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Predator-Induced Selection on Phenotypes by Sparrowhawks (*Accipiter nisus*) in House sparrows (*Passer domesticus*)

Master's thesis in Natural Science with Teacher Education

Supervisor: Thor Harald Ringsby

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Abstract

Predation can act as a selective agent on the phenotypic and genotypic distribution of traits in the prey, the demographic structure and spatiotemporal variation in mortality. This study investigates the effect of predation by sparrowhawks (*Accipiter nisus*) on mortality, demography and phenotypes over eight years in three insular house sparrow (*Passer domesticus*) populations in northern Norway. The effect of increasing sparrowhawk density on the probability of mortality differed spatially, with decreasing probability of mortality in two of the populations and increasing probability of mortality in one population. The effect of sparrowhawk density on mortality probability varied among juveniles and adults. There was evidence for predator density induced selection on body size and body mass, where lighter and smaller individuals suffer a high mortality probability with low sparrowhawk densities, while heavier and larger individuals have an increased mortality probability with high sparrowhawk densities. The mortality-induced selection on phenotypes could act balancing on intermediate body sizes and body mass. There were no signs of a difference in predator-induced mortality between sexes, in different population densities or between individuals with different wing length or wing load. These results increase our understanding of how predator-prey dynamics can be heterogeneous among populations, and how predator-induced mortality can be selective and influence adaptive evolution in the prey species. Disparity in predator-prey relationships provides opportunities to study anti-predatory behaviours, adaptive evolution, food webs and potential phenological mismatches.

Sammendrag

Predasjon kan påvirke fenotypisk og genotypisk distribuering av trekk i byttedyret, samt ha en innflytelse på demografisk struktur og variasjon i mortalitet ved tid og rom. Denne studien undersøker hvordan predasjon av spurvehauken (*Accipiter nisus*) induserer mortalitet i gråspurvpopulasjoner (*Passer domesticus*) demografisk og fenotypisk gjennom åtte år i tre insulære gråspurvpopulasjoner i Nord-Norge. Effekten av spurvehauktetthet på gråspurvens mortalitetssannsynlighet varierte mellom øyene, der sannsynligheten ble redusert hos to av øyene med økt spurvehauktetthet, mens for én økte mortalitetssannsynlighet med økt spurvehauktetthet. Spurvehauktettheten påvirket juvenile og adult gråspurv ulikt. Det var seleksjon på fenotypene kroppsstørrelse og kroppsmasse i løpet av studien. Ved lave spurvehauktettheter hadde små og lettere individer en større sannsynlighet for mortalitet, mens ved høye spurvehauktettheter hadde store og tyngre individer en større mortalitetssannsynlighet. Denne mortalitets-induserte seleksjonen på fenotypene kan ha virket balansere på intermediaære kroppsstørrelser og kroppsmasse. Det var ingen klare tegn til differensiert mortalitetssannsynlighet mellom kjønn, populasjonstettheter, vingelengde og vingebelastning. Disse resultatene kan øke forståelsen for hvordan predator-byttedyr dynamikk kan være heterogen mellom populasjoner, og hvordan mortalitet grunnet til predasjon kan påvirke adaptiv evolusjon hos byttedyret. Ulikheter i predator-byttedyr relasjoner gir grunnlag og muligheter for å studere antipredatorisk adferd, adaptiv evolusjon, næringsnett og potensielle fenologiske "mismatches".

Preface

The work described in this master thesis is carried out in the Department of Biology at Norwegian University of Science and Technology, during the spring of 2022, in the field of ecology, behaviour, evolution and biosystematics. This thesis was written as a part of Gråspurvprosjektet founded by Thor Harald Ringsby and Henrik Jensen, and takes part in the integrated master Natural Science with Teacher Education. This thesis has provided me with mathematical, statistical and biological tools and abilities improving my in-depht knowledge for the subjects, and has been invaluable for my personal development as a teacher.

I want to thank my supervisors Thor Harald Ringsby, Thomas Kvalnes and Peter Sjolte Ranke for guidance and support throughout the process of project planning, fieldwork, data handling, statistical analysis and writing. Your interest and curiosity for this thesis has been tremendously encouraging.

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Abbreviations

Age₁ Age category 1.

Age₂ Age category 2.

HD House sparrow population density.

SD Sparrowhawk density.

WL Wing load.

1 Introduction

Predation is a key ecological process that may affect the ecology and evolution of prey species (Buxton and Sperry, 2017; Kolb et al., 2007; Wilson, 1990). In prey species, predation may act as a selective agent influencing the phenotypic and genotypic distribution of traits, and may generally affect the abundance, vital rates and the age structure of populations (Lees and Creed, 1977; Roos et al., 2018; Sinclair and Krebs, 2002; Urban, 2007; Young, 1970). The presence of predators may also induce predator avoidance behaviour in the prey populations, as a means to reduce predation risk and mortality (Gotmark and Post, 1996; San-Jose et al., 2019; Suhonen, 1993). However, because predator-prey interactions are notoriously challenging to study in wild populations there is a need for more empirical studies estimating the effects of spatial and temporal variation in predator densities on life history traits in prey species. As the dynamic between predator and prey can vary temporally and spatially due to habitat heterogeneity and variance in the demography of the prey population (Ciechanowski et al., 2007; Palmer et al., 2017), it is important to study how predator-prey dynamics may vary over time in a larger geographical scale. Obtaining this knowledge will give more in-depth knowledge of interspecific dynamics and their role in the ecology such as food webs, niches, adaptive evolution and potential phenological mismatches.

The realized niche for a prey population gives insight into biotic factors that limit the population abundance (Hutchinson, 1957). Accordingly, predators are being one of the biotic limitations on the abundance of prey species, and influence their spatial and temporal variation in abundance (Roos et al., 2018). A number of theories aim to explain the fluctuations in prey populations abundance as a response to the abundance of predator populations (Arditi and Ginzburg, 1989) such as Lotka-Volterra predator-prey model (Volterra, 1928) and the Rosensweig-MacArthur predator prey model (Rosenzweig and MacArthur, 1963). One classical empirical example of such synchronized fluctuations between predator and prey is between snowshoe hare (*Lepus americanus*) and Canadian lynx (*Lynx canadensis*) (MacLulich, 1937). However, later experimental studies have revealed the significance of several other factors that contribute to the population dynamics in the hare (*L. americanus*) populations such as habitat quality (Krebs, 1996), food availability (Krebs et al., 1995) and demography (Oli et al., 2020). As there can be numerous factors influencing prey populations dynamics, the impact of a predator on the prey population can therefor be difficult to unravel.

Lindström et al. (1994) have shown the impact of predators on prey population size in the relationship between red fox (*Vulpes vulpes*) and mountain hares (*Lepus timidus*) in Sweden. In this example, the population sizes of red fox were severely reduced in the period 1973-1992 due to the parasite mange mite (*Sarcoptes scabiei*). This resulted in a numerical response where population size of mountain hares increased. It has also been found that impact of predators can have both negative and positive influence on preys'

population sizes (Chamberlain et al., 2009). For instance, Chamberlain et al. (2009) showed that increase in sparrowhawk abundance had both positive and negative impacts on the abundance and survival rates of different prey species' populations. Great tit (*Parus major*), blue tit (*Cyanistes caeruleus*) and collared dove (*Streptopelia decaocto*) responded positively to increased sparrowhawk abundance, while starling (*Sturnus vulgaris*), chaffinch (*Fringilla coelebs*) and greenfinch (*Carduelis chloris*) declined in abundance. The difference between species was attributed to dissimilarity in post-breeding population sizes, and disparity in behavioural responses to increased risk of predation (Chamberlain et al., 2009).

The probability of predation can be affected by the density of the prey species (Holling, 1959a, 1959b). For instance, risk of predation can decrease as prey population density increases as handling time and predator saturation may reduce the hunting efficiency of the predator (Götmark and Andersson, 2005; Götmark and Post, 1996). Götmark and Andersson (2005) conducted an experiment where the nest box density for great tit (*P. major*) were increased within sparrowhawk (*Accipiter nisus*) territories. Sparrowhawk did not regulate the great tit population density during summer, and it was suggested that dilution could explain the observed inverse density-dependent pattern. For instance, Holling (1959a) showed that the percentage of European pine sawfly (*Neodiprion sertifer*) consumed by the masked shrew *Sorex cinereus cinereus*, the short-tail shrew *Blarina brevicauda* and deer mouse *Peromyscus maniculatus bairdii* declined with their increased cocoon density. Theory predicts that prey density should increase the predators feeding rate proportionally when the ratio of prey and predator abundance are taken into account (Arditi and Ginzburg, 1989). Holling (1959a) outlined 3 different functional responses where the relationship between predators feeding rate is positive in response to prey density. Predators feeding rate can be linear, curvilinear and sigmoid. These functional responses could further explain preys mortality rates as different dome-shaped responses with increased prey population density (Arditi and Ginzburg, 1989; Holling, 1959b; Jeschke et al., 2004). Moreover, theory predicts an individual decline in predation risk with increased prey densities (Holling, 1959a, 1959b).

The impact a predator can have on preys' populations can be common (Donazar and Ceballos, 1989) or vary across separate populations (Durant, 1998; Ripple and Beschta, 2004, 2007; Thaker et al., 2011; Valeix et al., 2009). Spatial heterogeneity among populations can alter variability in behavioural responses to predation (Ripple and Beschta, 2004) such as selection on habitat (Creel et al., 2005; Lima, 1998; Wirsing et al., 2007) and success of antipredator strategies (Andruskiw et al., 2008). For instance, in the bridled goby (*Coryphopterus glaucofraenum*), Forrester and Steele (2004) showed with the presence of predators that spatial variation in refuge and prey population density affected mortality rates. The antipredator strategy to seek refuge was successful with high densities of refuges, compared to sites with low refuge densities, showing spatial variation in predation risk. Dissimilarity in predator-induced mortality among populations is not

always seen. Two different biographical populations of rabbits (*Oryctolagus cuniculus*) in northern Spain showed the same predator-prey relationship with eagle owl (*Bubo bubo*), a case in point (Donázar and Ceballos, 1989). This study exemplifies that there can be a general predator-prey relationship spatiotemporally as the young were selected on and predator-induced mortality fluctuated synchronous among the populations. As predation risk can vary through time (Lima and Bednekoff, 1999; Lima and Dill, 1990; Palmer et al., 2017) and space (Durant, 1998; Ripple and Beschta, 2004, 2007; Thaker et al., 2011; Valeix et al., 2009), subpopulations may be affected differently by predation.

