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Stefan J.G. Vriend

# On the roles of density dependence and environmental fluctuations in driving eco-evolutionary dynamics of hole-nesting passerines

Doctoral thesis

**NTNU**  
Norwegian University of Science and Technology  
Thesis for the Degree of  
Philosophiae Doctor  
Faculty of Natural Sciences  
Department of Biology



Norwegian University of  
Science and Technology



Stefan J.G. Vriend

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Trondheim, April 2022

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**“The only thing that makes life possible is  
permanent, intolerable uncertainty:  
not knowing what comes next.”**

*Faxe the Weaver*

*Ursula K. Le Guin — The Left Hand of Darkness (1969)*



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## Acknowledgements

The other day I was reading Frank Herbert's *Dune* and I came across this passage of a man who said:

*"I've always prided myself on seeing things the way they truly are.  
That's the curse of being a [...]. You can't stop analyzing your data."*

It made me think of science and research. Not so much the first sentence, even though there surely are researchers who think as such, but the last pair of sentences describe the work of a scientist quite precisely, I thought.

It has been five years since this journey started. It has been a wonderful and remarkable experience even though the pandemic and, even more so, the fact that half of me lived in another country made it extra challenging, to say the least. Yet here we are. *We*—for I have not undertaken this journey alone.

My first words of thanks go to *Bernt-Erik*, *Marlène*, *Vidar*, and *Steinar*. I have been fortunate to have had such a unique and complementary team of supervisors. *Bernt-Erik*, thank you for your continuous creation of ideas, which were always paired with a healthy portion of gloomy expectations and an even larger portion of enthusiasm if things worked out fine in the end, and your undisguised assessment of the results and writings I lay in front of you. *Steinar*, thank you for making sense of *Bernt-Erik*'s ideas – and being honest when you had no clue what he meant –, transcribing them into complex but testable theories, and reassuring me that my opponents would not understand some of the complex equations that you came up with either. *Vidar*, I envy your skill of translating *Bernt-Erik*'s plans and *Steinar*'s math into working scripts and codes, and of elaborately clarifying the loose ends and acknowledging the limitations of our methods and analyses. *Marlène*, thank you for your optimism and encouragement, your readiness to help and give advice, wherever and whenever, and your ability to identify the right moment to lift the curse and spur me to start writing. Even though the four of you routinely made my head spin or my thoughts cloudy, I am absolutely sure that I would not have reached this milestone without your navigation.

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thoughtfulness have encouraged and comforted me many times. I value your persuasion and perseverance. I will never forget the evenings and parties we had, but I am not sure whether I will remember the amusement and joy, or the misery and suffering of the day after. *Laura*, your enthusiasm is radiating. Thank you for sharing your happiness, your helping hand, your listening ear. I am amazed by your initiative and your ability to bring people together. Thank you, *Tof* for your humour and wit, *Kate* for your cheerfulness and adventurousness, *Thomas* for your brightness and brilliance, *Lara* for your fascination and anticipation, *Semona* for your boldness and earnestness, *Bart* for your fairness and understanding, *Chris* for your gentleness and calm. Thanks to the many other kind hearts that I met during my time in the north and travels abroad.

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Throughout these years, I have repeatedly realized that friendship goes beyond borders, and that the habits and quirks that come with such friendships can carry on as if we still shared the same house, city, or country. Thank you, *Paul, Tessa, Tim, Marc, Sebas, Judith*, and *Paula*. Thank you for your spirit and joy, the catchy songs and creative, little dances at festivals, the road trips and the third day of Christmas dinners. Thank you, *Steeph, Steve, Joe*, and *Rens*. Thank you for the undeterred frequency of our meetups, the late-night games and chatter, the daily exchange of pleasantries; I believe that their regular rhythm kept me sane and my mind at ease.

None of the opportunities I have been given would have been possible without the support of my family. Thank you, *Dominique* and *Jeroen*. You have always been there for me, irrespective of the distance between us and our homes. Thank you, *pap* and *mam*, for your unlimited encouragement. You always sheered the loudest, whether that was for school, sports, or studies. I learned a lot from the four of you; I treasure your stubborn, down-to-earth and compassionate hearts.

My greatest appreciation goes to you, *Susan*. Thank you for your motivation and inspiration, for challenging me and standing up for me, for your never-ending care and support. I admire you—your eagerness to learn, your determination and consideration, your warm generosity and absolute patience. I am proud of us, of what we have achieved despite the time and distance apart. As the northern adventure is coming to an end, I cannot wait for our new adventures to begin.

## List of papers

- Paper I** Sæther B.-E., Engen S., Gustafsson L., Grøtan V., and **Vriend S.J.G.** 2021. Density-dependent adaptive topography in a small passerine bird, the collared flycatcher. *American Naturalist* 197, 93–110. DOI: [10.1086/711752](https://doi.org/10.1086/711752).
- Paper II** **Vriend S.J.G.**, Engen S., Gustafsson L., Sæther B.-E., and Grøtan V. The effect of stochastic environmental fluctuations on phenotypic selection: a feedback loop between ecology and evolution. Manuscript in review at *Evolution*.
- Paper III** Gamelon M., **Vriend S.J.G.**, Engen S., Adriaensen F., Dhondt A.A., Evans S.R., Matthysen E., Sheldon B.C., and Sæther B.-E. 2019. Accounting for interspecific competition and age structure in demographic analyses of density dependence improves predictions of fluctuations in population size. *Ecology Letters* 22, 797–806. DOI: [10.1111/ele.13237](https://doi.org/10.1111/ele.13237).
- Paper IV** **Vriend S.J.G.**, Gamelon M., Adriaensen F., Cole E.F., Dhondt A.A., Matthysen E., Orell M., Rytkönen S., Sheldon B.C., Vatka E., Visser M.E., and Sæther B.-E. The contribution of intra- and interspecific competition to phenotypic selection on fitness-related traits: a comparative study in hole-nesting passerines. Manuscript.
- Paper V** **Vriend S.J.G.**, Grøtan V., Gamelon M., Adriaensen F., Ahola M.P., Álvarez E., Bailey L.D., Barba E., Bouvier J.-C., Burgess M.D., Bushuev A., Camacho C., Canal D., Charmantier A., Cole E.F., Cusimano C., Doligez B.F., Drobnik S.M., Dubiec A., Eens M., Eeva T., Erikstad K.E., Ferns P.N., Goodenough A.E., Hartley I.R., Hinsley S.A., Ivankina E., Juškaitis R., Kempnaers B., Kerimov A.B., Kålås J.A., Lavigne C., Leivits A., Mainwaring M.C., Martínez-Padilla J., Matthysen E., van Oers K., Orell M., Pinxten R., Reiertsen T.K., Rytkönen S., Senar J.C., Sheldon B.C., Sorace A., Török J., Vatka E., Visser M.E., and Sæther B.-E. Temperature synchronizes temporal variation in laying dates across European hole-nesting passerines. Revised manuscript in review at *Ecology*.

## Declaration of contributions

- Paper I** B-ES and SE conceived this study. LG provided the data and information about relevant auto-ecological aspects of the biology of the species. B-ES, SE, VG and **SJGV** developed the statistical models. **SJGV** and VG wrote the R scripts and produced the figures and tables. All authors contributed to the interpretation and discussion of the results, and the writing of the manuscript.
- Paper II** SE developed the theory in discussion with B-ES, VG, and **SJGV**. LG provided the data and biological information about the species and study site. VG led the analysis, with substantial input from **SJGV**, and with advice from SE and B-ES. **SJGV** drafted the manuscript with substantial input from SE and B-ES. All others provided feedback on later versions of the manuscript.
- Paper III** MG, SE, FA, EM, BCS, and B-ES conceived the study. FA, EM, AAD, and BCS contributed to data collection. FA, SRE, and **SJGV** prepared the datasets. MG conducted the analyses. MG and **SJGV** visualised the results graphically. MG wrote the manuscript and all other authors contributed to revisions on later versions of the manuscript.
- Paper IV** B-ES and **SJGV** conceived the study. FA, EFC, AAD, EM, MO, SR, BCS, EV, and MEV contributed to data collection. **SJGV** collated the data, performed the analyses, and drafted the manuscript with substantial input from B-ES and MG. All other authors provided feedback on later versions of the manuscript.
- Paper V** **SJGV**, VG, MG, and B-ES conceived the study. FA, MPA, EÁ, EB, J-CB, MDB, AB, CCa, DC, AC, EFC, CCu, BFD, SMD, AD, ME, TE, KEE, PNF, AEG, IRH, SAH, EI, RJ, BK, ABK, JAK, CL, AL, MCM, JM-P, EM, KvO, MO, RP, TKR, SR, JCS, BCS, AS, JT, EV, MEV provided the data. **SJGV** and LDB compiled the dataset. **SJGV** conducted the analyses with advice from VG, MG, and B-ES. **SJGV** wrote the first draft of the manuscript. All other authors provided feedback on later versions of the manuscript.

## A. Introduction

Ecology and evolution are intrinsically linked through an inevitable struggle for existence (Malthus, 1798; Wallace, 1858; Darwin, 1859). That is, populations have the potential to grow exponentially, but in reality, their growth is limited by resources, and natural selection consequently favours individuals who compete best for those limited resources (Kokko & López-Sepulcre, 2007).

Since the birth of both disciplines, the interaction between ecology and evolution over very long timescales has been undisputed (Post & Palkovacs, 2009; Hendry, 2017), with examples as the coevolution among predators and prey, or competitors, or more generally, the adaptation of organisms to the diverse environments across the globe. Yet, over very short timescales, the intertwined relationship between ecology and evolution has been mostly ignored or overlooked (Post & Palkovacs, 2009; Govaert et al., 2019), with few exceptions (e.g., genetic feedback, Pimentel, 1961; *r*- & *K*-selection, MacArthur, 1962; evolutionary ecology, Orians, 1962). Indeed, adaptation has mostly been considered a mere response to changes in the environment (Kokko & López-Sepulcre, 2007), and evolution has often been ignored when studying ecological dynamics because evolution was considered to occur too slowly (Slobodkin, 1961; Schoener, 2011). In the last

decades, however, the feedback between ecology and evolution on shorter time scales received increased attention as a result of the growing evidence that evolution *can* act on contemporary timescales (Thompson, 1998; Hendry & Kinnison, 1999).

Contemporary or “rapid” evolution has been observed, both experimentally and naturally, across a wide range of taxa and biological contexts (Reznick & Ghalambor, 2001; Carroll et al., 2007). This notion of a “convergence of ecological and evolutionary time” (Hairston et al., 2005) instigated the synthesis of ecology and evolution into a single framework: eco-evolutionary dynamics.

### **Eco-evolutionary dynamics: interactions and feedbacks**

Eco-evolutionary dynamics can be defined as “interactions between ecology and evolution that play out on contemporary time scales” (Hendry, 2017). In the broad sense, eco-evolutionary dynamics include the classic unidirectional effects of ecology on evolution, such as the adaptation of medium ground finches (*Geospiza fortis*) to drought-induced changes in the seed distribution on the Galápagos island of Daphne Major (Grant & Grant, 1995), or vice versa, the effects of evolution on ecology, such as the effect of the

selection and distribution of body sizes on the population dynamics of Soay sheep (*Ovis aries*) on Hirta, St. Kilda (Pelletier et al., 2007).

In addition, eco-evolutionary dynamics include reciprocal interactions referred to as “eco-evolutionary feedbacks” (Post & Palkovacs, 2009) or “ecogenetic feedbacks” (Kokko & López-Sepulcre, 2007). These interactions can be considered loops or cycles of ecological processes that drive evolutionary change in traits that, in turn, drive changes in ecological processes (Post & Palkovacs, 2009). For example, camouflage maladaptation in the stick insect *Timema cristinae* resulted subsequently in increased predation, decreased population size, and increased selection against the non-cryptic (i.e., maladapted) morph (Farkas & Montejo-Kovacevich, 2014). As another example, cyclic population size fluctuations in side-blotched lizards (*Uta stansburiana*) resulted in an evolutionary stable state maintaining both throat-colour morphs (Sinervo et al., 2000). High-density years, in which yellow-throated females with few, large offspring are favoured, alternated with low-density years, in which orange-throated females with many, small offspring are favoured, resulting in a two-year oscillation between the two morphs (Sinervo et al., 2000). The common denominator of these two examples is the key role of density in linking ecology and evolution.

## Density dependence

Density dependence is the process that limits populations at high density by decreasing population growth rate and its components, survival and reproduction (Lande et al., 2002). It formed the root of the “struggle for existence” and the resulting theory of evolution by natural selection (Wallace, 1858; Darwin, 1859) and consequently has been the focus of attention in many studies in both ecology and evolution. On the one hand, population ecologists attempt to identify and understand the density-dependent and density-independent factors that together drive population size fluctuations (Lack, 1954), whilst community ecologists study the role of density dependence in the coexistence of competing species or, more generally, the maintenance of biodiversity (Chesson, 2000). For evolutionary biologists, on the other hand, density dependence is an agent of natural selection, and provides important insights for life history evolution and trade-offs (Bassar et al., 2010). Density dependence has also been assigned a central role in many of the models of eco-evolutionary feedbacks. For example, MacArthur (1962) laid the foundation for density-dependent selection, which results from the assertion that different genotypes have higher fitness values at different levels of population density. In a multi-species or community context, Pimentel described a

“genetic feedback” between density and genetic change, such that a change in the density of a competitor or parasite population would change the selection and resulting genotypic proportions of the focal or host population (Pimentel, 1961). Despite that density dependence is ubiquitous in nature, both within and between species (Newton, 1998; Brook & Bradshaw, 2006), empirical evidence for density-dependent selection in natural populations is scarce (but see Sæther et al., 2016; Gamelon et al., 2018; Hunter et al., 2018). The detection of density dependence and estimation of its strength and direction are also complicated because the negative effects of high density on demographic rates might be delayed (e.g., due to interactions with other species in the community; Royama, 1992) and because individuals’ competitive abilities might change throughout their lives (e.g., by age; Charlesworth, 1972; Gamelon et al., 2016). The strength of density dependence may also vary with habitat characteristics (Dhondt, 2010) or climate conditions (Stenseth et al., 2015). In addition, competition between individuals of different species and the resulting interspecific density dependence is often asymmetric (i.e., the effect of one species on the other is stronger than vice versa), though the prevailing species in one situation may be the worse competitor in another (Dhondt, 1989), or apparent, if both are affected by a shared natural enemy, like a

predator or parasite (Newton, 1998). Resolving these challenges will be an important move forward in exploring the role of density dependence as a facilitator of eco-evolutionary feedbacks.

### **Environmental fluctuations and stochasticity in time and space**

In their struggle for existence, individuals face more challenges than competition with others; they also brave their environments. The environment is ever-changing, stochastic, and hence, a continuous influence on populations and individuals in all natural systems across the globe. The challenges that individuals living in today’s world are confronted with are exacerbated by human-induced threats as climate change, habitat degradation, and overexploitation (Brook et al., 2008). When individuals face challenges with predictable fitness consequences, they may acclimate through phenotypic plasticity (i.e., the ability of individuals with a given genotype to adjust their phenotype in response to environmental variation; Ghalambor et al., 2007). In fluctuating or stochastic environments, when temporal variation in the environment is unpredictable or its consequences uncertain, individuals are at an advantage when they “hedge their bets” (Slatkin, 1974). By reducing the variance in their fitness (i.e., conservative bet-hedging) or between-individual

correlation in fitness (i.e., diversified bet-hedging), individuals effectively become less vulnerable to years with severe weather or environmental catastrophes (e.g., flooding, droughts), at the cost of reduced mean fitness (Starrfelt & Kokko, 2012). Environmental stochasticity is a universal feature of natural ecosystems and often assumed to affect the vital rates of individuals (within an age or stage class) similarly (Lande, 1993). Yet, there is increasing evidence that stochastic environmental fluctuations and environmental perturbations affect individuals differently depending on their phenotypes (Marrot et al., 2018; Acker et al., 2021), possibly generating a feedback between ecology and evolution (Lande, 2007; Engen et al., 2020).

Temporal fluctuations of environmental conditions are often correlated, or synchronized, over large spatial extents, sometimes spanning entire continents (Koenig, 2002). This environmental synchrony is, besides dispersal and species interactions, one of the known drivers of spatial population synchrony, i.e., correlated temporal fluctuations of population sizes among

spatially distinct populations (Liebhold et al., 2004). Spatial population synchrony has been observed in a wide range of taxa (Elton, 1924; Moran, 1953; Hansen et al., 2020). Recently, environmentally driven spatial synchrony has also been observed in other vital rates, such as survival (Olmos et al., 2020) and breeding success (Olin et al., 2020), and fitness-related traits, such as body size (Herfindal et al., 2020). Understanding spatial and temporal variation in trait values (Berven & Gill, 1983; Jetz et al., 2008), particularly traits that have a direct link to fitness, and identifying the environmental variables that underlie this variation have been central to ecological and evolutionary research. However, aside from a few exceptions (e.g., Herfindal et al., 2020; Olin et al., 2020), little is known about spatial synchrony in trait values and to what degree that is driven by environmental variation. Especially those traits that follow distinct spatial patterns and have close links to environmental variables, such as phenology (Bailey et al., 2020; Samplonius et al., 2021), are likely to display synchronous fluctuations across large spatial scales.



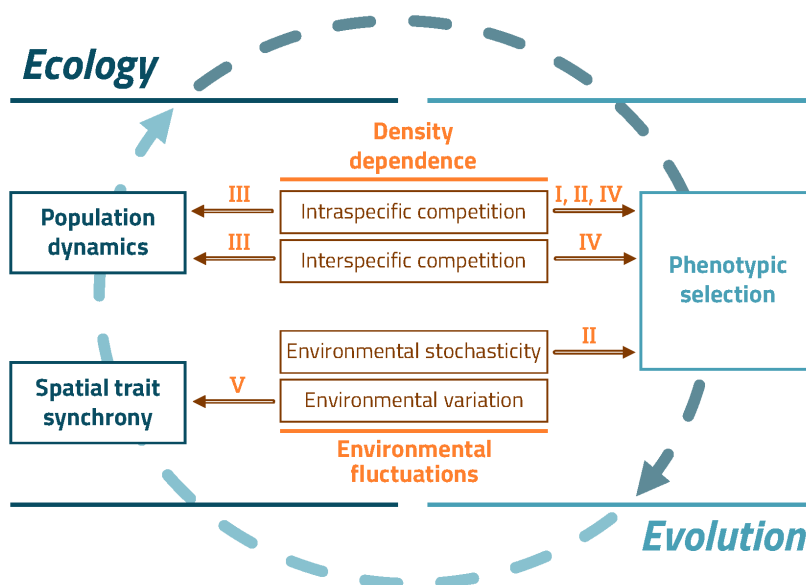
## B. Thesis objectives

In this thesis, I aim to improve our understanding of how density dependence and environmental fluctuations shape ecological and evolutionary processes, and the intertwined relationships between them. I explore these relationships across different levels of organisation: within single populations, across multiple populations of the same species, and across multiple populations of competing species. Comparative analyses across multiple populations of the same or closely related species are a powerful tool to examine the variation in ecological and evolutionary processes as well as capture potential general patterns that are otherwise unobservable.

Fundamental to this work are the long-term, individual-based data from an extensive collection of secondary hole-nesting bird populations across Europe. Throughout the thesis, I use data from different sets of populations and species to address four questions concerning the impact of density dependence (i.e., intraspecific and interspecific competition) on phenotypic selection and population dynamics, and of environmental variability on phenotypic selection and spatial trait synchrony (**Figure 1**):

1. How does intraspecific density dependence affect phenotypic selection of fitness-related traits? (**Papers I-II**)
2. What are the relative contributions of intra- and interspecific competition to phenotypic selection of fitness-related traits, and the population dynamics of competitors? (**Paper III-IV**)
3. How are the fitnesses of individuals and the phenotypic selection on their fitness-related traits affected by stochastic environmental fluctuations? (**Paper II**)
4. To what degree do spatiotemporal fluctuations in the environment contribute to the spatial synchrony of fitness-related traits? (**Paper V**)

In **paper I**, we studied how density dependence affected the adaptive topography of four fitness-related traits (i.e., timing of egg laying, clutch size, fledgling number, and mean tarsus length of chicks) in an island population of collared flycatchers (*Ficedula albicollis* Temminck). Here, the adaptive topography refers to Simpson's (1944) phenotypic equivalent of Wright's (1932) adaptive topography for allele frequencies. This "phenotype landscape" visualizes the relationship between mean phenotype and the mean fitness in the population, and consequently, how natural selection may lead



**Figure 1.** Thesis overview. Roman numerals refer to the focus of each paper included in this thesis.

to the evolution phenotypic trait. In addition to density-dependent selection analyses on each of the four traits separately, we examine how density dependence influences correlated selection on pairs of traits. That is, selection on a particular trait will affect its own distribution in the population as well as the distributions of correlated traits (Lande & Arnold, 1983).

Classic models of natural selection in temporally fluctuating environments assume that all individuals are similarly affected by stochastic fluctuations in the environment (Engen et al., 2013). However, individuals may vary in the impact that the environment has on their fitnesses, depending on their phenotypes (Lande, 2007) or the population density (Engen et al., 2020), and this may generate stochastic variation in selection. In [paper II](#), using the

same data as in [paper I](#), we examined how stochastic environmental fluctuations, the mean phenotype (i.e., causing frequency dependence) and the population size (i.e., causing density dependence) affected the fitness of individuals and the selection on three fitness-related traits (i.e., timing of egg laying, clutch size, and fledgling number).

While [papers I](#) and [II](#) dealt with intraspecific density dependence within a single population, [papers III](#) and [IV](#) covered both intra- and interspecific density dependence across multiple study sites. Species co-occur in ecological communities. Particularly species that interact directly with each other, like species that compete for shared resources, may influence each other's evolutionary (Johansson, 2008) and ecological

dynamics (Keddy, 1989). At the same time, the strength of intraspecific competition may vary with age (Gamelon et al., 2016). Yet, empirical studies of the consequences of interspecific competition for population growth in natural systems have so far discerned no age differences. In [paper III](#), we therefore examined how age-specific competition affected the population growth of two competitors. Using the model system of blue tits (*Cyanistes caeruleus* Linnaeus) and great tits (*Parus major* Linnaeus), who compete for food and nest sites, we quantified the relative contribution of age-specific intra- and interspecific competition to the population growth rates of each species across several study sites in Europe. In [paper IV](#), we used an extended set of study sites at which blue tits and great tits were sympatric to study the effects of intra- and interspecific competition on fitness and the selection on three fitness-related traits (i.e., timing of egg laying, clutch size, and fledgling number).

Lastly, timing of egg laying, clutch size, and fledgling number in birds are among the best studied traits in ecology and evolution. Besides their contributions to studies of natural selection and evolution, as demonstrated in papers I, II, and IV, the striking spatial and temporal patterns in the values of these traits, like the increase in clutch size and fledgling number (Moreau, 1944), and the delay in timing of egg laying (Slagsvold, 1976)

with increasing latitudes, and the environmental drivers of this variation have fascinated researchers for long. In [paper V](#), we examined the spatiotemporal variation in the values of these three traits and identified the environmental factors driving this variation using an extensive dataset of in total 86 populations of blue tits, great tits, and pied flycatchers (*Ficedula hypoleuca* Pallas). Particularly, we quantified how the spatial correlation in temporal trait fluctuations (i.e., spatial trait synchrony) changed with distance and the extent to which variation in local spring temperature and precipitation contributed to these spatial synchrony patterns.

The objective of this thesis is relevant for three reasons. First, density dependence and environmental fluctuations are omnipresent; virtually all populations in the natural world are, to varying degrees, limited by density-dependent factors and subject to environmental fluctuations. Second, as species are part of communities in which they directly or indirectly interact with other species, including interactions between species in models of population dynamics and natural selection will improve our understanding of eco-evolutionary dynamics in communities. Third, understanding the mechanisms through which ecology and evolution feedback into one another may help us predict how species and communities respond in the context of global change.

## C. Methods

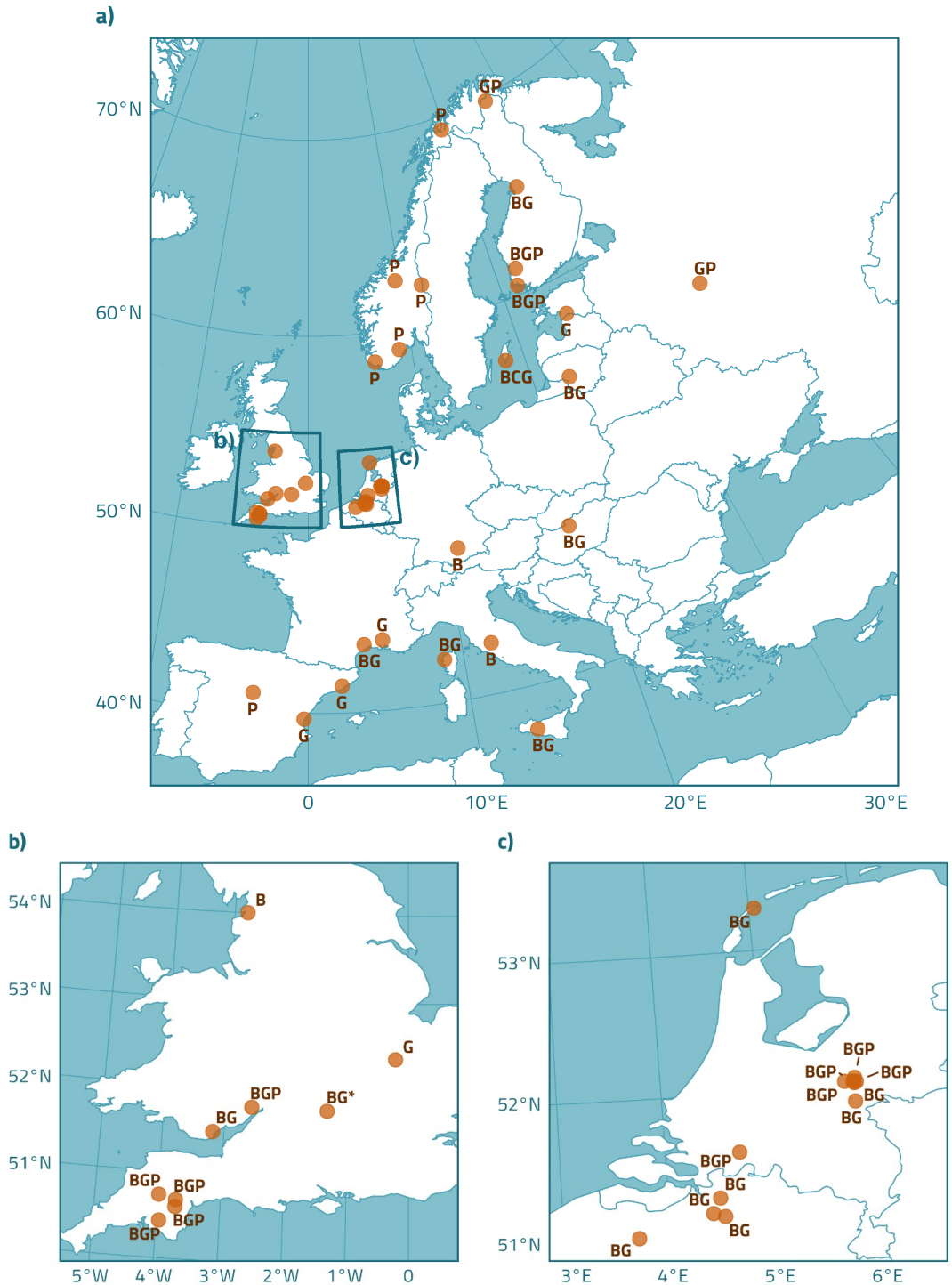
### **Study system: individual-based data from nestbox schemes in time and space**

Blue tits, great tits, collared flycatchers, and pied flycatchers are small secondary hole-nesting (or cavity-nesting) passerine bird species that breed in natural cavities or artificial nestboxes. The two tits, or parids, are mostly year-round residents or partial migrants (Smallegange et al., 2010), whilst the two flycatchers are obligate migrants that travel to sub-Saharan Africa in fall and return in spring. They occupy a range of woodland habitats, from rural woodlands and mixed forests to parks and gardens in (semi-)urban areas, where they primarily feed on insects and other arthropods during the breeding season. Great tits, and seldomly blue tits, are facultative multiple breeders and may occasionally have two successful broods in a single breeding season (Perrins, 1970, 1979), whilst the two flycatchers are single brooded.

