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Spatial and temporal variation in
hippoboscid parasitism by *Ornithomya*
chloropus on house sparrows (*Passer*
domesticus) and its effect on survival

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Biology

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Summary

1. I examined how the *Hippoboscidae Ornithomya chloropus* is spatially and temporally distributed in an insular metapopulation of house sparrows in northern Norway from 2004-2011, whether there were demographic differences in abundance as well the relationship between abundance and morphology, and abundance and survival in juvenile house sparrows.
2. I found a handling effect on the abundance of *O. chloropus* which reduced the number of flies found on individuals from their first to their second catch.
3. There was considerable variation in abundance between years and islands as well as within seasons, and abundance of *O. chloropus* differed between age-classes.
4. There was a negative relationship between abundance and the three morphological traits; body condition index, body mass and tarsus length. There was also a positive effect of age on these morphological traits and a negative effect of late hatch days.
5. There was a positive relationship between juvenile survival and body condition index, and survival and tarsus length.
6. These results indicate a relationship between the abundance of *O. chloropus* and the fitness of juvenile house sparrows with morphology while there was no clear relationship between juvenile survival and abundance.

Sammen drag

1. Jeg undersøkte om distribusjonen av hippobosciden *Ornithomya chloropus* varierte gjennom sesongen, mellom år og mellom øyer i en gråspurvmeta-populasjon på Helgelandskysten i Nord-Norge fra 2004 - 2011, om det fantes demografiske forskjeller i abundans og om det var et forhold mellom abundans og morfologi, og abundans og overlevelse for juvenile gråspurver.
2. Det var en håndteringseffekt på abundansen til *O. chloropus* som reduserte antall fluer som ble funnet på individer mellom deres første og andre fangst.
3. Det var betydelig variasjon i abundans gjennom året, samt mellom år og øyer. Det var også forskjell i abundans mellom aldersklassene adult og juvenil.
4. Forholdet mellom abundans og de tre morfologiske trekkene kondisjonsindeks, masse og tarslengde var negativt ved høye abundansverdier. Det var også en positiv effekt av alder på de morfologiske trekkene og en negativ effekt av klekkedag.
5. Jeg fant et positivt forhold mellom juvenil overlevelse og både kondisjonsindeks og tarslengde.
6. Resultatene indikerer et forhold mellom abundans av *O. chloropus* og den fysiske helsen til juvenile gråspurver og det ikke var et klart forhold mellom juvenil overlevelse og abundans.

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1. Introduction

There is a growing consensus that parasites may play an important role for the population dynamics of its host species (Anderson & May 1978; May & Anderson 1978; Hudson 2002), as well as influence the structure in ecological communities (Tompkins *et al.* 2002; Hudson *et al.* 2006; Dunn *et al.* 2012). Generally, parasites may reduce reproduction (Møller 1993; Richner *et al.* 1993; Mouritsen & Poulin 2002), survival (Chapman & George 1991; Sol *et al.* 2003) or individual growth (Senar *et al.* 1994). Effects are reviewed in Lehmann (1993) and Hudson (2002). The influence of parasites on host vital rates and dispersal may in turn affect host population dynamics (Richner *et al.* 1993).

A parasite is defined as an organism which feeds on the contents, tissues or body fluids of a host species, and which causes harm to its host (Campbell 2008). Thus, the parasite may spend parts of, or the majority of its life in association with its host (Campbell 2008). Researchers in parasitology have traditionally focused on the effects of certain parasites and their consequences on welfare and fitness of domesticated species or humans (Altizer *et al.* 2003; Sindermann 1987). Until recently, less attention had been given to the ecological and evolutionary role of parasites on individual fitness and population dynamics of wild host species (Ebert 2005). Historically, it was the general opinion that parasites could not have a significant negative fitness effect on their hosts as this would reduce the parasite's own fitness (see Hudson 2002). This view largely failed to account for parasites' short generation time compared to their host, their high reproductive rate, high dispersal ability, and the fact that parasites

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act purely to maximize their own individual fitness above all else (Hudson 2002).

In their milestone study from 1978, Anderson & May developed two theoretical models describing how parasites could potentially affect host population dynamics which would in turn reflect on the parasite's population dynamics. Accordingly, Anderson and May's model assumed that parasites could have an effect on their host's birth and mortality rates (Anderson & May 1978). Based on their models Anderson & May (1978) demonstrated that parasites may regulate the host population growth rate only if the parasite birth rate (leading to transmission within the host population) is higher than parasite death rate (both due to natural and parasite induced host deaths) plus host birth rate. This theoretical model framework is central as it represents a tool for quantifying and predicting the dynamics of host and parasite populations. Hudson *et al.* (1998) conducted a study on the effect of the parasite *Trichostrongylus tenuis* in populations of red-grouse (*Lagopus lagopus*) in Northern England. They showed that a reduction in parasite prevalence (defined as the number of host individuals infected by a parasite species divided by the total number of host individuals examined (Holmes 1982)) may regulate wild host populations by preventing a decline in population size. This effect came from the parasite decreasing the variance in the host population growth rate and thus stabilizing the population. This was also shown by Pedersen & Greives (2008) where the removal of internal nematodes from two species of mice (*Peromyscus leucopus* and *Peromyscus maniculatus*) decreased oscillations in population size in a natural population.

Research on the effect of avian ectoparasites on fitness components of their hosts is somewhat scarce and inconclusive. On one hand, there are studies which have demonstrated an effect of ectoparasites on fitness components, as for instance Chapman & George (1991) who found that ectoparasites (*Oeciacus vicarus*, *Argas cooleyi* and *Ornithodores concanensi*) reduced the survival of nestlings in a population of cliff swallows (*Hirundo pyrrhonota*). Likewise, Richner *et al.* (1993) found that both the body mass of the offspring and the number of chicks fledged were affected by hen fleas (*Ceratophyllus gallinae*) in the great tit (*Parus major L.*). Senar *et al.* (1994) found that body condition was re-

duced by 3% in parasitized birds in the European serin (*Serinus serinus*), and a review by Møller *et al.* (1990) on the effects of parasites found that parasites generally had a negative effect on fledgling body mass and survival in passerine birds. In contrast, several studies have not documented significant effects, such as Tompkins *et al.* (1996) who found no negative effects of the chewing louse fly (*Dannysus hirundis*) nor flightless louse fly (*Crataerina pallida*) on nestling growth or survival until fledging in the common swift (*Apus apus*) (Walker & Rotherham 2011). Further, body condition did not differ between parasitized and non-parasitized birds in the common swift (Hutson 1981) or the alpine swift (*Apus melba*) (Tella *et al.* 1995). The results are inconclusive for reproduction as well where Fitze *et al.* (2004) found a reduction in current reproduction in female great tits due to ectoparasite load, while Raveh *et al.* (2011) found no effect of parasite load on male reproductive success.

The prevalence of parasites has often been found to vary among age-classes and sexes in the host species. Most such studies have found that juvenile birds have a higher prevalence than adults (Corbet 1956; Sychra *et al.* 2008). A study by Sol *et al.* (2003) on *Haemoproteus columbae* in pigeons (*Columba livia*) suggested that the difference in parasite prevalence between adult and juvenile birds may be due to an acquired immunity of adults from being previously exposed to the parasite as a juvenile. A study of the difference in prevalence between the sexes found that male great tits (*Parus major*) had a higher prevalence of haematozoan parasites than females when reproductive effort was high (Norris *et al.* 1994). It was suggested that this difference may be due to an increased exposure to parasites because of time spent searching for food. However, alternative explanations such as a reduced immune system function in males due to a higher level of stress from mate guarding and mate feeding was also proposed (Norris *et al.* 1994)(see also other proposed explanations reviewed in Zuk & McKean (1996)).