Individual vulnerability to predation can be age-dependent, affected by the behaviour or antipredator strategies at the given age (Lingle et al., 2008). Juveniles often suffer a higher risk of predation than adults (Hammill and Smith, 1991; Hoy et al., 2015). Immature individuals may lack the experience or be ineffective at escaping predators when compared to older individuals (Fitzgibbon, 1990). Andreasson et al. (2019) found that juvenile and adult great tit (*P. major*) and blue tits (*C. caeruleus*) were prone to use different behavioural responses with increased perceived predation risk. However, predation can also be higher for older individuals due to senescence (Dhondt et al., 1998). Generally, differences between age classes in their susceptibility to predation will depend on the size and hunting tactics of the predator (Downes, 2002; Kunkel et al., 1999; Paquet, 1992).

A hunting tactic not resulting in an additive effect on the mortality rate of the prey population is called compensatory predation. Compensatory predation means that predators are more likely to kill prey individuals that typically may be in poor condition, do not contribute to population growth by non-reproducing, or was likely to die within a short time period due to diseases or starvation (Bender and Rosas-Rosas, 2016; Caughley et al., 1980; Errington, 1946). In such cases, presence of predators would not reduce the prey's population size. Rather, a decline in prey population mortality could be due to other causes and predation would be purely compensatory (Bartmann et al., 1992; Boyce et al., 1999; Errington, 1967). This is suggested to be the case for reindeer (*Rangifer tarandus*) in northern Norway, with predators such as the lynx (*Lynx lynx*), wolverine (*Gulo gulo*) and golden eagle (*Aquila chrysaetos*) (Tveraa et al., 2003).

Predation-induced mortality may cause evolutionary changes in phenotypic traits in the prey population (Lees and Creed, 1977). This occurs when a predator has a preference towards a particular range of the phenotypic distribution in the prey population. The peppered moth (*Biston betularia*) population in Great Britain during 1850 until 1950 is a classic example of such an influence on phenotype by the predator. There where a shift in high frequency from the salt-and-pepper phenotype to the melanic black as changes in the environment transpose camouflage opportunities from birds (Cook, 2003; Lees and Creed, 1977; as cited in Grant et al., 1996). Phenotypical traits such as body mass can affect the predation risk (Green and Côté, 2014; Lafferty, 1993; Selås, 1993; Werner et al., 1983 but see Gosler et al., 1995). The phenotypical trait body mass could

affect the ability to escape an attack by predators in birds, as a lower body mass may increase maneuverability (Gosler et al., 1995; Lima, 1986). For instance, Witter et al. (1994) found that elevated body mass in fat reserves decreased aerial maneuverability in the European starling (*Sturnus vulgaris*), and could increase the risk of predation. Several avian studies have shown corresponding results for other phenotypic traits. For instance, individuals being killed can be selected on due to poor condition (Green, 2001; Vedder et al., 2014) or the heaviest individuals due to reduced flight maneuvering (Witter and Cuthill, 1993; Gotmark and Post, 1996). The flying ability could be reduced with increased fat reserves giving a higher wing load (Hedenström, 1992; Norberg, 1995). However, wing load is often found not to influence on the predation risk (Kullberg, 1998; Kullberg et al., 1998; MacLeod et al., 2006 van der Veen and Lindström, 2000; Veasey et al., 1998).

Phenotypical differences can often be found between sexes (Clutton-Brock, 2007; Darwin, 1871; Lloyd and Webb, 1977). Traits such as colors (Endler, 1995), ornaments (Hernandez-Jimenez and Rios-Cardenas, 2012) and size (Ercit, 2014) can make individuals easier to detect or catch for a predator (Endler, 1995; but see Bókony et al. (2008)). For instance, the sexually size-dimorphic grasshopper *Tetrix japonica* with body-color marking variations differ in predation risk among the sexes. Predator-induced mortality is seen in spotted females and not in males, as being both larger and spotted are more conspicuous for predators (Tsurui et al., 2013). In the bird species barn swallows (*Hirundo rustica*), males have sexually exaggerated tail feathers, making them more prone to predation by sparrowhawk (*A. nisus*) as male barn swallows were easier to catch (Møller and Nielsen, 1997). These examples show that predator-induced mortality can differ between sexes and phenotypes. Differences between sexes are not only found to be phenotypical, but can be behavioural such as investment in breeding (Gray and Hamer, 2001; Ringsby et al., 2009) and foraging (Götmark et al., 1997; Lewis et al., 2002). For instance, female chaffinches (*Fringilla coelebs*) with cryptic plumage have suffered higher predator-induced mortality rate than males' bright plumage due to difference in foraging time (Götmark et al., 1997). Also female house sparrows (*Passer domesticus*) are found to forage more, as they feed offspring at an higher frequency than males (Ringsby et al., 2009). The sexes could then differ in predator-induced mortality due to phenotypical and behavioural differences.

In an insular metapopulation of house sparrows in northern Norway, individuals in 18 populations have been closely monitored using capture-mark recapture methods since 1993 (Ranke et al., 2021). Individuals were captured and banded with unique combinations of plastic colour rings, and measured for phenotypic traits at the juvenile and adult life stage. On three of the island-populations, the daily presence of sparrowhawks during winter (January - April) has been monitored in the period 2011-2018. This provided a unique opportunity to study temporal and spatial variation in the relationship between predator abundance and its effects on prey dynamics. In particular, the present study

will investigate the following objectives. First, I investigate if the annual mortality rate of house sparrows were influenced by the density of observed sparrowhawks during winter period. In these analyses I also test whether the mortality rate of house sparrows could be explained by among-island differences along with demographical factors such as their individual variation in sex, age classes and the annual house sparrow population density. Second, I investigate to which degree these factors (i.e. age, sex, island and population density) influenced house sparrow mortality through interaction with sparrowhawk density. Thirdly, I investigated to which degree the sparrowhawk acted as a selective agent on the phenotype of the house sparrow populations.

2 Method

2.1 Study species

2.1.1 House sparrow

House sparrows (*Passer domesticus*) are passerine birds, found on every continent except Antarctica (Cramp et al., 1994). Their total body length is in the range 14-16 cm, and their weights are in the range 25-35 gram (Anderson, 2006). As a sedentary and urban species the house sparrow find food and shelter in and near human settlements (Anderson, 2006; Lowther, 1977). Seeds are the primarily food source for adults, but they also use other available food items to supplement the diet (Anderson, 2006). The house sparrow is socially monogamous, with biparental care (Ringsby et al., 2009). Sexual maturity is reached after one year (Anderson, 2006), and each female can lay up to three broods within a season where each brood consist on average of 4.6 eggs (Anderson, 2006; Ringsby et al., 1998). The breeding season in the study area lasts from early May to mid-August (Jensen et al., 2003). The eggs are incubated at median of 11 days, and nestlings fledge at around 14 days of age (Anderson, 2006; Kvalnes et al., 2013). House sparrows have many natural predators worldwide. These includes reptiles, mammals and raptors (McLeod and Thompson, 2002; Paralkar, 1995; Storer, 1966). In Norway one of the most numerous predators is the Eurasian sparrowhawk (*Accipiter nisus*) (Shimmings and Øien, 2015).

2.1.2 Sparrowhawk

The sparrowhawk *Accipiter nisus* is commonly found in woodlands and cultivated areas (Gotmark and Post, 1996). It is a generalist raptor with many different prey species depending on the habitat and availability (Kramer, 1973; Opdam, 1978). Passerine birds within the weight class 51-120 grams constitute the main diet of sparrow hawks (Selås, 1993). However, when it comes to number of preys, passerine birds within the weight class 21-50 gram cover 30% of the number of preys (Selås, 1993). The house sparrow is an important food source during winter season (September - March), covering up to 1/3 of the winter diet in some studies (Glutz et al., 1973; Kramer, 1973; Opdam, 1978, as cited in Newton, 1986).

2.2 Study area

The study area consists of the insular house sparrow populations on Selvær, Lovund and Træna located in an archipelago along the coast of Helgeland in northern Norway (66°N13E'). The populations are part of a larger metapopulation, where house sparrows

have been monitored on a total of 18 islands since 1993. The islands consist of land with agriculture, gardens, heathland and mountains with oceanic climate, usually snow-free despite being in the Arctic Circle (Sæther et al., 1999). The fish industry is dominant on the islands along with aquaculture and sheep farming. The breeding of house sparrows primarily takes place in artificial nest boxes, but also in cavities found on houses and sometimes in trees. On these islands the weather fluctuates substantially and supplementary feeding in gardens are common.

2.3 Data collection

The study period lasted from 2010 until 2019. Daily observations of sparrowhawks have been collected since winter 2010-2011 until winter 2018-2019 by experienced local inhabitants during the winter period (defined as 1st of January till 1st of April, i.e. 13 weeks in total). Fieldwork has been conducted annually during the breeding season of house sparrows lasting from early May until mid August (Ringsby et al., 1998) as well as for one or two weeks during the autumn (September - October). In the house sparrow populations, each individual was marked with a numbered metal ring and a unique combination of three plastic color rings. Phenotypic traits were measured, such as body mass (± 0.05 gram with spring weight), wing length (± 0.05 mm with wing ruler) and tars length (± 0.005 mm with Vernier slide calliper) as well as the gender for each individual based on molecular genetic analysis (Jensen et al., 2003; Jensen et al., 2008). Measurements of left and right wing and tarsus length were averaged for each record.

House sparrows were marked either as fledglings in the nest (7-13 days of age) or captured as full grown juvenile or adult individuals using mist nets. Marked individuals were recaptured using mist nets and resighted using binoculars. Age was categorized as 0, 1 and 2, where age category 0 represents juveniles, category 1 first time breeders being 1 year old. Age category 2 represent individuals being 2 years or older. If an individual was not recaptured or observed the following year between 1st of April till 31st of December it was assumed dead and mortality recorded as 1 (otherwise 0 if it was observed alive in the same period). The 1747 individuals that were captured or resighted outside the nest (Table 1) were included in the study, this excludes the high mortality rate of fledglings that is less likely to be related to sparrowhawk predation.

