size; the prevalence of the larger-sized females decrease with increasing climatic harshness, as illustrated by the Köppen–Geiger classifications across Sweden (Kottek *et al.* 2006). As the climate harshness increase toward the north, fewer

individuals without any ecological gains from residency should theoretically reside. It adds evidence to Arrival Time theory by displaying that the gain of early arrival offset the elevated cost of residing even in Nordic winter conditions. Throughout the study period (1973–2014), males resided at the same latitudes, while in females gradually moved southwards at a rate of approx. 900 m annually (Table 8). A possible explanation could be milder climate allowing an increasing number of small males to reside, which in turn might further lead to increased competition and poorer wintering conditions for females. While my results do not suggest males traversing northwards, the detectability could be dampen by 1) small-scale southbound migration prior to the observer period used in my study, and 2) asymmetric latitudinal density of winter census routes.

Within an average winter, individuals (regardless of sex) were observed at increasing latitudes as the season progressed, probably reflecting a mid-winter avoidance of the areas at higher latitudes. This pattern provided surprising evidence for a third or intermediate migratory strategy, suggesting that many “resident” individuals indeed perform migration, but on a much smaller scale than earlier emphasized. Thus, they might combine the best of two worlds; moving away from the most acute winter conditions, still being able to arrive early in spring. By not crossing major migratory passages in the migration period, such movements would not be picked up by Bird Observatories; the data used in most studies of migration, also being the measure for migratory behaviour in this study.

In fact, this does again support the arrival time hypothesis, but on a scale not earlier considered for partial migrants. Several studies have approached and supported the arrival time hypothesis (Table 2) by focussing on intraspecific migration distances in fully migratory species (*i.e.* differential migration) (Cristol *et al.* 1999), for which the theory was originally

proposed. If the spatial gap between breeding and wintering areas increase for northerly residents (given stationary or retracting winter areas), this would actually initiate migratory behaviour occurring predominantly on a small spatial scale. If this means that northerly individuals wander south into areas dense with southern residents, this could perhaps trigger full-scale migratory behaviour due to a “leap-frog migration” effect (Boland 1990; Cristol *et al.* 1999). Further detailed studies are needed to validate these movements, and their extent among species and between areas.

5 Conclusions & Future studies

In this thesis, I studied several aspects of how partial migrants could be affected by both short-term weather and long-term climate change. This was addressed by the several hypotheses raised in this thesis.

1. Effects of the harshness last winter on the proportion of migrants

This study is to my knowledge the first that show carry-over effect from last winter on the proportion of migrants. While such effects could in part be expected, the lack of evidence up to now might largely be due to the lack of similar studies. Since partial migration could be partially affected by many factors simultaneously, this stresses the need for future studies to sort out the many factors which could be involved. The results on Fieldfare presented a typical situation where several, not mutually exclusive, explanations could be suggested. Accounting for individual life history would greatly improve our understanding of the topic, either by using modern tracking devices or opportunistically studying species where such data are easy to collect.

2. Effects of autumn temperature on the proportion of migrants

There was a lack of effect on the six study species from early autumn temperature. It suggests in part that my study species is not sensitive to climatic cues so early in autumn, and in part be due to not accounting for food abundance. Food might be the most important single factor affecting migration, visualised by the irruptive migration patterns of facultative species. Additionally, the actual response on food abundance is probably highly species-specific, and should be included in future similar studies.

3. Temporal response in migratory propensity to climate change

4 out of 6 species showed long-term trends in migratory propensity. This has important implications for future population dynamics if global warming persists. Especially, this could have large effects on marine and aquatic species which depends on open water. Studying seabirds at higher latitudes would be particularly interesting as the ice melts. However, the opposite response than expected shown in Sparrowhawk indicate response to larger underlying patterns that is not currently known. This might be due to a northern traverse in of the breeding ranges. Future studies should also address changes in breeding ranges, and perhaps also account for altered conditions in the winter areas for the birds that migrate south.

4-6. Arrival Time, Body size and Dominance

The evidence for Arrival Time hypothesis is clear; the smaller males reside more than the larger females. Additionally, it seems like males exploit the opportunity to increase in residency as warmer climate reduce the winter mortality. As far as my knowledge, this is the first study that allows a separation between Arrival Time and Body Size/Dominance by studying species with reversed size dimorphism. By studying more species simultaneously,

preferably with reversed size dimorphism, would give more insights of the generality of this hypothesis.