Birds that breed in nestboxes can be marked, identified and monitored systematically throughout their lives (Lambrechts et al., 2010). Starting with the pioneering works by Kluijver (1951) and Lack (1954), long-term, individual-based studies involving nestbox schemes have been model systems for ecology and evolutionary biology (Clutton-Brock & Sheldon, 2010) for at least

two reasons. First, long-term, individual-based nestbox studies allowed researchers to study ecological and evolutionary processes over long periods of time. They have proven pivotal in our understanding of, among others, phenotypic selection (Chevin et al., 2015; Cao et al., 2019) and evolution (Merilä et al., 2001; Garant et al., 2004) in fluctuating environments, and individual- and population-level responses to environmental and climate change (Charmantier et al., 2008; Reed et al., 2013; Evans & Gustafsson, 2017). Second, combining multiple long-term, individual-based datasets from spatially distinct study sites enabled the study of the same ecological and evolutionary processes in a spatial context and across different ecological systems (Both et al., 2004; Stenseth et al., 2015; Burgess et al., 2018; Samplonius et al., 2018; Culina et al., 2021).

The work in this thesis is based on individual-based data from in total 87 populations of blue tits ( $n = 31$ ), great tits ( $n = 35$ ), collared flycatchers ( $n = 1$ ), and pied flycatchers ( $n = 20$ ) that had been monitored for at least 9 years. These populations came from nestbox schemes at 44 different study sites throughout Europe (**Figure 2**), ranging latitudinally from Sicily, Italy ( $37^{\circ}35'$  N) to Kevo, Finland ( $69^{\circ}45'$  N) and longitudinally from Okehampton, United Kingdom ( $3^{\circ}59'$  W)



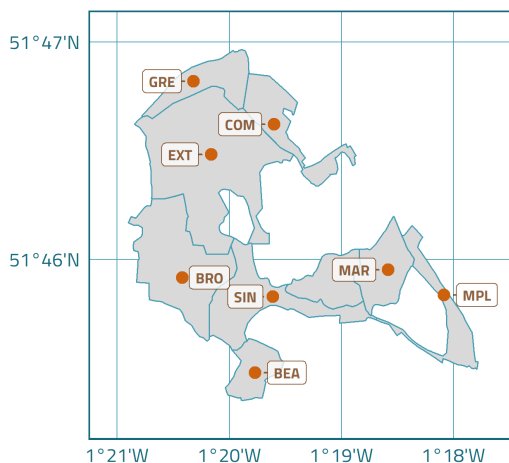
**Figure 2.** Map of the 87 populations of blue tits (B,  $n = 31$ ), collared flycatchers (C,  $n = 1$ ), great tits (G,  $n = 35$ ), and pied flycatchers (P,  $n = 20$ ) included in this thesis, originating from 44 different study sites in Europe (a), with insets of the United Kingdom (b), and the Netherlands and Belgium (c). \*Data from the Wytham Woods, a woodland characterised by high heterogeneity, were also analyzed at the sub-population level (see [Figure 3](#)).

to Zvenigorod, Russia ( $36^{\circ}51'$  E). The studied populations occupied various woodland habitats, dominated by deciduous, evergreen, or mixed forests. Meta-data for most of these populations are available through the Studies on Populations of Individual Birds (SPI-Birds, [www.spibirds.org](http://www.spibirds.org); Culina et al., 2021).

**Papers I** and **II** concentrated on the isolated population of collared flycatchers in the southern parts of Gotland, a Swedish island in the Baltic Sea. The nestboxes were located in seven study plots, six of which occurred in deciduous forests and one in a coniferous forest (Pärt & Gustafsson, 1989).

**Papers III** and **IV** used data from several study sites at which both blue tit and great tit were monitored. For **Paper III**, we included data from Boshhoek, Ghent, and Peerdsbos in Belgium, and Wytham Woods in the United Kingdom. For **Paper IV**, we included the same study sites, expanded by Hoge Veluwe and Vlieland in the Netherlands, and Oulu in Finland. Wytham Woods is a heterogeneous woodland divided into nine sectors (**Figure 3**) that differ in vegetation characteristics, physical geography, and nestbox density (Minot & Perrins, 1986; Garant et al., 2005). In both papers, analyses involving data from the Wytham Woods were carried out for the entire population (i.e., all sectors pooled) as well as for eight out of nine sectors for which sample sizes were sufficient.

**Paper V** used data from all 86 populations of blue tits, great tits, and pied flycatchers that were collated for this thesis. Only the population of collared flycatchers on Gotland was not part of this paper.



**Figure 3.** Map of the Wytham Woods, United Kingdom, and eight out of nine sectors for which additional analyses were carried out. Three-letter codes refer to sector names.

## Data collection

### *Breeding, individual, and demographic data*

For all nestbox schemes, the general procedure of data collection involved regular (at least weekly) visits to all nestboxes throughout the breeding season. If nestboxes were occupied, information on laying date (i.e., the day on which the first egg was laid, where 1 = 1<sup>st</sup> of April; note that smaller numbers are earlier in the year), clutch size (i.e., the

maximum number of eggs) and fledgling number (i.e., the number of nestlings that successfully fledged from the nest) and/or tarsus lengths of fledglings were collected.

In the nestbox schemes included in **papers I-IV**, individuals were marked with uniquely numbered leg rings when first captured, allowing them to be easily tracked throughout their lives, which made the data suitable for the analyses planned in these four papers. Nestlings were captured on the nest, and adults were mostly captured when incubating or when providing nestlings with food. From these capture-recapture data we derived individual-level information on apparent survival, recruitment, and age.

Throughout this thesis, two different measures of recruitment were used. In **paper III**, locally ringed nestlings recruited into the breeding population if they were observed breeding in their first year. In **papers I, II and IV**, locally ringed nestlings recruited into the breeding population if they were observed breeding in *any* future breeding season.

In **papers I, II and IV**, we calculated breeding females' individual fitnesses as their contribution to the next breeding season, i.e., an integrated measure of survival and recruitment. In **papers I and II**, following Sæther et al. (2000), individual fitness was calculated as  $W = I + B/2$ , where  $I$  is the apparent survival of the breeding female, and  $B/2$  the number of female recruits (i.e., half of

the number of recruits of both sexes, assuming equal sex ratio). In **paper IV**, individual fitness was calculated as  $W = I + F$ , where  $F$  is the number of female recruits.

In **papers I-IV**, the annual number of occupied nestboxes was used as a proxy of the total number of breeding pairs or the total number of breeding females in the population. This proxy is adequate because recapture rates of breeding females in these populations are high (range: 73-97%; Karvonen et al., 2012; Choquet et al., 2013) and most females start to breed at one year of age (Dhondt et al., 1990).

For all analyses, we excluded broods that were subjected to any experiments that could have affected the viability of parents or nestlings (e.g., clutch size manipulation or supplemental feeding). For **papers III and IV**, we summed the number of fledglings and number of recruits if individuals had multiple successful clutches in a single breeding season, whereas for **paper V**, we only used first clutches.

#### *Climatic data*

For **paper V**, we used data from two local (mean temperature and precipitation) climatic variables. Mean temperature and precipitation have been widely associated with variation in bird breeding parameters (Bowers et al., 2016; Bailey et al., 2020) and identified as drivers of spatiotemporal variation in fitness-related

traits (Herfindal et al., 2020). For each study site, we extracted daily mean temperatures (°C) and daily precipitation (mm) from the E-OBS gridded dataset version 20.0e (Cornes et al., 2018), or in the case of the study site located on the island of Vlieland, from the Royal Dutch Meteorological Institute.

## Phenotypic selection

### *Density-dependent phenotypic selection in fluctuating environments*

The foundation for how evolution operates in constant environments was laid by Fisher's fundamental theorem of natural selection (1930) and Wright's adaptive topography (1932). They showed that the mean Malthusian fitness, or intrinsic population growth rate, equals the additive genetic variance in fitness (Fisher, 1930), and that evolution maximizes the mean fitness of individuals in a population (Wright, 1932). This theory, however, ignored two important processes that affect the ecological and evolutionary dynamics of populations in natural, fluctuating environments: density dependence and environmental stochasticity (Engen et al., 2013; Sæther & Engen, 2015). Incorporating more ecological realism in models of selection led to the finding that the long-run growth rate is the relevant measure of fitness in a fluctuating but density-independent environment (Lewontin & Cohen,

1969; Tuljapurkar, 1982), whilst MacArthur (1962) showed that fitness decreases with increasing population size in a constant but density-dependent environment. In [paper I](#), following Lande et al. (2009) and Engen et al. (2013), we modelled the expected fitness of an individual with phenotype  $\mathbf{z}$  in a fluctuating environment  $\varepsilon$  with density dependence as

$$\begin{aligned} m(\mathbf{z}, N) &= \ln EW(\mathbf{z}, N, \varepsilon) \\ &= r_0(\mathbf{z}) - \sigma_\varepsilon^2/2 - \gamma(\mathbf{z})N, \end{aligned} \quad (1)$$

where  $m(\mathbf{z}, N)$  is the fluctuating Malthusian fitness,  $r_0(\mathbf{z}) - \sigma_\varepsilon^2/2$  the density-independent long-run growth rate with  $r_0(\mathbf{z})$  being the deterministic growth rate at small population sizes and  $\sigma_\varepsilon^2$  the environmental variance (i.e., the average variance in the Malthusian fitness through time), and  $\gamma(\mathbf{z})N$  captures the strength of density regulation and density-dependent selection.

In [paper I](#), density-dependent phenotypic selection was modelled on four fitness-related traits (i.e., laying date, clutch size, fledgling number, and mean fledgling tarsus length) separately as well as on pairs of traits. The density-independent component of the expected fitness (i.e.,  $r_0(\mathbf{z})$ ) was modelled as a second-degree approximation, including both directional and stabilizing selection on each trait, and correlated selection on the pair of traits in the two-trait (i.e., bivariate) models. The density-dependent component of the



expected fitness (i.e.,  $\gamma(\mathbf{z})N$ ) was of the exponential form, ensuring negative density dependence and allowing for density-dependent selection.

Lande et al. (2009) and Engen et al. (2013) also showed that the expected evolution of the mean phenotype  $\bar{\mathbf{z}}$  in density-regulated populations subject to environmental stochasticity tends to maximize

$$Q(\bar{\mathbf{z}}) = \bar{s}(\bar{\mathbf{z}})/\bar{\gamma}(\bar{\mathbf{z}}), \quad (2)$$

which is an adaptive topography in terms of expected population size and balances the long-run growth rate of the population ( $\bar{s}(\bar{\mathbf{z}})$ ) and the average strength of density regulation in the population ( $\bar{\gamma}(\bar{\mathbf{z}})$ ). In [paper I](#), we quantified the optimal values for each trait and pair of traits, maximizing  $Q(\bar{\mathbf{z}})$ .

#### *Individual variation in the impact of environmental stochasticity on fitness*

Additional ecological realism in phenotypic selection and evolution theory was provided by Lande (2007), who developed a model in which the fitnesses of individuals are differently affected by stochastic fluctuations in the environment, generating stochastic fluctuations in selection other than the stochasticity generated by fluctuations in population size. Engen et al. (2020) expanded this model by including frequency-dependent and density-dependent selection.

Consequently, in [paper II](#), we modelled the expected fitness of an individual with phenotype  $\mathbf{z}$  as

$$m(\mathbf{z}, N) = r_0(\mathbf{z}) - \bar{c}(\mathbf{z}, \bar{\mathbf{z}}, N) - \psi(\mathbf{z})N, \quad (3)$$

where  $\bar{c}(\mathbf{z}, \bar{\mathbf{z}}, N)$  is the environmental covariance between the growth rate of an individual with phenotype  $\mathbf{z}$  and that of the population with mean phenotype  $\bar{\mathbf{z}}$ , and captures the differential individual effects of environmental stochasticity, and  $\psi(\mathbf{z})N$  is identical to  $\gamma(\mathbf{z})N$  in eq. 1 but with different notation. If all individuals are similarly affected by stochastic fluctuations in the environment, the environmental covariance equals the constant environmental variance  $\sigma_e^2$ , the model in eq. 3 becomes identical to the model in eq. 1.

In [paper II](#), we quantified density-dependent selection on the multivariate phenotype of laying date, clutch size, and fledgling number, and examined the differential effects of environmental stochasticity on individuals dependent on their (multivariate) phenotype  $\mathbf{z}$ , the mean phenotype in the population  $\bar{\mathbf{z}}$ , and the size of the population  $N$ . The density-independent component of the expected fitness included directional selection, and the density-dependent component was of the same form as in paper I. The environmental covariance between two individuals, with phenotypes  $\mathbf{y}$

and  $\mathbf{z}$  respectively, was of the form:  $c(\mathbf{z}, \mathbf{y}, N) = \sigma(\mathbf{y}, N)\sigma(\mathbf{z}, N)\rho(\mathbf{y}, \mathbf{z})$ . Here  $\sigma(\mathbf{y}, N)$  and  $\sigma(\mathbf{z}, N)$  are the standard deviations of  $r_0(\mathbf{y})$  and  $r_0(\mathbf{z})$ , and capture the magnitude of environmental stochasticity, or the sensitivity of individual growth rates to environmental fluctuations as a function of their phenotypes and the population size.  $\rho(\mathbf{y}, \mathbf{z})$  is the correlation between  $r_0(\mathbf{y})$  and  $r_0(\mathbf{z})$ , which is expressed in terms of the difference in phenotypes  $\mathbf{v} = \mathbf{z} - \mathbf{y}$ , such that two individuals with identical phenotypes have correlation 1, and the two individuals with the biggest difference in phenotypes have correlation 0.

*Density-dependent phenotypic selection between competitors in fluctuating environments*

In ecological communities species often compete for resources, and in doing so, affecting each other's ecological and evolutionary dynamics, leading to phenomena such as character displacement (Grant & Grant, 2006) and competitive exclusion (Vallin et al., 2012). In [paper IV](#), we extended the model of density-dependent selection used in paper I to include both intra- and interspecific density-dependent selection. We modelled the expected fitness of an individual with phenotype  $\mathbf{z}$  as

$$m(\mathbf{z}, N) = r_0(\mathbf{z}) - \sigma_e^2/2 - \gamma(\mathbf{z})N - \gamma(\mathbf{z})M, (4)$$

where  $\gamma(\mathbf{z})N$  describes the strength of intraspecific density regulation and intraspecific density-dependent selection, and  $\gamma(\mathbf{z})M$  the strength of interspecific density regulation and interspecific density-dependent selection.

In [paper IV](#), similar to paper II, we quantified selection on the multivariate phenotype of laying date, clutch size, and fledgling number. The density-independent component of the expected fitness was of the same form as in paper I, including both directional and stabilizing selection. The density-dependent component was of the logistic form, including intra- and interspecific density dependence and intra- and interspecific density-dependent selection.

## Population dynamics

In age-structured populations subject to density-dependent feedbacks, the "critical age class" (*sensu* Charlesworth, 1972) is the age class in which the variation in the number of individuals contributes most to the density regulation. Gamelon et al. (2016) showed that in a Dutch population of great tits, the youngest breeding females (i.e., age 1) out of four age classes were the critical age class. In [paper III](#), we extended the age-specific model of density dependence to the blue tit and great tit model system and examined how age-specific competitive effects influence the

population growth rates of sympatric species using the model

$$\begin{aligned} \ln \lambda_{A,t} = & \alpha_A + \beta_{1A}(N_{1A,t} + \omega_A N_{1B,t}) \\ & + \beta_{2A}(N_{2A,t} + \omega_A N_{2B,t}) \\ & + \beta_{3A}(N_{3A,t} + \omega_A N_{3B,t}) \\ & + \beta_{4A}(N_{4A,t} + \omega_A N_{4B,t}) + \varepsilon_t, \end{aligned} \quad (5)$$

where  $\ln \lambda_{A,t} = N_{A,t+1}/N_{A,t}$  is the total population growth of species A from year  $t$  to  $t + 1$ ,  $\alpha_A$  the intercept<sup>1</sup>,  $\beta_{iA}$  the strength of density regulation of age class  $i$  on species A,  $N_{iA,t}$  and  $N_{iB,t}$  the number of breeding females in age class  $i$  of species A and B, respectively.  $\omega_A$  is the relative importance of intra- versus interspecific competition on the total density regulation in species A, where 0 indicates no effect of interspecific competition and 1 an equal effect of intra- and interspecific competition.  $\varepsilon_t$  are the residuals of the regression and correspond to variation in  $\ln \lambda_{A,t}$  not explained by variation in population size. The model in eq. 5 describes the density dependence for species A only; for species B, the model is similar except that the indices A and B are swapped.

Instead of using annual age-specific count data directly, more accurate age-specific numbers were retrieved by jointly analysing count data, capture-mark-recapture data, and recruitment data in an integrated population model. This framework allowed us to account for observation error commonly associated

with population censuses, incomplete information on the age of breeding females, and demographic stochasticity (Schaub & Abadi, 2011).

### Spatial synchrony in trait values

Environmental fluctuations and population dynamics are linked in such a way that spatially synchronous environmental fluctuations may induce spatial synchronous population size fluctuations (Hansen et al., 2020). Traits also have strong links to the environment; yet, whether synchronous fluctuations in environmental conditions can generate spatial synchrony in the values of traits is not well understood. In [paper V](#), we examined whether temperature and precipitation in spring (i.e., average of February-May, which corresponds to the period before and during breeding; Both et al., 2004) can drive spatial synchrony in laying dates, clutch sizes, and fledgling numbers across a large number of European populations of secondary hole-nesting passerines. For each year in each population, we calculated median laying date, mean clutch size, and mean fledgling number. These values were linearly detrended to remove common climatic trends and normalized to explore the temporal fluctuations in traits relative to long-term population averages. Following Engen et

1: In paper III,  $\gamma_{\lambda_A}$  and  $\gamma_{\lambda_B}$  are the notations used for the intercepts. I changed the notation here to distinguish them from the density-dependent components in the models of phenotypic selection (eqs. 1, 2, 4).

al. (2005), we quantified the spatial synchrony in trait values as function of the distance  $d$  between populations

$$\rho(d) = \rho_{\infty} + (\rho_0 - \rho_{\infty})e^{-d^2/2l^2}, \quad (6)$$

where  $\rho_0$  and  $\rho_{\infty}$  are the correlation as distance approaches zero and infinity, respectively, and  $e^{-d^2/2l^2}$  is a Gaussian

positive definite spatial autocorrelation function, where  $l$  is the standard deviation of the Gaussian probability distribution, representing the spatial scale of synchrony. In contrast to non-parametric models of spatial synchrony, the three parameters of this parametric model can be compared across different species and ecological contexts in a standardized way.

## D. Results and discussion

1. How does intraspecific density dependence affect the phenotypic selection on fitness-related traits? (Papers I-II)

Our analyses in [papers I](#) and [II](#) revealed evidence for density-dependent selection on fitness-related traits in the collared flycatcher population on Gotland, Sweden. Density-dependent selection occurs when variation in population sizes (or densities) have differential effects on individual fitnesses dependent on their phenotypes. In the univariate model from [paper I](#) and the multivariate model from [paper II](#), we found that earlier laying dates and larger fledgling numbers were favoured at smaller population sizes than at larger population sizes. This stronger selection for more fledglings at small population sizes is in line with the low occurrences of complete brood failure and high recruitment rates at small population sizes in this population, resulting in increased population growth. The stronger selection for earlier laying at small population sizes might result from an increased availability of nesting locations of better quality (Doligez et al., 2004) or improved timing of breeding irrespective of spring temperature (Ahola et al., 2012). In the model of correlated selection on these two traits ([paper I](#)), the density-dependent selection on fledgling number found in the univariate case

was no longer evident, likely because of the decrease in fledgling number with later laying (Perrins, 1970), such that selection for more fledglings results indirectly from selection for earlier laying. We found no evidence for density-dependent selection on clutch size, which has previously been shown to be only affected through indirect selection in this population (Sheldon et al., 2003). This is interesting because in other secondary hole-nesting passerines, clutch size has been shown to be under direct density-dependent selection (Both et al., 2000; Ahola et al., 2012; Engen & Sæther, 2016).

Density-dependent selection can be considered the simplest form of an eco-evolutionary feedback loop (Kokko & López-Sepulcre, 2007; Travis et al., 2013). That is, individuals favoured at small population sizes have trait values (e.g., more fledglings) that lead to an increase in population size, which will, in turn, select for individuals that deal well with high population densities. This ongoing loop is represented by an adaptive peak (i.e.,  $Q(\bar{z})$  in [paper I](#)), often at intermediate trait values, at which fluctuations in population size due to fluctuations in the environment will cause the mean phenotype to move away from its optimum value (Engen et al., 2013).

2. What are the relative contributions of intra- and interspecific competition to phenotypic selection of fitness-related traits, and the population dynamics of competitors? ([Papers III-IV](#))

Density-dependent interactions between competing species are another example of an eco-evolutionary feedback loop. Competition-induced selection pressures might change the distribution of trait values, which, in turn, might alter the strength of competition between the competitors (Govaert et al., 2019). A classic example of intra- and interspecific competition is the interaction between the smaller blue tit and the larger great tit. They compete both directly for nesting sites during the breeding season (Minot & Perrins, 1986) and roosting sites in winter (Dhondt & Eyckerman, 1980), as well as indirectly for food throughout the year (Lack, 1954; Dhondt, 1977). Our analyses in [papers III](#) and [IV](#) showed that the relative contributions of intra- and interspecific competition to the population growth rate and density-dependent selection of the two species vary considerably across the different study sites. In both papers, we found that interspecific competition had a stronger negative effect on the population growth or fitness of blue tits than of great tits. This asymmetry in competition has been demonstrated earlier in these two species

(Dhondt, 2012; Stenseth et al., 2015). Yet, this finding was not consistent across all study sites, potentially because of within-population habitat heterogeneity (Dhondt et al., 1992), or the double asymmetry in competition due to blue tits exploitation competitor (i.e., due to a more variable diet; Török & Tóth, 1999) and great tits being the better inference competitor (Dhondt, 2012). In addition, the differential contributions of the age classes to density regulation varied also between the study sites ([paper III](#)), including sites with the largest contribution from the youngest age class and sites with the largest contribution from age class 3 or 4.

In [paper IV](#), we found no clear evidence of intra- and interspecific density-dependent selection on any of the traits studied, with a few exceptions such as the negative relationship between blue tit densities and the selection on great tit clutch sizes in Hoge Veluwe. The lack of a consistent pattern across study sites might be attributed to the variation in the ecological contexts of each study site, such that a site's specific environmental conditions determine the evolutionary consequences of competition. Sector-level analyses of the heterogeneous Wytham Woods indeed showed within-population variation in the density effects on fitness and phenotypic selection, possibly generating a mosaic of competition strengths (Blondel et al., 1993).

3. How are the fitnesses of individuals and the phenotypic selection on their fitness-related traits affected by stochastic environmental fluctuations? (Paper II)

Stochastic fluctuations in the environment are commonly assumed to affect all individuals or groups of individuals (e.g., within age or stage classes) in the population equally (Lande, 1993). In [paper II](#), however, we showed that environmental stochasticity may impact the fitnesses of individuals differently depending on their phenotypes, the mean phenotype, and the size of the population. Individuals with large clutches or few fledglings experienced the strongest negative fitness consequences of environmental stochasticity, whereas their laying date had little contribution to these stochastic effects. This is the result of the magnitude of environmental stochasticity  $\sigma(\mathbf{z}, N)$  being the most sensitive to changes in clutch size, and the environmental correlation between individuals  $\rho(\mathbf{y}, \mathbf{z})$  to changes in fledgling number. All of these traits have strong, but often complicated, links to environmental variation and perturbations (Boyce & Perrins, 1987; Siikamäki, 1996; Eeva & Lehikoinen, 2010). The finding that negative impacts of environmental stochasticity on individual fitnesses were irrespective of laying date might indicate that laying date in this population is plastic, so that individuals experience little to no fitness consequences

when adjusting their laying dates, or that environmental stochasticity primarily acts at the later stages in the breeding season.

Negative impacts of the environment on the population may either be amplified (Jaatinen et al., 2021) or mitigated (Reed et al., 2013) when population densities are high. In [paper II](#), we found that the magnitude of environmental stochasticity decreased with increasing population size, thus behaving like demographic stochasticity (i.e., chance events of births and deaths), which diminishes with increasing population size.

Through the differential effects on the fitnesses of individuals with different phenotype stochastic environmental fluctuations induce frequency-dependent selection (Engen et al., 2020), illustrating a third route through which ecology and evolution may feedback into each other (Smallegange et al., 2018; Govaert et al., 2019).

4. To what degree do spatiotemporal fluctuations in the environment contribute to the spatial synchrony of fitness-related traits? (Paper V)

In [paper V](#), we showed that temporal fluctuations in the values of fitness-related traits may be spatially synchronous over large spatial extents. We found a high degree of spatial synchrony in laying date and lower degree of in clutch size and fledgling number, a

pattern that was consistent across all three secondary hole nesters. We further showed that a large degree of the spatial synchrony in laying dates of blue tits and great tits could be attributed to variation in local spring temperatures. This comes as no surprise because their timing of laying is strongly influenced by the onset of spring, and consequently the food availability for their offspring (Perrins, 1970). The smaller contribution of temperature to the spatial synchrony in laying dates of pied flycatchers might be attributed to the greater range of environmental conditions that they experience to time their spring arrival and the start breeding (Rushing et al., 2017).