2.3.1 Estimating annual variation in sparrowhawk density

The annual sparrowhawk density index was estimated for each island during the 13 weeks winter period (see above) as the number of weeks with at least one observation of a sparrowhawk, divided by 13 weeks (from 1st January to 1st April). The annual index was then standardized to a mean of 0 and variance of 1 within each island. This was done

as it was not possible to know the number of individuals observed, just their presence. The islands were seen as independent, since the mortality rate was assumed to be island-specific depending on habitat heterogeneity between the islands. In addition, the local observers differed among the 3 islands. At Lovund, there was one observer recording dates when sparrowhawks were seen. Whereas at Træna and Selvær, one and one till two observers contributed with data through the winter period respectively. Additionally a fieldworker observed annually for short periods.

2.3.2 House sparrow phenotypes

The sample size for this analysis was 668 (See Table 2). For each year the mean of all measured tarsus length was calculated independent of age, as it is fully grown at fledging stage (Ringsby et al., 1998). For adults (age category 2) the annual means of all weight and wing length recordings were based on samples obtained during summer season (April - August). Later measurements during the autumn were excluded due to seasonal changes in traits. For the juveniles, last measurements of body mass and mean wing length during their hatch year was used, as the last measurement was likely to be more closely related to their adult phenotypic size during winter. For all individuals, an annual wing load index was estimated as the residual deviance from the mean of a regression model. Body mass was set as response to wing length and estimated in separate models of both females and males, for all age categories, as well for each island.

2.3.3 House sparrow population density

For each island the size of house sparrow population was estimated with a capture-mark-recapture (CMR) (Ranke et al., 2021). Estimates were based on the recapture rate, where an individual is assumed dead if not recaptured or observed. Differences in annual recapture probability among islands were accounted for basing the model on ringed, breeding adults. As the rate of unmarked individuals varied annually the population estimates could potentially be biased. To account for such variations, resight rates below 0.60 were not included in the analysis. Due to variations in population sizes among the islands, the population sizes were mean centered and scaled to a variance of 1 to provide estimates of population density that was comparable between populations.

2.4 Statistical analysis

The Software R version 4.0.5 by R Core Team (2021) was used to analyse the data. Generalized linear mixed-models fitted with binomial error distribution and a complementary clog-log function were used to analyse the data (Bates et al., 2015). All models estimated

house sparrow mortality as a response variable and included the effect of year as a random effect. A priori defined candidate models were ranked according to Akaike's information criterion corrected for small sample size (AIC_c) to identify the most parsimonious models (Burnham and Anderson, 2002). The most parsimonious models were defined with lowest AIC_c value and used for further statistical analyses. Models were considered equally good if they fit the criteria of $\Delta AIC_c \leq 2$ compared to the model with lowest AIC_c value. If so, the model having fewer parameters including 0 in their confidence estimates were chosen. Aikake weight (AIC_c Weight), a model's relative likelihood, was used to evaluate the probability of the best fit models (Burnham and Anderson, 2002).

In the statistical analyses I first investigated if annual mortality of house sparrows was influenced by the sparrowhawk density by constructing four models. Since there were theoretical reasons to believe that variation in house sparrow mortality potentially varied among islands, sex and age classes, all the four candidate models in this section accounted for these factors. In addition, the candidate models investigated the effects of house sparrow population density and sparrowhawk density. The most parsimonious model was used as baseline model for further analyses. Secondly, I investigated if variation in house sparrow mortality was influenced by sex, age classes, population densities and islands in interaction with sparrowhawk density. To investigate if such differences occurred, analyses were conducted where the model fit of the baseline model was compared with a candidate model including an interaction with a focal variable and sparrowhawk density. In total 8 models have been analyzed in this section. Thirdly, I investigated if the mortality of house sparrows was influenced by selective sparrowhawk predation with respect to house sparrow phenotypes. To investigate if there were selection in phenotypes, the best fitted model explaining probability of mortality of house sparrows including the effect of sparrowhawk densities were used. Along with this model, the different phenotypes were added as explanatory factors individually and pairwise compared to a model including an interaction between the given phenotype and sparrowhawk density. In all analyses the explanatory variables such as house sparrow population density, sparrowhawk density, tarsus, weight and wing length were centered by their grand mean prior the analysis to improve model convergence. Estimated parameters are given with 95% confidence estimates (CI = [lower, upper]). Pearson's product moment correlation (r_p) was estimated between numeric explanatory variables to avoid multicollinearity due to highly correlated explanatory variables ($r_p < 0.05$) (Graham, 2003).

3 Results

The sparrowhawk density fluctuated between years (Figure 1), and the mean sparrowhawk density over the 8 year study period was 0.373 on Træna (SD = 0.210, range = [0.000, 0.615]), 0.243 on Selvær (SD = 0.110, range = [0.077, 0.385]) and 0.243 on Lovund (SD = 0.165, range = [0.000, 0.462]). Lovund and Selvær showed a similar pattern in the annual fluctuations, while Træna showed a different pattern. Træna had a mean of 100.1 individuals (SD = 28.6) over the 8 years study period, while Lovund and Selvær had mean population sizes of 48.9 (SD = 22.3) and 56.9 (SD = 22.0), respectively (Figure 2).

The most parsimonious model out of the 4 candidate models explaining the variation in annual mortality in house sparrows included a difference between age classes, a tendency for an increase in mortality with increasing house sparrow population density and a decrease in mortality with increasing sparrowhawk density (AIC_c Weight = 0.44, Tables 3 and 4). The confidence interval for the effect sparrowhawk density did not include zero (Table 4), and was not present in the second highest ranked model (Table 3 and S1). Thus, sparrowhawk density had a clear negative effect on the mortality of house sparrows (See Table 3 and 4).

The second section of pairwise analyses provided no evidence of an interaction effect between house sparrow population density and sparrowhawk density ($\beta_{SD*HD} = 0.098$, CI = [-0.044, 0.240], $\Delta AIC_c = 0.19$, AIC_c Weight = 0.48, Table S2). Thus, there was no support for the mortality of house sparrows being dependent on the combined effect of predator and prey density. In contrast, the pairwise model comparison revealed that the effect of sparrowhawk density differed substantially between the three populations (Table S3 and S4, AIC_c Weight = 0.98, Figure 3). At Lovund and Selvær, the probability of mortality decreased with increasing sparrowhawk density (Table S4, Figure 3), while at Træna there was an increase in house sparrow mortality with increasing sparrowhawk density (Table S4, Figure 3).

There was no support in the data for a difference in mortality with increasing predator density between sexes ($\Delta AIC_c = 1.94$, AIC_c Weight = 0.28, Table S5). However, there was support for a difference in rates of predation between age classes ($\Delta AIC_c = 0.00$, AIC_c Weight = 0.84, Table S6 and S7, Figure 4). There was a reduction in mortality with increasing sparrowhawk density for juveniles and only weak tendencies of a similar effect in the older individuals (Table S7, Figure 4).

The sparrowhawk was found to act as a selective mortality agent on both body mass ($\beta_{SD:Weight} = 0.059$, CI = [0.005, 0.113], $\Delta AIC_c = 0.00$, AIC_c Weight = 0.84, Table S8 and S9, Figure 5) and tarsus length ($\beta_{SD:Tarsus} = 0.224$, CI = [0.217, 0.231], $\Delta AIC_c = 0.00$, AIC_c Weight = 0.93, Table S10 and S11, Figure 6). Thus, at low densities of spar-

rowhawks, individuals with a low body mass (weight) or small body size (tarsus length) had a higher probability of mortality. Correspondingly at high densities of sparrowhawks, large house sparrow individuals with high body mass and long tars had a higher probability of mortality (Figure 5 and 6). At intermediate sparrowhawk densities mortality was approximately equal for all body mass and tarsus lengths (Figure 5 and 6, respectively). There was no support in the data for a difference in the effect of sparrowhawk density with increasing wing length ($\beta_{SD:Wing} = 0.033$, CI = [-0.012, 0.079], $\Delta AIC_c = 0.04$, AIC_c Weight = 0.49, Table S12, Figure S1) or wing load ($\beta_{SD:WL} = 0.045$, CI = [-0.015, 0.106], $\Delta AIC_c = 0.00$, AIC_c Weight = 0.51, Table S13 and S14, Figure S2).

4 Discussion

The present study revealed that increasing sparrowhawk density is related to both positive and negative effects on the mortality rate among three house sparrow populations (Table 3, 4 and 5, Figure 3). Accordingly, the presence of sparrowhawks during winter period is likely to affect the regional variance in metapopulation dynamics which a study in only one population would not detect. This study also revealed that sparrowhawk density has an effect on mortality on age classes (Table S6 and S7, Figure 4), where adult individuals are less responsive to increased predator density than juveniles. The results further showed a predator-induced selection on body size and mass (Table S8, S9, S10 and S11, Figure 5 and 6). Individuals with low body mass or small body size are prone to mortality at low sparrowhawk densities, while individuals with high body mass and long tars has a higher probability of mortality at high densities of sparrowhawks. This is seen in Figure 5 and 6.

The effect of sparrowhawk density on the mortality probability among islands was found in the present study (Table 5, S3 and S4, Figure 3). The present study demonstrates a heterogeneous pattern among the three local populations suggesting that the predator-prey dynamic between sparrowhawks and house sparrow is more complex than a general interspecific relationship, which may depend on local demography and habitat characteristics. The spatial variation could result from differences in behavioural responses to predation risk. At Lovund and Selvær the probability of mortality declined with increased sparrowhawk density (Figure 3), indicating an increase in the avoidance of high-risk situations of predation. For instance, there could be more easily available hiding spots to seek refuge for some populations and less need for exposure at high predator densities. Change in distribution to predation risk is found to vary with habitat for passerine birds in response to predation risk (Forsman et al., 2001; Møller et al., 2017). At Træna, the probability of mortality increased with increasing sparrowhawk density (Figure 3). An increase in mortality in the same predator-prey relationship is seen in Britain during the years 1970 till 2004, where an increased sparrowhawk density occurred simultaneously as house sparrow populations' density decreased (Bell et al., 2010). The same pattern of house sparrow density decline correlating to increased sparrowhawk density is found in Paris over a 15 year period (2003-2017) (Mohring et al., 2021). However, the volume of decline varied among the house sparrow populations. Accordingly, spatial variation in refuges due to habitat heterogeneity could influence how sparrowhawks affect the mortality probability in house sparrows. Interestingly, there has been found spatial variation in mortality rates among island populations in the house sparrow metapopulation at Helgeland (Ringsby et al., 1999).