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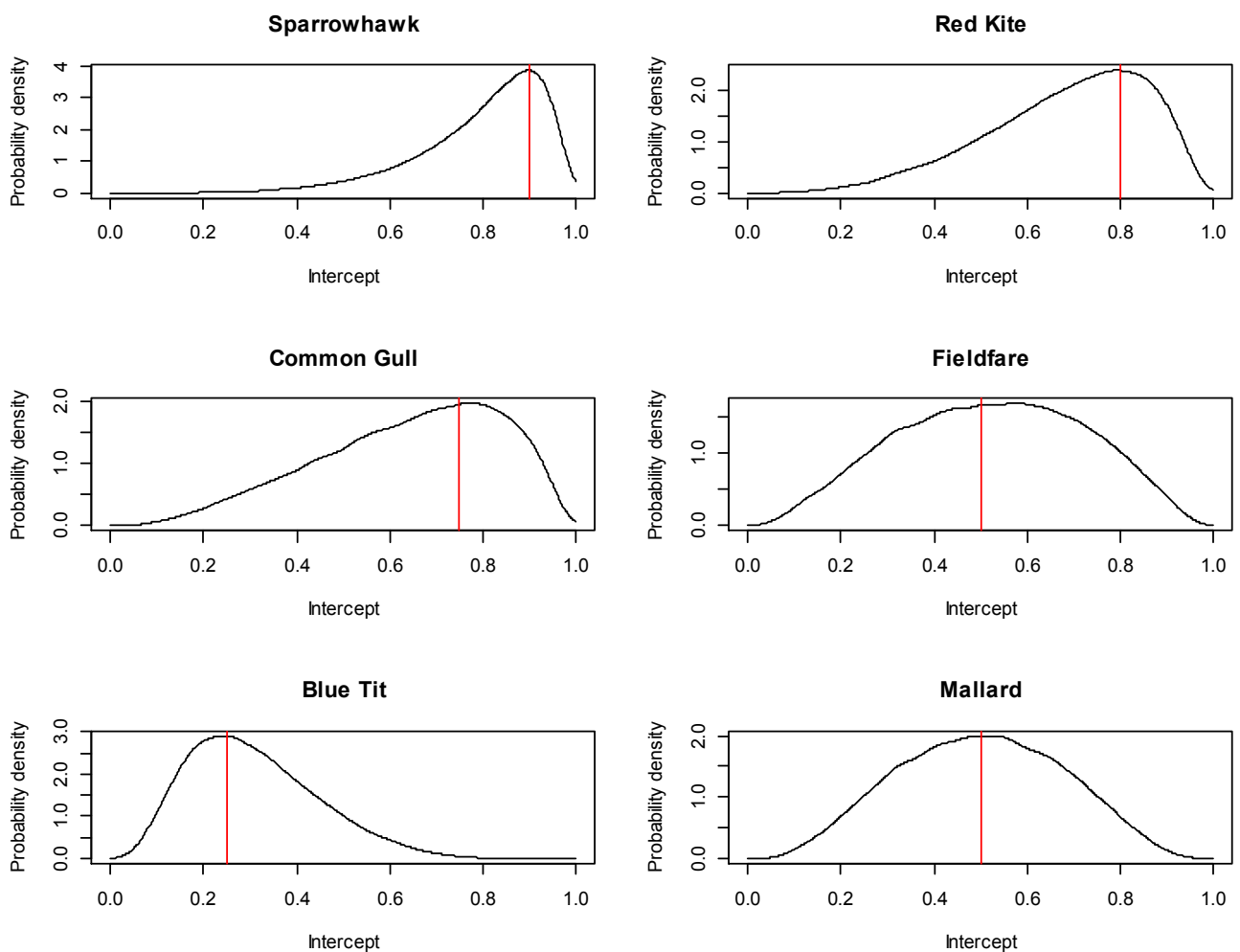
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Appendices

Appendix 1

The prior uncertainty of the intercept (a_0) in the six study species is assumed to be normally distributed. With centred continuous variables, the assumptions for the average proportion migrating can be illustrated using expit-transformed normal distributions. The figures are constructed by kernel density estimation from 50 000 pseudorandom normal and expit-transformed numbers. The red vertical lines indicate typical values around which the prior probabilities are most likely.