Local precipitation in spring did not contribute to spatial synchrony in any species-trait combination, possibly because it can have opposing effects on individuals throughout the breeding season (Radford et al., 2001; Eeva et al., 2020). After accounting for variation in temperature and precipitation, spatial

synchrony in laying date remained high at shorter distances, and spatial synchrony in clutch size and fledgling number was unaffected. This indicates that other local ecological factors play an important role in driving the spatiotemporal dynamics of these traits, including but not limited to the spatial heterogeneity of habitat quality (Blondel et al., 1993) and density dependence (Walter et al., 2017), the incidence of double brooding in great tits (Husby et al., 2009), the spatial synchrony of food supplies, such as beech mast in winter (Grøtan et al., 2009).

The spatial scale of synchrony in laying date and clutch size surpassed that of population abundances in blue tits and great tits (Sæther et al., 2007). As the pattern of spatial synchrony is consistent across the three species, it is likely that spatial trait synchrony is common for other traits that show such consistent responses to specific environmental variables as laying date, or phenology in general, does to temperature.



## E. Conclusions and perspectives

This thesis illustrates that intraspecific density dependence, interspecific density dependence, and environmental stochasticity constitute three processes through which ecology and evolution are impacted and intertwined.

Density dependence, within and between species, may affect the fitness of individuals and populations, and is an agent of natural selection on fitness-related traits. Overall, density-dependent effects on fitness and population growth are mainly negative as competition for resources increases, and phenotypic selection may consequently act towards increased reproduction or avoiding competition. Yet, the large heterogeneity in the strength and direction of density effects among populations and study sites suggests that the evolutionary outcome or consequences of intra- and interspecific competition may be dependent on the trait, population, species, and system under study.

Stochastic environmental fluctuations are a continuous impact on individuals and populations in natural systems. These impacts are similar when individuals are similar, or populations are near. As an inevitable consequence, the effects of the environment vary considerably when individuals vary in terms of phenotypes, or populations are distant. Variation or heterogeneity at the essence of both evolutionary biology and

population and community ecology (Vindenes et al., 2008; Bolnick et al., 2011), and may provide the means to link the two. Ignoring individual heterogeneity (Vindenes & Langangen, 2015) or spatial heterogeneity (Senner et al., 2018) may mask the strength and presence of eco-evolutionary processes, and hence bias predictions of population response to current and future global threats.

Environmental stochasticity and density dependence may also interact. On the one hand, density dependence may buffer against the detrimental effects of environmental perturbations (Reed et al., 2013; Hansen et al., 2019). On the other hand, environmental fluctuations may impact small populations more strongly (Jaatinen et al., 2021) or increase competition between species (Wittwer et al., 2015). The consequences for organisms vary greatly between the two interactions, underlining the importance of including both environmental stochasticity and density dependence when studying and predicting eco-evolutionary dynamics.

Like all scientific studies, irrespective of the field, this thesis has yielded more questions than answers. As both density dependence and environmental fluctuations are virtually everywhere, and the availability of meticulously collected long-term, individual-

based data is increasing, there are plenty of opportunities left to study the intricacies of eco-evolutionary dynamics in natural systems.

Species co-occur in ecological communities, in which they are often part of diverse competitive networks that are more than just the sum of pairwise interactions. Blue tits and great tits, for example, also compete with other secondary hole-nesting passerines, such as other parids and *Ficedula* flycatchers (Dhondt, 2012). In addition, competition is not constant through time; the winner in one situation may be the loser in the next. Incorporating these competitive loops in which no single species outcompetes all others (i.e., competitive intransitivity; Laird & Schamp, 2006) into a models of density-dependent selection may help us improve our understanding of the eco-evolutionary dynamics of each species involved in the network as well as the dynamics of the whole community.

One way forward in elucidating the influence of environmental stochasticity on phenotypic selection is through improving our understanding of its ecological causes of phenotypic selection (MacColl, 2011). This requires the development of models that directly incorporate environmental variation in models of phenotypic selection (e.g., adding an environmental dimension to the adaptive landscape; Chevin et al., 2010) because simply relating selection coefficients to variation in

environmental variables might misrepresent the complex relationship of traits, fitness, and the environment (Hunter et al., 2018).

There are multiple pathways through which environmental variation may impact populations. This may happen directly, such as the spatiotemporal variation in environmental conditions synchronizing the temporal dynamics of populations across a region or continent. However, this may also happen indirectly through variation in traits and vital rates (McLean et al., 2016), for instance when environmentally driven spatial synchrony of traits and vital rates would lead to spatial synchrony in population size fluctuations. Spatial population synchrony tends to increase the risk of extinction (Heino et al., 1997) because there is a greater chance that environmental perturbations will negatively affect all or most populations the region simultaneously (Koenig & Liebhold, 2016). A crucial next step is, therefore, to examine the extent to which traits and/or vital rates mitigate or intensify the synchronizing effect of the environment on population dynamics. Environmentally driven spatial trait synchrony may also contribute to our understanding of spatial variation in phenotypic selection (Siepielski et al., 2013), which is likely to have notable consequences for ecological and evolutionary processes alike (Jetz et al., 2009; Hadfield, 2016; Engen & Sæther, 2019).

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# Paper I

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## Density-Dependent Adaptive Topography in a Small Passerine Bird, the Collared Flycatcher

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**ABSTRACT:** Adaptive topography is a central concept in evolutionary biology, describing how the mean fitness of a population changes with gene frequencies or mean phenotypes. We use expected population size as a quantity to be maximized by natural selection to show that selection on pairwise combinations of reproductive traits of collared flycatchers caused by fluctuations in population size generated an adaptive topography with distinct peaks often located at intermediate phenotypes. This occurred because  $r$ - and  $K$ -selection made phenotypes favored at small densities different from those with higher fitness at population sizes close to the carrying capacity  $K$ . Fitness decreased rapidly with a delay in the timing of egg laying, with a density-dependent effect especially occurring among early-laying females. The number of fledglings maximizing fitness was larger at small population sizes than when close to  $K$ . Finally, there was directional selection for large fledglings independent of population size. We suggest that these patterns can be explained by increased competition for some limiting resources or access to favorable nest sites at high population densities. Thus,  $r$ - and  $K$ -selection based on expected population size as an evolutionary maximization criterion may influence life-history evolution and constrain the selective responses to changes in the environment.

**Keywords:** collared flycatcher, density dependence, eco-evolutionary dynamics, fitness variation, life-history evolution,  $r$ - and  $K$ -selection.

### Introduction

Wright (1932) introduced the concept of adaptive topography in evolutionary biology by demonstrating that evolution of gene frequencies in a constant environment will

maximize the mean fitness of the individuals in the population, assuming constant genotypic fitnesses over time, random mating, and no linkage disequilibrium among loci. Natural selection will then cause gene frequencies to change so that the population moves upward on the adaptive topography, resulting in an increase in the mean fitness of the population. Wright's shifting balance theory of evolution showed that this process could, by introducing the effects of random genetic drift, lead to multiple fitness peaks. The formation of such an adaptive topography has provided a theoretical foundation for analyses of many problems in evolutionary biology (Gavrilets 2004; Svensson and Cal-sbeek 2012).

Lande (1976, 1979, 1982) and Lande and Arnold (1983) provided an important conceptual advancement by developing a quantitative genetic theory for selection of the mean phenotype that showed that the adaptive topography for a normally distributed character is the mean Malthusian fitness as a function of the mean phenotype. Stochasticity was introduced by random genetic drift, causing variance in stochastic changes to be proportional to the inverse of the population size  $N$  (Lande 1976). This theory was later expanded by Lande (2007) to include a fluctuating environment, showing that the adaptive topography for the expected selection was the gradient of the long-run population growth rate (Lande et al. 2003) expressed as a function of the mean phenotype. In this model, individuals with different phenotypes are differently affected by environmental fluctuations but are similarly affected by density dependence.

Numerous studies covering a wide range of taxa have documented a decrease in mean individual fitness with increasing population density (e.g., Royama 1992; Fowler et al. 2006; Bassar et al. 2010; Travis et al. 2013; Sæther et al. 2016a). However, despite the presence of such a general pattern, empirical evidence for density-dependent

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selection in natural populations is still rare (Mueller 1997; Coltman et al. 1999; Sinervo et al. 2007; Svanbäck and Persson 2009). A major reason for this is that it can be challenging to show that genotypes or phenotypes favored at small population sizes differ from those that have higher fitness at large population densities, which is a prerequisite for density-dependent selection to occur (Reznick et al. 2002; Travis et al. 2013). Fortunately, an increasing number of experimental manipulations of population density have now revealed that density-dependent selection is an important selective agent on fitness-related characters in many natural populations (Sinervo et al. 2000; Svensson and Sinervo 2000; Reznick et al. 2012; Bassar et al. 2013; Travis et al. 2014; Hayward et al. 2018; Handelsman et al. 2019). As all natural populations fluctuate in size, this introduces a general mechanism of how the mean fitness of individuals in the population will change through time and ultimately influence the rate of evolutionary responses to changes in the environment (Sæther and Engen 2015). Density-dependent selection also represents the simplest form for feedback between ecology, described by the patterns in population dynamics, and evolution, characterized by the selective response to these population fluctuations (Kokko and Lopez-Sepulcre 2007; Travis et al. 2013; Govaert et al. 2019; Handelsman et al. 2019). This eco-evolutionary interaction may, in turn, influence trophic interactions and ecosystem processes (Svanbäck and Persson 2004; Reznick and Travis 2019). The aim of the present study is to quantify how fluctuations in population size may affect phenotypic selection in a small passerine bird.

An influential concept of density-dependent selection was the dichotomy between  $r$ - and  $K$ -selection introduced by MacArthur and Wilson (1967). They suggested, on the basis of a theory originally developed by MacArthur (1962), that phenotypes favored at small densities were selected against when population size approaches the carrying capacity because of competitive inferiority or poorer ability to utilize sparse resources (Bell 2008; Engen and Sæther 2017a). Another important implication of MacArthur's (1962) classical result is that in a stable environment evolution tends to maximize the carrying capacity  $K$ , a result that was later generalized to age-structured populations by Charlesworth (1994 and references therein). Thus, the adaptive topography in this deterministic model is simply described by the carrying capacity  $K$  as a function of the mean phenotype.

Lande et al. (2009) generalized, for a haploid population, MacArthur's (1962) classical result for deterministic models to include environmental stochasticity. They showed that in a fluctuating environment, evolution tends to maximize the expected population size  $Q = g(N)[1 - \sigma_e^2/2r_0]$ , where  $g(N)$  is an increasing function of population size

$N$  that describes the form of the density regulation (e.g.,  $g(N) = N^\theta$  for the theta logistic model, where  $\theta$  is a parameter determining the form of density regulation [Gilpin et al. 1976], and  $g(N) = N$  for the logistic model of density regulation),  $\sigma_e^2$  is the environmental variance, and  $r_0$  is the population growth rate at low densities. Evolution of the mean phenotype  $\bar{z}$  under density-dependent selection will always be toward the value  $z^*$  maximizing  $Q(\bar{z})$ . This maximum is never reached because environmental stochasticity always perturbs it toward values smaller than the maximum, but the mean phenotype still has some stationary fluctuations around the optimal phenotypic value  $z^*$  (Engen et al. 2013a). Thus,  $Q(\bar{z})$  is the adaptive topography of the population, describing how expected selection will depend on the mean phenotype.

One of the major challenges in analyses of density-dependent selection is to account for the effects of environmental variables that often strongly affect individual fitness. For example, clutch size of small hole-nesting passerine birds is affected by variation in climate variables that influences the timing of egg laying and the amount of food available to nestlings (Visser et al. 2004). Variation in climate explains a large proportion of annual variation in the number of recruits produced per female and hence is an important determinant of individual fitness (Reed et al. 2013b). In addition, intermediate clutch sizes often produce a larger number of recruits than both small and large clutches (Lack 1966; Pettifor et al. 1988). These effects result in stabilizing selection toward an optimal intermediate clutch size (Boyce and Perrins 1987), which also affects the within-population distribution of clutch sizes (Haukioja 1970). Experimental evidence indicates that this optimum is strongly affected by fluctuations in population density (Both et al. 2000). Accordingly, strong directional selection on optimal seasonal timing of reproduction can therefore be counteracted by demographic buffering through increased juvenile survival in years with low fledging rates (Reed et al. 2013a). However, statistical analyses of annual variation in selection have revealed that the total number of eggs produced per breeding season can be subject to  $r$ - and  $K$ -selection (Sæther et al. 2016b): females producing a large number of eggs have higher fitness at low population densities but have lower fitness close to the carrying capacity  $K$  than those females producing a small clutch when the population size is small. In this study, we will apply the long-run growth rate as a measure of fitness, defined as the mean of the fluctuating Malthusian fitness (Sæther and Engen 2015). This measure has the advantage that it includes density-dependent selection as well as environmental stochasticity, which both may strongly affect evolutionary processes in density-regulated populations (Roughgarden 1971; Travis et al. 2013; Engen and Sæther 2016).

A challenge in analyses of natural selection is that selection on one trait can be affected by correlated selection on other traits (Lande and Arnold 1983). In temperate passerine birds, there are strong interactions between different reproductive traits. For example, Lack (1947, 1954) indicated that the optimal clutch size of small passerines, maximizing the number of offspring surviving to the next breeding season, was less than the maximum number of eggs that could be laid because of reduced survival of fledglings or adults (Williams 1966) from the larger broods. Such indirect selection can even induce opposing selection on correlated characters. However, Kingsolver and Diamond (2011) found that opposing selection on different components of fitness rarely was so strong that it resulted in no net directional selection. Still, indirect selection has the potential for influencing the strength of selection acting on a character, affecting the evolution of life-history differences.

Here, we apply the evolutionary maximum principle of Lande et al. (2009) and Engen et al. (2013a) to calculate the adaptive topography of four different reproductive traits (timing of egg laying, clutch size, number of fledglings, and mean tarsus length) in the collared flycatcher *Ficedula albicollis* as well as functions of pairwise combinations of them. This enables us to explore the influence of directional and stabilizing selection acting on these reproductive traits. In particular, we focus on the effects of density-dependent selection, that is, whether those phenotypes with the lower fitness at small population sizes are superior close to the carrying capacity  $K$ , compared with those with higher fitness at small population densities. This will generate  $r$ - and  $K$ -selection toward an optimal reproductive strategy (Ricklefs 2000) at intermediate trait values. By comparing the actual values of different life-history traits with the location of these maxima, we will be able to evaluate the influence of  $r$ - and  $K$ -selection on different reproductive traits in this species.

## Methods

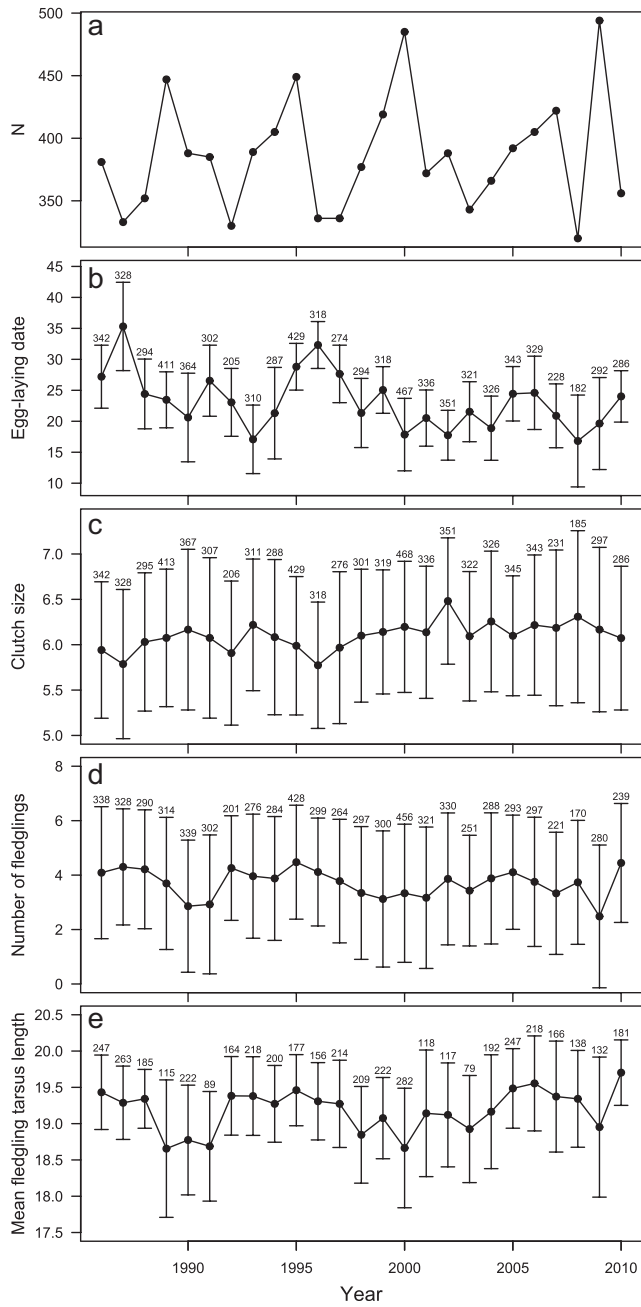
### Study Species

The collared flycatcher is a small (~13 g), insectivorous, hole-nesting passerine breeding mainly in deciduous forests in eastern parts of central Europe. It is a long-distance migrant, returning from the overwintering areas in sub-Saharan Africa in April and May. Collared flycatchers are sexually dimorphic. The distribution in the population of several male characters is influenced by sexual selection (Gustafsson et al. 1995; Ellegren et al. 1996; Pärt and Qvarnström 1997; Sheldon et al. 1997) as well as fluctuating selection caused by environmental variation (Evans and Gustafsson 2017).

### Study Population and Field Procedures

The collared flycatcher has been studied in the southern part of the island of Gotland in the Baltic Sea between 1980 and 2018 (57.2°N, 18.2°E). The individuals included in this study breed in nest boxes in a set of plots within the core study area, which was continuously monitored between 1986 and 2010. Most of the study plots were located in deciduous woodlands dominated by oak (*Quercus rubur* L.) and ash (*Fraxinus excelsior* L.) with a dense understory of hazel (*Corylus avallana* L.), whereas one study plot was also located in a pine forest (*Pinus sylvestris* L.). In this study, we pooled the data from all of these plots using the total number of occupied nest boxes as an estimate of population size. In total, the plots contained approximately 955 nest boxes throughout the study period, of which 35%–40% were occupied by collared flycatchers (Pärt and Gustafsson 1989; Doligez et al. 1999; Doncaster and Gustafsson 1999). The population size in these plots (i.e., the number of nest boxes occupied) fluctuated between 320 nesting pairs in 2008 and 494 pairs in 2009 (fig. 1a). A large proportion of breeding females remained in the same study plots when they were recorded breeding more than 1 year, resulting in a median breeding dispersal distance of less than 200 m (Pärt and Gustafsson 1989). In this study area, the ratio between the number of immigrants and emigrants in a study plot was close to 1, independent of fluctuations in population size (Doncaster et al. 1997).

A detailed description of the field procedures is found in Pärt and Gustafsson (1989). All nestlings were fitted with a uniquely numbered leg ring. Breeders were caught during the breeding season at their nest boxes and marked with a uniquely numbered ring if unringed. This provides the data for calculating survival rates, considering the whole study system as a single population. The probability that an actual female present in the population was recorded was very high (>0.97; Choquet et al. 2013). By regularly visiting the nest boxes throughout the breeding season, data were obtained on several reproductive traits: egg-laying date was defined as the date of laying of the first egg in April days (where the first of April is 1), clutch size equals the total number of eggs laid, and the number of fledglings is the number of nestlings at the end of nesting season (usually between day 15 and day 18 after hatching). As a phenotypic characteristic of the nestlings we used the mean tarsus length at 13 days of age (mean fledgling tarsus length). Annual variation in the reproductive traits is shown in figure 1b–1e. The estimates of heritability  $h^2$  of these traits ranges from 0.19 for clutch size (Sheldon et al. 2003) to 0.35 for timing of egg laying (Sheldon et al. 2003) and tarsus length (Husby et al. 2013), whereas Gustafsson (1986) found no heritability in the number of fledglings produced ( $h^2 = -0.016$ ).





In some years, this population has been subject to experimental manipulations of clutch size, brood size, or hatching date (e.g., Gustafsson and Sutherland 1988; Wiggins et al. 1994b; Gustafsson et al. 1995). In this study we excluded all broods ( $n = 1,596$ ) that included experiments affecting reproductive output or the size of the nestlings. For the numbers included in the analyses, see figure 1.

#### Modeling Eco-Evolutionary Dynamics

We model variation in females' individual fitness  $W = I + B/2$ , where  $I$  is an indicator for survival and  $B$  is the number of recruits of both sexes, which are distributed dependent on phenotype  $\mathbf{z}$  (Sæther and Engen 2015). Here,  $I$  has a value of 1 if the female survives from one breeding season to the next and 0 otherwise and  $B$  is the total number of recruits entering the population the next or a later breeding season, so that  $B/2$  is the expected number of new female recruits provided an equal sex ratio. Thus,  $W$  is a female's total contribution, in terms of individuals for the next breeding season, produced in a given year. This approach does not distinguish between permanent emigration and mortality and includes the first-year survival of the offspring in the mother's fitness. This means that we consider only individuals that contribute genetically to the local population. Furthermore, we also include only the female segment of the population, assuming that a sufficient number of males is present to mate with all available females, which is a common approach in demographic analyses (Caswell 2001).

Individual fitness  $W$  is a stochastic variable dependent on  $\mathbf{z}$ , including both demographic and environmental stochasticity (Engen and Sæther 2014) as well as population size and other aspects of the environment (Sæther and Engen 2015). The expected fitness of an individual with phenotype  $\mathbf{z}$  at population size  $N$  in an environment defined by the vector  $\boldsymbol{\varepsilon}$  can be written as  $E(W|\mathbf{z}, N, \boldsymbol{\varepsilon}) = e^{M(\mathbf{z}, N, \boldsymbol{\varepsilon})}$ , which is the expectation  $E$  with respect to demographic noise in  $I$  and  $B$ . In a large population, the mean fitness  $\bar{W}(\mathbf{z}, N, \boldsymbol{\varepsilon})$  equals this theoretical expectation, and the function  $M(\mathbf{z}, N, \boldsymbol{\varepsilon}) = \ln \bar{W}(\mathbf{z}, N, \boldsymbol{\varepsilon})$  is the Malthusian parameter of a hypothetical population of individuals with phenotype  $\bar{\mathbf{z}}$  at population size  $N$  in a constant environment  $\boldsymbol{\varepsilon}$ . Thus, the relevant measure of fitness in a stochastic environment with expectation denoted  $E_c$  is the mean of the fluctuating Malthusian fitness defined as  $m(\mathbf{z}, N) = E_c M(\mathbf{z}, N, \boldsymbol{\varepsilon}) = E_c \ln \bar{W}(\mathbf{z}, N, \boldsymbol{\varepsilon})$ , which in the absence of density regulation is equal to the long-run growth rate of

the population (Sæther and Engen 2015). The environmental variance, which is the variance of the Malthusian fitness, is in general a function of  $\mathbf{z}$  and  $N$ . If we approximate this by its mean value through time—say,  $\sigma_c^2$ —then the first-order approximation of the mean Malthusian fitness is

$$m(\mathbf{z}, N) \approx r(\mathbf{z}, N) - \frac{1}{2} \sigma_c^2, \quad (1)$$

where  $r(\mathbf{z}, N) = \ln E\bar{W}(\mathbf{z}, N, \boldsymbol{\varepsilon})$ . This ignores temporal autocorrelations in the environmental noise, which in general are small, even in long-lived species (Morris et al. 2011; Engen et al. 2013b). Assuming that selection is weak, so that population size  $N$  changes much faster than the mean phenotype  $\bar{\mathbf{z}}$ , and that  $r(\mathbf{z}, N) = r_0(\mathbf{z}) - \gamma(\mathbf{z})N$ , the infinitesimal mean and variance of the diffusion approximation for  $\ln N$  for a given  $\bar{\mathbf{z}}$  are the mean Malthusian fitness  $\bar{m}(\bar{\mathbf{z}}, N) = \bar{s}(\bar{\mathbf{z}}) - \bar{\gamma}(\bar{\mathbf{z}})N$  and the environmental variance  $\sigma_c^2$ , respectively, where  $\bar{s}(\bar{\mathbf{z}}) = \bar{r}_0(\bar{\mathbf{z}}) - \sigma_c^2/2$  is the long-run growth rate for densities close to zero and  $\bar{\gamma}(\bar{\mathbf{z}})$  is the average strength of density regulation acting on the population growth rate. Then the selection differential, according to Lande and Arnold (1983) and Lande et al. (2009), is  $\mathbf{P}\bar{\nabla}\bar{m}(\bar{\mathbf{z}}, N)$ , where  $\mathbf{P}$  is the phenotypic variance-covariance matrix.

Lande et al. (2009) and Engen et al. (2013a) showed that the expected evolution of the mean phenotype in density-regulated populations subject to a fluctuating environment always tends to increase the function

$$Q(\bar{\mathbf{z}}) = \frac{\bar{s}(\bar{\mathbf{z}})}{\bar{\gamma}(\bar{\mathbf{z}})} = \left[ 1 - \frac{\sigma_c^2}{2\bar{r}(\bar{\mathbf{z}})} \right] g(K(\bar{\mathbf{z}})). \quad (2)$$

Here,  $\bar{s}(\bar{\mathbf{z}}) = \bar{r}(\bar{\mathbf{z}}) - (1/2)\sigma_c^2$  is the long-run growth rate of the population in the absence of density regulation, where  $\bar{r}(\bar{\mathbf{z}})$ , the mean of  $r(\mathbf{z})$  in the population, is the deterministic growth rate of the mean phenotype  $\bar{\mathbf{z}}$  in the average environment,  $K(\bar{\mathbf{z}})$  is the carrying capacity for a given mean phenotype  $\bar{\mathbf{z}}$ , and  $\sigma_c^2$  is the environmental variance, assumed to be independent of phenotype. The expected evolution of the mean phenotype will thus be directed toward the value  $\mathbf{z}^*$  maximizing  $Q(\bar{\mathbf{z}})$ , but it will be moved away from this value by stochastic fluctuations in the environment (Engen et al. 2013a).