Parasites are typically aggregated in a small portion of the host population (Shaw & Dobson 1995). This may be caused by a variation in exposure to infective stages among host individuals, variation in susceptibility to parasitism,

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as well as higher mortality in highly infected individuals (Wilson *et al.* 2002). Aggregation may in turn lead to misinterpretation of the actual effects of parasites on the dynamics of a population. Anderson (1995) demonstrated in a theoretical study that a parasite may regulate the host population even at low prevalence of infection (0.18 %) if the parasite induced mortality rate is high (50 %). Hence, one should be cautious when interpreting parasite-host systems with low levels of prevalence in order to avoid the pitfall of wrongfully concluding a weak effect of the parasite on the host's population dynamics (Tompkins *et al.* 2002).

The objectives of this Master's project were to investigate the spatial and temporal variation in the prevalence of *O. chloropus* using eight years of data from four populations of house sparrows (*Passer domesticus*) located in an insular metapopulation at the coast of Helgeland in northern Norway. In the analyses I accounted for seasonal variation in prevalence, and age-classes and sex. Next, I investigated if juvenile morphology of house sparrows was related to the individual variance in *O. chloropus* abundance, defined as the number of parasites present on a host (Holmes 1982). Finally I investigated whether there was a relationship between juvenile survival and *O. chloropus* abundance.

The results from this study will contribute to our knowledge of parasite-host relationships and the effect of an ectoparasite on the fitness of its host in a metapopulation of a wild passerine species. Generation of such knowledge is vital in order to fully understand the effect ectoparasites may have on the population dynamics of its host.

2. Methods

2.1 The parasite: *Ornithomya chloropus*

The *Hippoboscidae* is a globally distributed dipteran insect family with 120 species (Maa 1963). The genus *Ornithomya* is a common parasite of birds. It can be found in large parts of Europe and occasionally in Egypt and Palestine (Corbet 1956). *Ornithomya fringillina*, *O. avicularia* and *O. chloropus* are known to parasitize the house sparrow in Europe. In the study area, house sparrows were parasitized by *O. chloropus*, identified by Preben Ottesen (Matilsynet) 2012, among others. This species also parasitizes other passerines and ground-feeding birds and is most likely distributed throughout the Holarctic region (Maa 1963).

The adult *Ornithomya* flies can be found as early as in April, but are most abundant in July and August (Corbet 1956). In the British Isles the last flies of the season may be found in late September and early October. The flies are found in the feathers of their hosts. Change of host occurs, though the parasites are mostly found on the individual host they first acquired (Corbet 1956). Host-shifts occur mostly within species due to proximity in roosting and feeding (Corbet 1956). Species which return to the same nest site year after year, such as blue tits (Tomas *et al.* 2007), house sparrows and winter wrens (Loye & Carroll 1998) are more prone to parasite infection as they return to sites which may already be infected and have larvae (Tomas *et al.* 2007).

The *Ornithomya* feed on their host's blood and have been found to have

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only one generation per year. They deposit already hatched larvae that pupate immediately after larviposition (Corbet 1956). The flies have been found to survive up to 50 days, and each fly may lay up to seven puparia (Corbet 1956). The pupae are not attached to the bird and most of them fall off.

2.2 The host: House sparrow

The house sparrow is a sedentary species which lives in close association with human settlements such as farms and areas populated by humans, both rural and urban. It is known to be the widest distributed wild bird species on the planet (Anderson 2006). House sparrows reach sexual maturity in their second year of life and build nests of grass and feathers in roofs, walls and nest boxes, with clutch size 4 - 6 eggs. In northern Norway, the breeding season lasts from May until August and the house sparrow can have up to three broods (Husby *et al.* 2006; Pärn *et al.* 2012).

Many endo- and ectoparasites have been recorded on house sparrows (Anderson 2006). House sparrow ectoparasites are mostly mites, ticks and feather lice (Anderson 2006) but also the *Hippoboscidae* have been recorded with two sub-families represented (Maa 1963). Because the house sparrow lives in loose colonies and performs communal feeding, roosting and display, parasites and diseases are easily transmitted (Valera *et al.* 2003).

2.3 Study area

The study area consisted of 18 islands in total, located in an archipelago covering 1600 km² off the coast of Helgeland in the northern part of Norway (66N, 13E) (Figure 1). The present study focused on four of these islands: Aldra, Gjerøy, Hestmannøy and Indre Kvarøy, where a high number of sparrows have been captured and checked for hippoboscids from 2004 to 2011. The landscape on these islands consists of agricultural land, heath land and mountains. The

climate is oceanic, and is usually free of snow for much of the winter (Sæther *et al.* 1999).

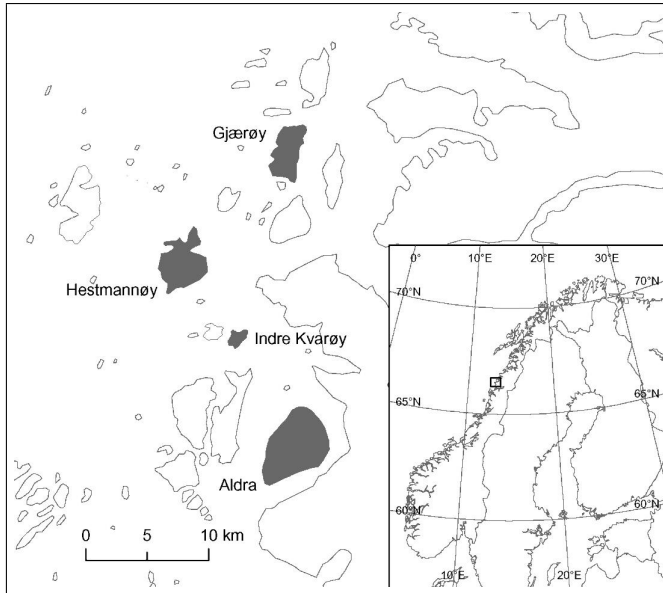


Figure 1: Map of study area in northern Norway from 2004 - 2011 with islands Aldra, Gjerøy, Hestmannøy and Indre Kvarøy marked.

2.4 General field procedures

Fieldwork was conducted during the breeding season from May until mid-August each year, and for another period from late September until early November. Each island was regularly searched for active nests throughout the breeding season, and nests were then revisited two to three times during the incubation and nestling period. At an age of 8 - 11 days fledglings were measured and marked with a unique combination of colored plastic bands and an aluminum ring with a unique identity number (Husby *et al.* 2006; Pärn *et al.* 2012). The

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fledged juveniles and adults were captured in barns and cow sheds, or outside in gardens of houses in small villages using mist nests (Jensen *et al.* 2008; Pärn *et al.* 2012). I categorized individuals into two age classes: juveniles (individuals in their first year) and adults (second calendar year or older). The sex of juveniles was difficult to determine before the first moult in the fall (Møller 2010). I therefore categorized individuals into life stage groups (LSG): adult males, adult females and juveniles. Slide calipers were used to measure tarsus length (to the nearest 0.1 mm) and a Pesola spring balance was used to measure body mass (to the nearest 0.1 g) (Husby *et al.* 2006). For detailed description of field work see Husby *et al.* (2006) and Jensen *et al.* (2004). Variation in the measurement of morphological traits for fledged juveniles and adults between field workers were adjusted for using regression techniques (Jensen *et al.* 2004). Birds were often caught several times within (average of 146 individuals recaptured each year) and between years, and the mean annual reencounter rate for the four study islands in the study period was > 0.8 (Holand *et al.*, unpublished results).

2.5 Parasite counts

The total number of visible *Hippoboscidae* present on each individual house sparrow was counted. This included flies present on the plumage and those that flew off during the general handling of a bird as described above, which lasted for approximately 10 - 15 minutes. Flies hiding under the feathers were not actively searched for. Thus, the estimated number of flies is presumably lower than the true number. Furthermore, the handling of the bird appeared to have a negative effect on the abundance of *O. chloropus* at the following captures.