Living in groups can be beneficial because increased density enables individuals to seek cover behind conspecifics and thereby reduce the probability of being killed (De Vos and O'Riain, 2010; Hamilton, 1971; King et al., 2012; McClure and Despland, 2010). Another

mechanism that has been suggested is that predators may be confused by prey moving in flocks (Calvert et al., 1979; Foster and Treherne, 1981; Hamilton, 1971), making it difficult to single out and track individual prey (Ioannou, Tosh, Neville, and Krause, 2008). For instance, Jeschke and Tollrian (2005) showed that *Daphnia magna* and *Daphnia obtusa* swarms confused their predator such that prey uptake decreased at high prey densities. It is theorized that group living is beneficial by decreasing individual risk of predation through improved vigilance (Bertram, 1980; Elgar, 1989), prompting expeditious alarm calls (Cäsar et al., 2013; Zuberbühler et al., 1999). The present study revealed no support for an interaction between house sparrow population density and sparrowhawk density on mortality probability for the house sparrow (Table S2). Thus, there was no support for a non-linear change in mortality probability of house sparrows depending on the combined effect of predator and prey density. Other limiting factors to population growth such as food availability (Ashmole, 1963; Krebs et al., 1995; Martin, 1987), diseases (Süld et al., 2014) and density (Sibly and Hone, 2002) could explain the increase in mortality with population density. Interestingly, a recent study found that limiting factors such as lack in food availability were not the cause of mortality in insular house sparrow populations, but annual environmental factors such as temperature strongly affected the populations (Simons et al., 2019). The study is not yet peer reviewed, but holds interesting content. Though, a study done by Peach et al. (2018) confirms that increased food abundance does not affect winter survival nor the population size in house sparrows.

With the presence of predators, prey may adjust foraging efficiency as a anti-predator behavioural response (Cresswell, 2008), increase vigilance with higher predation risk (Lima, 1994), or increase predation avoidance behaviour (Bertleff et al., 2021; Clinchy et al., 2013). As juveniles often suffer a higher risk of predation, anti-predator behaviour in the juveniles could explain the decrease in juvenile mortality rate with increased sparrowhawk densities (Andreasson et al., 2019; Lingle et al., 2008, Figure 4). Sodhi (1992) investigated differences in risk-taking behaviour between juvenile and adult house sparrows and found that juveniles were less exposed than adults during the breeding season. Given that house sparrow were the most numerous prey for merlins (*Falco columbarius*) in the study by Sodhi (1992), the results may not be directly transferable to the present study. Since predators may have different hunting tactics within and among predator species (Cresswell, 1996; Lima, 1993; Parrish, 1993; Rudebeck, 1950), anti-predator behaviour in house sparrows may therefore differ with specific predator-prey relationships. The sparrowhawk has a hunting technique characterized by surprise attacks (Selås, 1993), Cresswell and Quinn (2010) showed in their studies that increased sparrowhawk density led to reduced attack success. Furthermore, the studies showed that increased prey density also led to reduced attack success (Cresswell and Quinn, 2010). An increase in vigilance with higher population density can counteract the sparrowhawks' surprise attack. In addition, an increased rate of predators can alter less risk-taking (Cresswell, 2008) and increased vigilance (Lima, 1994; Xu et al., 2013) in the prey.

There was evidence for predator-induced selection on mortality, with a higher mortality probability for smaller house sparrows at low sparrowhawk densities and for larger house sparrow at high sparrowhawk densities during the winter period (Table S8, S9, S10 and S11, Figure 5 and 6). Interestingly, MacLeod et al. (2006) have demonstrated that house sparrow respond to predation risk by adjusting their body mass, with a trade-off between predation risk and starvation risk during winter period. At high predation risk, MacLeod et al. (2006) found that house sparrows kept their mass low. This supports the present study's findings where lighter individuals have a lower probability of mortality with high sparrowhawk density. In sociable weavers (*Philetairus socius*) Covas et al. (2002) found that probability of survival was highest for individuals with intermediate body mass, where lighter and heavier individuals suffered lower survival probabilities due to predation and risk of starvation. There was a survival disadvantage for individuals deviating from the mean in body mass in light of predation shown by (Covas et al., 2002). Fluctuating temporal variation in sparrowhawk density (Figure 1) and predator-induced mortality probabilities for phenotypes (Table S8, S9, S10 and S11, Figure 5 and 6) could act as balancing selection of intermediate body sizes and body masses of house sparrows over time.

There was no evidence for predator-induced selection in the present study on wing length (Table S12) and wing load (Table S13 and S14). Theory predicts reduction in flight maneuvering due to increased body mass relative to wing area, along with selection for low wing loads in order to escape attacks from predators (Gotmark and Post, 1996; Witter and Cuthill, 1993). This receives no support in the present study as there was no selection on wing load. Wing load has earlier not been found to influence predation risk (Kullberg, 1998; Kullberg et al., 1998; Veasey et al., 1998) as individuals compensate their weight by modifying flight techniques (Kullberg et al., 1998).

House sparrows are sexually dimorphic (Anderson, 2006) and their difference in color and behaviour could have influenced predation risk as males' ornament could be more conspicuous to predators (Kotiaho, 2001). However, the result in the present study did not reveal any sex-specific selection related to sparrowhawk densities (Table S5). This is in accordance with Bókony et al. (2008) where no difference in house sparrows' risk-taking with their ornament were found, and phenotypical traits such as larger throat patches or ornamented wing-bars had no impact on probability of survival. Predation density was measured during winter period in the present study, where difference in predator-induced mortality may be indistinguishable since behavioural differences between sexes may not be as distinct during the winter period as opposed to the breeding season (Summers-Smith, 1956). For the house sparrows other studies has not found a clear difference in mortality between the sexes (Anderson, 2006; Dobson, 1987; Ringsby et al., 1999).

Correlated environmental factors not included in the study could have potentially explained the variance in the observed relationship between sparrowhawk density and house sparrow population density. For instance, in years of mild climate, both species could

benefit with decline in annual probability of mortality of house sparrows (Ringsby et al., 2002), and corresponding increase in winter sparrowhawk densities due to high reproductive success and/or increased survival probability (Newton, 1988). House sparrow juvenile survival rate during winter are strongly influenced by factors during breeding season, such as body condition and body size (Ringsby et al., 1998). Accordingly, climatic data could be included to investigate the synchronous influence on both species and potentially enlighten how the annual variance influence this predator-prey relationship.

For house sparrows there has been shown annual fluctuations in breeding success as a response to annual climatic change, and not due to biotic factors (Kavanagh, 2011). A study conducted within the same metapopulation of house sparrows as the present study suggests annual and temporal variation influences mortality rates (Ringsby et al., 1999). Interestingly, as the different populations in the present study is influenced by the same climatic changes, there is spatial variation in mortality among the islands. Another study conducted within the metapopulation along Helgeland tackles how large-scale regional climate affects mortality among islands and populations (Ringsby et al., 2002), where recruitment rates were significantly influenced by an interaction between island and year. These mentioned studies, and the present one, support that mortality probability is island specific. In addition to predation, environmental factors could be a predictor for the observed mortality rates.

Being sensitive to environmental changes could be a potential threat to the population when considering climate change. As supplementary food have earlier not been found to conserve a decline in house sparrow populations (Peach et al., 2018), other conservation initiatives may be needed if unfavourable climate prolongs in the populations. In contrast, the sparrowhawk is found insensitive to changes in climate (Nielsen and Møller, 2006), but can respond to changes in the prey community composition (Millon et al., 2009). Whether the predator-prey relationship between sparrowhawk and house sparrow is influenced by the environment, as well as their population dynamics, is yet unknown.

In the present study the mortality rates were overestimated, as resighting rates were not accounted for in our analysis (Lebreton et al., 1992). However, using simpler models simplifies the interpretation of the results on sparrowhawk density and demography on house sparrow mortality. To account for the overestimating of house sparrow mortality rates, CMR data could be applied in the mortality estimate as such models deals with survival probabilities with recapture rates. However, while mortality rates are overestimated, the relative magnitude of the effects of predation is not likely to be compromised as there is not to be expected a difference in resighting rates for different densities of sparrowhawk. In this data set, juveniles dominated (55,1%) the sample size. Incorporating CMR data in the estimation of mortality would not have major influence, since the resight rates are based on breeding adults as they reflect the population size.

5 Conclusion

This study has shown that probability of mortality in house sparrows is affected by sparrowhawk density, where it varies between age classes and spatially. There is mortality-induced selection on phenotypical traits in the house sparrow by the sparrowhawk. Lighter and smaller individuals suffer a high mortality probability with low sparrowhawk densities, while heavier and larger individuals have an increased mortality probability with high sparrowhawk densities. The sparrowhawk seems to act balancing on intermediate body sizes and body mass due to temporal fluctuations in predator density and predator-induced mortality probabilities for the phenotypes. Island specific temporal variation in environmental factors could be a confounding effect on the house sparrow mortality. In addition, age-specific differences in predation avoidance behaviour and potential habitat heterogeneity could explain variability in mortality probabilities for the house sparrow. The present study has given a deeper understanding of the interspecific dynamic between sparrowhawks and house sparrows, predator-prey relationships, and how predator-induced selection on phenotypes vary spatiotemporally. Disparity in predator-prey relationships provides opportunities to study anti-predatory behaviours, adaptive evolution, food webs and potential phenological mismatches.