We modeled selection on four reproductive traits (egg-laying date, clutch size, number of fledglings, and mean tarsus length of the brood) of the collared flycatcher separately as well as for pairs of traits. All of these traits are associated with variation in individual fitness  $W$  in the collared flycatcher (Gustafsson 1986; Brommer et al. 2004,

**Figure 1:** Annual variation in the number of breeding pairs of collared flycatcher (*a*) and in the mean values of egg-laying date (*b*;  $n = 7,937$ ), clutch size (*c*;  $n = 7,990$ ), number of fledglings (*d*;  $n = 7,406$ ), and mean fledgling tarsus length (*e*;  $n = 4,551$ ). Bars show standard deviations, and numbers indicate annual sample sizes.

2007). Many studies have even used variation in these traits as indices for individual differences in fitness (Wilson and Nussey 2010). Here, we use an alternative measure of fitness  $m(z, N)$ , which relates directly to ecological and evolutionary dynamics (Sæther and Engen 2015). In the first step, following Engen et al. (2013a) and Sæther et al. (2016b), we modeled the density-dependent dynamics of the deterministic growth rates  $r(z, N) = r_0(z) - \gamma(z)N$  for individuals considering each trait separately, so that  $z = z$ . For the deterministic growth rate at small population sizes, we used the second-degree approximation  $r_0(z) = \beta_1 + \beta_2z + \beta_3z^2$ , allowing for variation in the deterministic growth rate with variation in trait  $z$ . If  $\beta_3 < 0$ , this indicates that the deterministic growth rate has a maximum. The strength of density regulation was modeled as  $\gamma(z) = e^{a+bz}$ , ensuring strictly negative density dependence, where  $b$  expresses how  $\gamma(z)$  changes with trait  $z$ . If  $b \neq 0$ , the effects of fluctuations in population size are phenotype specific, indicating the presence of  $r$ - and  $K$ -selection.

In the second step, in accordance with the model for a single trait, we extended the model of the dynamics of the deterministic growth rate to include a function of a pair of traits  $z = (z_1, z_2)$  as  $r(z_1, z_2, N) = r_0(z_1, z_2) - \gamma(z_1, z_2)N$ , where  $r_0(z_1, z_2)$  is the deterministic growth rate at small population sizes and  $\gamma(z_1, z_2)$  is the strength of density regulation. We also included stabilizing selection as a second-degree approximation and correlated selection among traits at low densities as  $r_0(z_1, z_2) = \beta_1 + \beta_2z_1 + \beta_3z_1^2 + \beta_4z_2 + \beta_5z_2^2 + \beta_6z_1z_2$ . We described how the strength of density regulation depends on  $z_1$  and  $z_2$  by the function  $\gamma(z_1, z_2) = e^{a+b_1z_1+b_2z_2}$  ensuring that  $\gamma(z_1, z_2) > 0$ , where  $b_1$  and  $b_2$  express how  $\gamma(z_1, z_2)$  changes with increasing values of  $z_1$  and  $z_2$ . If  $b_1 \neq 0$  or  $b_2 \neq 0$ , the effects of fluctuations in population size are phenotype specific, indicating the presence of  $r$ - and  $K$ -selection. Thus, this approach enabled us to account for density-dependent variation in fitness, which provides an important extension of Lande and Arnold (1983), who assumed density-independent population growth only.

#### Estimation Procedures

We assumed that the dependent variable  $2W = 2I + B$ , taking integer values  $0, 1, 2, \dots$  follows a Poisson distribution with log link function, so that

$$\ln E(2W|z, N, \varepsilon) = \beta'_1 + \beta_2z + \beta_3z^2 - Ne^{a+bz} + \varepsilon \quad (3a)$$

for the univariate model and

$$\begin{aligned} \ln E(2W|z_1, z_2, N, \varepsilon) = & \beta'_1 + \beta_2z_1 + \beta_3z_1^2 \\ & + \beta_4z_2 + \beta_5z_2^2 + \beta_6z_1z_2 \\ & - Ne^{a+b_1z_1+b_2z_2} + \varepsilon \end{aligned} \quad (3b)$$

for the bivariate model, where  $\beta'_1 = \beta_1 + \ln 2 - (1/2)\sigma_\varepsilon^2$  and environmental variance  $\sigma_\varepsilon^2$  is the temporal variation in the random effects  $\varepsilon$ . For a description of estimation procedures, see the supplemental PDF (available online).

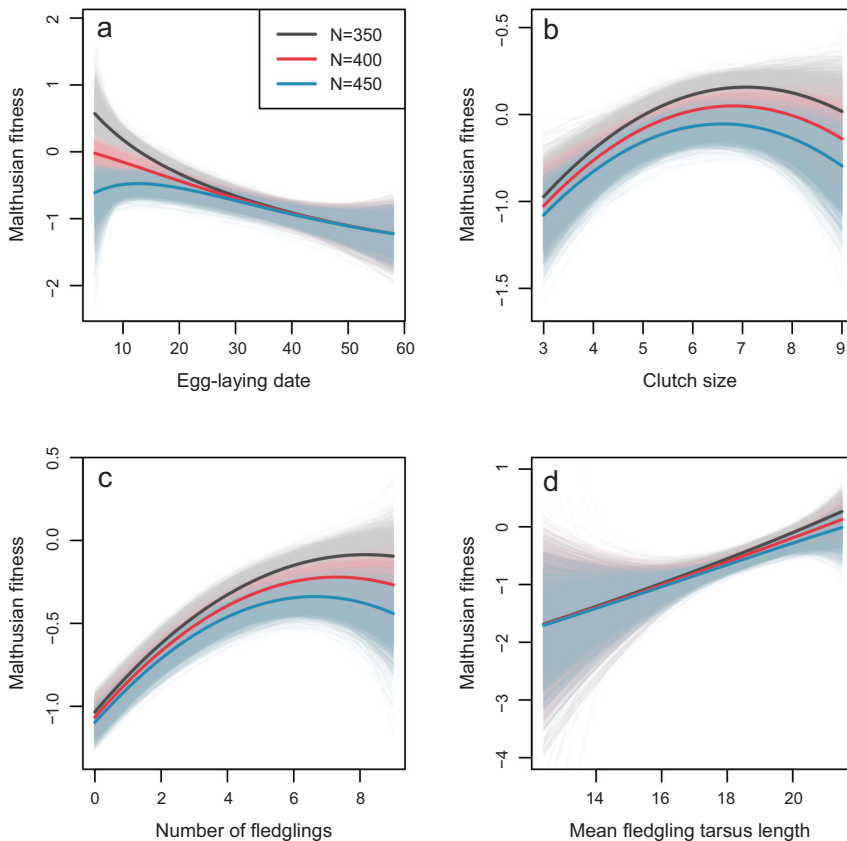
To determine whether density-dependent selection acted through the survival component of  $W$ , we estimated the phenotype-specific effects of  $N$  on juvenile and adult survival. Juvenile survival was measured as the probability that a fledgling was recorded in a later breeding season, and adult survival was measured as the probability that a breeding female was recorded in a subsequent breeding season. In collared flycatchers the probability of breeding dispersal is independent of whether the female was a successful breeder (Pärt and Gustafsson 1989). Similarly, natal dispersal in this population is not associated with population density and is independent of the laying date and the size of the clutch from which they hatched (Pärt 1990).

In accordance with most capture-mark-recapture data, it was not possible to separate between mortality and emigration. Emigrants were implicitly treated as dead individuals, and estimates of adult survival and number of recruits (which includes first-year survival) are biased low. This means that we consider the contribution of individuals and alleles only to the local population. Accordingly, estimates of  $\bar{s}(\bar{z})$  will be too low (and even negative) if immigration is not accounted for. In many populations of small temperate passerines, the proportion of immigrants is quite high (Grøtan et al. 2009; Gamelon et al. 2017). To obtain a stationary process for the population fluctuations, we therefore included an immigration component in the expression for  $Q(\bar{z})$  (see the supplemental PDF for details). Uncertainty in  $z^*$  values was based on all posterior samples (see the supplemental PDF for details). All analyses were performed in R version 3.5.1 (R Core Team 2019).

## Results

### *The Pattern of Selection*

The Malthusian fitness decreased with increasing population size for all reproductive traits examined (fig. 2; table 1). The slopes of the relationships between the Malthusian fitness indicated that fitness increased with early laying of the first egg ( $\beta_2 < 0$ ) and with increasing clutch size, number of fledglings, and mean fledgling tarsus length. In addition, significant stabilizing selection ( $\beta_3 < 0$ ) also occurred in two traits (clutch size and number of fledglings), indicating that an intermediate value of the phenotype exists that maximizes the Malthusian fitness (table 1; fig. 2b, 2c). However, uncertainties in the estimates were large.



**Figure 2:** Malthusian fitness for mean values of egg-laying date (a), clutch size (b), number of fledglings (c), and mean fledgling tarsus length (d) at different population sizes  $N$  for 4,500 posterior samples. Thick lines show posterior means.

At all population levels, there was significant directional selection for early egg laying (fig. 2a) and large mean fledgling tarsus lengths (fig. 2d). The strength of directional selection on egg-laying date was dependent on population size, being stronger at smaller population sizes.

The presence of  $r$ - and  $K$ -selection requires that phenotypes with high fitness at low densities have smaller fitness close to the carrying capacity than those with inferior fitness at low population densities (Sæther et al. 2016b). Such a statistically significant interaction was present for number of fledglings. This implies that a larger reduction in Malthusian fitness with increasing  $N$  occurred among those females

producing the largest number of fledglings at low population densities (fig. 2c,  $b$  significantly larger than zero; table 1). Similarly, increased population size had a stronger fitness effect on early-laying compared with late-laying females, but there was still directional selection for early laying of eggs at every level of population size (table 1). In addition, no significant ( $P > .1$ ) interaction with  $N$  was present for survival of either juveniles or adult females. Thus, density-dependent selection in this population of collared flycatcher operates through the breeding component of the Malthusian fitness (i.e., the reproductive output) because there were no phenotypic-specific effects of  $N$  on the survival components of  $W$ .

**Table 1:** Analyses of variation in fitness  $W_z$  of breeding females of collared flycatcher as a function of different phenotypic characters  $z$  and population size  $N$

Parameter	Egg-laying date	Clutch size	No. fledglings	Mean fledgling tarsus length
$\beta_1$	.205*** (.116 to .293)	.244*** (.192 to .296)	.281*** (.227 to .334)	.362*** (.302 to .420)
$\beta_2$	-.198*** (-.228 to -.168)	.047*** (.026 to .068)	.278*** (.254 to .303)	.150*** (.119 to .181)
$\beta_3$	.011 (-.005 to .028)	-.024*** (-.037 to -.012)	-.089*** (-.116 to -.062)	.001 (-.013 to .015)
$a$	-2.430*** (-4.170 to -1.703)	-2.254*** (-2.926 to -1.852)	-2.634*** (-3.626 to -2.118)	-2.380*** (-3.336 to -1.890)
$b$	-.689** (-1.574 to -.327)	.126 (-.057 to .363)	.392* (.091 to .982)	.175 (-.125 to .577)
$\sigma^2$	.206*** (.153 to .286)	.114*** (.083 to .161)	.103*** (.073 to .147)	.126*** (.088 to .181)

Note: The effects of  $z$  are approximated by a second-order polynomial  $\beta_1 + \beta_2z + \beta_3z^2$ , representing stabilizing selection if  $\beta_3 < 0$ . The strength of density dependence on  $z$  is assumed to be linear, so the mixed model takes the form  $\ln E(2W) = \beta_1 + \beta_2z + \beta_3z^2 - Ne^{r+z} + \epsilon$ , where  $\epsilon$  is the residual variation, year is entered as a random effect to account for environmental stochasticity ( $\sigma^2$ ), and  $a$  and  $b$  express how  $\gamma(z)$  changes with increasing value of  $z$ . If  $a \neq 0$  and  $b \neq 0$ , the effects of fluctuations in population size are phenotype specific, indicating the presence of  $r$ - and  $K$ -selection. Shown in parentheses are the 95% confidence intervals of the parameter estimates. Traits were standardized (mean = 0, SD = 1) prior to estimating parameters.

\*  $P < .05$ .

\*\*  $P < .01$ .

\*\*\*  $P < .001$ .

Our next step was to examine how density-dependent selection depended on the interaction between different traits (table 2). There was no significant correlated selection ( $\beta_6$  not significantly different from zero) on any but one pair of traits (i.e., egg-laying date and clutch size). All reproductive traits were subject to density-dependent selection, as in the univariate case ( $a < 0$ ). The interaction between phenotype and population density was significant for egg-laying date both with clutch size and number of fledglings (table 2). Egg-laying date was still subject to directional selection, as in the one-dimensional case. Finally, no directional or stabilizing selection on clutch size was present when including correlated selection on one of the other three traits (table 2). This suggests that selection acting on the clutch size of collared flycatchers is strongly affected by indirect selection on other reproductive traits.

### The Adaptive Topography

These relationships were used to calculate the adaptive topography  $Q(\bar{z})$  in terms of expected population size as function of the mean of each of the reproductive traits (eq. [2]). The stochastic population growth rate  $\bar{s}(\bar{z})$  increased with the mean of clutch size, number of fledglings, and fledgling tarsus length, whereas it decreased with mean egg-laying date (fig. 3). Similar trends were present for the relationship between the strength of density dependence and mean phenotype  $\bar{z}$  (fig. 3): the effects of population size fluctuations on the Malthusian fitness

were stronger with early egg laying, large clutch size and number of fledglings, and long fledgling tarsi. Consequently, for egg-laying date, clutch size, and number of fledglings, an intermediate mean value that maximized fitness under the influence of  $r$ - and  $K$ -selection was present (figs. 3, S1a–S1c; figs. S1–S3 are available online). For fledgling tarsus length, the value that maximized fitness was estimated at the upper limit of possible values, indicating directional selection (fig. S1d). Comparisons of these maxima ( $z^*$ ) with the mean value of the trait in the population ( $\bar{z}$ ; fig. 3) indicate univariate selection for an advance of egg laying ( $\bar{z} = 23.34$  [mean]  $\pm$  7.10 [SD] vs.  $z^* = 13.11$  [mode];  $-1.12$  to  $18.62$  [95% credible interval]), increased number of fledglings ( $\bar{z} = 3.69 \pm 2.39$  vs.  $z^* = 6.47$ ;  $5.69$  to  $7.92$ ), and larger fledglings (mean fledgling tarsus length  $\bar{z} = 19.20 \pm 0.71$  vs.  $z^* = 22.2$ ;  $20.2$  to  $22.21$ ), whereas the mean value of clutch size ( $\bar{z} = 6.10 \pm 0.79$  vs.  $z^* = 6.76$ ;  $6.43$  to  $7.76$ ) was close to the value maximizing  $Q(\bar{z})$ .

Analyses of the two-dimensional fitness adaptive topography revealed that for three of the six pairwise combinations of traits, the expected Malthusian fitness was maximized at intermediate values (fig. 4). For example, laying 7.09 eggs on day 8 was the combination of mean phenotypes maximizing  $Q(\bar{z}_1, \bar{z}_2)$ . This shows that correlated density-dependent selection can induce stabilizing selection even on reproductive traits subject to univariate directional selection (fig. 2a). Finally, it is notable that including correlated selection had only a minor

**Table 2:** Analyses of variation in individual fitness  $W_z$  of breeding females of collared flycatcher as a function of two different phenotypic characters ( $z_1$  and  $z_2$ ) and population size  $N$

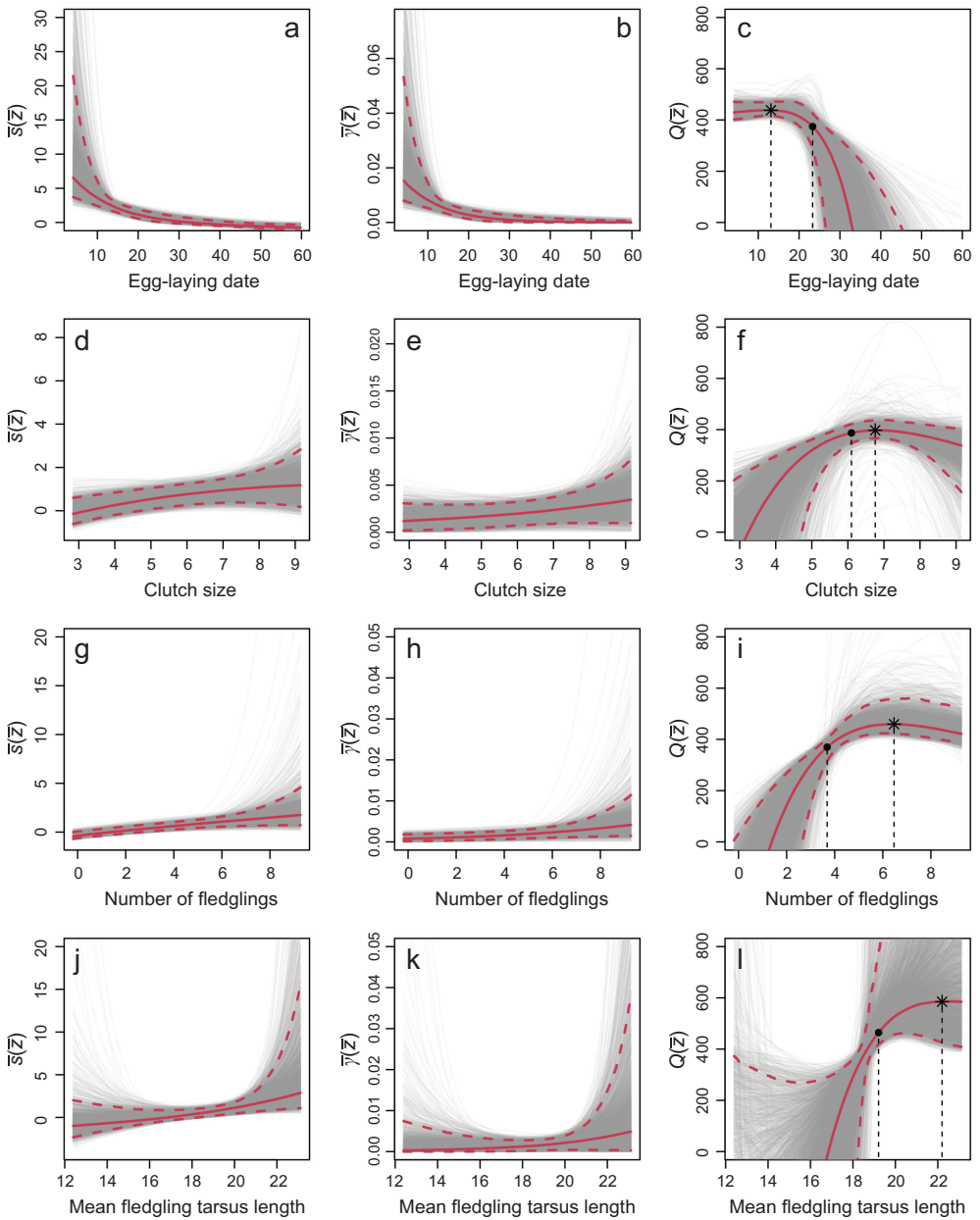
Parameter	Egg-laying date and clutch size	Egg-laying date and no. fledglings	Egg-laying date and mean fledgling tarsus length	Clutch size and proportion fledged	Clutch size and mean fledgling tarsus length	No. fledglings and mean fledgling tarsus length
$\beta_1$	.223*** (.132 to .312)	.289*** (.218 to .358)	.357*** (.270 to .440)	.290*** (.233 to .345)	.372*** (.310 to .432)	.366*** (.303 to .428)
$\beta_2$	-.198*** (-.230 to -.166)	-.112*** (-.144 to -.080)	-.133*** (-.173 to -.093)	.001 (-.023 to .025)	.031 (.005 to .056)	.101*** (.071 to .130)
$\beta_3$	.003 (-.016 to .022)	-.001 (-.018 to .016)	.003 (-.018 to .024)	-.010 (-.025 to .004)	-.010 (-.025 to .004)	-.010 (-.032 to .011)
$\beta_4$	.001 (-.022 to .024)	.257*** (.231 to .282)	.134*** (.102 to .165)	.277*** (.250 to .305)	.155*** (.122 to .183)	.112*** (.080 to .144)
$\beta_5$	-.021** (-.036 to -.007)	-.098*** (-.125 to -.071)	.001 (-.013 to .015)	-.086*** (-.117 to -.055)	.002 (-.013 to .015)	.010 (-.005 to .024)
$\beta_6$	-.030* (-.055 to -.005)	-.015 (-.040 to .011)	.003 (-.027 to .033)	-.004 (-.032 to .024)	-.001 (-.028 to .026)	-.012 (-.040 to .017)
$a$	-2.421*** (-4.176 to -1.692)	-2.552*** (-3.747 to -1.941)	-3.162** (-7.279 to -1.909)	-2.613*** (-3.624 to -2.105)	-2.353*** (-3.242 to -1.875)	-2.406*** (-4.037 to -1.894)
$b_1$	-.676* (-1.576 to -.306)	-.638** (-1.283 to -.292)	-1.062 (-3.120 to -.309)	.040 (-.286 to .342)	.110 (-.139 to .410)	.087 (-.237 to .898)
$b_2$	.028 (-.165 to .219)	.144 (-.053 to .412)	.047 (-1.67 to .262)	.358 (.040 to 1.065)	.166 (-.133 to .537)	.155 (-.208 to .796)
$\sigma^2$	.207*** (.154 to .289)	.144*** (.103 to .207)	.187*** (.133 to .267)	.102*** (.073 to .147)	.125*** (.088 to .181)	.126*** (.082 to .182)

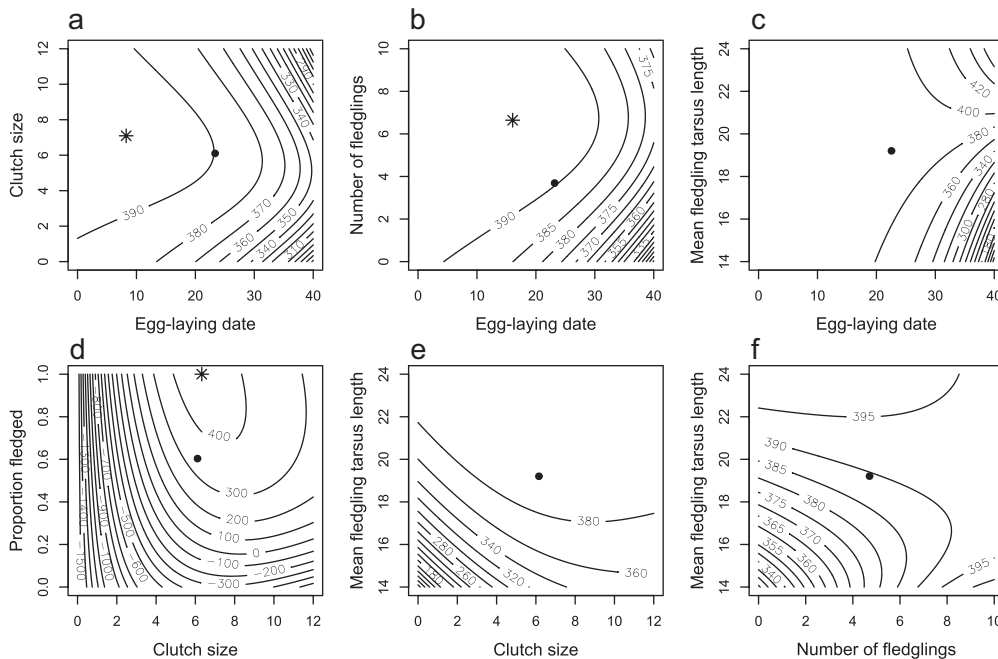
Note: In addition to stabilizing and density selection on each trait, we also include the effects of interaction between themselves, the interaction between the characters and  $N$ , and the three-way interaction including the characters and  $N$ . The effects of  $z$  are approximated by a second-order polynomial  $\beta_1 + \beta_2 z_1 + \beta_3 z_2 + \beta_4 z_1^2 + \beta_5 z_2^2$  representing stabilizing selection if  $\beta_i < 0$  or  $\beta_i > 0$ . Correlated selection on the two characters is estimated as  $\beta_6 z_1 z_2$ . The mixed model then takes the form  $\ln E(2W) = \beta_1 + \beta_2 z_1 + \beta_3 z_2 + \beta_4 z_1^2 + \beta_5 z_2^2 + \beta_6 z_1 z_2 - N e^{\beta_7 z_1 + \beta_8 z_2} + \varepsilon$ , where  $\varepsilon$  is the residual variation, year is entered as a random effect to account for environmental stochasticity ( $\sigma^2$ ), and  $a$ ,  $b_1$ , and  $b_2$  express how  $\gamma(z)$  changes with increasing values of  $z_1$  and  $z_2$ . If  $a \neq 0$  and  $b_1 \neq 0$  or  $b_2 \neq 0$ , the effects of fluctuations in population size are phenotype specific, indicating the presence of  $r$ - and  $K$ -selection. Shown in parentheses are the 95% confidence intervals of the parameter estimates. Traits were standardized (mean = 0, SD = 1) prior to estimating parameters.

\*  $P < .05$ .

\*\*  $P < .01$ .

\*\*\*  $P < .001$ .





**Figure 4:** Bivariate adaptive topography for mean value pairs of reproductive traits  $(z_1, z_2)$  described by expected population size  $Q(\bar{z}_1, \bar{z}_2)$  as evolutionary maximum criteria. Lines show combinations of traits with equal fitness, with values indicated by the small numbers. Stars show combinations of mean values of the phenotypic traits maximizing  $Q(\bar{z}_1, \bar{z}_2)$  (i.e.,  $z_1^*$  for the trait on the X-axis and  $z_2^*$  for the trait on the Y-axis), whereas circles show the mean value of the pairs of the reproductive traits in the population. In the analyses involving clutch and brood size, the number of fledglings was constrained to be equal to or less than the number of eggs. For c, e, and f, estimates  $z_1^*$  and  $z_2^*$  were outside the data range (i.e., for c,  $z_1^* = 4.52 \times 10^3$  and  $z_2^* = 108$ ; for e,  $z_1^* = 2.69$  and  $z_2^* = 25.05$ ; for f,  $z_1^* = 1.15 \times 10^4$  and  $z_2^* = -5.98 \times 10^3$ ).

impact on the strong directional selection (fig. 2d) for increased mean nestling tarsus length.

### Discussion

Our results revealed that density-dependent selection in collared flycatchers acts on egg-laying date and number of fledglings (fig. 2; table 1). This generates an adaptive topography influenced by changing population size; phenotypes favored at low densities were different from those with higher fitness at population sizes close to carrying

capacity  $K$  (figs. 2, 3; table 1). In addition, fluctuations in population size induced correlated selection among different reproductive traits (fig. 4; table 2). Consequently, intermediate phenotypes are often those that maximize the Malthusian fitness (fig. 4), suggesting that  $r$ - and  $K$ -selection may affect the evolution of reproductive strategies of small temperate passerines such as the collared flycatcher.