Appendix 2

Code for the R-function used to study the annual migrating proportion in a single population, based on abundance indices of autumn migration, wintering and breeding. The code is written by Andreas Lindén as part of another piece of work in preparation, and published here with the consent of the author.

```
#MIGR.PROP.PENALIZED: Estimate and explain variation in the migrating proportion
# of birds in a population. The function does penalized maximum likelihood
# fitting of the model:
#
#  $P[t] = \text{expit}(a_0 + X[t,1]*b[1] + X[t,2]*b[2] \dots + X[t,k]*b[k])$ 
#  $M[t] = a_1 * N[t] * P[t] * \exp(\text{Err}[t,1])$ 
#  $W[t] = a_2 * N(t) * (1-P[t]) * \exp(\text{Err}[t,2])$ 
#  $\text{Err}[t,:] \sim \text{Bivariate Normal}([0 \ 0], \text{Cov})$ 
#
# SYNTAX: migr.prop.penalized(M, W, N, X = NA, a0.m = 0, a0.sd = 0, boot = 200)
#
# INPUT:
#
# M      - Index for number of migrating individuals
# W      - Index for number of wintering individuals
# N      - Index for post-breeding density (or breeding density)
# X      - Matrix of covariates affecting the proportion migrating
# a0.m   - Average intercept in normally distributed prior (default 0)
# a0.sd  - Standard deviation in normally distributed prior
#        (by default 0; i.e. a0 fixed)
# boot   - Number of bootstrap repetitions for SEs (by default 200)
#
# OUTPUT: All output is given in a list, with the following parts
#
# $b      - Estimated regression coefficients
# $SE.b   - Standard errors of estimates
# $Cov.b  - Variance-covariance matrix of estimates
# $Wald   - Wald statistics for estimated effects compared to zero (df = 1)
# $p.val  - Wald test p-values for null hypothesis of zero coefficients
# $a      - Constant parameters a1 and a2
# $Cov.R  - Variance-covariance matrix of residuals
# $neg.LL - The minimized negative log likelihood
# $K      - Number of estimated parameters
# $AIC    - Akaike information criterion
# $P      - Fitted proportion of migrants
# $R      - Residuals (estimated Err(t,:))
#
# © Andreas Lindén, 23th August 2015
# Last updated: 23rd August 2015
#
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migr.prop.penalized = function(M, W, N, X = NA, a0.m, a0.sd = 0, boot = 200){

#####
migr.prop.eval = function(b,M,W,N,X,a0.m,a0.sd){

# Number of observations
n = length(M)

# Calculate the probability of migrating
Xb = X %*% b
P = 1 / (exp(-Xb)+1)

# Bivariate data matrix
```

```

Y = cbind(log(M)-log(N)-log(P), log(W)-log(N)-log(1-P))

# Bivariate normal residuals
m = apply(Y,2,"mean")
R = cbind(Y[,1]-m[1], Y[,2]-m[2])

# Estimate variance covariance matrix
C = t(R) %*% R / n

# Calculate log-likelihood evaluated at a0
const = n*2*log(2*pi)+n*log(det(C))
dY = (R %*% solve(C)) * R
mvLL = -(const+sum(dY)) / 2

# Evaluate penalized neg. log likelihood
lnL.a0 = dnorm(b[1], mean = a0.m, sd = a0.sd, log = TRUE)
nLL = -(lnL.a0+mvLL)
return(nLL)
}

#####

# Build design matrix
n = length(M)

if (all(is.na(X))){
  X = matrix(1,n,1)
} else {
  X = cbind(matrix(1,n,1),X)
}

# Number of explanatory parameters
k = ncol(X)

# Find the maximum likelihood estimate of "b"
# (minimize the neg. log-likelihood)
ctrl = list(maxit = 20000, reltol = 1e-15)
par0 = rep(0,k)
par0[1] = a0.m
opt.result = optim(par0, migr.prop.eval, method = "Nelder-Mead",
  control = ctrl, hessian = TRUE, M = M, W = W,
  N = N, X = X, a0.m = a0.m, a0.sd = a0.sd)
b = opt.result$par
neg.LL = opt.result$value

# Calcualte AIC
K = k+5
AIC = 2*neg.LL + 2*K

# Calculate the probability of migrating
P = 1/(exp(-X %*% b)+1)

# Get the other parameters
Y = cbind(log(M)-log(N)-log(P), log(W)-log(N)-log(1-P))
m = apply(Y,2,"mean")
R = cbind(Y[,1]-m[1], Y[,2]-m[2])
a1 = exp(m[1])
a2 = exp(m[2])
Cov.R = (t(R) %*% R) / n

# Estimate SE:s through parametric bootstrap
if (boot > 0){
  B = matrix(NA,k,boot)
  Xi = X[,2:k]
  library(mvtnorm)

  for (i in 1:boot){
    lnZi = cbind(log(N)+log(P), log(N)+log(1-P)) + rmvnorm(n,m,Cov.R)

```

```

        Mi = exp(lnZi[,1])
        Wi = exp(lnZi[,2])
        mod.i = migr.prop.penalized(Mi,Wi,N,Xi,a0.m,a0.sd,boot = 0)
        B[,i] = mod.i$b
    }

    Cov.b = cov(t(B))

} else {
    Cov.b = matrix(NA,k,k)
}

# Standard errors
SE.b = sqrt(diag(Cov.b))

# Wald tests
Wald = (b/SE.b)^2
p.val = 1-pchisq(Wald,1)

# Assign statistics
return(list(b = b, SE.b = SE.b, Cov.b = Cov.b, Wald = Wald, p.val = p.val,
          a1 = a1, a2 = a2, Cov.R = Cov.R, neg.LL = neg.LL, K = K,
          AIC = AIC, P = P, R = R))
}