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Figures

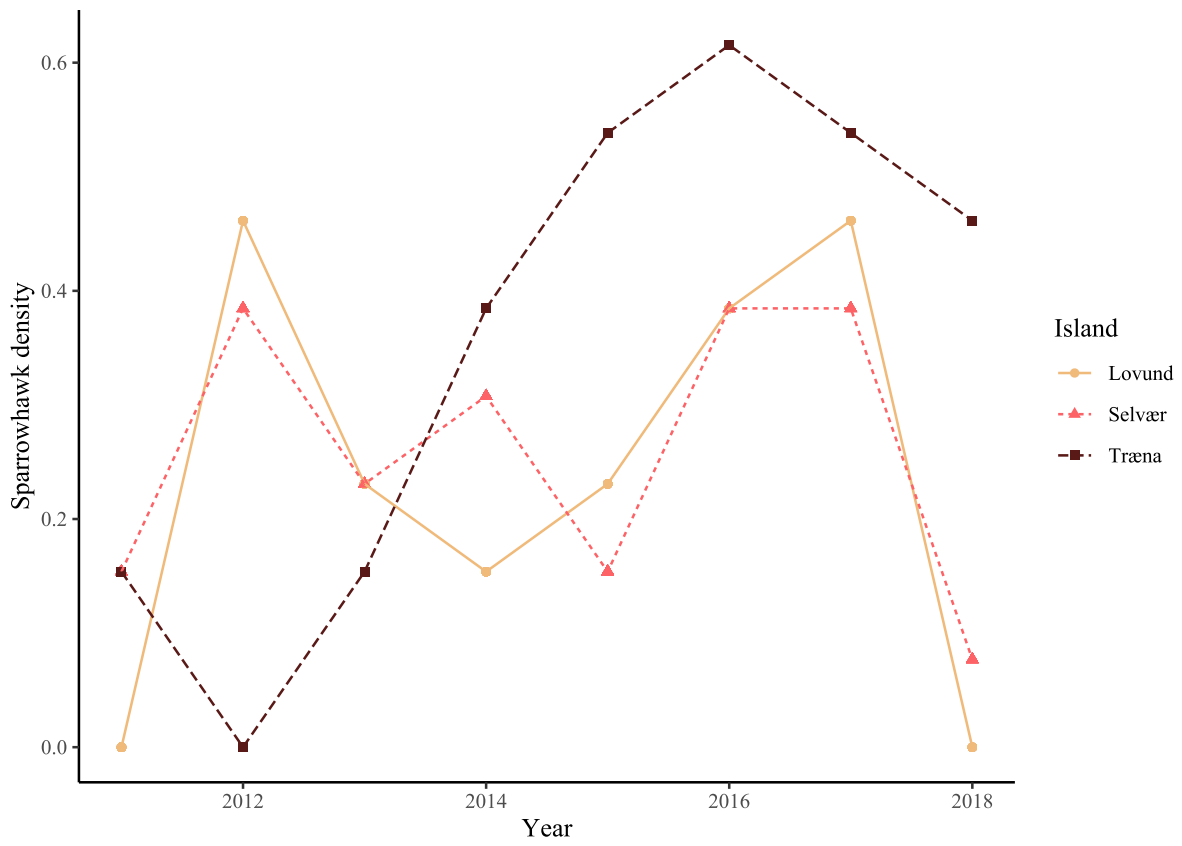


Figure 1: Sparrowhawk (*Accipiter nisus*) densities in islands Lovund, Selvær and Træna during the years of 2011-2018.



Figure 2: Population sizes of house sparrow (*Passer domesticus*) in islands Lovund, Selvær and Træna during the years of 2011-2018.

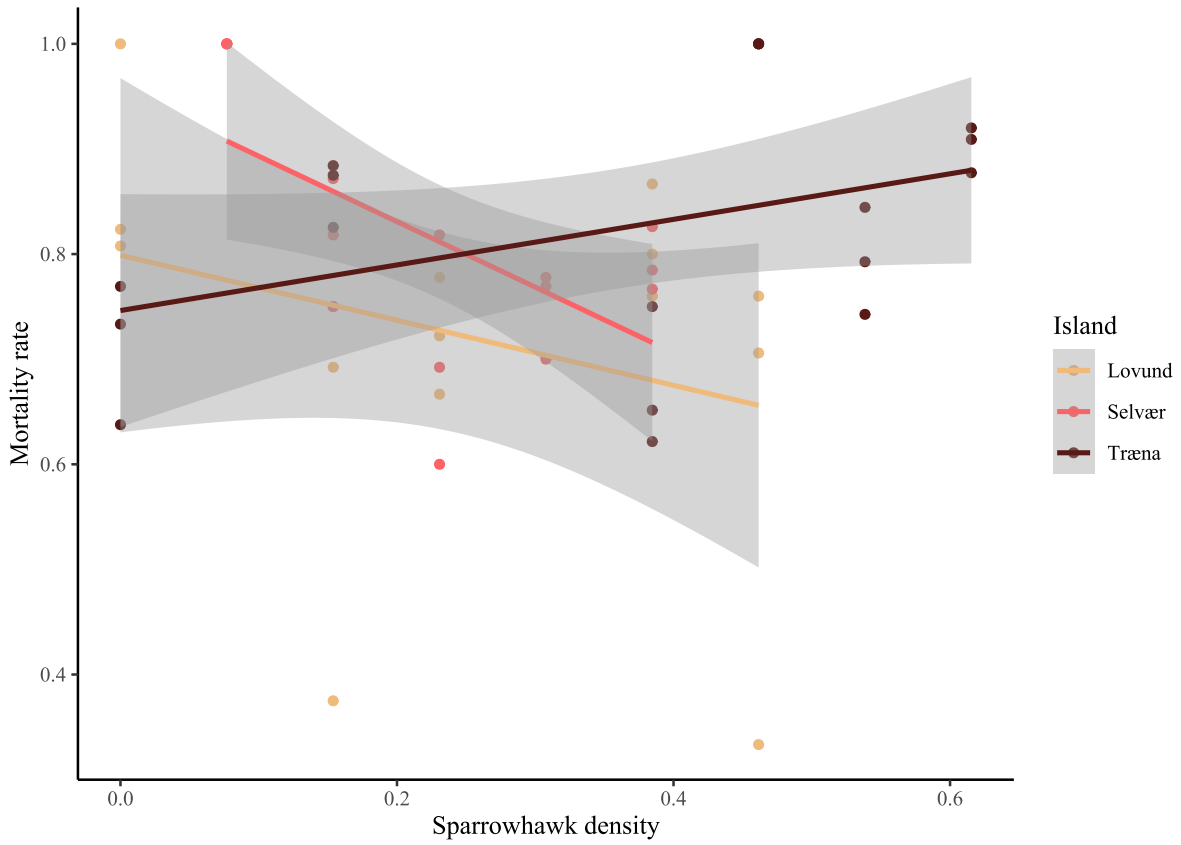


Figure 3: Mortality rate of house sparrows (*Passer domesticus*) in islands Lovund, Selvær and Træna as a response to sparrowhawk (*Accipiter nisus*) rate during the years of 2011-2018. Confidence intervals are represented as the gray areas around each linear functional response.

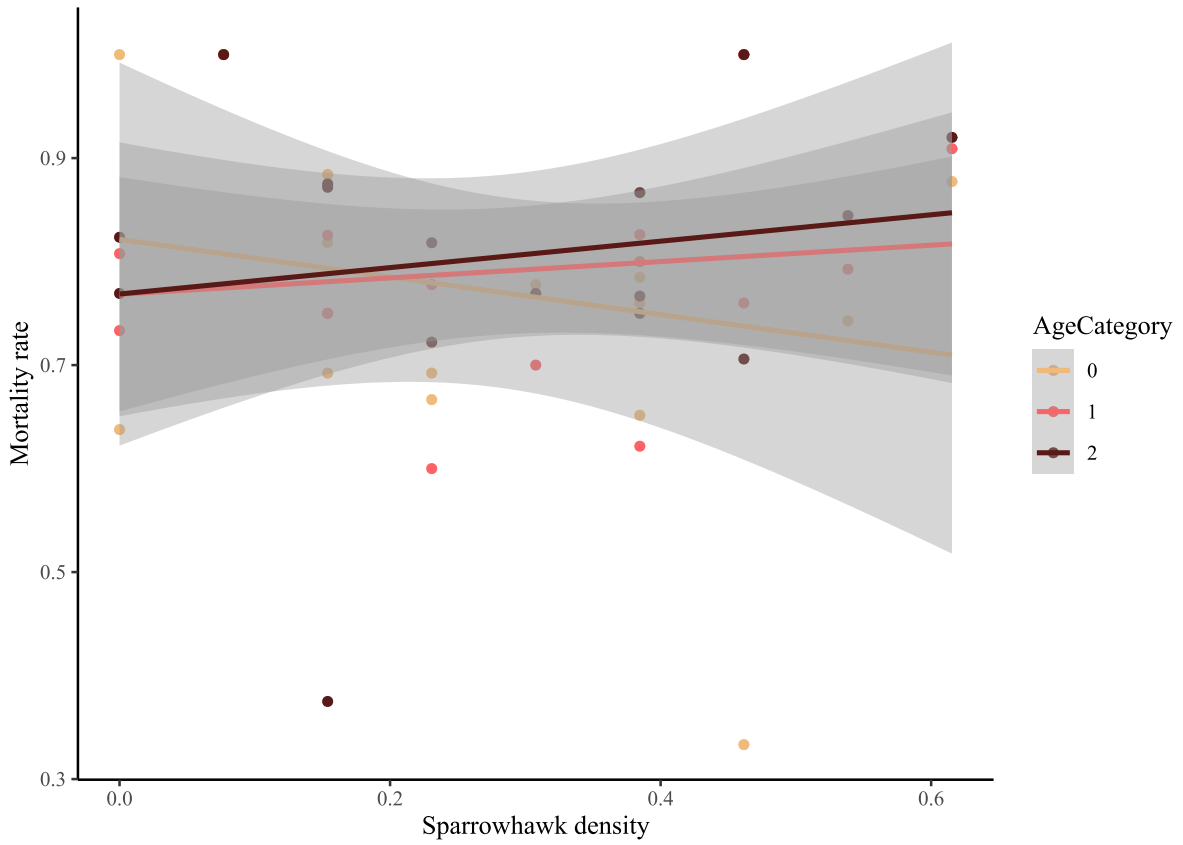


Figure 4: Mortality rate of house sparrow (*Passer domesticus*) for different age categories 0 (juveniles), 1 (1 CY) and 2 (2+ CY) as a response to sparrowhawk (*Accipiter nisus*) density during the years of 2011-2018. Confidence intervals are represented as the gray areas around each linear functional response.