This effect can be seen in Figure 2a where the number of flies at the first and second captures are shown for juvenile birds caught twice during the summer season with fewer than 14 days between the two captures. Mean capture day for the first catch day was ca. 25th of July and for the second catch day ca. 30th of July. Figure 2b shows the distribution of *O. chloropus* on the same individuals included in Figure 2a. Many of the previously infected individuals were found

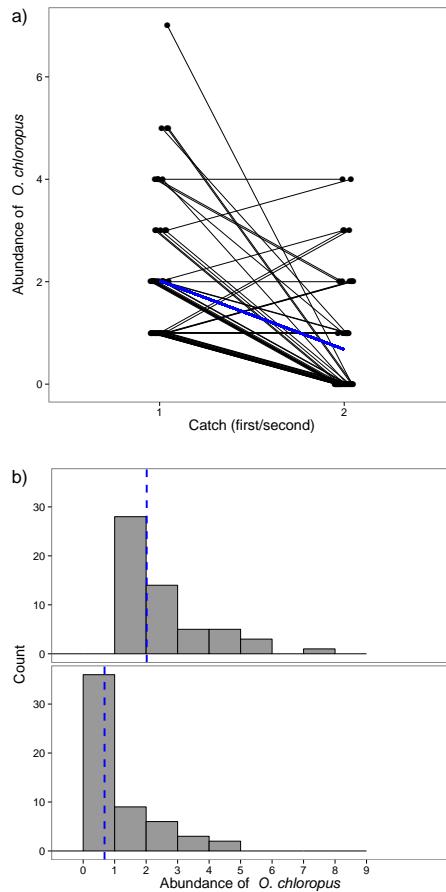


Figure 2: a) Effect of handling on abundance of *O. chloropus* on juvenile house sparrows, with at least one *O. chloropus* at first registration, captured twice within 14 days during the summer season (May 1st - August 30th) ($n = 56$). Line drawn between first and second catch for all individuals. b) Frequency distributions for the abundance of *O. chloropus* at first and second capture with mean abundance indicated as dashed line.

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to have no flies at the second capture, and there was a general decrease in abundance between the first and second capture. A paired student's t-test between the two captures shows that the mean number of flies is significantly different ($t = 10.4401$, $P < 0.001$) and thus there appears to be a negative effect of handling on *O. chloropus* abundance in juveniles. To account for this handling effect I used the first registration only for each year for each individual.

2.6 Statistical analyses

This study consisted of three main sets of analyses. First I focused on temporal and spatial variation in *O. chloropus* abundance and prevalence (2.6.3). Then I investigated the relationship between individual morphology and the abundance of *O. chloropus* (2.6.4). In the third section I investigated whether *O. chloropus* influenced the survival of juvenile house sparrows (2.6.5). However, I begin by addressing how I handled correlation between predictor variables (2.6.1), and describe the model inference approach that was applied (2.6.2). All statistical analyses in this study were conducted using the software R (R 2013, Development Core Team, version 2.15.1).

2.6.1 Accounting for correlation between explanatory variables

All morphological measures were log (base e) transformed to reduce heteroscedasticity (Larsen & USDA 1978). In order to account for the problem of collinearity in multiple regression analyses (Graham 2003), the correlation of the morphological variables among juveniles was examined. There was a positive correlation between body mass and tarsus length ($r_p = 0.42$, $P < 0.001$, $n = 271$). Thus, in order to account for collinearity as well as disentangle the variance components of body condition from the component of variation due to structural size (Graham 2003), I calculated a body condition index (BCI) as the residuals from a linear regression model of body mass on tarsus length. Because of the

positive correlation between body mass and tarsus length, and body mass and BCI ($r_p = 0.91$, $P < 0.001$, $n = 271$), body mass was not included in any model containing BCI or tarsus length.

All continuous explanatory variables used in morphology and survival analyses (including age of juveniles in days at first capture, hatch day in relation to season day number (SDN) centered on July 29th and abundance of *O. chloropus* (AOC)) were tested for inter-correlations using Pearson correlation analyses. SDN was centered on July 29th to reduce covariance among predictor variables (Aiken & West 1991). All correlations were non-significant except between hatch day and juvenile age ($r_p = -0.51$, $P < 0.001$, $n = 271$). In order to explore the possible effect of multicollinearity I thoroughly investigated whether the slope estimates and the standard errors remained the same both in models with age and hatch day present and with only one or the other. I tested this in a generalized linear model containing response variable juvenile survival with explanatory variables year, island, AOC, BCI and tarsus length as well as either hatch day or age or both included. The parameter estimates and standard errors were for all intents and purposes similar for models with either variable and models containing both. The potential bias due to the multicollinearity effect of combining these two in the same model was therefore considered to be negligible (Graham 2003).

2.6.2 Multi-model inference based on AIC_c

Candidate models were constructed based on relevant and sound ecological theory. Akaike's Information Criteria accounting for small sample sizes (AIC_c) was calculated for each model. The lowest AIC_c value identifies the best model given the data and the candidate models. Models with a ΔAIC_c less than 2.0 can be considered equally good (Burnham & Anderson 2002). AIC_c weights (w_i) can be interpreted as the probability that a model is the best among the candidate models considered. The model with the lowest AIC_c was selected for detailed analysis.

2.6.3 Spatial and temporal variation in abundance and prevalence of *O. chloropus*

In the first section of analyses I investigated whether individual AOC varied among island populations and among years. The data used for modeling AOC included all age classes from 2004 - 2011 captured between May 1st and October 31st ($n = 3187$). In order to avoid bias in the parasite count due to the handling effect (see above), I only included data from the first individual capture each year. Initially I considered modeling AOC as a negative binomial distribution, which is commonly used in studies of parasites in order to account for the aggregated distribution (Crawley 2007; Lloyd-Smith 2007). However, such models had convergence problems, possibly due to the small number of observations per individual. I therefore applied a generalized linear mixed model with a Poisson distributed response variable (i.e. with AOC) and a zero inflation term, using the glmmADMB package version 0.7.2.12 (Bolker 2009). I used individual identity as a random effect (with standard deviation σ) to account for dependency within individuals among years. I included a zero inflation term because of the higher probability of zeros in our data due to the natural aggregation exhibited by parasites in host populations (Tompkins *et al.* 2002), as well as the potential effect of not detecting flies hiding under feathers.

The predictor variables in the full model were year, island, and seasonal day number (SDN). To account for non-linear seasonal effects, I also included SDN². I tested whether within- and between-year variation in AOC differed between islands by including the interactions SDN and island, SDN² and island, and year and island. I also tested if the seasonal effect on AOC varied between years by including SDN and year, and SDN² and year. An interaction between two variables was never included in a model without the respective variables present as main factors (Pasta 2011), which also went for higher order terms such as SDN² where the main effect SDN was present. When the best model had been selected based on the AIC_c criterion, I extracted mean prevalence for each combination of year and island throughout the season (see outline of

calculations in Appendix I). After identifying the best model according to the AIC_c criterion for spatial and temporal variables, I investigated whether the model could be further improved by extending the model with an LSG or age-class variable. I did not include these variables in the initial set of candidate models as this would involve an inexpedient number of candidate models as relevant interaction terms should be included as well. Because the LSG variable contained three levels (male adult, female adult and juvenile) and the age-class variable separated between adults and juveniles, the LSG and the age-class variables were partly overlapping and therefore not included together in the same model.

2.6.4 Morphology and abundance of *O. chloropus*

In the second section of analyses I investigated whether morphology was related to number of flies. As only 14 % of the adults included in modeling morphology were infected compared to 33 % of the juveniles I concentrated the analyses on the juvenile data from the summer season (May 1st - October 31st) from the years 2004 - 2010 in order to obtain the highest statistical power possible by ensuring a high prevalence in the sample data (271 juvenile individuals in total while 183 adults) (Cohen 1992). Separate sets of models were run with BCI, tarsus length and body mass as response variables, respectively. The global models all contained AOC and AOC², year and island as well as age and hatch day as explanatory variables. Interactions included AOC with island, age and hatch day, as well as AOC² with age and hatch day, and year and island with hatch day. The number of candidate models differed for each morphological measure as a varying number of interactions were included. For BCI I ran 62 candidate models, 49 for body mass and 39 candidate models for tarsus length. For all analyses I used generalized linear models (i.e. the `glm()`-procedure, Gaussian error distribution, R Development Core Team, 2013).