```

Appendix 3

Calculating discontinuity effects of the observer shift in 2001

```
#####
# 0. Loading and adjusting data

remove(list = ls())

# Open Species_trendprop_Dataset5.csv
X = read.csv("")

head(X)
str(X)
X$Observer_ID = as.factor(X$Observer_ID)

#####
# 1. Testing the effect of observer effect on migration counts

# Fit negative binomial GAM
library(mgcv)

# Sparrowhawk
Accnis_results = gam(Accnis_M_corr ~ s(Year) + Observer_ID, family = nb(link=log),
data = X)
summary(Accnis_results)

# Blue Tit
Cyacaer_results = gam(Cyacaer_M ~ s(Year) + Observer_ID, family = nb(link=log),
data = X)
summary(Cyacaer_results)

# Common Gull
Larcan_results = gam(Larcan_M_corr ~ s(Year) + Observer_ID, family = nb(link=log),
data = X)
summary(Larcan_results)

# Red Kite
Milmil_results = gam(Milmil_M ~ s(Year) + Observer_ID, family = nb(link=log), data
= X)
summary(Milmil_results)

# Fieldfare
Turpil_results = gam(Turpil_M ~ s(Year) + Observer_ID, family = nb(link=log), data
= X)
summary(Turpil_results)

# Mallard
Aplatyr_results = gam(Aplatyr_M ~ s(Year) + Observer_ID, family = nb(link=log),
data = X)
summary(Aplatyr_results)

#####
# 2. Calculating correction coefficients and adjust data (in Xadj)

Xadj = X
i.adj = (Xadj$Observer_ID == "3")

# Correction coefficients:
# How much many times more birds did Kjellen [3] see compared to Roos [2]?
# cc > 1 means Kjellen had more
# cc < 1 means Roos had more
```

```

#cc_Accnis = 1/exp(coef(Accnis_results)[2])
#Xadj$Accnis_M[i.adj] = round(cc_Accnis * Xadj$Accnis_M[i.adj])

#cc_Cyacaer = 1/exp(coef(Cyacaer_results)[2])
#Xadj$Cyacaer_M[i.adj] = round(cc_Cyacaer * Xadj$Cyacaer_M[i.adj])

cc_Larcan = 1/exp(coef(Larcan_results)[2])
Xadj$Larcan_M[i.adj] = round(cc_Larcan * Xadj$Larcan_M[i.adj])

#cc_Milmil= 1/exp(coef(Milmil_results)[2])
#Xadj$Milmil_M[i.adj] = round(cc_Milmil * Xadj$Milmil_M[i.adj])

#cc_Turpil = 1/exp(coef(Turpil_results)[2])
#Xadj$Turpil_M[i.adj] = round(cc_Turpil * Xadj$Turpil_M[i.adj])

#cc_Aplatyr = 1/exp(coef(Aplatyr_results)[2])
#Xadj$Aplatyr_M[i.adj] = round(cc_Aplatyr * Xadj$Aplatyr_M[i.adj])

#####
# 3. Plotting the migration data for all species

par(mfrow = c(2,3))

# Plot Accnis
M.hat_Accnis = fitted.values(Accnis_results)
plot(X$Year, X$Accnis_M, type = "p", xlab = "Year", ylab = "N migrating",
      main = "Sparrowhawk", ylim = c(1, 50000))
points(Xadj$Year[i.adj], Xadj$Accnis_M[i.adj], col = "red")
lines(X$Year, M.hat_Accnis)
abline(v = 2000.5, col = "red")

# Plot Milmil
M.hat_Milmil = fitted.values(Milmil_results)
plot(X$Year, X$Milmil_M, type = "p", xlab = "Year", ylab = "N migrating",
      main = "Red Kite", ylim = c(0, 4000))
points(Xadj$Year[i.adj], Xadj$Milmil_M[i.adj], col = "red")
lines(X$Year, M.hat_Milmil)
abline(v = 2000.5, col = "red")

# Plot Larcan
M.hat_Larcan = fitted.values(Larcan_results)
plot(X$Year, X$Larcan_M, type = "p", xlab = "Year", ylab = "N migrating",
      main = "Common Gull", ylim = c(1, 14000))
points(Xadj$Year[i.adj], Xadj$Larcan_M[i.adj], col = "red")
lines(X$Year, M.hat_Larcan)
abline(v = 2000.5, col = "red")

# Plot Turpil
M.hat_Turpil = X$Turpil_M
M.hat_Turpil[!is.na(M.hat_Turpil)] = fitted.values(Turpil_results)
plot(X$Year, X$Turpil_M, type = "p", xlab = "Year", ylab = "N migrating",
      main = "Fieldfare", ylim = c(0, 60000))
points(Xadj$Year[i.adj], Xadj$Turpil_M[i.adj], col = "red")
lines(X$Year, M.hat_Turpil)
abline(v = 2000.5, col = "red")

# Plot Cyacaer
M.hat_Cyacaer = fitted.values(Cyacaer_results)
plot(X$Year, X$Cyacaer_M, type = "p", xlab = "Year", ylab = "N migrating",
      main = "Blue Tit", ylim = c(1, 400000))
points(Xadj$Year[i.adj], Xadj$Cyacaer_M[i.adj], col = "red")
lines(X$Year, M.hat_Cyacaer)
abline(v = 2000.5, col = "red")

# Plot Aplatyr
M.hat_Aplatyr = X$Aplatyr_M
M.hat_Aplatyr[!is.na(M.hat_Aplatyr)] = fitted.values(Aplatyr_results)

```

```

plot(X$Year, X$Aplatyr_M, type = "p", xlab = "Year", ylab = "N migrating",
     main = "Mallard", ylim = c(0, 800))
points(Xadj$Year[i.adj], Xadj$Aplatyr_M[i.adj], col = "red")
lines(X$Year, M.hat_Aplatyr)
abline(v = 2000.5, col = "red")

#####
# 5. Falsterbo annual mean temperatures for Aug-Sep

# Open Falsterbo_temp_full_dataset.csv
Temp_data = read.csv("C:/Users/Andreas/Dropbox/Rovfugl/Partial
Migration/Arbeidsmappe høst
15/Proportion migration/Falsterbo data beregning
observer/Falsterbo_temp_full_dataset.csv")
na.omit(Temp_data)
head(Temp_data)

# Create subset with temperature data from month 8-9, and 1975-2013
Temp_data.fall = Temp_data[Temp_data$Month == 8 | Temp_data$Month == 9, ]
Temp_data.fall = Temp_data.fall[Temp_data.fall$Year > 1974,]
Temp_data.fall = Temp_data.fall[Temp_data.fall$Year < 2014,]

# Get annual means and put into the data frames
Mean_temp = aggregate(Temp ~ Year, data = Temp_data.fall, FUN = mean)
X$Temp = Mean_temp$Temp
Xadj$Temp = Mean_temp$Temp
Xadj$Temp

## ADDITIONALLY:
# How did the mean temperature increase during 1975-2013 month 8-9?
plot(Mean_temp, main= "Mean annual temperature Aug-Sep", ylab= "Mean T Aug-Sep")

# Testing with linear model
Temp_trend = lm(Temp~Year, data= Mean_temp)
summary(Temp_trend)

# Adding the regression line to the former plot
abline(Temp_trend, lwd=1)

#####
# Previous Winter NAO:

NAO_INDX = read.table("")
head(NAO_INDX)

# naming columns
colnames(NAO_INDX)[1] == "Year"
colnames(NAO_INDX)[2] == "Win.index"

# Subset according to year.
NAO_INDX = NAO_INDX[which(NAO_INDX$Year > 1974 & NAO_INDX$Year < 2014),]

# Include subset winter NAO to the data frame "X" and "Xadj"
X$NAO_W = NAO_INDX$Win.index
Xadj$NAO_W = NAO_INDX$Win.index

#####
# 6. Partial migration population analysis

# Set current working directory (path for where the files are stored)
setwd("")

# Source function