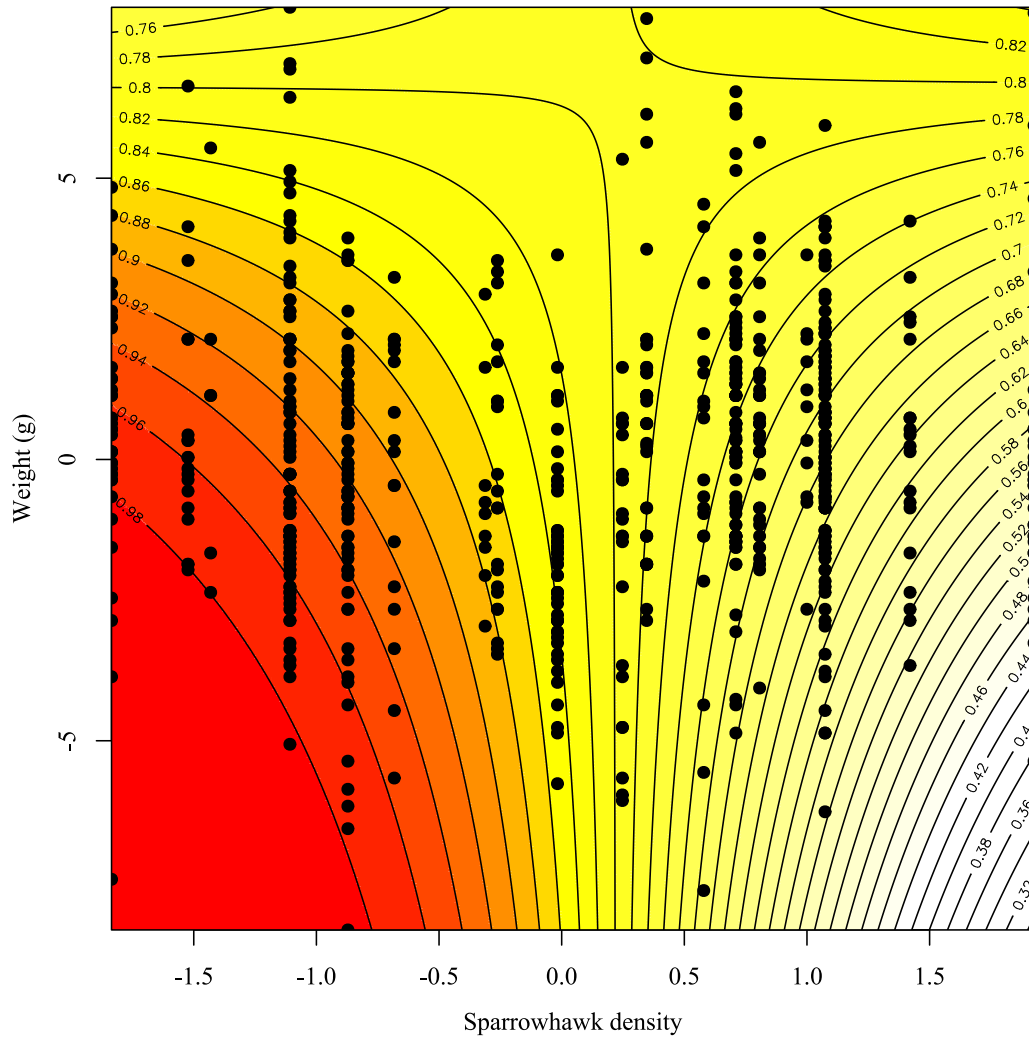


Figure 5: Probability of mortality of house sparrow (*Passer domesticus*) as a response to the interaction between body mass in weight (g) in house sparrow and z-scored sparrowhawk (*Accipiter nisus*) density during the years of 2011-2018.

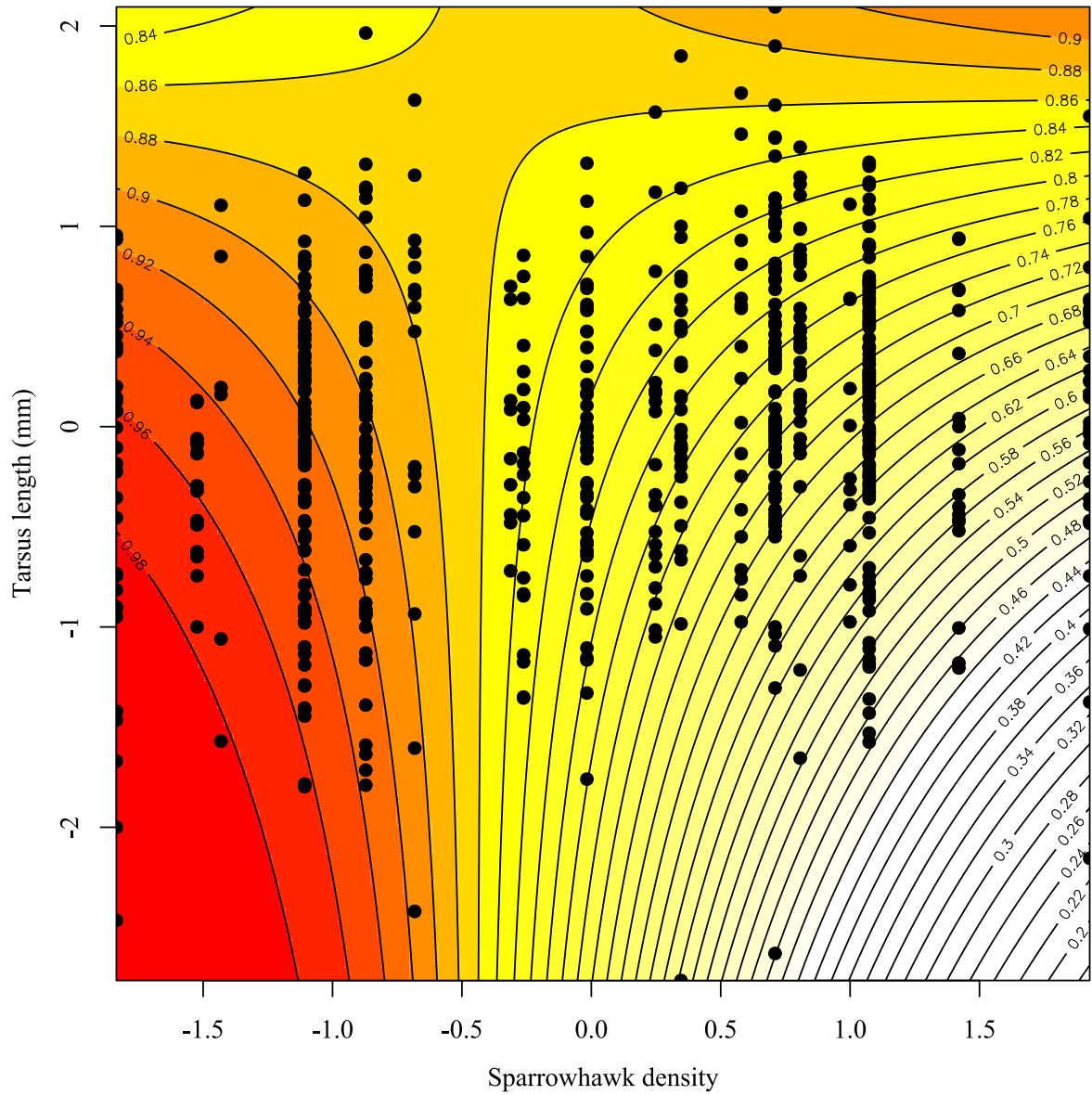


Figure 6: Probability of mortality of house sparrow (*Passer domesticus*) as a response to the interaction between tarsus length in house sparrow and z-scored sparrowhawk (*Accipiter nisus*) density during the years of 2011-2018.

Tables

Table 1: Overview of sample sizes n for the statistical analysis of mortality on house sparrow (*Passer domesticus*) in three islands located in northern Norway.

Age Category	Lovund	Selvær	Træna	Total
0	158	279	625	960
1	129	108	265	467
2	79	106	149	314
Total	322	442	997	1741

Table 2: Overview of sample sizes n for the statistical analysis of mortality on house sparrow (*Passer domesticus*) with sparrowhawk (*Accipiter nisus*) density and phenological measurements as explanatory factor in three islands located in northern Norway.

Age Category	Lovund	Selvær	Træna	Total
0	82	140	30	527
1	21	26	67	114
2	3	5	19	27
Total	106	171	391	668

Table 3: Ranking of models explaining mortality in house sparrow (*Passer domesticus*) population in northern Norway in light of sparrowhawk (*Accipiter nisus*) density. Models are binomial generalized linear mixed-effect models fitted with year as random intercept. The difference in AIC_c values from top ranked model is ΔAIC_c , and the Akaike weight is noted as AIC_c Weight.

Rank	Model Parameters	ΔAIC_c	AIC_c Weight
1	Sex + Island + Age + SD + HD	0.00	0.44
2	Sex + Island + Age + SD	0.85	0.29
3	Sex + Island + Age	1.70	0.16
4	Sex + Island + Age + HD	3.49	0.08

Table 4: Parameter estimates and their 95% confidence intervals of explanatory effects in the most parsimonious model (Table 3) describing variation in the probability of mortality in house sparrow (*Passer domesticus*) populations in light of sparrowhawk (*Accipiter nisus*) density in northern Norway. The random effect is presented with variance and standard deviation (SD). Variables with significance $p < 0.05$ are bolded.

Fixed effects			
Variable	Estimate	95 % Confidence Interval	
		Lower limit	Upper limit
Intercept	0.376	-0.047	0.799
Sex male	-0.168	-0.295	-0.042
Age ₁	0.019	-0.130	0.169
Age ₂	0.203	0.029	0.377
Island Selvær	0.235	0.038	0.431
Island Træna	0.264	0.093	0.434
SD	-0.161	-0.297	-0.025
HD	0.092	-0.014	0.199
Random effect			
	Variance	SD	
Year	0.295	± 0.544	

Table 5: Parameter estimates of the model best fitted to the data set and their 95% confidence intervals of explanatory effects without interactions as age and population size, and with interaction as sparrowhawk density with island and sparrowhawk density with age category. The model describes variation in the probability of mortality in house sparrow (*Passer domesticus*) populations in light of sparrowhawk (*Accipiter nisus*) density. The random effect is presented with variance and standard deviation (SD). Interactions are presented with ”*”. Variables with significance $p < 0.05$ are bolded.