When modeling individual variation in tarsus length, one observation with an unusually high number of flies (9) was highly influential (Cook's distance

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> 20) and strongly affected the regression parameter estimates for AOC. I fit the data with models with and without the outlier, and compared and discussed the results. In models of BCI and body mass the outlier affected the regression estimates to a lesser extent, according to Cook's distance (Burnham & Anderson 2002).

2.6.5 Juvenile survival and abundance of *O. chloropus*

In the third section of analyses I investigated whether probability of recruitment, i.e. juvenile survival from first to second calendar year was affected by AOC. The global model contained the binomial response variable survived/not survived and I used a generalized linear model (i.e. the `glm()`-procedure, Binomial error distribution, R Development Core Team, 2013). The model included the explanatory variables main effects and second order terms of AOC, BCI, tarsus length, hatch day and age at first capture. In addition, year and island were included as categorical variables (i.e. fixed effects). The two-way interaction terms which were included were BCI with tarsus length, hatch day, age, island and year, as well as AOC with BCI, hatch day, age, island and year. Candidate models were evaluated by AIC_c values.

3. Results

3.1 Spatial and temporal variation in abundance and prevalence of *O. chloropus*

The highest ranked model indicated that the AOC varied considerably within and between years as well as between islands (Appendix II, Table A). This model was also used to derive the seasonal variation in prevalence of *O. chloropus* among islands and years (Figure 3) as described in Appendix I. The highest ranked model had an Akaike weight of 0.7 and AIC_c was 2.58 lower than the second model, which suggests that this model was the best given the data and the candidate models. The model indicated considerable within-year variation in AOC, and the peak appeared to vary between years and islands, although the parameter estimates were uncertain (Appendix II, Table B, see also the derived spatiotemporal prevalence in Figure 3). The peak in number of flies occurred between mid-June to mid-July on Indre Kvarøy, and in mid-July to August on Aldra. Timing of the peak varied between years. The peak in AOC on Hestmannøy and Gjerøy occurred in mid-July.

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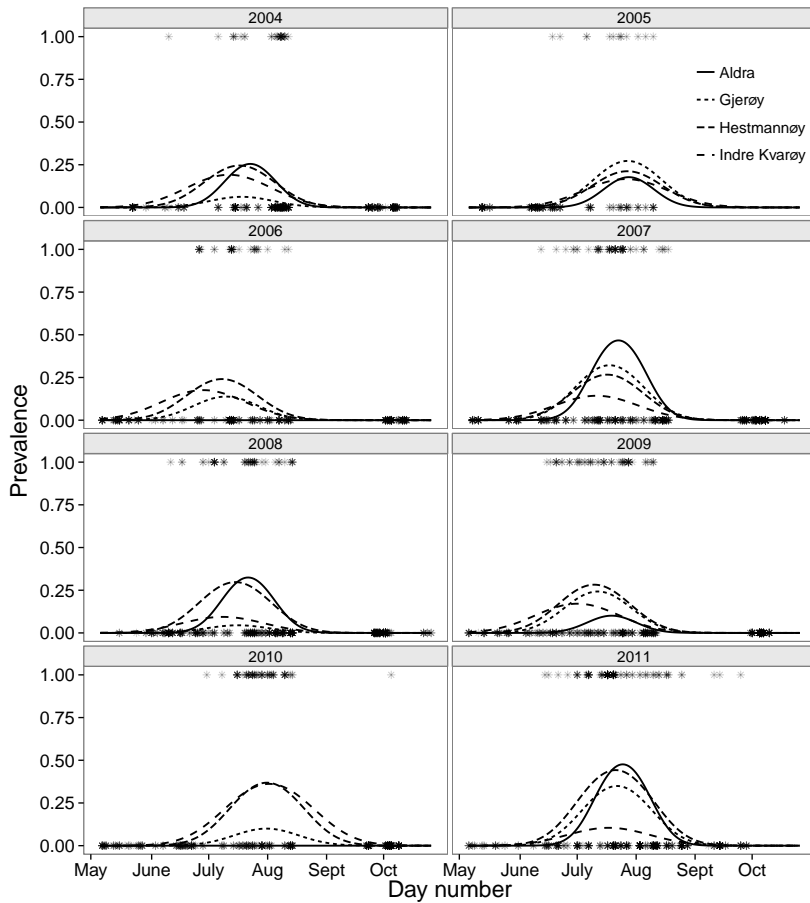


Figure 3: Estimated prevalence for the highest ranked model explaining the spatial and temporal variation in the abundance of *O. chloropus* in an insular metapopulation of house sparrows in northern Norway. Island, year, season day number (SDN) and SDN^2 were included as explanatory variables, including their two way interaction terms. Individual identity was included as a random factor in a zero-inflated Poisson model. For more details see Appendix II.

When LSG and age-class were added separately to the best model including spatial and temporal variation in parasite abundance, the ΔAIC_c values indicated that there was little difference ($\Delta\text{AIC}_c = 0.64$) between the two candidate models. The candidate model which included age-class was ranked highest and therefore considered the best ($\Delta\text{AIC}_c = 126.18$ between age-class and the previous best model). The abundance of *O. chloropus* was higher in juveniles than in adults ($\beta = 1.6900$, $\text{SE} = 0.1550$).

3.2 Morphology and abundance of *O. chloropus*

When investigating the relationship between individual BCI as response variable and the abundance of *O. chloropus*, the highest ranked model contained a positive effect of abundance of *O. chloropus* (AOC) ($\beta = 0.0036$, $\text{SE} = 0.0096$) and a negative effect of AOC^2 ($\beta = -0.0025$, $\text{SE} = 0.0017$), which suggested a decrease in BCI at high abundances. However, the standard errors indicate that effect of AOC on BCI is uncertain. The model also suggested a positive relationship between BCI and age ($\beta = 0.0015$, $\text{SE} = 0.0004$), and the presence of hatch day in seven of the ten highest ranked models indicate a possible effect of hatch day on BCI as well (Appendix II, Table C).

Correspondingly, when examining the relationship between individual variation in body mass as response variable and the abundance of *O. chloropus*, the analyses revealed a similar pattern as found in the above analysis with BCI (Appendix II, Table D). The highest ranked model included only the main effects AOC, AOC^2 , age, hatch day and hatch day². However, based on ΔAIC_c values from the second- and third highest models respectively, these models may also be considered good candidate models (Appendix II, Table D). The parameter estimates from the highest ranked model showed a positive main effect of AOC ($\beta = 0.0035$, $\text{SE} = 0.0029$) and the quadratic term was negative ($\beta = -0.0029$, $\text{SE} = 0.0019$). The standard errors were high relative to the estimates, though (as for BCI) AOC was included in 8 of the top 10 models. In contrast, the estimates for age ($\beta = 0.0021$, $\text{SE} = 0.0005$), hatch day ($\beta = -0.0017$, SE

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$= 0.0013$) and hatch day² ($\beta = -3.03 \cdot 10^{-5}$, $SE = 1.43 \cdot 10^{-5}$) have low uncertainty which indicates relationships between these variables and body mass. Body mass appears to increase with age as well as hatch day, though juveniles born on late hatch days have a slight decrease in body mass from the maximum.