```



```

source("migr.prop.penalized.R")

# Set data, remove rows with NAs, center covariates (Year and Temp)
ANIS = data.frame(Year = X$Year, M = X$Accnis_M, W = X$Accnis_W , N = X$Accnis_N,
                  Temp = X$Temp, NAO = X$NAO_W)
ANIS = na.omit(ANIS)
ANIS$Year.C = ANIS$Year - mean(ANIS$Year)
ANIS$Temp.C = ANIS$Temp - mean(ANIS$Temp)

CCAEX = data.frame(Year = X$Year, M = X$Cyacaer_M, W = X$Cyacaer_W , N =
X$Cyacaer_N,
                  Temp = X$Temp,NAO = X$NAO_W)
CCAEX = na.omit(CCAEX)
CCAEX$Year.C = CCAEX$Year - mean(CCAEX$Year)
CCAEX$Temp.C = CCAEX$Temp - mean(CCAEX$Temp)

D = Xadj # only species applied with correction factor
LCAN = data.frame(Year = D$Year, M = D$Larcan_M, W = D$Larcan_W , N = D$Larcan_N,
                  Temp = D$Temp,NAO = D$NAO_W)
LCAN = na.omit(LCAN)
LCAN$Year.C = LCAN$Year - mean(LCAN$Year)
LCAN$Temp.C = LCAN$Temp - mean(LCAN$Temp)

MMIL = data.frame(Year = X$Year, M = X$Milmil_M, W = X$Milmil_W , N = X$Milmil_N,
                  Temp = X$Temp,NAO = X$NAO_W, boot = 10000)
MMIL = na.omit(MMIL)
MMIL$Year.C = MMIL$Year - mean(MMIL$Year)
MMIL$Temp.C = MMIL$Temp - mean(MMIL$Temp)

TPIL = data.frame(Year = X$Year, M = X$Turpil_M, W = X$Turpil_W , N = X$Turpil_N,
                  Temp = X$Temp,NAO = X$NAO_W)
TPIL = na.omit(TPIL)
TPIL$Year.C = TPIL$Year - mean(TPIL$Year)
TPIL$Temp.C = TPIL$Temp - mean(TPIL$Temp)

APLT = data.frame(Year = X$Year, M = X$Aplatyr_M, W = X$Aplatyr_W , N =
X$Aplatyr_N,
                  Temp = X$Temp,NAO = X$NAO_W)
APLT = na.omit(APLT)
APLT$Year.C = APLT$Year - mean(APLT$Year)
APLT$Temp.C = APLT$Temp - mean(APLT$Temp)

##### TEMP & NAO #####
# Fit the models through penalized maximum likelihood estimation
ANISX = cbind(ANIS$Year.C, ANIS$Temp.C, ANIS$NAO)
ANIS.res = migr.prop.penalized(ANIS$M, ANIS$W, ANIS$N, ANISX, 2.3, 0.5, boot =
10000)

CCAEX = cbind(CCAEX$Year.C, CCAEX$Temp.C, CCAEX$NAO)
CCAEX.res = migr.prop.penalized(CCAEX$M, CCAEX$W, CCAEX$N, CCAEX, -0.7, 1.44,
boot=10000)

LCANX = cbind(LCAN$Year.C, LCAN$Temp.C, LCAN$NAO)
LCAN.res = migr.prop.penalized(LCAN$M, LCAN$W, LCAN$N, LCANX, 0.8, 0.6, boot=10000)

MMILX = cbind(MMIL$Year.C, MMIL$Temp.C, MMIL$NAO)
MMIL.res = migr.prop.penalized(MMIL$M, MMIL$W, MMIL$N, MMILX, 1.4, 0.3, boot=10000)

TPILX = cbind(TPIL$Year.C, TPIL$Temp.C, TPIL$NAO)
TPIL.res = migr.prop.penalized(TPIL$M, TPIL$W, TPIL$N, TPILX, 0.1, 0.7, boot=10000)

APLTX = cbind(APLT$Year.C, APLT$Temp.C, APLT$NAO)
APLT.res = migr.prop.penalized(APLT$M, APLT$W, APLT$N, APLTX, -0.0, 0.8,
boot=10000)

#####