Fixed effects			
Variable	Estimate	95 % Confidence Interval	
		Lower limit	Upper limit
Intercept	0.350	-0.158	0.860
Sex male	-0.170	-0.298	-0.042
HD	0.217	0.079	0.356
SD	-0.397	-0.637	-0.157
Island Selvær	0.303	0.097	0.510
Island Træna	0.257	0.080	0.433
Age ₁	0.042	-0.110	0.196
Age ₂	0.232	0.055	0.410
SD*Island Selvær	0.415	0.144	0.686
SD*Island Træna	-0.049	-0.276	0.177
SD*Age ₁	0.210	0.040	0.380
SD*Age ₂	0.183	-0.012	0.380
Random effect			
	Variance	SD	
Year	0.459	± 0.677	

Supplementary materials

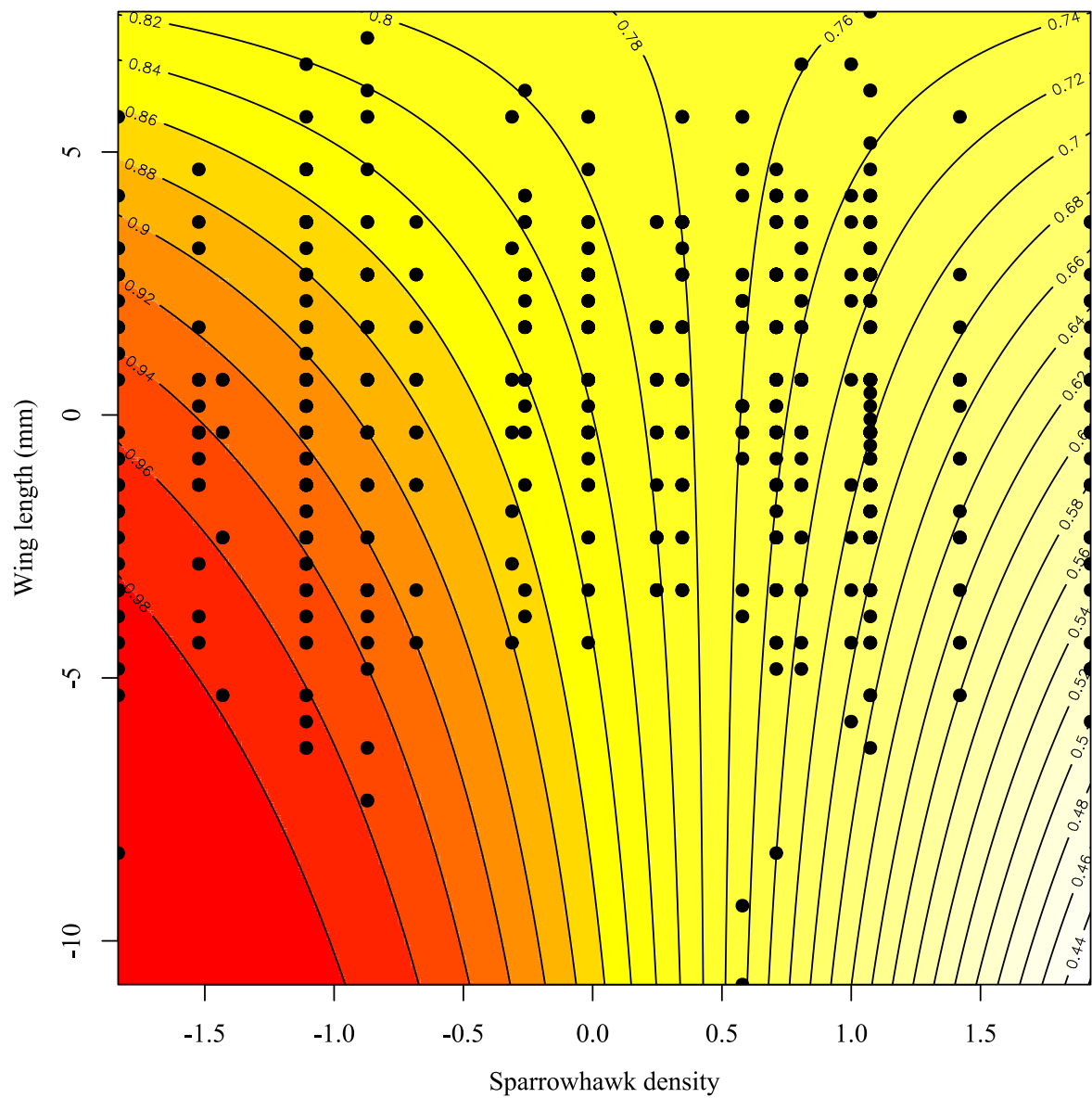


Figure S1: Probability of mortality of house sparrow (*Passer domesticus*) as a response to the interaction between wing length (mm) in house sparrow and sparrowhawk (*Accipiter nisus*) density during the years of 2011-2018.

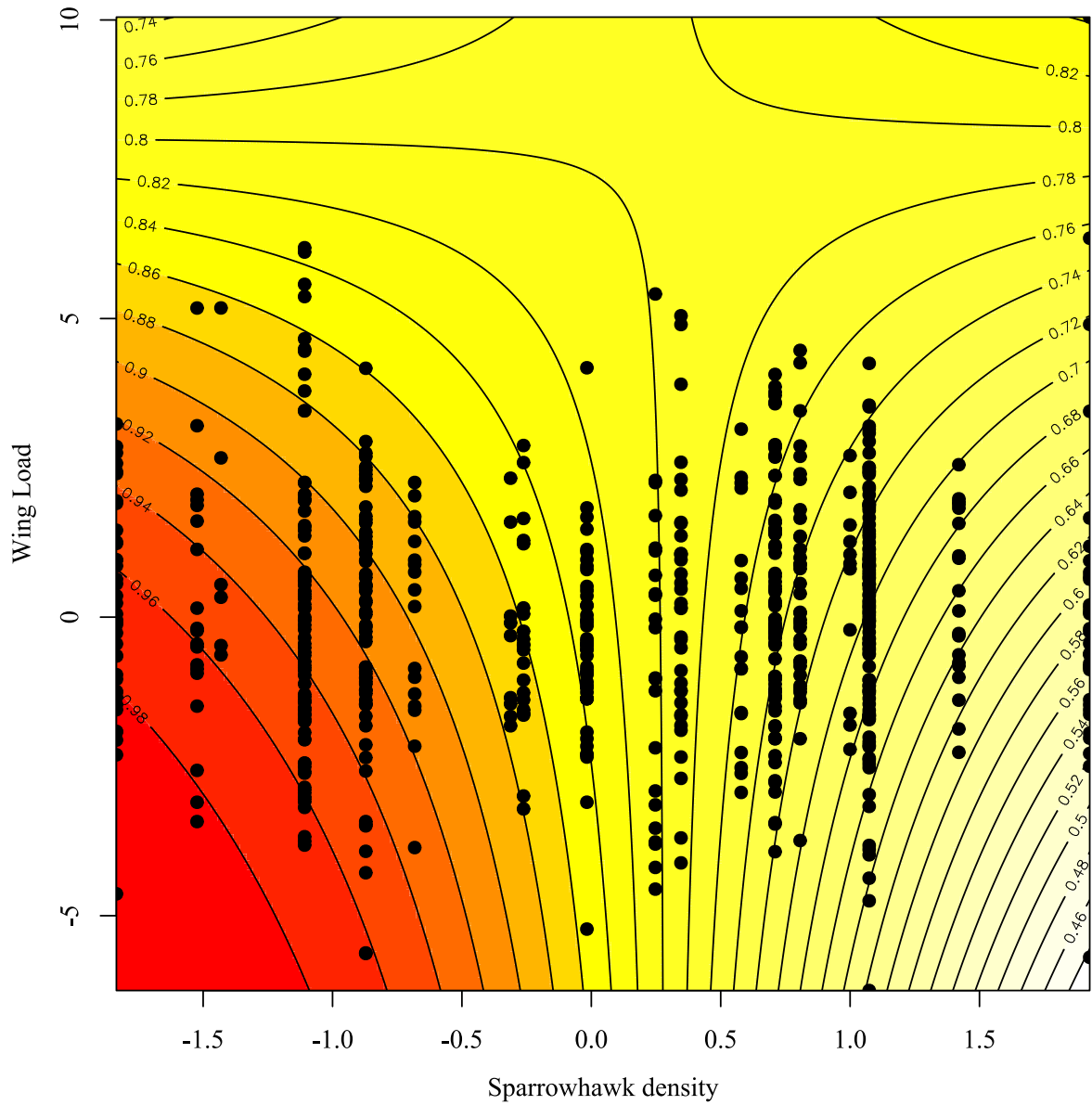


Figure S2: Probability of mortality of house sparrow (*Passer domesticus*) as a response to the interaction between wing load in house sparrow and sparrowhawk (*Accipiter nisus*) density during the years of 2011-2018.

Table S1: Parameter estimates and their 95% confidence intervals of explanatory effects in the models ranked 2nd, 3rd and 4th (Table 3) describing variation in the probability of mortality in house sparrow (*Passer domesticus*) populations in northern Norway. Parameter estimates are represented with the 95% confidence interval [lower limit, upper limit]. The random effect is also presented with variance explained and standard deviation [\pm SD]. Variables with significance $p < 0.05$ are bolded.

Fixed effects	Models		
	Rank 2	Rank 3	Rank 4
Intercept	0.386[-0.032, 0.806]	0.406[-0.008, 0.820]	0.406[-0.006, 0.819]
Sex male	-0.165[-0.292, -0.039]	-0.167[-0.294,-0.041]	-0.168[-0.295, -0.042]
Age ₁	0.029[-0.120, 0.178]	0.023[-0.126, 0.171]	0.020[-0.130, 0.169]
Age ₂	0.202[0.028, 0.376]	0.197[0.024,0.371]	0.197[0.023, 0.370]
Island Selv�er	0.247[0.051, 0.442]	0.231[0.038,0.425]	0.226[0.031, 0.421]
Island Tr�ena	0.263[0.093, 0.433]	0.263[0.094,0.432]	0.263[0.093, 0.432]
SD	-0.096[-0.208, 0.015]	-	-
HD	-	-	0.021[-0.067, 0.111]
Random effect			
Year	0.293[\pm 0.541]	0.287[\pm 0.536]	0.284[\pm 0.533]

Table S2: Ranking of models explaining mortality in house sparrow (*Passer domesticus*) populations in northern Norway in light of sparrowhawk (*Accipiter nisus*) density and selection. Models are binomial generalized linear mixed-effect models fitted with year as random intercept. The difference in AIC_c values from top ranked model is ΔAIC_c , and the Akaike weight is noted as AIC_c Weight. Interactions are represented with "*".