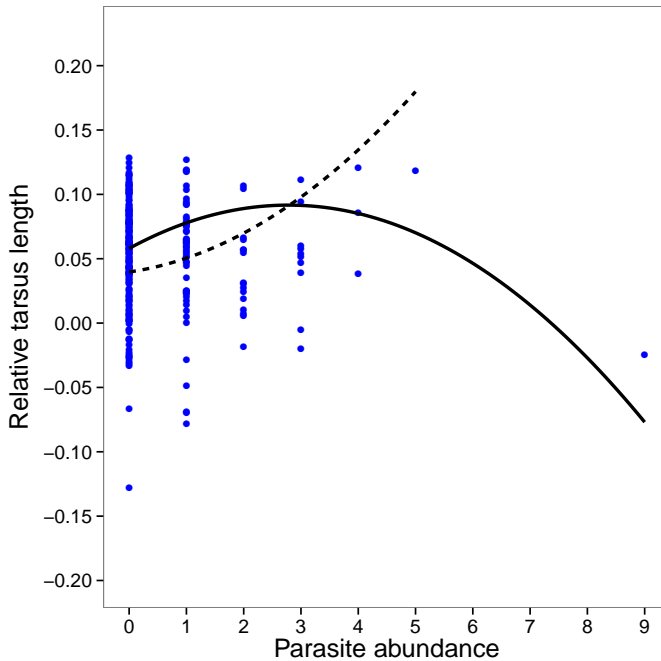


Figure 4: Relationship between tarsus length ($\log e$ transformed and centered) and abundance of *O. chloropus* with (full line) and without (dotted line) the outlier present. Age, hatch day, and hatch day² were also included as explanatory variables and set to their respective means 35.35 and -37.69 and multiplied by their parameter coefficients. Individual captures are marked with blue dots.

When investigating the relationship between individual tarsus length as response variable and the abundance of *O. chloropus* the model selection performed with the outlier present revealed that the highest ranked model (Appendix II, Table E) contained a positive relationship with AOC ($\beta = 0.0177$,

SE = 0.0114) and a negative relationship between AOC² ($\beta = -0.0039$, SE = 0.0014) and tarsus length. This suggests that the tarsus length of juveniles increased as the abundance of *O. chloropus* increased, but decreased at intermediate to high abundances (Figure 4). The small standard errors of the parameter estimates suggest that a relationship was present between AOC and tarsus length among juvenile house sparrows. In addition, the highest ranked model included two interaction terms which enhance the effects of AOC and AOC² as the interaction between AOC and hatch day showed a positive relationship ($\beta = 0.0008$, SE = 0.0003) while the interaction between AOC² and hatch day showed a negative relationship ($\beta = -0.0002$, SE = 0.0003) with tarsus length. Finally, age showed a positive relationship with tarsus length ($\beta = 0.0004$, SE = 0.0002) as well as hatch day ($\beta = 0.0007$, SE = 0.0002) while hatch day² had a negative estimate ($\beta = -0.0008$, SE = 0.0006). The ΔAIC_c values indicated that models 1 - 3 may all be considered good candidate models (Appendix II, Table E).

When repeating the analysis of tarsus length after excluding the outlier the model selection resulted in a different highest ranked model which included AOC, AOC², age, hatch day, hatch day² and the interaction between AOC and hatch day (the interaction between AOC² and hatch day was not included). The parameter estimate for AOC was positive ($\beta = 0.0060$, SE = 0.0109), as well as for AOC² ($\beta = 0.0043$, SE = 0.0021). There was a positive interaction between AOC and hatch day ($\beta = 0.0005$, SE = 0.0002), which indicates that the effect of AOC on tarsus length differs with hatch day. Tarsus length increased with age ($\beta = 0.0004$, SE = 0.0002), while hatch day ($\beta = -0.0008$, SE = 0.0006) and hatch day² ($\beta = -1.54 \cdot 10^{-5}$, SE = 0.0002) had negative parameter estimates. Accordingly, excluding the outlier strongly affected the relationship between the abundance of *O. chloropus* and the variation in tarsus length, as can be seen in Figure 4. Even though there was no reason to believe that the outlier was caused by a sampling error I found it valuable to evaluate the statistical effect of the outlier on the explanative model.

3.3 Juvenile survival and abundance of *O. chloropus*

In the third section of analyses I investigated if AOC could explain the probability of recruitment of juveniles, i.e. survival until second calendar year. Even though six of the highest ranked models contained AOC as an explanatory variable the two highest ranked models did not (Appendix II, Table F). The highest ranked model included positive effects of tarsus length, BCI, hatch day and age at capture on the probability of survival until recruitment (Appendix II, Table G). In addition, the model contained a negative relationship for the interactions between BCI and tarsus length as well as BCI and age with probability of juvenile survival (Appendix II, Table G), which indicates that the effect of BCI on juvenile survival will depend on tarsus length as well as age.

However, as emphasized by Anderson & May (1978) it is important to consider the effect of parasites on the probability of survival even if they do not have a strong overall effect on the survival probability in the population but may lower the survival probability for only a small fraction of the population. Accordingly, among the 10 highest ranked models, 6 included AOC as an explanatory variable. The highest ranked model including AOC was ranked as third with an $AIC_c = 0.92$ from the highest ranked model, and may be considered equivalent to the highest ranked model in describing the variation in survival. Here AOC had a negative coefficient ($\beta = -0.2535$, $SE = 0.2345$) as well as hatch day ($\beta = -0.0278$, $SE = 0.0126$). BCI ($\beta = 38.6991$, $SE = 8.6667$), tarsus length ($\beta = 11.69653$, $SE = 5.1933$) and age ($\beta = 0.0309$, $SE = 0.0159$) all had positive coefficients. The two interaction terms; BCI with tarsus length ($\beta = -127.5073$, $SE = 57.7382$) and BCI with age ($\beta = -0.6239$, $SE = 0.1981$) had negative coefficients, showing that the effect of BCI on juvenile survival will depend on tarsus length as well as age. The high standard error for the parameter estimate of AOC shows that the relationship between abundance of *O. chloropus* and juvenile survival is uncertain.

4. Discussion

In this study I have documented large spatiotemporal variation in the abundance and prevalence of *Ornithomya chloropus* in an insular metapopulation of house sparrows on the coast of Helgeland in northern Norway (Figure 3, Appendix II, Table B). This is, to my knowledge, the first study which has documented substantial spatiotemporal variance in prevalence of *O. chloropus* within a restricted geographical area of a wild passerine host species. Furthermore, the prevalence of louse flies differed considerably between juveniles and adults. Although we found no conclusive relationships between morphology and AOC, there were indications of a negative relationship between tarsus length and AOC. There was no relationship between the juvenile survival and AOC.

Spatial and temporal variation in prevalence has previously been documented for other hippoboscids species. For instance Senar *et al.* (1994) found that prevalence of *Ornithoica turdi* varied within and between years in European serins in Spain and Corbet (1956) found within-year variation in *Ornithomya fringillina*. I have found evidence for spatial and temporal distribution of hippoboscids in the study system, as is shown in Figure 3. There appears to be differences in peak between islands as well as start and end of season between years as the interactions between year and SDN, and island and SDN² were included in the best model. The spatial variation in abundance of *O. chloropus* may be due to spatial heterogeneity in the distribution of the host (Tripet *et al.* 2002) on the various islands combined with habitat heterogeneity (von Post *et al.* 2012) and variation in demography among populations (Robillard *et al.*

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2013) while the temporal variation may be caused by weather conditions such as precipitation (Senar *et al.* 1994).