```

```

# Put main results in neat tables
Accnis.result = data.frame(Parameter = c("Intercept", "Year.C", "Temp.C", "NAO_Win"),
                            Estimate = ANIS.res$b, SE = ANIS.res$SE.b,
                            Wald.stat = ANIS.res$Wald, df = c(1,1,1,1), p =
ANIS.res$p.val)
Accnis.result$pSig = (Accnis.result$p <= p.sig)
Accnis.result$p = round(Accnis.result$p, digits = 3)
Accnis.result$Wald.stat = round(Accnis.result$Wald.stat, digits = 3)
Accnis.result$SE = round(Accnis.result$SE, digits = 3)
Accnis.result$Estimate = round(Accnis.result$Estimate, digits = 3)
Accnis.result

Cyacaer.result = data.frame(Parameter = c("Intercept", "Year.C", "Temp.C", "NAO_Win"),
                            Estimate = CCAE.res$b, SE = CCAE.res$SE.b,
                            Wald.stat = CCAE.res$Wald, df = c(1,1,1,1), p =
CCAER.res$p.val)
Cyacaer.result$pSig = (Cyacaer.result$p <= p.sig)
Cyacaer.result$p = round(Cyacaer.result$p, digits = 3)
Cyacaer.result$Wald.stat = round(Cyacaer.result$Wald.stat, digits = 3)
Cyacaer.result$SE = round(Cyacaer.result$SE, digits = 3)
Cyacaer.result$Estimate = round(Cyacaer.result$Estimate, digits = 3)
Cyacaer.result

Larcen.result = data.frame(Parameter = c("Intercept", "Year.C", "Temp.C", "NAO_Win"),
                            Estimate = LCAE.res$b, SE = LCAE.res$SE.b,
                            Wald.stat = LCAE.res$Wald, df = c(1,1,1,1), p =
LCAE.res$p.val)
Larcen.result$pSig = (Larcen.result$p <= p.sig)
Larcen.result$p = round(Larcen.result$p, digits = 3)
Larcen.result$Wald.stat = round(Larcen.result$Wald.stat, digits = 3)
Larcen.result$SE = round(Larcen.result$SE, digits = 3)
Larcen.result$Estimate = round(Larcen.result$Estimate, digits = 3)
Larcen.result

Milmil.result = data.frame(Parameter = c("Intercept", "Year.C", "Temp.C", "NAO_Win"),
                            Estimate = MMIL.res$b, SE = MMIL.res$SE.b,
                            Wald.stat = MMIL.res$Wald, df = c(1,1,1,1), p =
MMIL.res$p.val)
Milmil.result$pSig = (Milmil.result$p <= p.sig)
Milmil.result$p = round(Milmil.result$p, digits = 3)
Milmil.result$Wald.stat = round(Milmil.result$Wald.stat, digits = 3)
Milmil.result$SE = round(Milmil.result$SE, digits = 3)
Milmil.result$Estimate = round(Milmil.result$Estimate, digits = 3)
Milmil.result

Turpil.result = data.frame(Parameter = c("Intercept", "Year.C", "Temp.C", "NAO_Win"),
                            Estimate = TPIL.res$b, SE = TPIL.res$SE.b,
                            Wald.stat = TPIL.res$Wald, df = c(1,1,1,1), p =
TPIL.res$p.val)
Turpil.result$pSig = (Turpil.result$p <= p.sig)
Turpil.result$p = round(Turpil.result$p, digits = 3)
Turpil.result$Wald.stat = round(Turpil.result$Wald.stat, digits = 3)
Turpil.result$SE = round(Turpil.result$SE, digits = 3)
Turpil.result$Estimate = round(Turpil.result$Estimate, digits = 3)
Turpil.result

Aplatyr.result = data.frame(Parameter = c("Intercept", "Year.C", "Temp.C", "NAO_Win"),
                            Estimate = APLT.res$b, SE = APLT.res$SE.b,
                            Wald.stat = APLT.res$Wald, df = c(1,1,1,1), p =
APLT.res$p.val)
Aplatyr.result$pSig = (Aplatyr.result$p <= p.sig)
Aplatyr.result$p = round(Aplatyr.result$p, digits = 3)
Aplatyr.result$Wald.stat = round(Aplatyr.result$Wald.stat, digits = 3)
Aplatyr.result$SE = round(Aplatyr.result$SE, digits = 3)
Aplatyr.result$Estimate = round(Aplatyr.result$Estimate, digits = 3)
Aplatyr.result

# CHECK RESIDUALS

```

```
dev.new()
par(mfrow = c(2,3))

#ANIS
plot(ANIS$Year.C,ANIS.res$R[,1])
abline(0,0)
plot(ANIS$Year.C,ANIS.res$R[,2])
abline(0,0)

#CCAE
plot(CCAE$Year.C,CCAЕ.res$R[,1])
abline(0,0)
plot(CCAE$Year.C,CCAЕ.res$R[,2])
abline(0,0)

#LCAN
plot(LCAN$Year.C,LCAN.res$R[,1])
abline(0,0)
plot(LCAN$Year.C,LCAN.res$R[,2])
abline(0,0)

#MMIL
plot(MMIL$Year.C,MMIL.res$R[,1])
abline(0,0)
plot(MMIL$Year.C,MMIL.res$R[,2])
abline(0,0)

#TPIL
plot(TPIL$Year.C,TPIL.res$R[,1])
abline(0,0)
plot(TPIL$Year.C,TPIL.res$R[,2])
abline(0,0)

#APLT
plot(APLT$Year.C,APLT.res$R[,1])
abline(0,0)
plot(APLT$Year.C,APLT.res$R[,2])
abline(0,0)
```