Rank	Model Parameters	ΔAIC_c	AIC_c Weight
1	Sex + Age + Island + SD + HD	0.00	0.52
2	Sex + Age + Island + SD*HD	0.19	0.48

Table S3: Ranking of models explaining mortality in house sparrow (*Passer domesticus*) populations in northern Norway in light of sparrowhawk (*Accipiter nisus*) density and spatial influence. Models are binomial generalized linear mixed-effect models fitted with year as random intercept. The difference in AIC_c values from top ranked model is ΔAIC_c , and the Akaike weight is noted as AIC_c Weight. Interactions are represented with "*".

Rank	Model Parameters	ΔAIC_c	AIC_c Weight
1	Sex + Age + HD + SD*Island	0.00	0.98
2	Sex + Age + Island + SD + HD	7.81	0.02

Table S4: Parameter estimates and their 95% confidence intervals of explanatory effects in the most parsimonious model (Table S3) describing variation in the probability of mortality in house sparrow (*Passer domesticus*) populations in light of spatial difference by sparrowhawk (*Accipiter nisus*) density in northern Norway. The random effect is also presented with variance explained and standard deviation (SD). Interactions are represented with "**". Variables with significance $p < 0.05$ are bolded.

Fixed effects			
Variable	Estimate	95 % Confidence Interval	
		Lower limit	Upper limit
Intercept	0.326	-0.156	0.857
Sex male	-0.168	-0.295	-0.040
Age ₁	0.014	-0.136	0.165
Age ₂	0.215	0.040	0.391
HD	0.227	-0.089	0.364
SD	-0.275	-0.494	-0.055
Island Selvær	0.294	0.089	0.498
Island Træna	0.264	0.089	0.440
SD*Island Selvær	0.374	0.108	0.640
SD*Island Træna	-0.103	-0.325	0.117
Random effect			
	Variance	SD	
Year	0.443	± 0.665	

Table S5: Ranking of models explaining mortality in house sparrow (*Passer domesticus*) populations in northern Norway in light of sparrowhawk (*Accipiter nisus*) density and selection on sexes. Models are binomial generalized linear mixed-effect models fitted with year as random intercept. The difference in AIC_c values from top ranked model is ΔAIC_c , and the Akaike weight is noted as AIC_c Weight. Interactions are represented with "*".

Rank	Model Parameters	ΔAIC_c	AIC_c Weight
1	Sex + Age + Island + SD + HD	0.00	0.72
2	Age + Island + HD + SD*Sex	1.94	0.28

Table S6: Ranking of models explaining mortality in house sparrow (*Passer domesticus*) populations in northern Norway in light of sparrowhawk (*Accipiter nisus*) density and selection on age classes. Models are binomial generalized linear mixed-effect models fitted with year as random intercept. The difference in AIC_c values from top ranked model is ΔAIC_c , and the Akaike weight is noted as AIC_c Weight. Interactions are represented with "*".

Rank	Model Parameters	ΔAIC_c	AIC_c Weight
1	Sex + Island + HD + SD*Age	0.00	0.84
2	Sex + Age + Island + SD + HD	3.26	0.16

Table S7: Parameter estimates and their 95% confidence intervals of explanatory effects in the most parsimonious model (Table S6) describing variation in the probability of mortality in house sparrow (*Passer domesticus*) populations in light of selection on age categories by sparrowhawk (*Accipiter nisus*) density in northern Norway. The random effect is also presented with variance explained and standard deviation (SD). Interactions are represented with "**". Variables with significance $p < 0.05$ are bolded.

Fixed effects			
Variable	Estimate	95 % Confidence Interval	
		Lower limit	Upper limit
Intercept	0.376	-0.058	0.812
Sex male	-0.170	-0.297	-0.043
Island Selv�er	0.236	0.038	0.433
Island Tr�ena	0.250	0.078	0.421
HD	0.089	-0.017	0.197
SD	-0.242	-0.392	-0.092
Age ₁	0.046	-0.106	0.198
Age ₂	0.220	0.044	0.395
SD*Age ₁	0.205	0.038	0.372
SD*Age ₂	0.175	-0.018	0.369
Random effect			
	Variance	SD	
Year	0.321	± 0.566	

Table S8: Ranking of models explaining mortality in house sparrow (*Passer domesticus*) populations in northern Norway in light of sparrowhawk (*Accipiter nisus*) density and weight of *P. domesticus*. Binomial generalized linear mixed-effect models fitted with year as random intercept. The difference in AIC_c values from top ranked model is ΔAIC_c , and the Akaike weight is noted as AIC_c Weight. Interactions are represented with “*”.

Rank	Model Parameters	ΔAIC_c	AIC_c Weight
1	Sex + HD + SD*Island + SD*Age + SD*Weight	0.00	0.80
2	Sex + HD + SD*Island + SD*Age + Weight	2.76	0.20

Table S9: Parameter estimates and their 95% confidence intervals of explanatory effects in the most parsimonious model (Table S8) describing variation in the probability of mortality in house sparrow (*Passer domesticus*) populations in light of sparrowhawk (*Accipiter nisus*) density and selection on *P. domesticus* weight in northern Norway. The random effect is also presented with variance explained and standard deviation (SD). Interactions are presented with "**". Variables with significance $p < 0.05$ are bolded.

Fixed effects			
Variable	Estimate	95 % Confidence Interval	
		Lower limit	Upper limit
Intercept	0.176	-0.369	0.723
Sex male	-0.050	-0.274	0.172
HD	0.118	-0.146	0.383
SD	-0.569	-1.031	-0.107
Island Selvær	0.243	-0.158	0.644
Island Træna	0.382	0.040	0.725
Age ₁	0.131	-0.166	0.429
Age ₂	0.904	-0.532	2.340
Weight	-0.013	-0.062	0.036
SD*Island Selvær	0.424	-0.113	0.962
SD*Island Træna	0.172	-0.297	0.643
SD*Age ₁	0.221	-0.136	0.578
SD*Age ₂	-0.690	-2.564	1.184
SD*Weight	0.059	0.005	0.113
Random effect			
	Variance	SD	
Year	0.353	± 0.594	

Table S10: Ranking of models explaining mortality in house sparrow (*Passer domesticus*) populations in northern Norway in light of sparrowhawk (*Accipiter nisus*) density and tarsus length of *P. domesticus*. Binomial generalized linear mixed-effect models fitted with year as random intercept. The difference in AIC_c values from top ranked model is ΔAIC_c , and the Akaike weight is noted as AIC_c Weight. Interactions are represented with “*”.

Rank	Model Parameters	ΔAIC_c	AIC_c Weight
1	Sex + HD + SD*Island + SD*Age + SD*Tarsus	0.00	0.93
2	Sex + HD + SD*Island + SD*Age + Tarsus	5.19	0.07

Table S11: Parameter estimates and their 95% confidence intervals of explanatory effects in the most parsimonious model (Table S10) describing variation in the probability of mortality in house sparrow (*Passer domesticus*) populations in light of sparrowhawk (*Accipiter nisus*) density and selection on *P. domesticus* tarsus length in northern Norway. The random effect is also presented with variance explained and standard deviation (SD). Interactions are presented with "**". Variables with significance $p < 0.05$ are bolded.

Fixed effects			
Variable	Estimate	95 % Confidence Interval	
		Lower limit	Upper limit
Intercept	0.178	-0.359	0.721
Sex male	-0.064	-0.272	0.198
HD	0.103	-0.149	0.376
SD	-0.538	-1.000	-0.078
Island Selvær	0.242	-0.164	0.639
Island Træna	0.347	0.015	0.702
Age ₁	0.142	-0.172	0.455
Age ₂	0.917	-0.500	2.357
Tarsus	0.100	-0.063	0.032
SD*Island Selvær	0.360	-0.124	0.953
SD*Island Træna	0.168	-0.251	0.688
SD*Age ₁	0.268	-0.188	0.545
SD*Age ₂	-0.693	-2.646	1.054
SD*Tarsus	0.224	-0.012	0.080
Random effect			
	Variance	SD	
Year	0.355	± 0.596	

Table S12: Ranking of models explaining mortality in house sparrow (*Passer domesticus*) populations in northern Norway in light of sparrowhawk (*Accipiter nisus*) density and wing length of *P. domesticus*. Binomial generalized linear mixed-effect models fitted with year as random intercept. The difference in AIC_c values from top ranked model is ΔAIC_c , and the Akaike weight is noted as AIC_c Weight. Interactions are represented with "**".

Rank	Model Parameters	ΔAIC_c	AIC_c Weight
1	Sex + HD + SD*Island + SD*Age + Wing	0.00	0.51
2	Sex + HD + SD*Island + SD*Age + SD*Wing	0.04	0.49

Table S13: Ranking of models explaining mortality in house sparrow (*Passer domesticus*) populations in northern Norway in light of sparrowhawk (*Accipiter nisus*) density and wing load of *P. domesticus*. Binomial generalized linear mixed-effect models fitted with year as random intercept. The difference in AIC_c values from top ranked model is ΔAIC_c , and the Akaike weight is noted as AIC_c Weight. Interactions are represented with "**".

Rank	Model Parameters	ΔAIC_c	AIC_c Weight
1	Sex + HD + SD*Island + SD*Age + SD*WL	0.00	0.51
2	Sex + HD + SD*Island + SD*Age + WL	0.05	0.49

Table S14: Parameter estimates and their 95% confidence intervals of explanatory effects in the most parsimonious model (Table S13) describing variation in the probability of mortality in house sparrow (*Passer domesticus*) populations in light of sparrowhawk (*Accipiter nisus*) density and selection on *P. domesticus* wing load in northern Norway. The random effect is also presented with variance explained and standard deviation (SD). Interactions are presented with "**". Variables with significance $p < 0.05$ are bolded.

Fixed effects			
Variable	Estimate	95 % Confidence Interval	
		Lower limit	Upper limit
Intercept	0.187	-0.355	0.730
Sex male	-0.075	-0.296	0.144
HD	0.112	-0.151	0.376
SD	-0.558	-1.021	-0.095
Island Selvær	0.254	-0.146	0.654
Island Træna	0.386	0.044	0.727
Age ₁	0.125	-0.172	0.422
Age ₂	0.902	-0.562	2.367
WL	-0.013	-0.070	0.044
SD*Island Selvær	0.407	-0.130	0.945
SD*Island Træna	0.191	-0.275	0.658
SD*Age ₁	0.237	-0.120	0.595
SD*Age ₂	-0.694	-2.614	1.225
SD*WL	0.045	-0.015	0.106
Random effect			
	Variance	SD	
Year	0.347	± 0.589	