The start of the parasite season depends on temperature as this will stimulate the exit of male parasites from the puparia (Walker & Rotherham 2010). Females exit at a later time (Walker & Rotherham 2010), which may be a reason for the rapid increase in parasite abundance further into the season. Clayton *et al.* (2010) found that host behavior such as preening and sand bathing along with a seasonal moult are defense mechanisms against harmful ectoparasites. This supports the findings of Corbet (1956) that there was an increase in damaged flies found on hosts from July until August. Waite *et al.* (2012) experimentally demonstrated that Rock Pigeons (*Columba livia*) infested with hippoboscids preened twice as much as control individuals without flies. Sychra *et al.* (2008) also suggested that the seasonal moult makes it easier for birds to rid themselves of ectoparasites. The decrease in parasite abundance towards the autumn in this study system (Figure 3) may therefore be a consequence of an increase in time available for activities such as preening and sand bathing (Stainton 1982) as well as a seasonal moult starting in July - August and ending in September (Ginn & Melville 1983). Møller (2010) suggested that ambient temperature would not affect ectoparasites present on hosts as the host's body would be a microclimate in itself underneath the plumage. Flies which are discarded from the host through anti-parasite behavior would therefore be subject to temperature, though flies present on hosts would not be affected by temperature, but rather by other factors such as the behavioral parasite defenses mentioned above. The decrease in *O. chloropus* abundance may be caused by juveniles increasingly leaving the nest and a decrease in time spent in nests for their parents, as it likely is the main area of novel infections. Hence there will be fewer reinfections (Tomas *et al.* 2007).

Another factor which contributes to a longer period of prevalence in the island populations is the fact that the house sparrow is a multi-brooded species which may typically produce 1 - 3 successful broods during the period May - August in the study area (Kvalnes *et al.* 2013). They are prone to nest reuse

(Anderson 2006), and Tomas *et al.* (2007) found that the blue tit was more prone to infection by ectoparasites due to their nest reuse. The house sparrow will spend more time in nests than a single brood species and are thus more exposed to infection and a higher individual parasite load. Loye & Carroll (1998) found that adult nest selection was important for nestling survival due to high parasite prevalence in low quality nests. Accordingly, this may partly explain the observed seasonal pattern in the present study as prevalence of *O. chloropus* will increase throughout the year as more flies emerge from puparia and have a constant supply of food throughout the host breeding season, and then decrease as breeding ends.

It has previously been demonstrated that the initiation of the breeding season varies significantly among islands in the study area (Ringsby *et al.* 2002), and that a significant interaction between islands and years was present. This suggests that the onset of breeding for a certain island population may occasionally deviate from the expected timing, most likely due to heterogeneity in habitat quality and spatiotemporal variation in phenology. This variation is likely to affect the spatial variation found in prevalence of *O. chloropus* in this study. As hatching success varies between islands (Sæther *et al.* 1999), so will also the respective proportion of juveniles in the populations vary among the populations, which will contribute to variation in prevalence as juveniles is the most infected age-class in the present study.

Depending on the habitat, such as closed up barn, open loft or nest box, there may be varying micro-climatic conditions such as variation in temperature, humidity and even wind speed which may lead to differences in emergence from puparia, which in turn could displace the parasite season (Walker & Rotherham 2010; Marshall 1981). Habitat heterogeneity may therefore cause differences in start, peak and end of season on the different islands depending on the quality of the farm or nesting area, as shown in the interaction between SDN and island. It may also be a cause of the difference in infection period length. Population density varied considerably in the study system depending on the habitat type, which may be an artifact of migration (Pärn *et al.* 2012), though other studies

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have found an effect of island size on prevalence as well (Lindström *et al.* 2004). This may affect the transfer rates of parasite between host (Corbet 1956) which may strongly influence the local prevalence.

Generally, the present study indicates that high abundances of *O. chloropus* was negatively related to the size of the morphological traits BCI, body mass and tarsus length (Figure 4). However due to the high uncertainty of the estimates in the best candidate models this does not seem to be a strong effect, compared to the effects of age and hatch day on morphology (Appendix II, Tables C - E). A number of studies have examined the effect of parasite abundance on morphological traits but there do not seem to be any general conclusions. For instance Hutson (1981) and Tella *et al.* (1995) did not find a relationship between body mass and abundance of lice or flies and the Common swift and Alpine swift, respectively. On the other hand, Senar *et al.* (1994) found a negative effect of abundance on body condition in the European serin. Because the present study has a correlational design we cannot determine whether the relationship between abundance of *O. chloropus* and morphological traits is causal or not, though there are studies which lend support to parasite abundance negatively affecting host morphology (Reviewed in Lehmann (1993) and Møller (1993)). However because parasites per definition extract energy one may *a priori* assume a negative effect on morphology. On the other hand, I cannot exclude the possibility that the negative relationship occurred because small individuals were more prone to infection. It is also possible that the “target hypothesis” (Hamilton & Zuk 1982), that larger individuals are more easily infected due to their size, may play a part in the positive relationship between morphology and abundance of *O. chloropus*.

This study did not find that the survival of juveniles to recruitment was strongly influenced by AOC, although AOC was present in many of the highest ranked models (Appendix II, Table F). The best model containing AOC indicated a possible negative relationship between AOC and juvenile survival though with a large standard error. It has previously been found that juvenile survival until recruitment is affected by both body condition and tarsus length

in juvenile house sparrows (Ringsby *et al.* 1998), and a study by Brown *et al.* (1995) found a negative long term effect of ectoparasites on survival of the cliff swallow (*Hirundo pyrrhonota*). Hence, the results on the relationship between morphological traits and parasite abundance lend support to the hypothesis that parasites may indirectly affect juvenile survival in the study populations. Some recurring variables when looking at juvenile survival seem to be traits such as BCI and tarsus length, as well as age and hatch day. Age may be important due to the increased likelihood of surviving through the winter with a higher age at the time of catching (see also Ringsby, Sæther & Solberg 2002), as well as a general increase in BCI with age, which is important for survival. Hatch day has been found influential in previous studies on juvenile survival in the study area (Ringsby *et al.* 1998; 2002) and may have a negative effect because of an increased probability of becoming infected with earlier hatch days.

The apparent lack of effect of *O. chloropus* on juvenile survival may also be due to the natural aggregation of parasites on hosts. Anderson (1995) suggested in a theoretical study that even a low level of infection could be responsible for regulation of populations where the fraction of host death by parasites is low if the parasite is the only density-dependent mechanism regulating the host population. Thus, *O. chloropus* may potentially have a regulatory effect on the population dynamics in house sparrows despite there being no apparent evidence for it in this study. It is reasonable that the documented handling effect (Figure 2) had a positive effect on the probability of juvenile survival as the decrease in *O. chloropus* abundance following handling may release the host from negative effects of the parasite and consequently result in artificially elevated survival rates in the present study. If abundance of *O. chloropus* in fact does have an effect on juvenile house sparrow survival it would most likely be negative as was found in the third model (Appendix II, Table F).

The occurring climate change may change the distribution patterns of parasites and as the study area is in the northern reaches of *O. chloropus*' range, there is reason to believe that *O. chloropus* will establish in further northern areas. One ecological mechanism that will contribute to extended geographical

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distribution is the increased dispersal rates in house sparrow populations which has been documented with increased spring temperatures (Pärn *et al.* 2012).

In the present study we have focused on the prevalence and potential effect of a single parasite species. However it is important to realize that the parasite community in a host species may be diverse, and even though the fitness effect of one single parasite species may be marginal, the interaction of several aggregated parasite species may have severe fitness consequences for the host population (Holmstad & Skorping 1998; Roberts *et al.* 2002; Holmstad *et al.* 2005). Such mechanisms may influence both the population dynamics of the host species as well as potentially affecting the structure of the avian community. Endoparasites, such as coccids and the caecal nematode *Syngamus trachea* (Holand *et al.* in press) are commonly recorded on house sparrows in the study system, and the combined effect may potentially contribute to lower fitness as covariation between these groups has been shown (Holmstad *et al.* 2008).

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Appendix I

Calculation of mean prevalence based on individual variation in AOC for different year - island combinations from May 1st till August 31st.