These analyses are based on several simplifying assumptions. First, we exclude age-specific effects on Malthusian fitness, although age has been found to be related to variation in reproduction and survival in the collared

**Figure 3:** Components of the adaptive topography due to the long-run population growth rate  $\bar{s}(\bar{z})$  and the strength of density dependence  $\bar{\gamma}(\bar{z})$  using expected population size  $Q(\bar{z})$  as evolutionary maximum criteria for single reproductive traits  $z$ , including egg-laying date (a-c), clutch size (d-f), number of fledglings (g-i), and mean fledgling tarsus length (j-l) for 4,500 posterior samples. Solid red lines show posterior medians, and dashed red lines show 95% credible intervals. Stars show the posterior mode of  $z^*$ —that is, the phenotype value maximizing  $Q(\bar{z})$ —whereas circles show the mean value of the reproductive traits in the population.



flycatcher (Gustafsson and Pärt 1990) as well as in small passerines in general (Sæther 1990; Forslund and Pärt 1995). Second, we assume that the distribution of  $2W$  follows a Poisson distribution. A common problem encountered in life-history studies is that such data can show both overdispersion and underdispersion (Lynch et al. 2014). In the present study, the mean ratio of the variance to the mean in the annual distributions of  $2W$  is 1.282, indicating only a slight overdispersion relative to the Poisson distribution (fig. S2). This facilitates analyses of selection (eq. [3]) by quite standard statistical models in which the parameters can be interpreted on the basis of a specified theoretical framework (Morrissey and Sakrejsa 2013). Third, we assume that the environment shows stationary fluctuations around a constant mean value. However, this ignores the effects of trends in the environment, which has been found to affect the strength of phenotypic and genotypic selection in this species (Evans and Gustafsson 2017). Fourth, fluctuations in the environment are assumed to affect all phenotypes similarly, so selection is determined only by fluctuations in  $N$  (Engen et al. 2013a). Fifth, no density-dependent phenotypic plasticity is included, which may affect estimates of the response to selection. Despite these simplifying assumptions, the number of parameters in the model still becomes large, especially in those analyses of correlated selection (table 2).

Our analyses revealed directional selection on all reproductive traits examined in the present study (tables 1, 2). Furthermore, our univariate analyses showed that stabilizing selection acted on clutch size and number of fledglings, which previously has been found in this population (Sheldon et al. 2003) as well as in other small passerines, such as the great tit *Parus major* (Boyce and Perrins 1987; Liou et al. 1993; Both et al. 2000; Pettifor et al. 2001) and the blue tit *Cyanistes caeruleus* (Svensson 1997). This can be caused by a larger proportion of pairs being forced to occupy suboptimal habitats at high population densities (Sutherland 1996; Both and Visser 2003), which is a pattern frequently recorded in small passerine species (Doncaster and Gustafsson 1999; Both and Visser 2003; Forsman et al. 2008). Accordingly, the proportion of nests that fail to produce any fledglings in this population increases with  $N$  (slope = 0.0011, SE = 0.0003,  $P = .0022$ ,  $n = 25$ ; fig. S3a), whereas the mean number fledglings produced per successful ( $\geq 1$  fledgling) nest was independent of  $N$  (slope = 0.0004, SE = 0.0012,  $P = .977$ ,  $n = 25$ ; fig. S3b). Other studies of small passerines have also revealed that complete losses of clutches or broods are an important determinant of individual differences in reproductive success (see Perrins 1979; Santema and Kempenaers 2018). However, the density-dependent increase in the proportion of unsuccessful nests may also be influenced by higher reproductive costs for the fe-

males (Gustafsson and Sutherland 1988; Schluter and Gustafsson 1993; Cichon et al. 1998; Doligez et al. 2002; Sendecka et al. 2007) at high population densities, resulting in more females abandoning their brood.

The strength of selection was strongly affected by fluctuations in population size (fig. 2; tables 1, 2). This implies that variation in population size is an important selective agent in collared flycatchers, as in other passerines (Both 1998; Both et al. 2000; Sæther et al. 2016b), affecting the evolution of the reproductive strategy of this species. At large population sizes, a delay in the timing of egg laying and a smaller clutch size were favored, which were associated by selection for a smaller number of fledglings with small tarsi (tables 1, 2). Accordingly, in collared flycatchers the timing of reproduction affects variation in several components of individual fitness (Wiggins et al. 1994b; Brommer et al. 2005; Evans and Gustafsson 2017). The timing of egg laying is, in turn, dependent on the weather during spring, being early in warm springs (Brommer et al. 2008; Evans and Gustafsson 2017).

As in many other small temperate passerines (Reed et al. 2013a, 2013b), the timing of egg laying covaries with several demographic traits in this population (Gustafsson 1986). Our analyses revealed that the Malthusian fitness decreases with a delay in the timing of egg laying especially at small densities, whereas the density-dependent fitness effects of variation in egg-laying date mainly occurs early in the season (fig. 2a). At large population sizes, variation in fitness is much less influenced by the timing of egg laying. An interaction between spring temperature and density dependence has also previously been assumed to affect the demography of small passerines (Reed et al. 2015). This indicates that fluctuating selection caused by variation in the environment—for example, due to climate fluctuations (Evans and Gustafsson 2017)—has stronger effects at smaller population sizes than at population densities closer to carrying capacity  $K$ . The larger variation in the mean Malthusian fitness at large clutch sizes and number of fledglings (fig. 2b, 2c) also indicates that environmental stochasticity affects larger phenotypes the most, which is expected according to a bad-year effect caused by temporal variation in food availability (Boyce and Perrins 1987). In addition, there was directional selection for fledglings with long tarsi (fig. 2d). This is in accordance with the results of Björklund and Gustafsson (2013, 2017), who showed consistent directional selection on fledgling body size in this population. This was closely related to a lower probability of survival of small juveniles (Linden et al. 1992).

In this study, we have calculated the adaptive topography, which is equivalent to the adaptive landscape (Arnold et al. 2008), for different reproductive traits (fig. 3) and pairs of traits (fig. 4) based on expected population



size as the quantity to be maximized by evolution, following Lande et al. (2009) and Engen et al. (2013a). This describes expected phenotypic selection over a long period of time (Lande 2007; Engen et al. 2013a; Kopp and Matuszewski 2014) as a function of population size  $N$ , which has been found to be the major driver of a genotype-environment interaction on selection of several phenotypic traits in the Soay sheep *Ovis aries* (Hayward et al. 2018). Applying such an approach is justified because density dependence has previously been found to affect the dynamics of this population (Sæther et al. 2016a). This operates through a density-dependent decrease in the number of fledglings produced (slope =  $-0.0049$ , SE =  $0.0021$ ,  $P = .028$ ; fig. S3b), which caused a decrease in the recruitment rate with increasing population size (slope =  $-0.0016$ , SE =  $0.0005$ ,  $P = .002$ ; fig. S3c). Annual variation in the date of egg laying (slope =  $-0.0263$ , SE =  $0.0200$ ,  $P = .201$ ; fig. S3d) and clutch size (slope =  $0.0010$ , SE =  $0.0007$ ,  $P = .136$ ; fig. S3e) were not associated with fluctuations in  $N$ . Similarly, mean nestling tarsus length was not significantly affected by  $N$  (slope =  $0.0000$ , SE =  $0.0016$ ,  $P = .978$ ; fig. S3f), but the mean tarsus length at larger brood sizes was more affected by fluctuations in population size than in smaller broods (interaction between number of fledglings and  $N = -0.0007$ , SE =  $0.0003$ ,  $P = .0038$ ; fig. S3f), which may affect the subsequent survival of fledglings in the largest broods (Linden et al. 1992). In contrast, our analyses revealed no effects of fluctuations in population size on either juvenile or adult survival. This suggests that  $r$ - and  $K$ -selection in this population mainly operates through an effect on the recruitment rate, influenced by a combination of larger losses of clutches and fledging of smaller nestlings from large-sized broods at high population sizes. Because the critical season for population regulation in small passerines such as the collared flycatcher is survival, especially during the nonbreeding season (Sæther et al. 2004, 2016a), this indicates that the vital rates with the highest contribution to this species' population dynamics are different from those most strongly affecting the phenotypic evolution.

Our study reveals a trade-off between the components of Malthusian fitness due to high stochastic population growth rate  $\bar{s}(\bar{z})$  at low densities and the effects on the mean phenotype of changes in population size  $\bar{\gamma}(\bar{z})$  (fig. 3), causing ongoing  $r$ - and  $K$ -selection in this population. This forms an adaptive peak, often at an intermediate value of  $z$  at which the fitness function achieves a maximum value (figs. 2c, 3, S1). Those females producing a large number of fledglings with long tarsi early in the season have lower fitness at high population sizes than those delaying egg laying (fig. 2). Consequently, the egg-laying date maximizing fitness expressed by  $Q(\bar{z})$  is later

at large population sizes than at low densities (figs. 2–4). Similarly, smaller broods are also favored closer to the carrying capacity than at small population sizes (fig. 2). This corresponds to a previous study showing  $r$ - and  $K$ -selection acting on the total number of eggs produced during a breeding season in great tits (Sæther et al. 2016b).

One important challenge in evolutionary biology is to identify characters covarying with fitness, thereby affecting the change in mean values from one generation to the next (Govaert et al. 2019). However, predicting such changes in fitness-related traits has been difficult (e.g., Merilä et al. 2001), and indirect selection has been proposed as the major sources for obtaining reliable estimates of selection acting on single characters (Morrissey et al. 2010). In the present analyses, bivariate fitness sets (fig. 4) produced maximum values that were only to a small degree located closer to the recorded mean values of the population than the value maximizing the  $Q(\bar{z})$  function computed for single traits alone (figs. 3, S1). Thus, the deviation of the recorded mean values from this maximum value indicates selection and potential for evolutionary changes in this population on timing of egg laying, number of fledglings, and mean nestling tarsus length. Such evolutionary responses will also be facilitated by the presence of heritabilities significantly larger than zero that have been recorded in three of the traits (Gustafsson 1986; Sheldon et al. 2003; Björklund et al. 2013; Husby et al. 2013) as well as additive genetic covariances among them (Sheldon et al. 2003). In particular, there should be strong directional selection for producing a large number of large fledglings (fig. 4). Such an evolutionary response may, however, be constrained by the timing of egg laying through the negative additive genetic covariance with clutch size (Sheldon et al. 2003). Furthermore, the timing of egg laying is also correlated with spring temperatures in collared flycatchers (Brommer et al. 2005) as well as in temperate small passerines in general (Both and Visser 2001; Visser et al. 2003; Both et al. 2004; Reed et al. 2013a), which will affect the response to density-dependent selection. Similarly, the large difference between the number of fledglings maximizing the  $Q(\bar{z})$  function and the recorded mean value in the population (figs. 3, 4) also indicates strong selection to reduce nestling loss. The clutch size maximizing the  $Q(\bar{z})$  function is also smaller than the corresponding value of the number of fledglings (fig. 2), which may indicate a constraint on the number of eggs produced, for example, by a cost of incubation of large clutches (e.g., Wiggins et al. 1994a).

In analyses of phenotypic selection in natural populations, several measures of fitness have been applied (Brommer 2000). Here, we have used the number of new individuals produced to the next or later breeding season as a proxy, which ignores complicating effects of age structure (Engen et al. 2014; Lande et al. 2017). This includes

offspring survival into the estimate of the mother's fitness (for an alternative approach, see Reid et al. 2019). One advantage of this approach is that this measure can be used to calculate the adaptive topography based on the criteria of maximizing the expected population size. This enables us to identify whether there exists some intermediate mean phenotype that has the highest mean fitness. Another advantage is that this maximization criterion includes several other measures of fitness. For instance, in a population with overlapping generations but no age structure, Engen and Sæther (2017b) showed, in a model in which birth and death rates depend on density through the same function, that this implies evolution maximizing a product of two functions. The first factor is an increasing function of  $r$ , and the other is an increasing function of lifetime reproductive success (LRS). This means that the continuum between  $r$ - and  $K$ -selection is equivalent to a continuum between selection for increased deterministic growth rate  $r_0$  and LRS, both measured at population sizes close to zero. If the population is subject to  $r$ -selection, some life-history traits may then have a larger contribution to  $Q(\bar{z})$  than under  $K$ -selection, under which other traits may be favored. In the present study, the population fluctuates around such high numbers that meaningful extrapolation down to very small population sizes is impossible, so we cannot reliably estimate  $r_0$  and LRS at small population sizes. However, within the range of recorded population sizes, the mean phenotypes maximizing  $r$ , LRS, and  $Q(\bar{z})$  are quite similar except that  $Q(\bar{z})$  is maximized by a larger number of fledglings than the other two measures of fitness.

Our analyses revealed that density-dependent selection influenced variation in several reproductive traits of collared flycatcher, resulting in adaptive topographies with distinct peaks in mean fitness (fig. 2). This is in contrast to previous multivariate analyses of phenotypic selection on morphological traits of adults of this species (Björklund and Gustafsson 2017), for which the fitness surfaces were relatively flat. Because of significant heritability in three of the traits (the exception is number of fledglings produced) examined in this study (Gustafsson 1986; Merilä and Sheldon 2000; Sheldon et al. 2003; Björklund et al. 2013),  $r$ - and  $K$ -selection is likely to result in phenotypic evolution toward an intermediate mean value (Engen et al. 2013a), where fluctuations caused by environmental stochasticity always tend to move the mean away from the value that maximizes the expected population size (Roughgarden 1971). Thus, fluctuations in population size may be an important selective agent affecting the evolution of reproductive strategies and constrain the selective responses to changes in the environment. This may operate by inducing trade-offs between life-history traits that maximize fitness at different population sizes.

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### Statement of Authorship

This study was conceived by B.-E.S. and S.E. Data were provided by L.G., who also provided information about relevant autoecological aspects of the biology of the species and discussed the outline of the analyses. Statistical models were developed by B.-E.S., S.E., V.G., and S.J.G.V. S.J.G.V. and V.G. wrote the R scripts and produced the figures and tables. All authors contributed to the interpretation of the results and the writing of the manuscript.

### Data and Code Availability

Data have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.prr4xgkxb>; Sæther et al. 2020).

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“Bird’s-eye view of the Terrace Cañons.” From the review of Powell’s *Exploration of the Colorado* (*The American Naturalist*, 1876, 10:102–105).

# Density-dependent adaptive topography in a small passerine bird, the collared flycatcher

Supplemental Material

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## Calculation of the immigration rate necessary for obtaining stationarity of the population fluctuations

Following Sæther et al. (2016b), the immigration rate to get a stationary distribution was

estimated as  $\hat{\mu} = -\ln \bar{W} + \frac{1}{2}\sigma_e^2$ , and  $\bar{W} = \left( \sum^T (2I + B) / 2 \right) / T$ , where  $T$  is the number of

years. The function  $Q(\bar{z}) = \bar{s}(\bar{z}) / \bar{\gamma}(\bar{z})$  can then be calculated using

$$\bar{s}(\bar{z}) = \beta_1 + \beta_2 \bar{z}_1 + \beta_3 (\bar{z}^2 + P) - \frac{\sigma_e^2}{2} + \mu \quad \text{and} \quad \bar{\gamma}(\bar{z}) = -e^{a+b\bar{z}},$$

where  $P$  is the phenotypic

variance. Correspondingly, for a pair of phenotypic traits the function

$Q(\bar{z}_1, \bar{z}_2) = \bar{s}(\bar{z}_1, \bar{z}_2) / \bar{\gamma}(\bar{z}_1, \bar{z}_2)$  becomes

$$\bar{s}(\bar{z}) = \beta_1 + \beta_2 \bar{z}_1 + \beta_3 (z_1^2 + P_1) + \beta_4 \bar{z}_2 + \beta_5 (\bar{z}_2^2 + P_2) + \beta_6 (\bar{z}_1 \bar{z}_2 + C_{12}) - \frac{\sigma_e^2}{2} + \mu,$$

where  $P_1$  and  $P_2$  are the variance of the two phenotypes,  $C_{12}$  is the phenotypic covariance

among the two traits, and  $\gamma(z_1, z_2) = -e^{a+b_1 z_1 + b_2 z_2}$ .

### Procedures for Estimation of Parameters

We use generalized linear mixed models (GLMM) to estimate the parameters in equations 3a and 3b of the main text. The estimation procedure was implemented in Template Model Builder (Kristensen et al. 2016). Traits were normalized (mean = 0, sd = 1), and confidence intervals were calculated by profile likelihoods and may in some cases be more accurate than  $p$ -values based on quadratic approximations (Bolker 2008, p. 196). Phenotypic variances and covariances were calculated among individuals within years and then averaged across years.

A proper assessment of uncertainty of predicted relationships between the traits and  $m(\bar{z})$ ,  $\bar{s}(\bar{z})$ ,  $\bar{\gamma}(\bar{z})$  and  $Q(\bar{z})$ , respectively (see equations 1 and 2 in the main text), requires



possible correlated parameter uncertainty to be accounted for. To obtain estimates of joint parameter uncertainty, we fitted the univariate models within the Bayesian framework as well. Using the no-U-turn sampler (NUTS) Markov chain Monte Carlo (MCMC) algorithm (Monnahan and Kristensen 2018), we ran three independent chains with different starting values for 30,000 iterations, with a burn-in of 15,000 iterations, and thinning every 10<sup>th</sup> observation, resulting in 4500 posterior samples (Tables S1-S4). Calculations of derived quantities (equations 1 and 2 in the main text) were performed using sets of parameters from each of the 4500 posterior samples, and thereby accounting for joint parameter uncertainty. We used the Brooks and Gelman diagnostic  $\hat{R}$  to assess chain convergence (Brooks and Gelman 1998) and the effective sample size and number of post-burn-in divergences to evaluate model precision and bias (Gelman et al. 2013; Betancourt 2017).

Uncertainty in  $z^*$  values was quantified by numerical optimization of each posterior sample, generating a distribution of  $z^*$  values, represented in the main text by the posterior mode and the 95% credible interval. The optimization interval included 1 standard deviation on either side of the observed phenotype values. For number of fledglings, the lower bound of the optimization interval was set to 0, as 1 standard deviation lower than the observed phenotype values resulted in negative values. All analyses were performed in R 3.5.1 (R Core Team 2019).

**Table S1** Analyses of variation in fitness  $W_z$  of breeding females of collared flycatcher as function of egg-laying date ( $z$ ) and population size  $N$ . The effects of  $z$  are approximated by a second-order polynomial  $\beta_1 + \beta_2 z + \beta_3 z^2$ , representing stabilizing selection if  $\beta_3 < 0$ . The strength of density dependence on  $z$  is assumed linear so the mixed model takes the form  $\ln E(2W) = \beta_1 + \beta_2 z + \beta_3 z^2 - Ne^{a+bz} + \varepsilon$ , where  $\varepsilon$  is the residual variation, year is entered as a random effect to account for environmental stochasticity ( $\sigma^2$ ), and  $a$  and  $b$  expresses how  $\gamma(z)$  changes with increasing value of  $z$ . If  $a \neq 0$  and  $b \neq 0$  the effects of fluctuations in population size are phenotype-specific, indicating presence of  $r$ - and  $K$ -selection. To obtain estimates of joint parameter uncertainty, the model was fitted within the Bayesian framework using the no-U-turn sampler (NUTS) Markov Chain Monte Carlo (MCMC) algorithm, resulting in 4500 posterior samples. The Brooks and Gelman diagnostic  $\hat{R}$  was used to assess chain convergence, and the effective sample size  $n_{\text{eff}}$  to assess model precision. Traits were standardized (mean = 0, sd = 1) prior to estimating parameters.

Parameter	Posterior mean	95% credible interval	$\hat{R}$	$n_{\text{eff}}$
$\beta_1$	0.205	0.109, 0.298	1	2636
$\beta_2$	-0.199	-0.230, -0.169	1	4500
$\beta_3$	0.011	-0.006, 0.028	1	4348
$a$	-2.688	-4.265, -1.766	1.001	3351
$b$	-0.807	-1.610, -0.357	1.001	3371
$\ln \sigma^2$	-1.498	-1.816, -1.163	1	4242

**Table S2** Analyses of variation in fitness  $W_z$  of breeding females of collared flycatcher as function of clutch size ( $z$ ) and population size  $N$ . The effects of  $z$  are approximated by a second-order polynomial  $\beta_1 + \beta_2 z + \beta_3 z^2$ , representing stabilizing selection if  $\beta_3 < 0$ . The strength of density dependence on  $z$  is assumed linear so the mixed model takes the form  $\ln E(2W) = \beta_1 + \beta_2 z + \beta_3 z^2 - Ne^{a+bz} + \varepsilon$ , where  $\varepsilon$  is the residual variation, year is entered as a random effect to account for environmental stochasticity ( $\sigma^2$ ), and  $a$  and  $b$  expresses how  $\gamma(z)$  changes with increasing value of  $z$ . If  $a \neq 0$  and  $b \neq 0$  the effects of fluctuations in population size are phenotype-specific, indicating presence of  $r$ - and  $K$ -selection. To obtain estimates of joint parameter uncertainty, the model was fitted within the Bayesian framework using the no-U-turn sampler (NUTS) Markov Chain Monte Carlo (MCMC) algorithm, resulting in 4500 posterior samples. The Brooks and Gelman diagnostic  $\hat{R}$  was used to assess chain convergence, and the effective sample size  $n_{\text{eff}}$  to assess model precision. Traits were standardized (mean = 0, sd = 1) prior to estimating parameters.

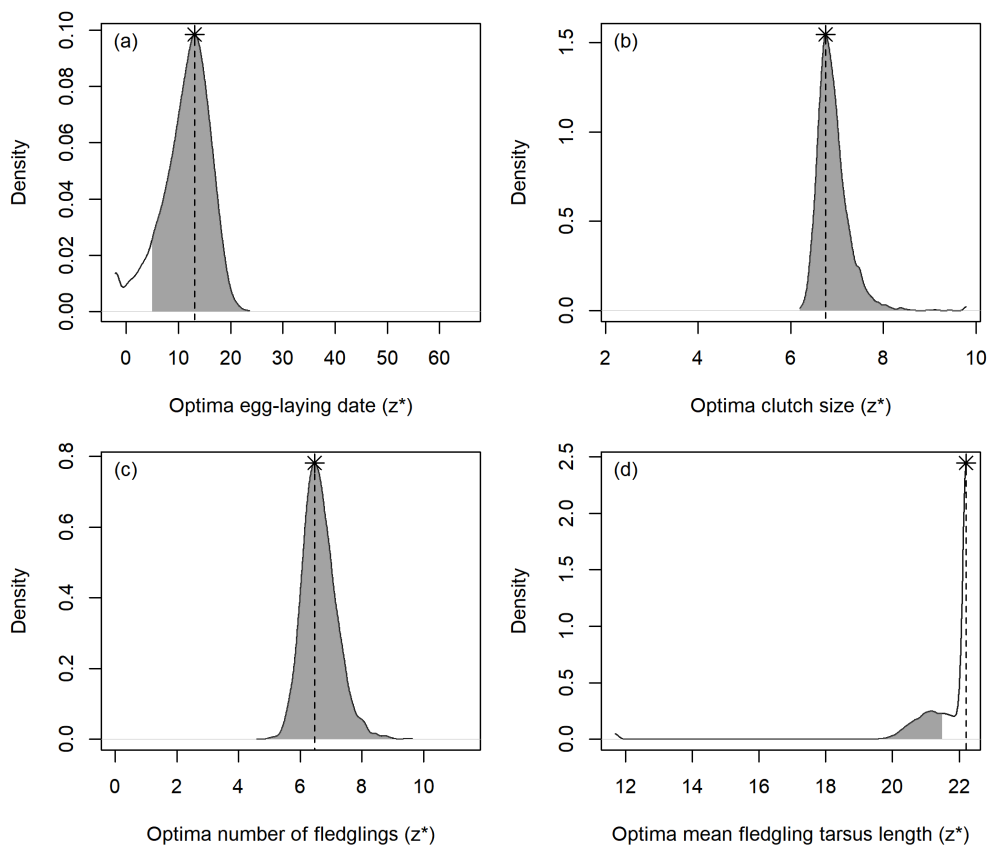
Parameter	Posterior mean	95% credible interval	$\hat{R}$	$n_{\text{eff}}$
$\beta_1$	0.245	0.189, 0.301	1.001	4094
$\beta_2$	0.047	0.026, 0.068	1	4181
$\beta_3$	-0.025	-0.037, -0.012	1.001	4500
$a$	-2.452	-3.450, -1.891	1	4213
$b$	0.143	-0.085, 0.425	1	4386
$\ln \sigma^2$	-2.071	-2.407, -1.709	1.001	4226

**Table S3** Analyses of variation in fitness  $W_z$  of breeding females of collared flycatcher as function of number of fledglings ( $z$ ) and population size  $N$ . The effects of  $z$  are approximated by a second-order polynomial  $\beta_1 + \beta_2 z + \beta_3 z^2$ , representing stabilizing selection if  $\beta_3 < 0$ . The strength of density dependence on  $z$  is assumed linear so the mixed model takes the form  $\ln E(2W) = \beta_1 + \beta_2 z + \beta_3 z^2 - Ne^{a+bz} + \varepsilon$ , where  $\varepsilon$  is the residual variation, year is entered as a random effect to account for environmental stochasticity ( $\sigma^2$ ), and  $a$  and  $b$  expresses how  $\gamma(z)$  changes with increasing value of  $z$ . If  $a \neq 0$  and  $b \neq 0$  the effects of fluctuations in population size are phenotype-specific, indicating presence of  $r$ - and  $K$ -selection. To obtain estimates of joint parameter uncertainty, the model was fitted within the Bayesian framework using the no-U-turn sampler (NUTS) Markov Chain Monte Carlo (MCMC) algorithm, resulting in 4500 posterior samples. The Brooks and Gelman diagnostic  $\hat{R}$  was used to assess chain convergence, and the effective sample size  $n_{\text{eff}}$  to assess model precision. Traits were standardized (mean = 0, sd = 1) prior to estimating parameters.