Appendix 3

Analysis of winter sex and age proportion, and the latitudinal distribution of sex.

```
# Load dataset
# Remove all observations with more than 1 individual
bort = which(Accnis_Svalan$Nr != 1)
Accnis_Svalan = Accnis_Svalan[-bort, ]

##### DATES TO DOY#####

# CONVERSION
# Extract all dates to independent columns
Accnisdate = Accnis_Svalan$Date
Accnisdateconv = as.Date(Accnisdate, "%d.%m.%Y")

# Convert dates to DOY
AccnisDOY = as.numeric(strftime(Accnisdateconv, format = "%j"))

# Convert from format "dd.mm.yyyy" to own columns:
AccnisYEAR = as.numeric(format(Accnisdateconv, "%Y"))
AccnisMONTH = as.numeric(format(Accnisdateconv, "%m"))
AccnisDAY = as.numeric(format(Accnisdateconv, "%d"))

# Convert DOY to -+ new years eve each year
# Preparing columns
DOY.adj = AccnisDOY
Year.adj = AccnisYEAR

# Identify autumn dates used
ind = which(DOY.adj >= 305)

# Subtract that from total DOY to get negative values when less than 365
DOY.adj[ind] = DOY.adj[ind]-365

# Assign spring autumn values to next year
# (i.e. winter season assigned to next year)
Year.adj[ind] = Year.adj[ind]+1

##### SEX, LATITUDE AND AGE #####

#Sex and number to own columns
AccnisSEX = Accnis_Svalan$Sex
AccnisNR = Accnis_Svalan$Nr
AccnisLAT = Accnis_Svalan$Latitude
AccnisLONG = Accnis_Svalan$Longitude

# Age2GROUPS 1k spring autumn =0, 2k after christmas
# winter = 1, rest= 1
AccnisAGE = (Accnis_Svalan$Age2groups)
AccnisAGE_K = (Accnis_Svalan$Age_K)

# FEMALE = "0", MALE = "1"
AccnisFEMALE = which(AccnisSEX == 0)
AccnisMALE = which(AccnisSEX == 1)

# Center Year
Year.adj_C = (Year.adj - mean(Year.adj))

# Center latitude
AccnisLAT_C = (AccnisLAT - mean(AccnisLAT))

# CREATE DATA FRAME
```

```

AccnisDATA=data.frame(Year.adj_C, AccnisLAT_C,
Year.adj,DOY.adj,AccnisDOY,AccnisSEX,AccnisNR,AccnisLAT,AccnisLONG,AccnisAGE)

# Dataset with rows for both M and F
as.factor(AccnisDATA$AccnisSEX)
AccnisDATA$AccnisSEX = factor(AccnisDATA$AccnisSEX, labels = c("female", "male"))

# Identifying the periods to throw away (between winter and next winter)
minusDOY= which(AccnisDATA$AccnisDOY <= 305 & AccnisDATA$AccnisDOY >= 91)

# Removing data with those identified dates from the dataset
AccnisDATA =AccnisDATA[-minusDOY,]

##### ANALYSIS OF LATITUDE LONGITUDE #####

# Identify spring dates used
ind2 =which(DOY.adj > 0 & DOY.adj < 92 & AccnisAGE_K == "2K")

# Assign 2k in spring to 1k
AccnisAGE[ind2] = AccnisAGE[ind2]-1
AccnisDATA$AccnisAGE = as.factor(AccnisDATA$AccnisAGE)

#### ANALYSES #####

library(mgcv) # required for GAM
result1=gam(AccnisAGE ~ s(DOY.adj) + Year.adj_C, family= "quasibinomial",
data=AccnisDATA)
summary(result1)
result2=gam(AccnisSEX ~ s(DOY.adj) + Year.adj_C, family= "quasibinomial",
data=AccnisDATA)
summary(result2)
result3=gam(AccnisLAT_C ~ AccnisSEX* Year.adj_C + s(DOY.adj), family="gaussian",
data=AccnisDATA)
summary(result3)

# Plot all models
par(mfrow=c(1,3))
plot.gam(result1, xlab="Centred Day of Winter", ylab="Age",shade=TRUE,
shade.col="gray90",cex.lab=1.5, cex.axis=1.5, cex.main=1.5, cex.sub=1.5)
abline(v=0)
plot.gam(result2, xlab="Centred Day of Winter", ylab="Sex",shade=TRUE,
shade.col="gray90",cex.lab=1.5, cex.axis=1.5, cex.main=1.5, cex.sub=1.5)
abline(v=0)
plot.gam(result3, xlab="Centred Day of Winter", ylab="Latitude",shade=TRUE,
shade.col="gray90",cex.lab=1.5, cex.axis=1.5, cex.main=1.5, cex.sub=1.5)
abline(v=0)

#####
# Max and min males
a = 0.35223
b = 0.014261 # year.adj.C

maxyear = max(Year.adj_C, na.rm = FALSE)
minyear = min(Year.adj_C, na.rm = FALSE)

yearmax = a + b*maxyear
sexyearmax =1/(exp(-yearmax)+1)
sexyearmax

yearmin = a + b*minyear
sexyearmin =1/(exp(-yearmin)+1)
sexyearmin

#####
# Max and min lat