The glmmADMB package models zero-inflation by assuming that the response takes a value of zero with probability p_z and that it alternatively comes from a Poisson distribution with mean with probability $1 - p_z$. The whole distribution thus takes the form

$$P(X = x) = \begin{cases} p_z + (1 - p_z) \frac{e^{-\lambda} \lambda^0}{0!} & \text{for } x = 0 \\ (1 - p_z) \frac{e^{-\lambda} \lambda^x}{x!} & \text{for } x \geq 1. \end{cases} \quad (1)$$

Using a log-link function for the relationship between the expected value of the Poisson component of the response and the linear predictor,

$$\ln(\lambda) = \mu + u, \quad (2)$$

where $u \sim N(0, \sigma^2)$ and μ is the non-random part of the linear predictor. Prevalence conditional on the random effect u is then

$$\begin{aligned} P(X \geq 1 \mid u) &= 1 - P(X = 0) \\ &= 1 - (p_z + (1 - p_z)e^{-\lambda}) \\ &= 1 - p_z - (1 - p_z)e^{-\lambda} \\ &= (1 - p_z)(1 - e^{-e^{\mu+u}}). \end{aligned} \quad (3)$$

Using the law of total probability, the expected prevalence when u has the density function $f(u)$ (a normal distribution with zero mean and variance σ^2) is then

$$\begin{aligned}P(X \geq 1 | u) &= \int P(X \geq 1 | u) f(u) du \\&= \int (1 - p_z) (1 - e^{-e^{\mu+u}}) f(u) du \\&= (1 - p_z) \left(1 - \int e^{-e^{\mu+u}} f(u) du\right).\end{aligned}\tag{4}$$

The integral must be computed numerically, for example using the `integrate` function in R (R Development Core Team, 2013).

Appendix II

Table A: Ranking of generalized linear mixed models (glmmADMB, Poisson family, R Development Core Team, 2013) of individual in *O. chloropus* abundance in a house sparrow metapopulation in northern Norway. The full model included island, year and season day number (SDN) and their two-way interaction as explanatory variables. Individual identity was included as a random factor. The table includes the ten highest ranked models of 36 based on the AIC_c criteria with model rank, number of parameters (K), AIC_c deviance (ΔAIC_c) and AIC_c weights (w_i).

	Model	K	ΔAIC_c	w_i
1	Year + Island + SDN + SDN ² + Year:SDN + Island:SDN ² + Year:Island	45	0.00	0.70
2	Year + Island + SDN + SDN ² + Year:SDN + Island:SDN + Island:SDN ²	27	2.58	0.19
3	Year + Island + SDN + SDN ² + Year:SDN + Island:SDN ²	24	4.22	0.09
4	Year + Island + SDN + SDN ² + Island:SDN + Island:SDN ² + Year:Island	41	7.06	0.02
5	Year + Island + SDN + SDN ² + Year:SDN ² + Island:SDN + Year:Island	45	11.34	0.00
6	Year + Island + SDN + SDN ² + Year:SDN ² + Island:SDN ²	24	12.14	0.00
7	Year + Island + SDN + SDN ² + Year:SDN ² + Year:Island	42	14.09	0.00
8	Year + Island + SDN + SDN ² + Year:SDN ²	21	15.57	0.00
9	Year + Island + SDN + SDN ² + Year:SDN + Year:SDN ² + Year:Island	49	15.60	0.00
10	Year + Island + SDN + SDN ² + Island:SDN + Island:SDN ²	20	17.75	0.00

Table B: Regression coefficients with standard errors (SE) for the highest ranked model explaining the spatial and temporal variation in the abundance of *O. chloropus* in an insular metapopulation of house sparrows in northern Norway, from 2004-2011. Island, year, season day number (SDN) and SDN² were included as explanatory factors, including their two way interaction terms. Individual identity was included as random factor in a zero-inflated Poisson model (i.e. glm()-procedure, poisson error distribution, R Development Core Team, 2013.)

Explanatory variables	β	SE	95% CI	
			Lower	Upper
Intercept	-1.4900	0.2820	-2.0394	-0.9334
Year 2005	0.0581	0.5330	-0.9873	1.1034
Year 2006	-0.0520	0.4070	-1.3184	0.2779
Year 2007	0.0827	0.3270	-0.5573	0.7227
Year 2008	0.1340	0.3370	-0.5247	0.7937
Year 2009	-0.2020	0.3740	-0.9337	0.5305
Year 2010	0.7130	0.3480	0.0303	0.5305
Year 2011	0.8650	0.3240	0.2289	1.5000
Island Aldra	0.1550	0.6230	-1.0672	1.3765
Island Gjerøy	-1.4600	0.5720	-2.5783	-0.3379
Island Indre Kvarøy	-0.3920	0.5320	-1.4343	0.6502
SDN	-0.0390	0.0160	-0.0390	-0.0155
SDN ²	-0.0017	0.0002	-0.0020	-0.0013
Year 2005 : SDN	0.0336	0.0228	-0.0112	0.0783
Year 2006 : SDN	-0.0303	0.0193	-0.0682	0.0076
Year 2007 : SDN	-0.0012	0.0760	-0.0356	0.0333
Year 2008 : SDN	-0.0072	0.0176	-0.0417	0.0273
Year 2009 : SDN	-0.0238	0.0179	-0.0589	0.0112
Year 2010 : SDN	0.0477	0.0190	0.0100	0.0849
Year 2011 : SDN	0.0132	0.0172	-0.0205	0.0469
Island Aldra : SDN ²	-0.0014	0.0008	-0.0032	0.0470
Island Gjerøy : SDN ²	-0.0002	0.0003	-0.0008	0.0004
Island Indre Kvarøy : SDN ²	-0.0005	0.0003	$3 \cdot 10^{-5}$	0.0044
Year 2005 : Island Aldra	-0.3520	1.2800	-2.8526	2.1476
Year 2006 : Island Aldra	-21.9000	32000	-62719	62675
Year 2007 : Island Aldra	0.6770	0.8480	-0.9846	2.3379
Year 2008 : Island Aldra	0.1070	0.7760	-1.4144	1.6285

Continued on next page

Table B – continued from previous page

Explanatory variables	β	SE	95% CI	
			Lower	Upper
Year 2009 : Island Aldra	-1.0100	1.0500	-3.0784	1.0489
Year 2010 : Island Aldra	-20.2000	13600	-26736	26696
Year 2011 : Island Aldra	-0.0038	0.8170	-1.6046	1.5971
Year 2005 : Island Gjerøy	1.7500	0.9640	-0.1404	3.6392
Year 2006 : Island Gjerøy	0.9130	0.7350	-0.5269	2.3532
Year 2007 : Island Gjerøy	1.7100	0.6920	0.3503	3.0643
Year 2008 : Island Gjerøy	-0.5570	0.9200	-2.3605	1.2459
Year 2009 : Island Gjerøy	1.3400	0.7320	-0.0965	2.7745
Year 2010 : Island Gjerøy	-0.0209	0.7180	-1.4275	1.3856
Year 2011 : Island Gjerøy	1.1600	0.6480	-0.1084	2.4308
Year 2005 : Island Indre Kvarøy	0.1170	0.9090	-1.6640	1.8974
Year 2006 : Island Indre Kvarøy	-0.3020	0.7170	-1.7077	1.1031
Year 2007 : Island Indre Kvarøy	-0.4230	0.6800	-1.7556	0.9089
Year 2008 : Island Indre Kvarøy	-1.0400	0.7450	-2.4977	0.4238
Year 2009 : Island Indre Kvarøy	-0.4600	0.7610	-1.9523	1.0318
Year 2010 : Island Indre Kvarøy	0.3620	0.6750	-0.9622	1.6854
Year 2011 : Island Indre Kvarøy	-1.3300	0.6580	-2.6148	-0.0037

Table C: Ranking of generalized linear models (glm()-procedure, Gaussian family, R Development Core Team, 2013) of individual body condition index (BCI) in a house sparrow metapopulation in northern Norway. The full model included island year, age at capture and hatch day and abundance of *O. chloropus* (AOC), and quadratic terms of age, hatch day and AOC. Two way interactions between AOC and year, AOC and age, AOC and hatch day, AOC² and age, AOC² and hatch day, year and hatch day and island and hatch day were included. The table shows the ten highest ranked models of 62 based on the AICc criteria with model rank, number of parameters (K), AICc deviance (ΔAIC_c) and AICc weights (w_i). For further model details see Methods.