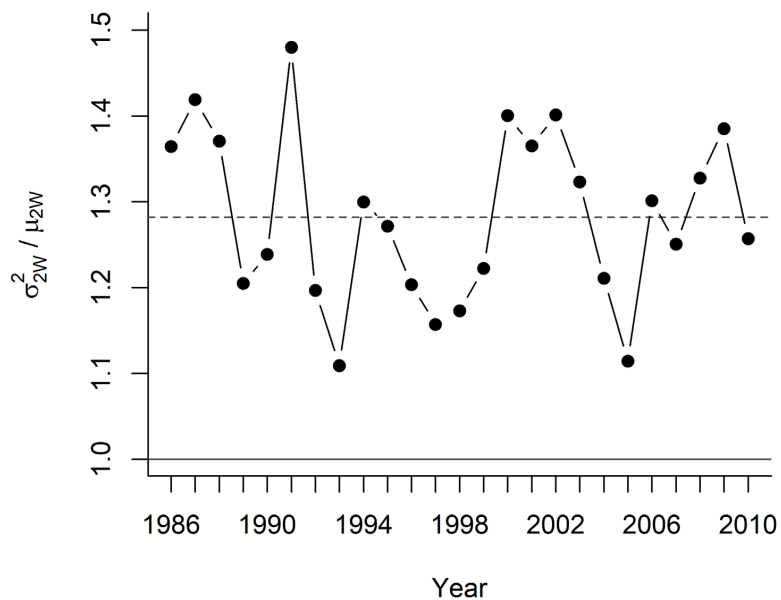
Parameter	Posterior mean	95% credible interval	$\hat{R}$	$n_{\text{eff}}$
$\beta_1$	0.281	0.225, 0.336	1	4500
$\beta_2$	0.278	0.254, 0.302	1	4414
$\beta_3$	-0.089	-0.115, -0.063	0.999	4376
$a$	-2.835	-3.930, -2.159	1	4209
$b$	0.454	0.079, 1.038	1	4500
$\ln \sigma^2$	-2.189	-2.535, -1.814	1	4468

**Table S4** Analyses of variation in fitness  $W_z$  of breeding females of collared flycatcher as function of mean fledgling tarsus length ( $z$ ) and population size  $N$ . The effects of  $z$  is approximated by a second-order polynomial  $\beta_1 + \beta_2 z + \beta_3 z^2$ , representing stabilizing selection if  $\beta_3 < 0$ . The strength of density dependence on  $z$  is assumed linear so the mixed model takes the form  $\ln E(2W) = \beta_1 + \beta_2 z + \beta_3 z^2 - Ne^{a+bz} + \varepsilon$ , where  $\varepsilon$  is the residual variation, year is entered as a random effect to account for environmental stochasticity ( $\sigma^2$ ), and  $a$  and  $b$  expresses how  $\gamma(z)$  changes with increasing value of  $z$ . If  $a \neq 0$  and  $b \neq 0$  the effects of fluctuations in population size are phenotype-specific, indicating presence of  $r$ - and  $K$ -selection. To obtain estimates of joint parameter uncertainty, the model was fitted within the Bayesian framework using the no-U-turn sampler (NUTS) Markov Chain Monte Carlo (MCMC) algorithm, resulting in 4500 posterior samples. The Brooks and Gelman diagnostic  $\hat{R}$  was used to assess chain convergence, and the effective sample size  $n_{\text{eff}}$  to assess model precision. Traits were standardized (mean = 0, sd = 1) prior to estimating parameters.

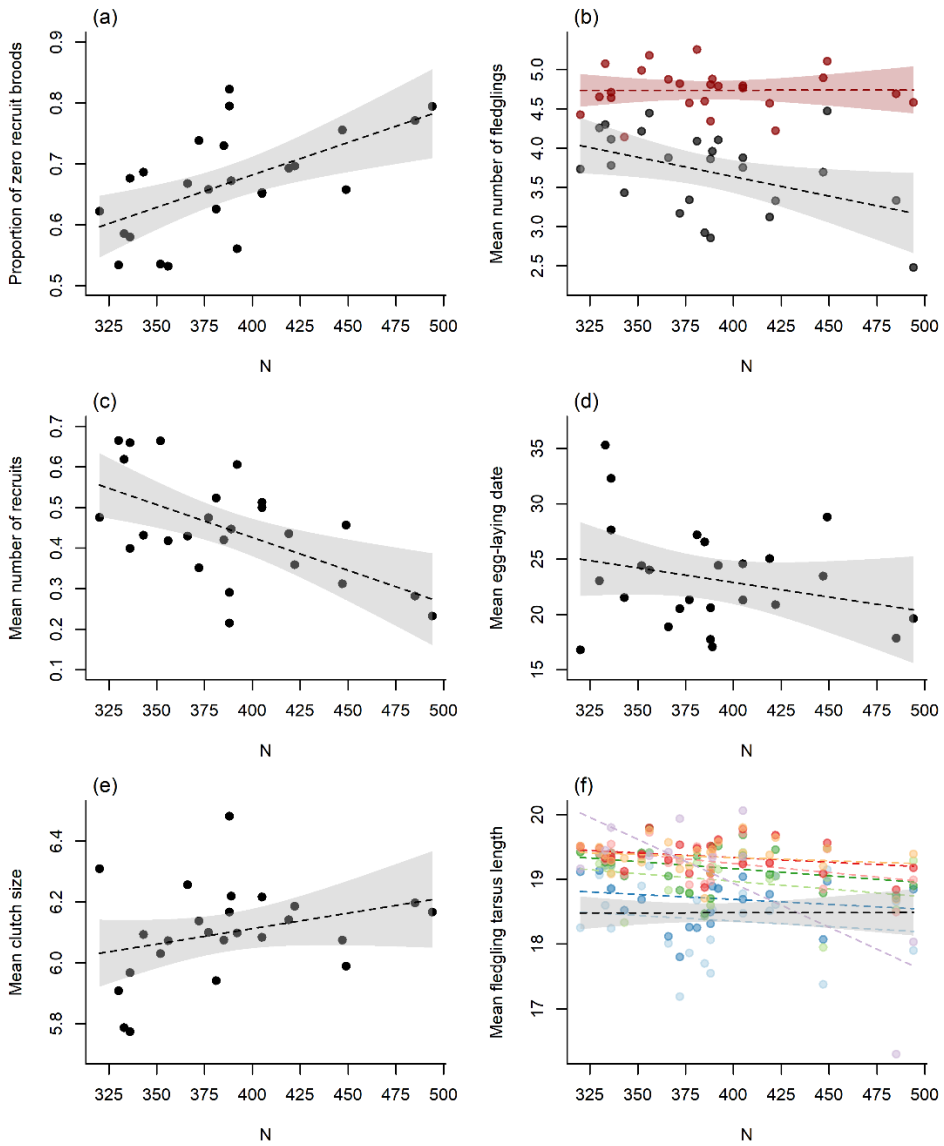
Parameter	Posterior mean	95% credible interval	$\hat{R}$	$n_{\text{eff}}$
$\beta_1$	0.362	0.297, 0.425	1.001	4416
$\beta_2$	0.151	0.120, 0.181	1	4255
$\beta_3$	0.001	-0.013, 0.015	1	4375
$a$	-2.708	-4.285, -1.975	1	4206
$b$	0.197	-0.178, 0.665	0.999	4224
$\ln \sigma^2$	-1.971	-2.343, -1.593	1	4015



**Figure S1.** Kernel density estimates of  $z^*$ , i.e. the mean phenotype that maximizes the adaptive topography  $Q(\bar{z})$ , for egg-laying date (a), clutch size (b), number of fledglings (c) and mean fledgling tarsus length (d) based on 4500 posterior samples. Grey shaded areas indicate the  $z^*$  values that are within the observed range of phenotype values. Stars indicate the mode of the distribution and the values for  $z^*$  displayed in Figure 3 of the main text. The ranges of the x axes correspond to the optimization intervals.



**Figure S2.** Annual variation in the dispersion (i.e., the ratio of the variance to the mean) of the fitness measure  $2W$ , which was modelled to follow a Poisson distribution. Values  $> 1$  indicate overdispersion; values  $< 1$  indicate under-dispersion. Dashed line displays the mean ratio throughout the study period (1.282) and indicates that there is some degree of overdispersion.



Broods (b)

- All broods
- Broods > 0 fledglings

Number of fledglings (f)

- 1
- 2
- 3
- 4
- 5
- 6
- 7
- 8



**Figure S3.** Effect of population size  $N$  on proportion of zero recruit broods (a), mean number of fledglings for all broods (black dots) and broods with at least 1 fledgling (red dots) (b), mean number of recruits (c), mean egg-laying date (d), mean clutch size (e) and mean fledgling tarsus length for all broods (black line) and broods of different sizes (colored lines) (f). Slopes are estimated through linear regressions, and ribbons represent the 95% confidence interval.

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# Paper II

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This paper is awaiting publication and is not included in NTNU Open




# Paper III

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## LETTER

## Accounting for interspecific competition and age structure in demographic analyses of density dependence improves predictions of fluctuations in population size

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## Abstract

Understanding species coexistence has long been a major goal of ecology. Coexistence theory for two competing species posits that intraspecific density dependence should be stronger than interspecific density dependence. Great tits and blue tits are two bird species that compete for food resources and nesting cavities. On the basis of long-term monitoring of these two competing species at sites across Europe, combining observational and manipulative approaches, we show that the strength of density regulation is similar for both species, and that individuals have contrasting abilities to compete depending on their age. For great tits, density regulation is driven mainly by intraspecific competition. In contrast, for blue tits, interspecific competition contributes as much as intraspecific competition, consistent with asymmetric competition between the two species. In addition, including age-specific effects of intra- and interspecific competition in density-dependence models improves predictions of fluctuations in population size by up to three times.

## Keywords

Competitive interactions, *Cyanistes caeruleus*, density dependence, density regulation, *Parus major*, population growth rate.

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## INTRODUCTION

Understanding species coexistence has long been a major goal in ecological studies (Ellner *et al.* 2019). Most species live in guilds or communities alongside other ecologically similar species, sometimes relying on common limiting resources. A major principle of coexistence theory for two competing species is that intraspecific density dependence should be stronger than interspecific density dependence (Chesson 2000). If interspecific competition is stronger than intraspecific competition, one species will ultimately be excluded (see e.g. Alatalo *et al.* 1985), which will change the composition of the entire ecological community (Kokkoris *et al.* 1999; Chesson 2000). A recent review showed that, in plant communities, intraspecific competition is indeed four to five times stronger than interspecific competition, providing the basis for the maintenance of diversity in natural communities (Adler *et al.* 2018). Assessing the relative contribution of inter- and intraspecific competition to density regulation is crucial to determine the chances of species persistence in a community.

Intraspecific density dependence causes a decrease in population growth rate with increasing density of the focal population (Royama 1992; Turchin 1995; Berryman *et al.* 2002; Lande *et al.* 2002; Brook & Bradshaw 2006). Classical

analyses of density dependence are based on time series of population fluctuations, assuming that all individuals in the population have an equal competitive effect (Krebs 2002). Evidence is accumulating, however, that in age-structured populations, the strength of competitive effects vary along an individual's lifetime (see e.g. Coulson *et al.* 2001; Lande *et al.* 2002; de Roos & Persson 2013). For example in a great tit (*Parus major*) population, the youngest birds have the strongest density-dependent effect on other individuals of the same age or older (Gamelon *et al.* 2016). Young birds constitute the critical age classes for density dependence (*sensu* Charlesworth 1972), in which the variation in the number of individuals most strongly affects density regulation. Until now, however, no field study has examined how age-specific competitive effects influence the population growth rates of sympatric species (see Cameron *et al.* 2007 for laboratory settings). The question of how age-specific competitive effects influence the growth rates of sympatric species has rarely been addressed because the classical models of competition between two species A and B use linear combinations of their two densities. For instance, the well-known Lotka (1925) and Volterra (1926) competition model in continuous time measures the effect of species-specific densities  $N_A$  and  $N_B$  on species-specific population growth rates  $\lambda_A$  and  $\lambda_B$ , where  $K_A$  and  $K_B$  are the species-specific carrying capacities:

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$$\log(\lambda_A) = r_A - \frac{r_A}{K_A}(N_A + \alpha_{AB}N_B),$$

$$\log(\lambda_B) = r_B - \frac{r_B}{K_B}(N_B + \alpha_{BA}N_A),$$

with  $\alpha_{AB}$  and  $\alpha_{BA}$  the competition coefficients corresponding to the per capita reduction in growth caused by each additional individual of the other species. However, such models are developed in the simple case of no age structure assuming the same ability for all individuals to compete. In the real world, this assumption is unrealistic, and it is thus important to test whether age structure can improve models of inter-specific competition.

Great tits and blue tits (*Cyanistes caeruleus*) are hole-nesting bird species that compete for cavities and food. Competition intensity varies across Europe (Møller *et al.* 2018) and between habitats (Dhondt 2011). Long-term, individual-based monitoring of these two species have been performed across Europe and two complementary approaches have been adopted to understand how they compete. The first is observational, meaning that vital rates (e.g. survival, fecundity) and emergent population descriptors (e.g. population size) are estimated for these two sympatric species without changing the density of cavities (i.e. the number of nest boxes remains constant throughout the study). The second approach is manipulative and involves a change in the number or type of nest boxes over time (Török & Tóth 1999; Dhondt 2011). Field experiments that manipulate density of one competitor and record the response of the other species have provided significant insight into the role of interspecific competition in the regulation of populations (see Connell 1983; Schoener 1983 for reviews).

Long-term studies of nestbox-breeding tits in the UK and in Belgium, consisting of both observational and manipulative approaches, provide an opportunity to explore how age classes of two competitive species affect each species' population growth rate. We adopted several approaches to address these issues. First, using an integrated population model (IPM) (see Schaub & Abadi 2011; Zipkin & Saunders 2018 for reviews), we estimated the age-specific numbers of the females of both species in all sites. This approach allows us to account for observation errors in population censuses, as well as uncertainty in the age of some individuals, which is crucial while investigating density dependence (Dennis *et al.* 2006; Lillegård *et al.* 2008; Abadi *et al.* 2012; Lebreton & Gimenez 2013; Schaub *et al.* 2013). Second, we compared the relative importance of intra- and interspecific competition for both species in geographically spread sites. Third, we examined how the number of individuals of both species in different age classes contributed to the observed variation in population growth rates of both species. One can hypothesise that including interspecific competition and age-specific contribution to density dependence in demographic analyses would improve predictions of population growth. We tested this hypothesis in all sites for both species by comparing predictions of population sizes from density-dependence models accounting or ignoring age structure and interspecific competition.

## MATERIAL AND METHODS

### Overview of different density-dependence models

#### Classical approach

The classical approach to studying density dependence consists of assessing the extent to which population growth rate decreases with population size. The Ricker model is a simple and common way of representing density-dependent feedback in the per-unit-abundance growth rate (Ricker 1954; Dennis & Taper 1994). The Ricker model is the phenomenological relationship between population growth rate in year  $t$  ( $\lambda_t = \frac{N_{t+1}}{N_t}$ ) and population size  $N_t$ . It takes the following form:

$$\log(\lambda_t) = \gamma_{\lambda'} + \beta_N N_t + res_{\lambda'_t} \quad (1)$$

where  $\gamma_{\lambda'}$  is the intercept,  $\beta_N$  is the regression coefficient providing a measure of the strength of the density regulation, and  $res_{\lambda'_t}$  are the residuals of the regression corresponding to the variation in  $\lambda$  not explained by population size.

#### Age-specific contribution to density dependence

To determine how the different age classes contributed to the observed variation in population growth rate, the previous phenomenological relationship (eqn 1) can be broken down by age-specific numbers  $N_{i,t}$  (see Gamelon *et al.* 2016). In the case where four age classes are considered, eqn 1 becomes:

$$\log(\lambda_t) = \gamma_{\lambda} + \beta_{N_1} N_{1,t} + \beta_{N_2} N_{2,t} + \beta_{N_3} N_{3,t} + \beta_{N_4} N_{4,t} + res_{\lambda_t} \quad (2)$$

where  $\beta_{N_i}$  are the age-specific regression coefficients.

#### Age-specific contribution to density dependence including interspecific competition

To determine how the number of individuals in the different age classes from species A and B contribute to the observed variation in population growth rate of species A ( $\lambda_{A,t}$ ) and B ( $\lambda_{B,t}$ ), we break down the previous phenomenological relationship (eqn 2) by species-specific numbers  $N_{iA,t}$  and  $N_{iB,t}$ . In the case where four age classes are considered, eqn 2 becomes:

$$\begin{aligned} \log(\lambda_{A,t}) &= \gamma_{\lambda_A} + \beta_{N_{1,A}}(N_{1A,t} + \omega_A \times N_{1B,t}) \\ &\quad + \beta_{N_{2,A}}(N_{2A,t} + \omega_A \times N_{2B,t}) \\ &\quad + \beta_{N_{3,A}}(N_{3A,t} + \omega_A \times N_{3B,t}) \\ &\quad + \beta_{N_{4,A}}(N_{4A,t} + \omega_A \times N_{4B,t}) + res_{\lambda_{A,t}}, \\ \log(\lambda_{B,t}) &= \gamma_{\lambda_B} + \beta_{N_{1,B}}(N_{1B,t} + \omega_B \times N_{1A,t}) \\ &\quad + \beta_{N_{2,B}}(N_{2B,t} + \omega_B \times N_{2A,t}) \\ &\quad + \beta_{N_{3,B}}(N_{3B,t} + \omega_B \times N_{3A,t}) \\ &\quad + \beta_{N_{4,B}}(N_{4B,t} + \omega_B \times N_{4A,t}) + res_{\lambda_{B,t}}. \end{aligned} \quad (3)$$

where  $\beta_{N_{iA}}$  and  $\beta_{N_{iB}}$  are the age-specific regression coefficients when interspecific competition is accounted for. In the first part of the equation, an  $\omega_A$  value of 0 indicates that only the age-specific numbers of species A matter. In this scenario, only intraspecific competition explains variations in  $\lambda_A$  and interspecific competition has no impact on growth rate (as in eqn 2). In contrast, an  $\omega_A$  value of 1 indicates



that an individual of species B has the same competitive effect on the population growth rate of species A as an individual of species A. Hence,  $\omega_A$  (and  $\omega_B$ ) provides a measure of the relative importance of inter- vs. intraspecific competition on the total density regulation acting on  $\lambda_A$  (and  $\lambda_B$ ). Noticeably,  $\omega_A$  corresponds to  $\alpha_{AB}$  in the Lotka–Volterra competition model and  $\omega_B$  to  $\alpha_{BA}$ . However, our model is more complex, since it includes density regulation acting among age classes. The strength of density regulation is given by the  $\beta_{Ni,A}$  coefficients (with high negative  $\beta_{Ni,A}$  indicating strong density regulation). If the required high-quality data are available, the above formula can easily be extended to more than two competing species and the competition coefficient  $\omega_A$  can be made age-specific to relax the assumption of similar age differences in competitive strength for inter- and intraspecific competition.

### Great tits and blue tits as a case study

Great tits and blue tits are two competing, short-lived birds abundant in European gardens and woodlands as year-round residents (Perrins & McCleery 1989). They are cavity-nesters and readily accept nest boxes as nesting sites, making it possible to monitor the entire breeding population. Nest boxes with a large entrance hole (32 mm) are suitable for both species, whereas nest boxes with a small entrance hole (26 mm) almost completely exclude great tits that are bigger than blue tits.

The data come from three long-term study sites near Antwerp (Boshoek and Peerdsbos) and Ghent in Belgium, and from eight sites ('rounds') within Wytham Woods, near Oxford in the UK (Table 1, Supporting Information 1). In all sites, both great and blue tit populations were monitored. In the case of Wytham Woods, substantial differences (up to five fold) in nest box density between rounds as well as differences in vegetation structure, physical geography, etc., coupled with the large sample size, suggested that it would be appropriate to estimate effects at the level of the round (see e.g. Garant *et al.* 2005). Lumping the rounds into one single population would neglect such heterogeneity and ignore differences in population density as determined by nestbox density. Furthermore, one might expect competition for sites to be more pronounced when boxes are at low density. Populations are open to immigration and emigration. At all sites except Peerdsbos, the number of nest boxes remained constant during the study period (see Minot & Perrins 1986; Dhondt *et al.* 1990; Nour *et al.* 1998; Visser *et al.* 2003; Garant *et al.* 2005; Dhondt 2010; Matthysen *et al.* 2011 and Table 1 for further details on the study sites). In Peerdsbos, 33% of both large-holed and small-holed nest boxes were removed in 1997.

### Demographic data

Nest boxes were visited during the breeding season and three types of demographic data were recorded:

- (1) For each species, the total number of breeding females ( $C_t$ ) was recorded. As most females start to breed at one year of age, the breeding population size is a good proxy

**Table 1** Eleven sites included in the study where intra- and interspecific density dependence were investigated.

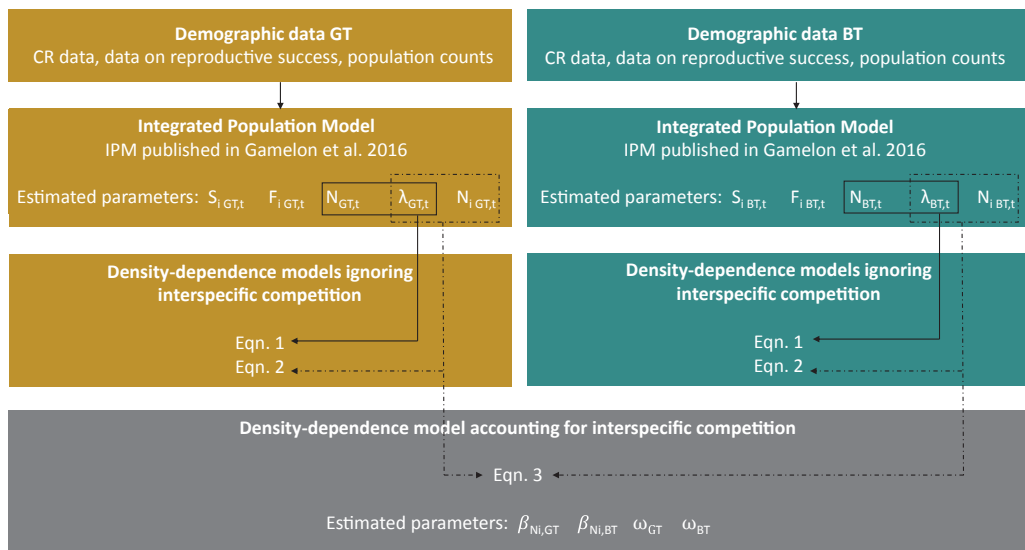
	Study sites	Study period	Monitored females
1	Boshoek	1994–2016	$N_{GT} = 1634$ ; $N_{BT} = 1348$
2	Ghent	1994–2011	$N_{GT} = 399$ ; $N_{BT} = 136$
3/4	Peerdsbos	1980–1996/1997–2016	$N_{GT} = 805$ ; $N_{BT} = 778$
5	Bean Wood	2001–2016	$N_{GT} = 379$ ; $N_{BT} = 372$
6	Broad Oak	2003–2016	$N_{GT} = 636$ ; $N_{BT} = 682$
7	Common Piece	2003–2016	$N_{GT} = 357$ ; $N_{BT} = 361$
8	Extra	2008–2016	$N_{GT} = 930$ ; $N_{BT} = 536$
9	Great Wood	2008–2016	$N_{GT} = 597$ ; $N_{BT} = 436$
10	Marley	2001–2016	$N_{GT} = 553$ ; $N_{BT} = 455$
11	Marley Plantation	2001–2016	$N_{GT} = 479$ ; $N_{BT} = 305$
12	Singing Way	2001–2016	$N_{GT} = 514$ ; $N_{BT} = 319$

Displayed are the study sites (in Belgium and the UK), the study period during which demographic data were collected on great tits and blue tits, and the number of marked great tit ( $N_{GT}$ ) and blue tit ( $N_{BT}$ ) females as part of capture-recapture programs. The number of nest boxes provided to tits was reduced at Peerdsbos in 1997 and remained constant in the other sites.

- for the total number of females in the population (Dhondt *et al.* 1990).
- (2) All nestlings and mothers were fitted with a uniquely numbered leg-ring to allow identification. Additionally, mothers were aged (first-years vs. adults [ $\geq 2$  years]) based on plumage characteristics. We assumed that previously unringed mothers recruited into the population in the first year in which they were recorded breeding; some of these could not be aged due to left-census truncation (those recruited as adults). The breeding females of known age that are marked and monitored throughout their life provide capture-recapture (CR) data of known age females. We grouped the breeding birds of known age into four age classes: 1, corresponding to the first year of breeding (i.e. second calendar year of life); 2, corresponding to the second year of breeding; 3 corresponding to the third year of breeding; and 4, which groups breeding females aged 4 or more.
- (3) Females locally ringed as nestlings were recorded as recruited to the breeding population if they were observed breeding in a subsequent year. This gave the number of females that successfully became a first-year breeding female in year  $t + 1$ , termed the breeding recruitment for year  $t$  ( $J_t$ ). This recruitment could be broken down by the age-class of the mother (see Dhondt 1989 for evidence of age-specific recruitment): first year breeder, second year, etc. This provided estimates of the number of recruits for mothers of age class  $i$  in year  $t$  ( $J_{i,t}$ ). Also, we recorded the total number of breeding females of each age class  $i$  in year  $t$  ( $B_{i,t}$ ).

### Annual age-specific numbers of females using an IPM

Our analyses were performed on each study site separately (see Fig. 1 for a schematic of the different analytical steps). For each species, we integrated the recorded number of breeding females ( $C_t$ ), CR data of females of known age and data on reproductive success (i.e.  $B_{i,t}$  and  $J_{i,t}$ ) into an integrated



**Figure 1** Schematic of the different analytical steps to investigate intra- and interspecific density dependence. In each study site, demographic data including capture-recapture (CR) data are collected on great tits (GT, yellow) and blue tits (BT, blue). In each site, data are analysed within an Integrated Population Model (IPM) and time series of population size ( $N_t$ ), population growth rate  $\lambda_t$ , age-specific survival rates ( $S_{i,t}$ ), fecundity rates ( $F_{i,t}$ ) and numbers ( $N_{i,t}$ ) are obtained for each species in each location. Outside the IPMs, these parameters then feed density-dependence models ignoring (eqns 1 and 2) or accounting (eqn 3) for interspecific competition. In this latter case,  $\beta_{N_i}$  corresponding to the age-specific contribution to density dependence and  $\omega$ , the relative importance of inter- vs. intraspecific competition, are estimated for both species at a given location.

population model (IPM) (Schaub & Abadi 2011). This framework provides estimates of all the vital rates (survival, fecundity), the true total number of females  $N_t$  and the true age-specific numbers of females  $N_{i,t}$  for each year  $t$  with improved precision and free of observation error (Besbeas *et al.* 2002; Abadi *et al.* 2010, 2012; Kéry & Schaub 2012). The joint analysis of these three datasets thus allowed us to account for observation error associated with the recorded number of counted breeding females (Lebreton & Gimenez 2013). It also allowed us to account for the incomplete information on age structure in the monitoring data (e.g. some females are of unknown age), for imperfect detection (e.g. recapture probability is not 1) and for demographic stochasticity (Lande *et al.* 2002).