```

```
c = 0.158565 #lat males
maxlat = max(AccnisLAT_C, na.rm = FALSE)
minlat = min(AccnisLAT_C, na.rm = FALSE)

latmalesmax = a+c*maxlat
latmalesmax
latmalesmin = a+c*minlat
latmalesmin

##### END SCRIPT #####
```

Appendix 4

Simulations of the kernel density distributions which fit each species probability mode and uncertainty for migration.

```
# Function which performs kernel density estimation
kernel.plot = function(x, xi, bw = 0.01, xlim, main){
  yi = rep(0,length(xi))

  for (j in 1:length(x)){
    yi = yi + dnorm(xi, mean = x[j], sd = bw)
  }

  yi = yi/length(x)
  plot(xi,yi,"l", xlab = "Intercept", ylab = "Probability density",
       xlim = xlim, main = main)
}

par(mfrow=c(3,2))

# Evaluere plotten for disse verdier
xi = seq(0,1,0.002)

# The number of normal distributed simulations
n = 50000
dev.new()
par(mfrow=c(3,2))

##### SPARROWHAWK #####
#####
# Target: 90% migr

# Simulating n normal distributed numbers
a0.sim.6 = rnorm(n, mean = 1.6, sd = 0.9)

# Expit transforming "a0.sim.6"
p0.sim.6 = 1/(exp(-a0.sim.6)+1)

# Kernel density plot with bandwidth 0.02
kernel.plot(p0.sim.6, xi, bw = 0.02, xlim = c(0,1),main= "Sparrowhawk")
abline(v=0.9, col= "red")

##### RED KITE #####
#####
# Target: 80% migr

# Simulating n normal distributed numbers
a0.sim.2 = rnorm(n, mean = 0.9, sd = 0.9)

# Expit transforming "a0.sim.2"
p0.sim.2 = 1/(exp(-a0.sim.2)+1)

# Kernel density plot with bandwidth 0.02
kernel.plot(p0.sim.2, xi, bw = 0.02, xlim = c(0,1), main= "Red Kite")
abline(v=0.8, col= "red")

##### COMMON GULL #####
#####
#Target: ca.75% migr

# Simulating n normal distributed numbers
a0.sim.1 = rnorm(n, mean = 0.7, sd = 1.0)

# Expit transforming "a0.sim.1"
p0.sim.1 = 1/(exp(-a0.sim.1)+1)
```

```

# Kernel density plot with bandwidth 0.02
kernel.plot(p0.sim.1, xi, bw = 0.02, xlim = c(0,1), main= "Common Gull")
abline(v = 0.75, col= "red")

##### FIELDFARE #####
# Target: 50% ? stor usikkerhet

# Simulating n normal distributed numbers
a0.sim.3 = rnorm(n, mean = 0.1, sd = 0.95)

# Expit transforming "a0.sim.3"
p0.sim.3 = 1/(exp(-a0.sim.3)+1)

# Kernel density plot with bandwidth 0.02
kernel.plot(p0.sim.3, xi, bw = 0.02, xlim = c(0,1), main= "Fieldfare")
abline(v=0.5, col= "red")

##### BLUE TIT #####
# Target: 0.25% migr

# Simulating n normal distributed numbers
a0.sim.5 = rnorm(n, mean = -0.9, sd = 0.7)

# Expit transforming "a0.sim.5"
p0.sim.5 = 1/(exp(-a0.sim.5)+1)

# Kernel density plot with bandwidth 0.02
kernel.plot(p0.sim.5, xi, bw = 0.02, xlim = c(0,1), main= "Blue Tit")
abline(v=0.25, col= "red")

##### MALLARD #####
# Target: 50% migr

# Simulating n normal distributed numbers
a0.sim.4 = rnorm(n, mean = -0.0, sd = 0.8)

# Expit transforming "a0.sim.4"
p0.sim.4 = 1/(exp(-a0.sim.4)+1)

# Kernel density plot with bandwidth 0.02
kernel.plot(p0.sim.4, xi, bw = 0.02, xlim = c(0,1), main= "Mallard")
abline(v=0.50, col= "red")

```


Appendix 5

R-code for studying the relationship between breeding onset and productivity in Sparrowhawk.

```
# Load dataset
Laydata = read.csv("Egg laying_OA_dataset.csv", header=TRUE)

# Extract all dates to independent columns
Laydate = Laydata$Egg.laying
Laydateconv = as.Date(Laydate, "%d.%m.%Y")

# Convert dates to DOY and YEAR
LayDOY = as.numeric(strftime(Laydateconv, format = "%j"))
LayYEAR = as.factor(strftime(Laydateconv, format = "%Y"))

# Center "LayDOY"
DOY.C = ((LayDOY)-mean(LayDOY))

#Seperate clutch size
LayCLUTCH = Laydata$Clutch.size

#Create dataset with Year, centered DOY and clutch size
Laydate = data.frame(LayYEAR,DOY.C,LayDOY,LayCLUTCH)
head(Laydate)

# Analysis
results = glm(LayCLUTCH ~ DOY.C + LayYEAR, data= Laydate, family="quasipoisson")
summary(results)

#removing outlier datapoint (nr 10) from the dataset
fix(Laydate) #identifying visually the point
Laydate = Laydate[-c(10), ]
results = glm(LayCLUTCH ~ DOY.C + LayYEAR, data= Laydate, family="quasipoisson")
summary(results)
```