	Model	K	ΔAIC_c	w_i
1	AOC + AOC ² + Age	5	0.00	0.22
2	AOC + Age	4	0.13	0.20
3	Age	3	0.23	0.19
4	AOC + AOC ² + Age + Hatch day	6	1.47	0.10
5	AOC + Age + Hatch day	5	1.77	0.08
6	AOC + Age + Hatch day + Hatch day ²	6	1.89	0.07
7	AOC + AOC ² + Age + Hatch day + Hatch day ²	7	2.16	0.01
8	AOC + AOC ² + Age + Island + Hatch day	9	7.11	0.00
9	AOC + Age + Island + Hatch day + Hatch day ²	9	7.32	0.00
10	AOC + AOC ² + Age + Island + Hatch day + Hatch day ²	10	7.75	0.00

Table D: Ranking of generalized linear models (glm()-procedure, Gaussian family, R Development Core Team, 2013) of individual body mass in a house sparrow metapopulation in northern Norway. The full model included island year, age at capture and hatch day and abundance of *O. chloropus* (AOC), and quadratic terms of age, hatch day and AOC. Two way interactions between AOC and year, AOC and age, AOC and hatch day, AOC² and age, AOC² and hatch day, year and hatch day and island and hatch day were included. The table shows the ten highest ranked models of 49 based on the AICc criteria with model rank, number of parameters (K), AICc deviance (ΔAIC_c) and AICc weights (w_i). For further model details see Methods.

	Model	K	ΔAIC_c	w_i
1	AOC + AOC ² + Age + Hatch day + Hatch day ²	7	0.00	0.32
2	AOC + Age + Hatch day + Hatch day ²	6	0.41	0.26
3	Age + Hatch day + Hatch day ²	5	1.20	0.17
4	AOC + AOC ² + Age + Hatch day	6	2.28	0.10
5	AOC + Age + Hatch day	5	3.84	0.05
6	Age + Hatch day	4	4.58	0.03
7	AOC + AOC ² + Age + Island + Hatch day + Hatch day ²	10	5.30	0.02
8	AOC + Age + Island + Hatch day + Hatch day ²	9	5.56	0.02
9	AOC + AOC ² + Year + Age + Hatch day + Hatch day ²	13	6.67	0.01
10	AOC + AOC ² + Age + Island + Hatch day	9	7.59	0.01

Table E: Ranking of generalized linear models (glm()-procedure, Gaussian family, R Development Core Team, 2013) of individual tarsus length in a house sparrow metapopulation in northern Norway. The full model included island year, age at capture and hatch day and abundance of *O. chloropus* (AOC), and quadratic terms of age, hatch day and AOC. Two way interactions between AOC and year, AOC and age, AOC and hatch day, AOC² and age, AOC² and hatch day, year and hatch day and island and hatch day were included. The table shows the ten highest ranked models of 39 based on the AICc criteria with model rank, number of parameters (K), AICc deviance (ΔAIC_c) and AICc weights (w_i). For further model details see Methods.

	Model	K	ΔAIC_c	w_i
1	AOC + AOC ² + Age + Hatch day + Hatch day ² + AOC:Hatch day + AOC ² :Hatch day	9	0.00	0.46
2	AOC + AOC ² + Hatch day + Hatch day ² + AOC:Hatch day + AOC ² :Hatch day	8	1.72	0.19
3	AOC + AOC ² + Island + Age + Hatch day + Hatch day ² + AOC:Hatch day + AOC ² :Hatch day	12	1.85	0.18
4	AOC + AOC ² + Island + Hatch day + Hatch day ² + AOC:Hatch day + AOC ² :Hatch day	11	3.68	0.07
5	AOC + AOC ² + Age + Hatch day + AOC:Hatch day + AOC ² :Hatch day	8	4.35	0.05
6	AOC + AOC ² + Island + Age + Hatch day + AOC:Hatch day + AOC ² :Hatch day	11	5.97	0.02
7	AOC + AOC ² + Hatch day + AOC:Hatch day + AOC ² :Hatch day	7	6.34	0.02
8	AOC + AOC ² + Year + Age + Hatch day + Hatch day ² + AOC:Hatch day + AOC ² :Hatch day	15	10.71	0.00
9	AOC + AOC ² + Year + Island + Age + Hatch day + Hatch day ² + AOC:Hatch day + AOC ² :Hatch day	18	12.14	0.00
10	AOC + AOC ² + Year + Island + Hatch day + Hatch day ² + AOC:Hatch day + AOC ² :Hatch day	17	13.93	0.00

Table F: Ranking of generalized linear models (glm()-procedure, Binomial family, R Development Core Team, 2013) for juvenile survival in a house sparrow metapopulation in northern Norway. The full model included island year, age at capture and hatch day as well as abundance of *O. chloropus* (AOC), body condition index (BCI) and tarsus length and quadratic terms of age, hatch day, AOC, BCI and tarsis length as explanatory variables. Two way interactions between BCI and tarsus length, BCI and hatch day, BCI and age, BCI and year and BCI and island. AOC and BCI, AOC and year, AOC and age, AOC and hatch day, AOC and island as well as AOC² and year and AOC² and BCI were also included. The table shows the ten highest ranked models of 110 based on the AICc criteria with model rank, number of parameters (K), AICc deviance (ΔAIC_c) and AICc weights (w_i). For further model details see Methods.

	Model	K	ΔAIC_c	w_i
1	BCI + Tarsus + Hatch day + Age + BCI:Tarsus + BCI:Age	7	0.00	0.14
2	BCI + BCI ² + Tarsus + Hatch day + Age + BCI:Tarsus + BCI:Age	8	0.69	0.10
3	AOC + BCI + Tarsus + Hatch day + Age + BCI:Tarsus + BCI:Age	8	0.92	0.09
4	AOC + BCI + BCI ² + Tarsus + Hatch day + Age + BCI:Tarsus + BCI:Age	9	1.62	0.06
5	AOC + BCI + Tarsus + Hatch day + Age + BCI:Tarsus + BCI:Age + BCI:AOC	9	1.63	0.06
6	AOC + AOC ² + BCI + Tarsus + Hatch day + Age + BCI:Tarsus + BCI:Age + BCI:AOC	10	2.23	0.05
7	BCI + Tarsus + Age + BCI:Tarsus + BCI:Age	6	2.31	0.05
8	AOC + AOC ² + BCI + Tarsus + Hatch day + Age + BCI:Tarsus + BCI:Age	9	2.34	0.04
9	BCI + BCI ² + Tarsus + Age + BCI:Tarsus + BCI:Age	7	2.68	0.04
10	AOC + BCI + BCI ² + Tarsus + Hatch day + Age + BCI:Tarsus + BCI:Age + BCI:AOC	10	2.77	0.04

Table G: The table shows regression coefficients and their respective standard errors (SE) for the highest ranked model explaining individual variance in juvenile survival in an insular metapopulation of house sparrows in northern Norway. The model included body condition index (BCI), tarsus length, hatch day and age as well as interactions between BCI and tarsus and BCI and age.

Explanatory variables	β	SE	95% <i>CI</i>	
			Lower	Upper
Intercept	-4.4416	0.7320	-5.9628	-3.0804
BCI	38.3234	8.5234	22.856	56.3840
Tarsus	11.7135	5.1746	1.9083	22.2781
Hatch day	-0.0265	0.0125	-0.0515	-0.0021
Age	0.0348	0.0156	0.0048	0.0663
BCI:Tarsus	-127.6333	57.3525	-245.1365	-18.8401
BCI:Age	-0.6184	0.1949	-1.0253	-0.2594