Inference is based on the joint likelihood, corresponding to the multiplication of the likelihoods from the single datasets (CR data, data on reproductive success and population count) (Kéry & Schaub 2012). The likelihoods of the different datasets were specified as follows. For CR data of breeding females of known age, we used the Cormack–Jolly–Seber model (Lebreton *et al.* 1992) which allows estimation of annual survival between age class  $i$  and  $i + 1$  ( $S_{i,t}$ ) and recapture ( $P_t$ ) probabilities. For data on reproductive success, the observed number of daughters locally recruited per age class  $i$  ( $J_{i,t}$ ) is Poisson distributed with  $J_{i,t} \sim \text{Poisson}(B_{i,t} \times F_{i,t})$ , where  $F_{i,t}$  is the recruitment rate of females of age class  $i$  at year  $t$ . For the population count data, we used a state-space model (de Valpine & Hastings 2002) that consisted of a

process model describing how the population size and structure changed over time as well as an observation model (Besbeas *et al.* 2002). We considered a pre-breeding age-structured model with the four pre-defined age classes. The true age-specific numbers of females  $N_{i,t}$  corresponds to the sum of locally born females and immigrants. Assuming independence among the datasets, the likelihood of the IPM corresponds to the product of the likelihoods of the three different datasets, namely population counts, reproductive success data and CR data (Kéry & Schaub 2012). The assumption of independence is violated in our study because some of the breeding females may be found in the different datasets but, as shown in a simulation study (Abadi *et al.* 2010), it is unlikely that it affects our parameter estimates and their precision with the kind of data we used here.

The model was fitted within a Bayesian framework. To assess convergence, we ran four independent chains with different starting values for a minimum of 100 000 MCMC iterations, with a burn-in of 50 000 iterations, thinning every 100th observation and resulting in 2000 posterior samples. We used the Brooks and Gelman diagnostic to assess the convergence of the simulations and used the rule to determine whether convergence was reached (Brooks & Gelman 1998). The analyses were implemented using JAGS version 3.4.0 (Plummer 2003) with package R2jags (Su & Yajima 2012). For a full description of the IPM, the priors used and the R code to fit the IPM, see an example on another great tit population (Gamelon *et al.* 2016).

To ensure that the priors for initial population numbers did not influence estimates of age-specific numbers during the first year of the study, we considered estimates provided by our IPM from the second year onwards (see Supporting Information 2).

#### Age-specific contribution to density dependence including interspecific competition

As a derived parameter from the IPM, we computed the 'observed' population growth rate of great tits (GT) in year  $t$  as  $\lambda_{GT,t} = \frac{N_{GT,t+1}}{N_{GT,t}}$  for each posterior sample (2000 in total) and recorded its posterior mean. To determine how the (posterior means of the) age-specific numbers of great tit  $N_{iGT}$  and blue tit  $N_{iBT}$  females contributed to the observed variation in  $\lambda_{GT}$ , we applied eqn 3 with species A corresponding to great tit and species B to blue tit (BT). As  $N_{GT,t}$ ,  $N_{iGT,t}$  and  $N_{iBT,t}$  were estimated in the IPM model, sampling variance and observation errors were accounted for. This approach thus precludes spurious detection of density dependence (see Freckleton *et al.* 2006; Schaub *et al.* 2013; Gamelon *et al.* 2016 for a similar approach). To determine the value of  $\omega_{GT}$  (i.e. the relative importance of inter- and intraspecific competition in the dynamics of great tits) that provides the best fit of eqn 3 to the data, we calculated the Akaike Information Criterion (AIC) (Burnham & Anderson 2002) of eqn 3 for  $\omega_{GT}$  ranging from 0 to 1 in increments of 0.005. The model with the lowest AIC was considered as the best one, and its corresponding value of  $\omega_{GT}$  was recorded. We did not consider competitive exclusion as a possible scenario and thus prevented interspecific competition from exceeding intraspecific competition in our analyses by restricting the competition coefficients  $\omega$  to values less than unity. By not allowing parameter values above unity, the parameters are tested in a region in accordance with biological *a priori* and the accuracy in the estimation is improved. We reported the estimates of the regression coefficients  $\beta_{N_{iGT}}$  from the best model retained, which indicate how the number of females of both species in age class  $N_i$  contributed to the observed variations in  $\lambda_{GT}$ .

For each site, we applied the same approach on blue tits to determine how the age-specific numbers of great tit ( $N_{iGT}$ ) and blue tit ( $N_{iBT}$ ) females contributed to the observed variation in blue tit population growth rate,  $\lambda_{BT,t}$ .

#### Implications for the dynamics of age-structured populations

For each blue tit population, from the estimates of  $\omega_{BT}$ ,  $\beta_{N_{iBT}}$  and  $\gamma_{\lambda_{BT}}$  and the true age-specific numbers of females  $N_{iGT,t}$  and  $N_{iBT,t}$  during the study periods, we calculated the expected population growth rate  $\lambda_{BT,expected1}$  (from eqn 3). We compared it to the observed annual growth rate  $\lambda_{BT}$  during this period (i.e. estimated with the IPM) through a simple linear regression.

Second, eqn 2 was fitted, meaning that interspecific competition was ignored. From these new estimates of  $\beta_{N_{iBT}}$  and  $\gamma_{\lambda}$  and from true age-specific numbers of blue tit females  $N_{iBT,t}$  we calculated the expected growth rate  $\lambda_{BT,expected2}$ . This was then compared to the observed growth rate  $\lambda_{BT}$  with a linear regression.

Finally, eqn 1 was fitted, meaning that both interspecific competition and age-specific contribution to density dependence were ignored. From the estimates of  $\beta_{N_{BT}}$  and  $\gamma_{\lambda}$ , and from true total number of blue tits  $N_{BT,t}$ , we calculated  $\lambda_{BT,expected3}$  and compared it to the observed growth rate  $\lambda_{BT}$ .

We applied the same approach for each great tit population. Analyses were performed with R software, version 3.4.3 (R Development Core Team 2017).

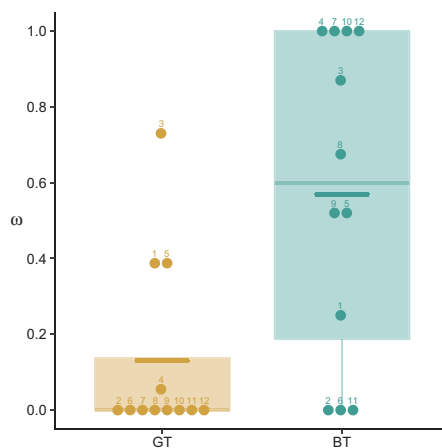
## RESULTS

### IPM

Age-specific numbers of females  $N_{iGT,t}$  and  $N_{iBT,t}$  varied over time, for both great tits and blue tits in all sites (Supporting Information 2). Survival and fecundity rates also fluctuated through years, and generally differed among age classes (Supporting Information 3,4). The recapture probability varied over years and was generally high in all sites for both species (Supporting Information 5).

### Relative importance of inter- vs. intraspecific competition

For each site and each species, we estimated the value of  $\omega_{GT}$  and  $\omega_{BT}$  that provided the best fit of the model described in eqn 3 (Fig. 2). At eight out of 10 sites (excluding the manipulative experiment at Peerdsbos),  $\omega_{GT}$  equals 0 (Fig. 2). This indicates small contribution of interspecific competition to the changes in population size of great tits, that is blue tits have little effect on the growth rate of the great tit population,  $\lambda_{GT}$ . At the two other sites,  $\omega_{GT}$  equals 0.39, indicating that two to three blue tits have the same competitive effect as one great tit.



**Figure 2** Boxplot showing the relative importance of inter- vs. intraspecific competition on the total density regulation acting on great tit's population growth rate  $\omega_{GT}$  (in yellow) and on blue tit's population growth rate  $\omega_{BT}$  (in blue) across sites. Values equal to 0 indicate no interspecific competition and values equal to 1 indicate a similar competitive effect of great tit and blue tit. Numbers refer to the study sites (see correspondence in Table 1).

For blue tits, at seven out of 10 sites, accounting for inter-specific competition (with  $\omega_{BT} > 0$ ) in eqn 3 better explains variation in population growth rate  $\lambda_{BT}$  than ignoring inter-specific competition (with  $\omega_{BT} = 0$ ). Thus, the number of great tits present at a site affects  $\lambda_{BT}$ . The relative importance of inter- vs. intraspecific competition  $\omega_{BT}$  even reached unity for some sites (Fig. 2), indicating that one great tit has the same competitive effect as one blue tit. At the three other sites,  $\omega_{BT}$  equals 0, indicating that the number of great tits has no effect on  $\lambda_{BT}$ .

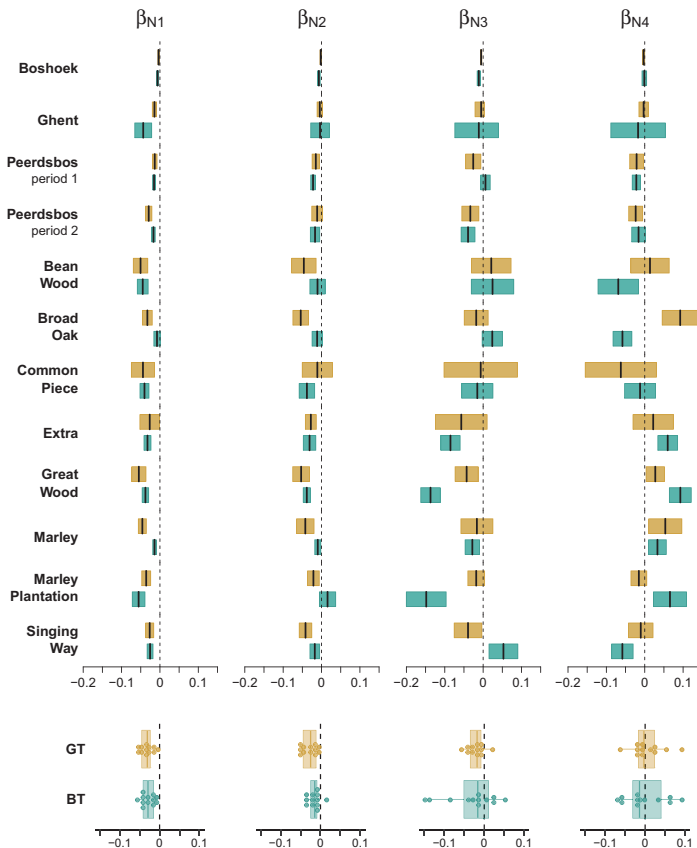
### Effects of age-class numbers on population growth rate

Negative  $\beta_{N_i}$  values indicate that higher number of females in age class  $N_i$  translates to lower population growth rate. The  $\beta_{N_i}$  values were negative, positive, or not significant depending on the species, the study sites and the age class (Fig. 3). Thus,

the different age classes did not contribute equally to the strength of density dependence. While in some sites, age 1 and 2 had the strongest negative effect on  $\lambda$  (e.g. at Common Piece, Fig. 3), older age classes contributed the most to density regulation in other areas (e.g. in the blue tit population at Singing Way). The effects of age-class numbers on  $\lambda$  have the same order of magnitude for both species (Fig. 3) indicating that they experience similar strength of density dependence.

### Change in the number of nest boxes over time

In Peerdsbos, the removal of some nest boxes during the study period provides an opportunity to explore the effect of a change in nest box number on the relative contribution of inter- and intraspecific competition to the population dynamics. Prior to the removal in 1997, the effects of interspecific competition were close to intraspecific competition in both



**Figure 3** Columns show the effects of the number of breeding females  $N_i$  in age class  $i$  of both species on great tit population growth rates  $\lambda_{GT}$  (log-transformed) (in yellow) and on blue tit population growth rates  $\lambda_{BT}$  (log-transformed) (in blue) in the eleven study sites (in rows). Displayed are the means of the regression coefficients  $\beta_{N_i}$  and their associated standard errors. Negative values indicate that higher number of females in the age class  $N_i$  translates to lower population growth rate. The boxplots summarise the effects of the number of breeding females  $N_i$  in age class  $i$  of both species on  $\lambda_{GT}$  and  $\lambda_{BT}$  across sites.

species ( $\omega_{GT} = 0.730$  and  $\omega_{BT} = 0.87$ , Fig. 2). One great tit had almost the same competitive effect as one blue tit on  $\lambda_{GT}$  and one blue tit had the same competitive effect as one great tit on  $\lambda_{BT}$ . In the second period (i.e. after 1997), the relative importance of interspecific competition dropped for great tits ( $\omega_{GT} = 0.055$ ) and increased for blue tits ( $\omega_{BT} = 1$ ). Thus, interspecific competition becomes negligible on  $\lambda_{GT}$ , whereas on  $\lambda_{BT}$ , one blue tit tended to have the same competitive effect as one great tit.

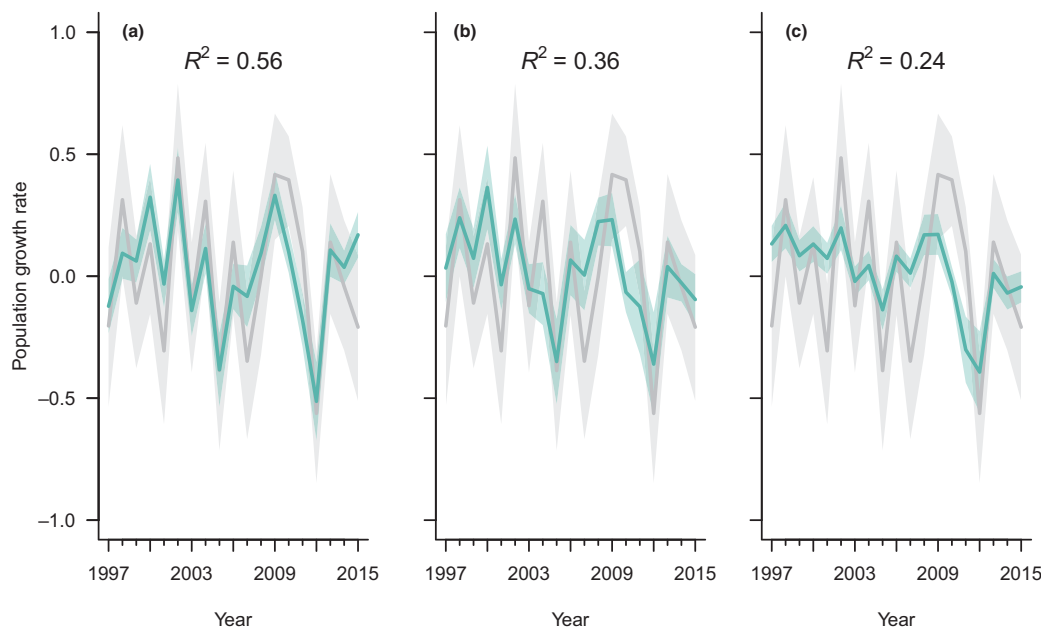
The removal of some nest boxes was associated with a two-fold increase in the strength of density regulation for great tits (Fig. 3). Together with a low  $\omega_{GT}$  reported during the second period, these results indicate that great tits play a major role in their own regulation. However, the strength of density regulation was not stronger in the second period for blue tits (Fig. 3). Together with a high  $\omega_{BT}$ , this means that blue tits were mainly limited by great tits in the second period, although with the same intensity as in the first period.

#### Implications for the dynamics of age-structured populations

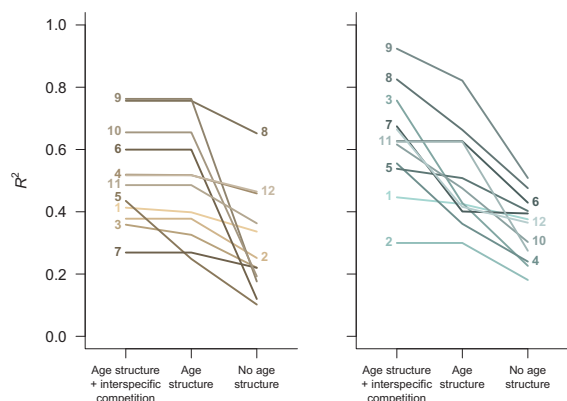
After the removal in 1997 in Peerdsbos, great tits contributed greatly to the strong density dependence acting on the dynamics of the blue tit population ( $\omega_{BT} = 1$ ). This population is a relevant case study for exploring how including interspecific competition in demographic analyses might help to predict variations in population growth rate  $\lambda_{BT}$ . The posterior means of  $\lambda_{BT}$  (on a log-scale) estimated through the IPM varied

between  $-0.56$  and  $0.48$ , indicating that the population decreased and increased over time (Fig. 4, grey lines). These fluctuations were caused by the combined effect of both density-dependent and -independent factors (such as climate variations). The expected growth  $\lambda_{BT,expected1}$  predicted by our density-dependent model accounting for age-specific contribution to density dependence and interspecific competition (eqn 3) matched well with the observed variations in  $\lambda_{BT}$  (Fig. 4a, blue line). This model explains 56% of the variance in  $\lambda_{BT}$ . However,  $\lambda_{BT,expected2}$  predicted by a density-dependent model accounting for age-specific contribution to density dependence but ignoring interspecific competition (eqn 2) provided a poorer fit (Fig. 4B, blue line), explaining only 36% of the variance in observed  $\lambda_{BT}$ . The classical approach (eqn 1) assuming equal contribution of all ages to density dependence and ignoring interspecific competition provided an even poorer fit (Fig. 4c, blue line), explaining only 24% of the variance in observed  $\lambda_{BT}$ .

The blue tit population at Peerdsbos is not an exception with regards to improved predictions of fluctuations in population size when both age structure and interspecific competition are accounted for. Accounting for age and interspecific competition in demographic analyses substantially improves our predictions of variations in growth rate for most of the blue tit populations, by up to three times (Fig. 5). For great tit populations, while accounting for age-specific contribution to density dependence improves the model fit (Fig. 5, comparison between eqn 1 and eqn 2), accounting for interspecific



**Figure 4** Blue tit population growth rate ( $\lambda_{BT}$ , on a log-scale) at Peerdsbos between 1997 and 2016. Grey lines correspond to the observed growth rate  $\lambda_{BT}$  (i.e. estimated through the IPM) with its 95% confidence interval. Blue lines (and their 95% confidence intervals) correspond to (a) growth rate  $\lambda_{BT,expected1}$  predicted by a density-dependent model accounting for age-specific contribution to density dependence and both intra- and interspecific competition (eqn 3); (b) growth rate  $\lambda_{BT,expected2}$  predicted by the same model as that in (a) but ignoring interspecific competition (eqn 2); (c) growth rate  $\lambda_{BT,expected3}$  predicted by the same model as that in (b) but assuming equal contribution of all ages to density dependence (i.e. classical approach, eqn 1).



**Figure 5** Coefficient of determination ( $R^2$ ) between observed population growth rates and predicted ones from eqn 3 (i.e. by a density-dependent model accounting for age-specific contribution to density dependence and both intra- and interspecific competition), eqn 2 (i.e. ignoring interspecific competition but accounting for age-specific contribution) and eqn 1 (i.e. classical approach) for great tit (in yellow, one colour per site) and blue tit populations (in blue, one colour per site). Numbers refer to the study sites (see correspondence in Table 1).

competition has rather little effect on the predictive power of the density-dependence model (Fig. 5, comparison between eqn 2 and eqn 3).

## DISCUSSION

Fluctuations in size of natural populations are due to temporal variation in climate (see e.g. Sæther *et al.* 2000, 2004; Coulson *et al.* 2001; Stenseth *et al.* 2003; Berryman & Lima 2006) and density dependence (Royama 1992; Turchin 1995). The relative importance of environmental stochastic and deterministic (i.e. density-dependent) factors in affecting population growth rates has long been debated (Andrewartha & Birch 1954; Nicholson 1957; Turchin 1995; Coulson *et al.* 2004) but it is now accepted that both play an important role (Leirs *et al.* 1997; Coulson *et al.* 2001; Boyce *et al.* 2006). Several studies of tits have shown that both climate variation and density dependence induce spatio-temporal variation in population dynamics (Sæther *et al.* 2003; Grøtan *et al.* 2009). Accordingly, in our study, density dependence was present in all populations (negative  $\beta$  parameters, Fig. 3) and account for up to 92% of the recorded variation in population growth (see e.g. the blue tit population at Great Wood, Fig. 5). Within a population, both intra- and interspecific competition contributed to the density regulation. These contributions were age-dependent. Our findings question the assumptions commonly made when estimating the strength of density dependence (Krebs 2002), that (1) interspecific competition is negligible; and (2) all individuals in the population have an equal competitive effect. Relaxing these assumptions greatly improves predictions of fluctuations in population size in age-structured populations. Variation in population growth rates is better predicted when interspecific competition and age-specific contribution to density dependence are accounted for. In

populations limited by intra- and interspecific competition such as blue tit populations, we strongly recommend the use of a scalar function describing how several age classes of competitive species affect the population growth rate negatively.

### Contribution of inter- and intraspecific competition to changes in population size

Classical models of competition between two species such as Lotka (1925) and Volterra (1926) use linear combinations of the two densities and ignore age structure. Here, we provide a straightforward method to estimate the relative importance of intra- vs. interspecific competition in age-structured populations. When close to 0, the competition coefficient (here called  $\omega$ ) indicates that only intraspecific competition explains variations in population growth rate  $\lambda$ , whereas close to 1, it indicates a similar contribution of intra- and interspecific competition to observed variations in  $\lambda$ . A value above unity would indicate that interspecific competition is higher than intraspecific competition, and that the coexistence between the two species only results from immigration. A proper evaluation of this hypothesis would require a spatially-explicit competition model.

On the basis of long-term monitoring of two competing species, we found that the relative contribution of interspecific competition to density dependence ( $\omega$  values) is species-specific, with interspecific competition being more important in blue tits than in great tits. This indicates asymmetric competition, in accordance with previous studies that have shown that when great tit population density is high, great tits direct high levels of aggression against blue tits during competition for food or breeding sites (Dhondt 2011). The increased relative importance of interspecific competition  $\omega_{BT}$  for the blue tit population at Peerdsbos after the removal of some nest boxes probably results from interspecific competition for roosting sites in winter, as shown in multiple experiments (Dhondt 2011). Great tits can even exclude most blue tits if all nest boxes are suitable for both species, through higher rates of dispersal in blue tits (Dhondt 2011). Conversely, great tit population growth was only slightly sensitive to blue tit population density and was mainly limited by intraspecific competition. Intraspecific competition is common in great tits and well documented (Both *et al.* 1999). An experimental study showed that competition among conspecifics in great tit could lead to higher juvenile dispersal (Kluyver 1971). Similarly, there is compelling evidence that at high density, great tits occupy lower quality territories, leading to reduced clutch size (Perrins 1979; Dhondt *et al.* 1992). In contrast to the situation for blue tits, our analyses suggest that density regulation in great tit populations mainly operates through intraspecific competition.

### Age-specific contribution to density regulation

We found that the strength of density regulation ( $\beta$  parameters) is comparable for great and blue tits. However, individuals differ in their contribution to density dependence dependent on their age. Previous work that focused on a single great tit population (Gamelon *et al.* 2016) provided support for the important role of the youngest age classes in density regulation. Our current findings suggest that,



even if young females consistently contribute to density regulation, older individuals also play an important role, in one-third of the populations. Although it is beyond the scope of this study, the fact that some ages appear to be important in driving density regulation at some sites but not others is deserving of further study, and could be attributable to variation in local environmental conditions.

## CONCLUSION

We studied the population dynamics of two co-occurring and ecologically competing bird species in the UK and Belgium. The two species exhibit similar strength of density regulation, and individuals of different ages play contrasting roles in that regulation. While in blue tits, interspecific competition can be as important as intraspecific competition in determining this regulation, great tit populations show little sensitivity to the local density of blue tits. Beyond the interspecific differences, we detected among-site differences in the strength of density regulation ( $\beta$  parameters) and the relative importance of interspecific competition ( $\omega$  values). Variation in ecological conditions (e.g. availability of food resources, cavities) could explain such discrepancies. While we focused on pairwise interactions, more complex interactions with other competitors present in some of the areas may affect the growth rates of great tit and blue tit populations. Expanding our approach to more than two competitor populations offers exciting avenues of research (Levine *et al.* 2017).

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## AUTHORSHIP

F.A., E.M., A.A.D. and B.C.S. contributed to data collection; F.A., S.R.E. and S.J.G.V. prepared the datasets; M.G., S.E., F.A., E.M., B.C.S. and B.E.S. conceived the study; M.G. conducted the analyses and wrote the manuscript and all authors contributed to revisions on later manuscript versions.

## DATA ACCESSIBILITY STATEMENT

The data and the R scripts supporting the results are archived in Dryad <https://doi.org/10.5061/dryad.45873cg>.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Editor, Roberto Salguero-Gomez

Manuscript received 11 October 2018

First decision made 26 November 2018

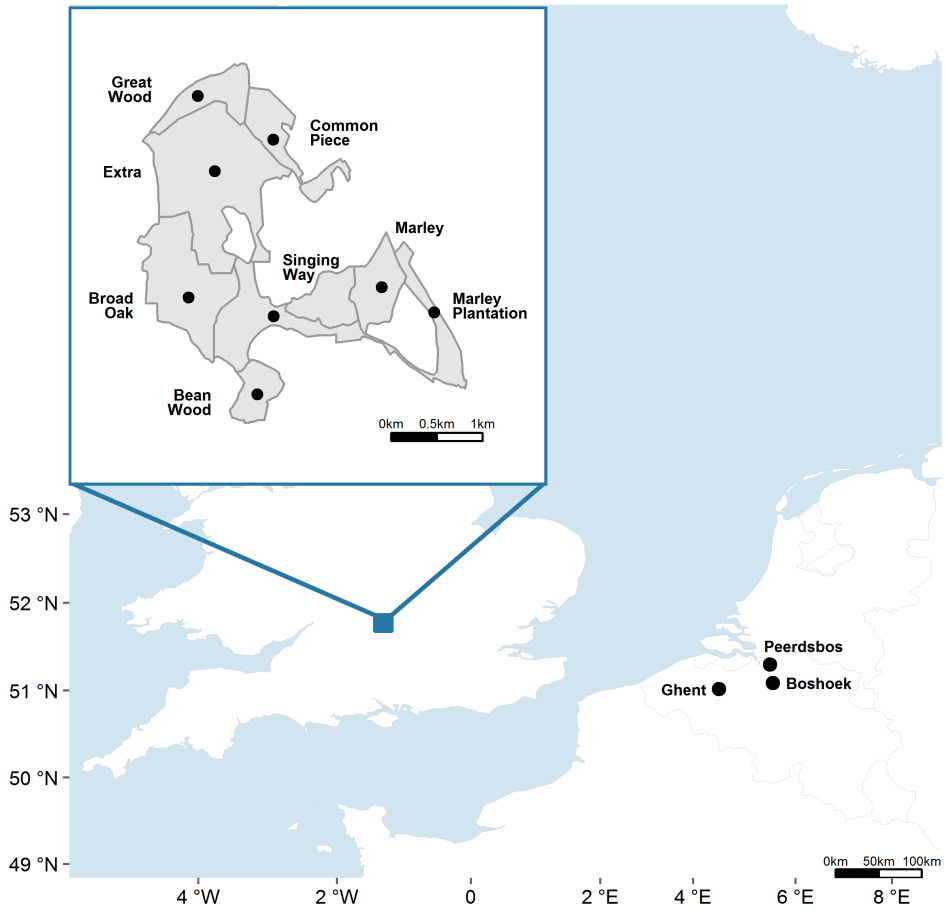
Second decision made 21 January 2019

Manuscript accepted 24 January 2019

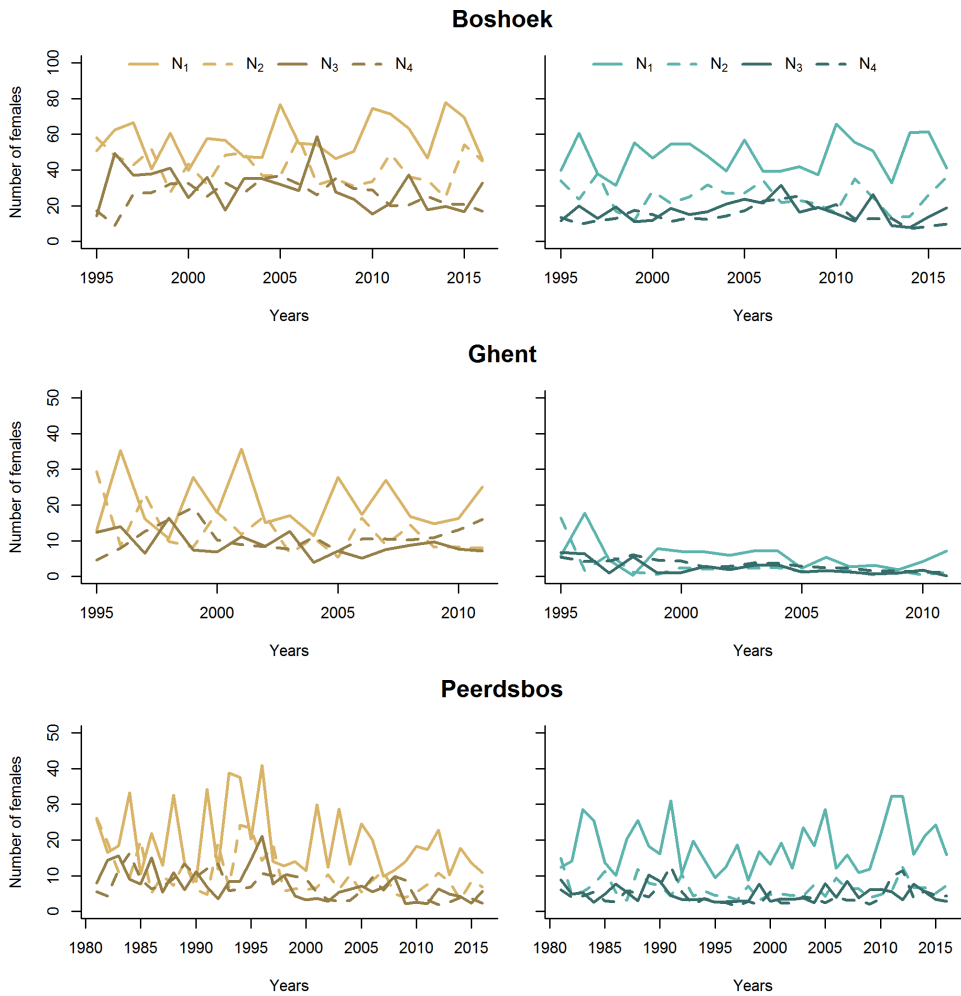


## Supporting Information

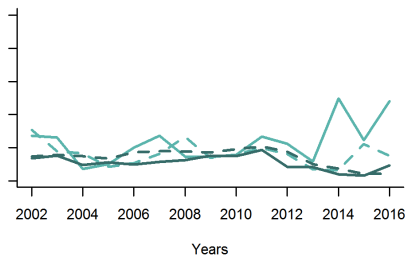
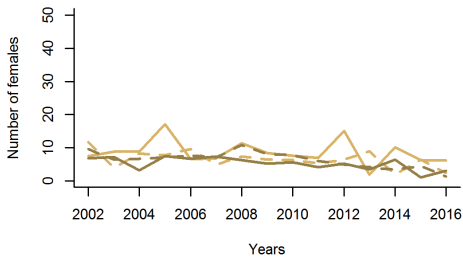
**Supporting Information S1** Map showing the eleven study sites included in the study.



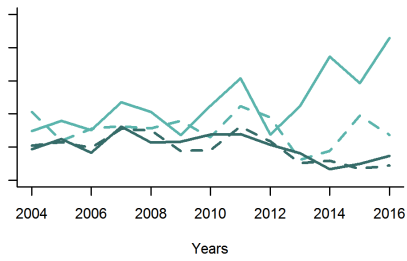
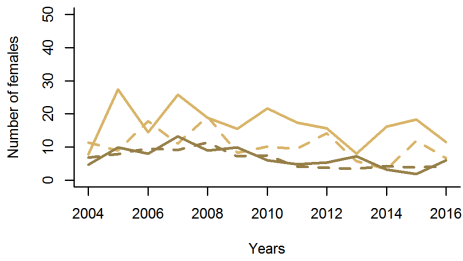
**Supporting Information S2** Posterior means of the annual age-class numbers of breeding females  $N_i$  estimated from the IPM in the great tit (in yellow) and blue tit (in blue) populations in Belgium and the UK.



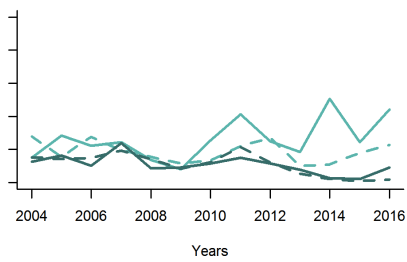
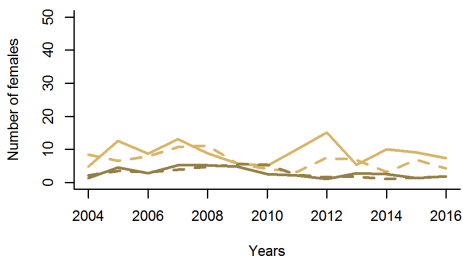
**Bean Wood**



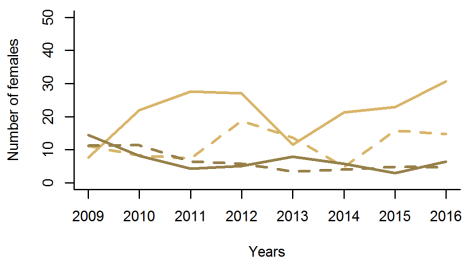
**Broad Oak**



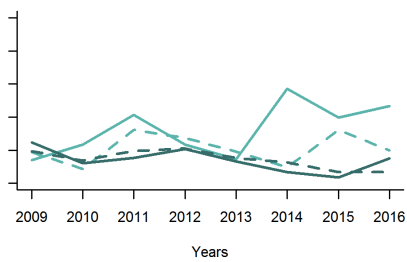
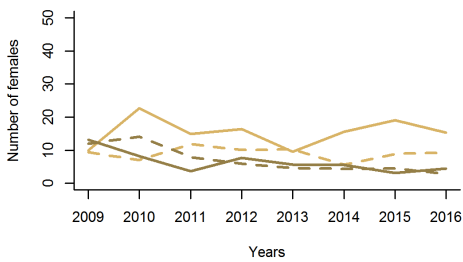
**Common Piece**



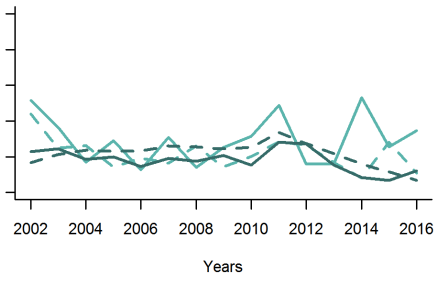
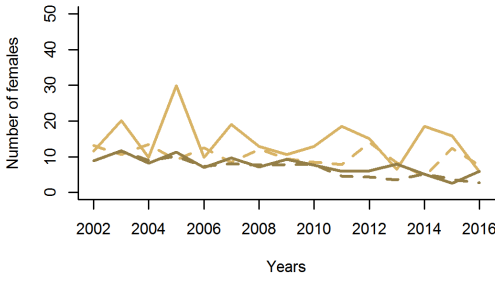
**Extra**



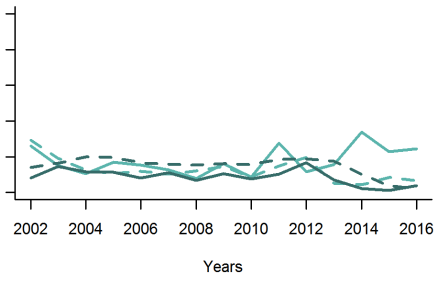
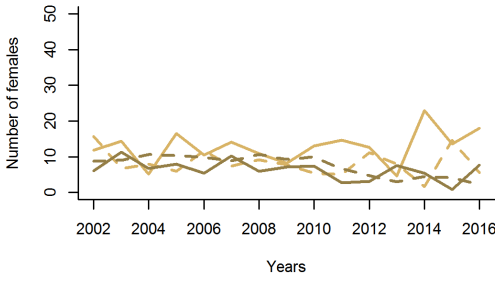
**Great Wood**



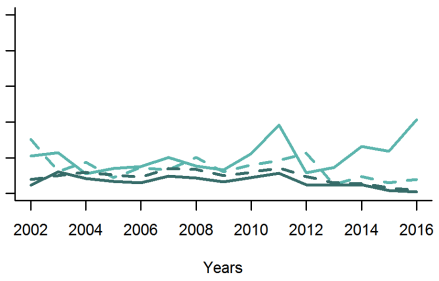
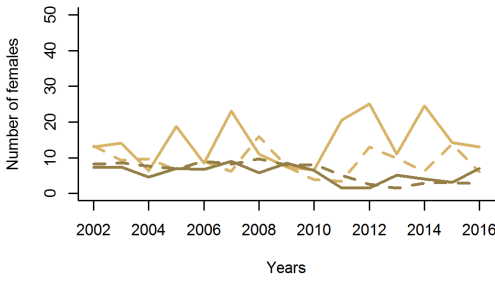
### Marley



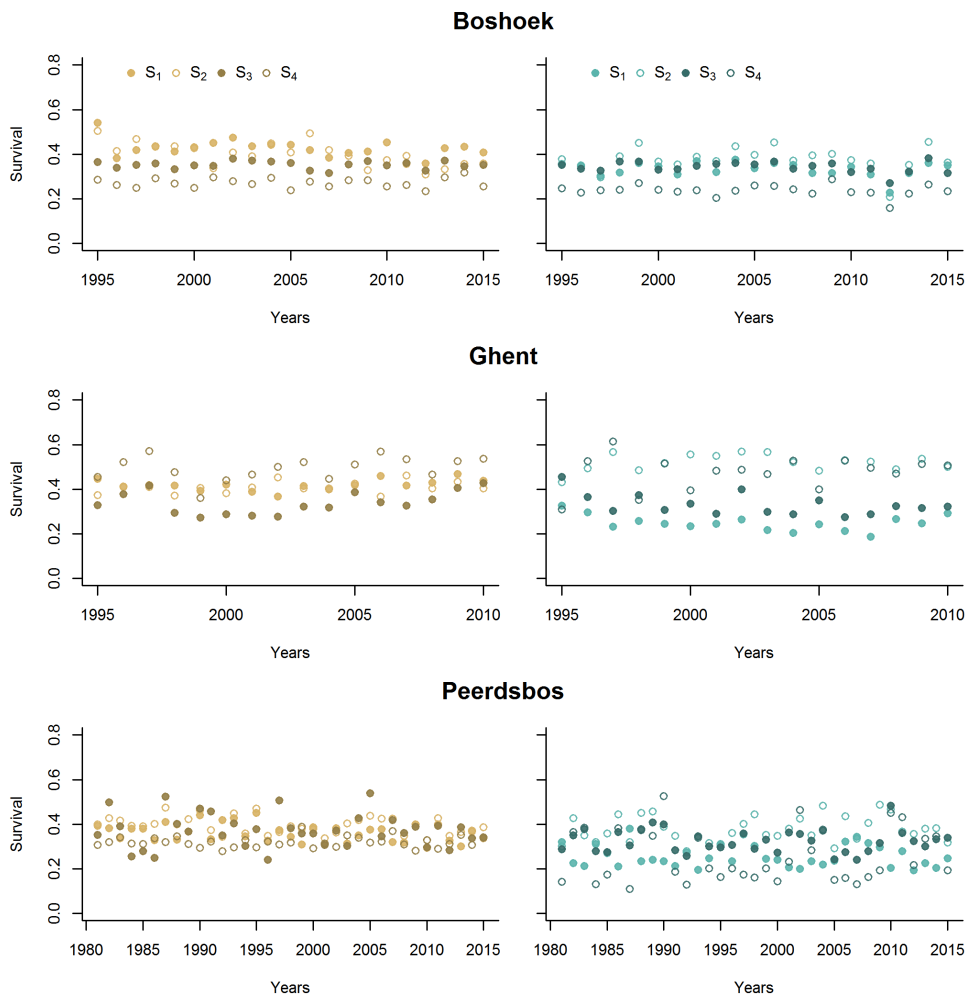
### Marley Plantation



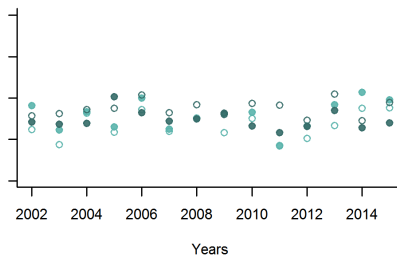
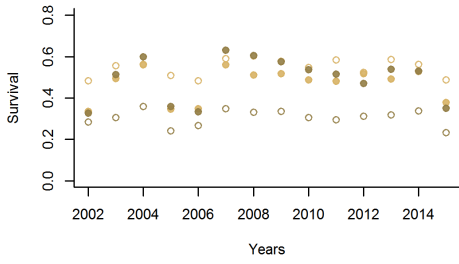
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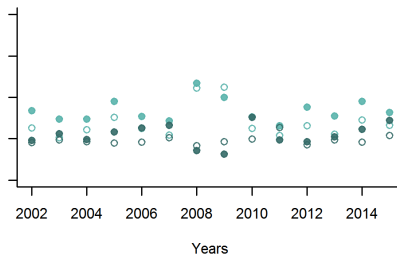
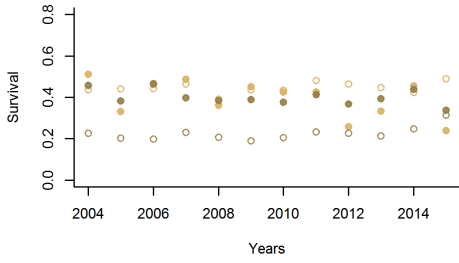
**Supporting Information S3** Posterior means of the annual age-specific survival rates estimated from the IPM in the great tit (in yellow) and blue tit (in blue) populations in Belgium and the UK.



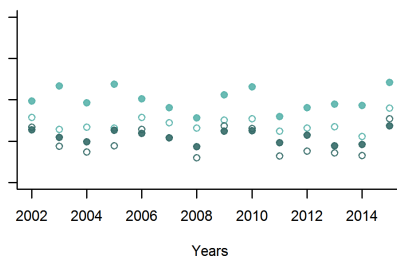
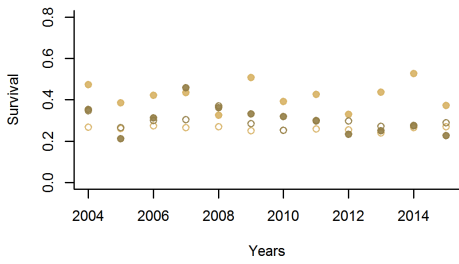
### Bean Wood



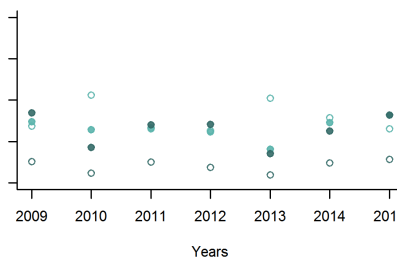
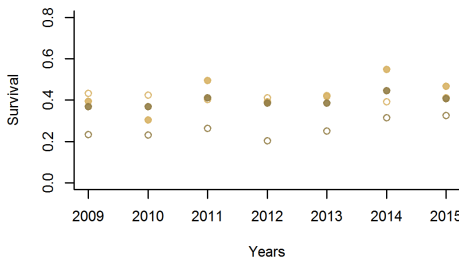
### Broad Oak



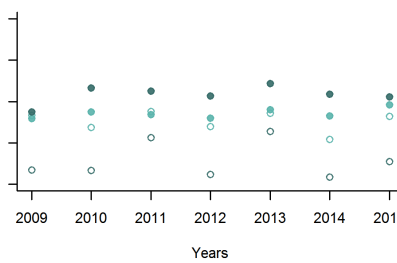
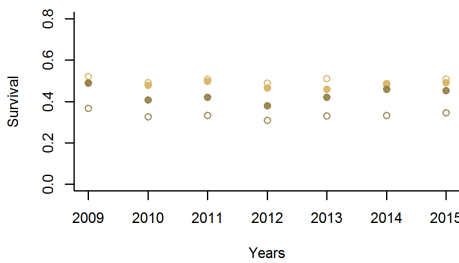
### Common Piece



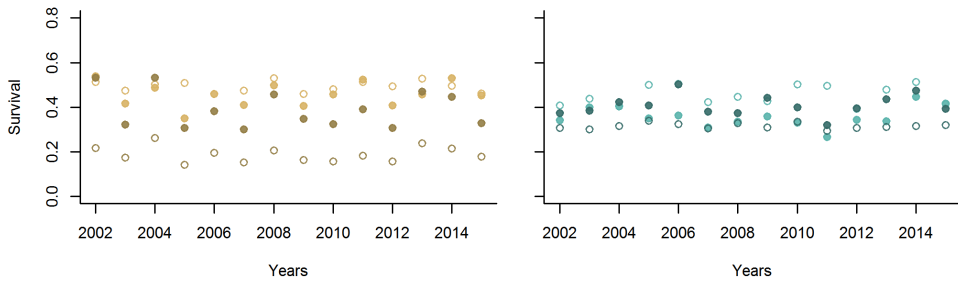
### Extra



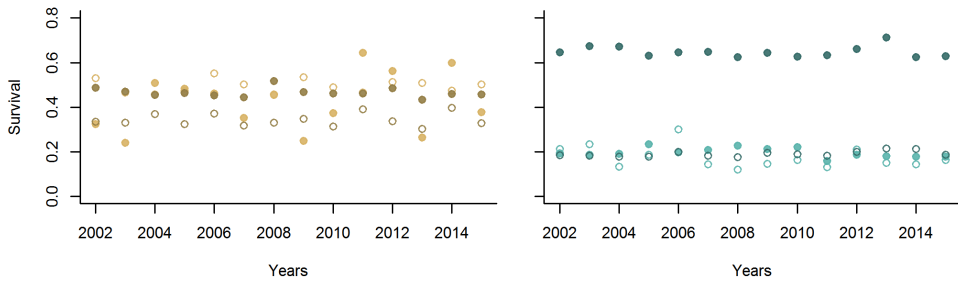
### Great Wood



### Marley



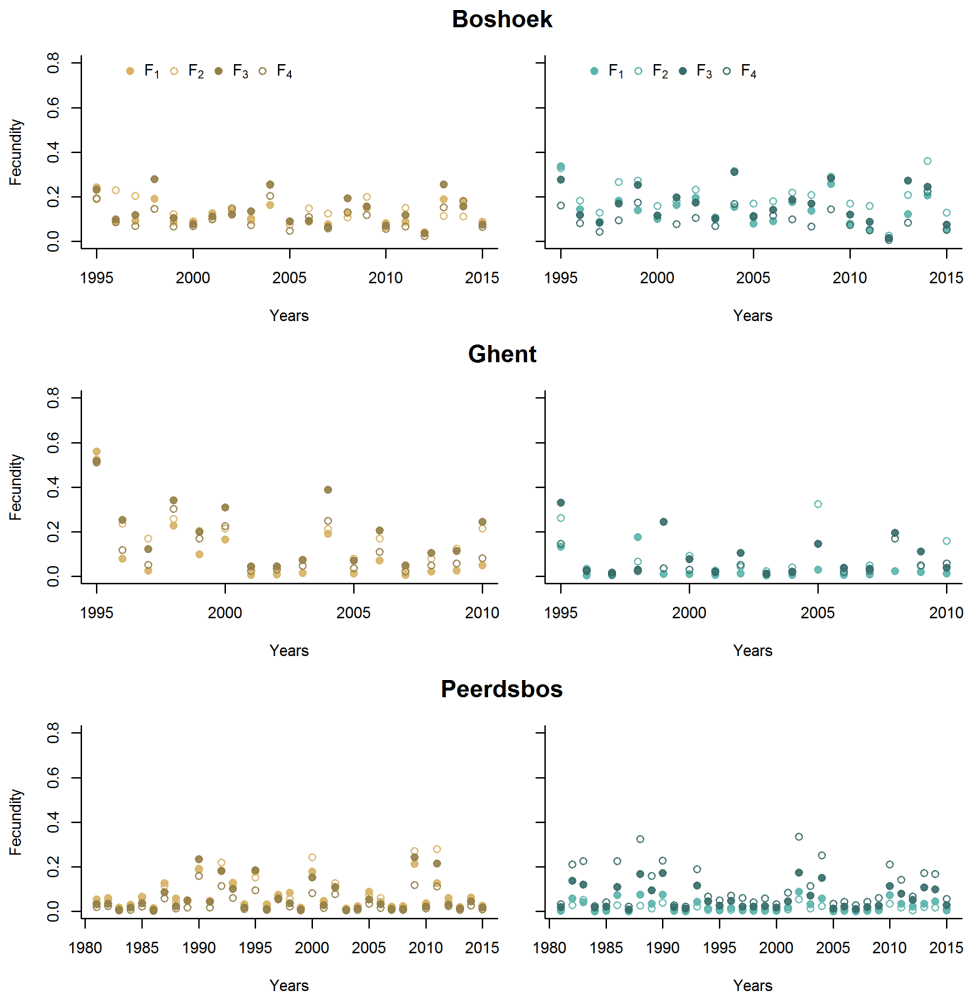
### Marley Plantation



### Singing Way

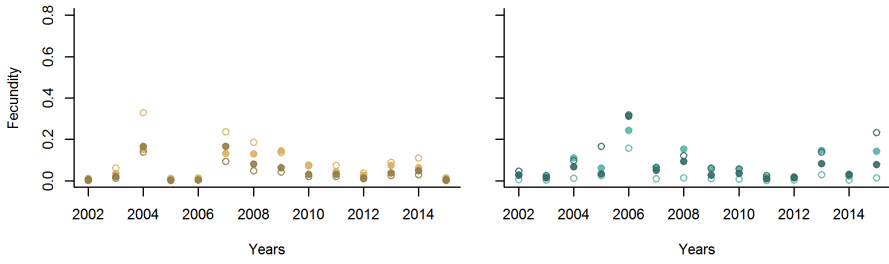


**Supporting Information S4** Posterior means of the annual age-specific fecundity rates estimated from the IPM in the great tit (in yellow) and blue tit (in blue) populations in Belgium and the UK.

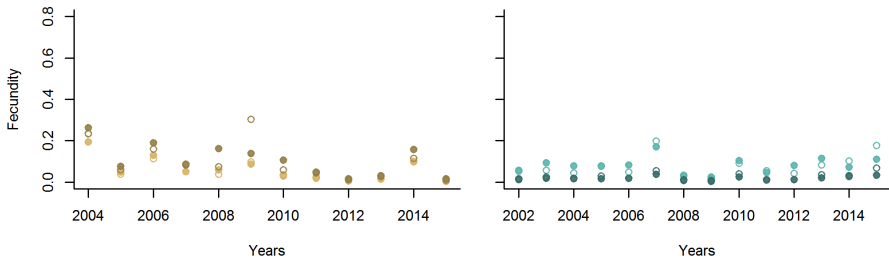




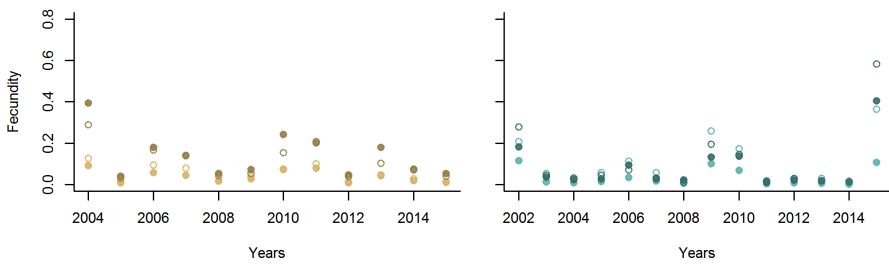
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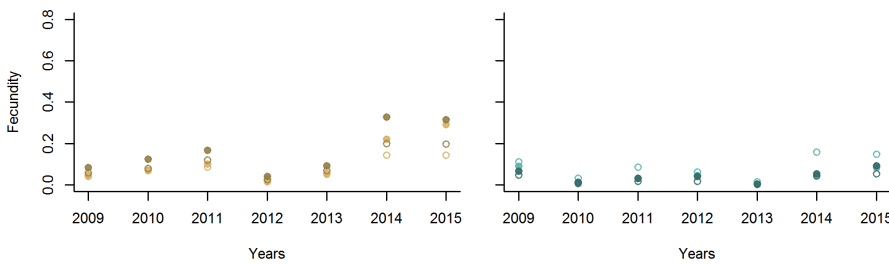
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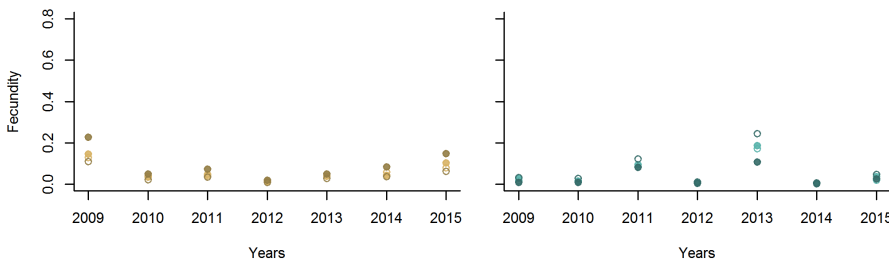
### Common Piece



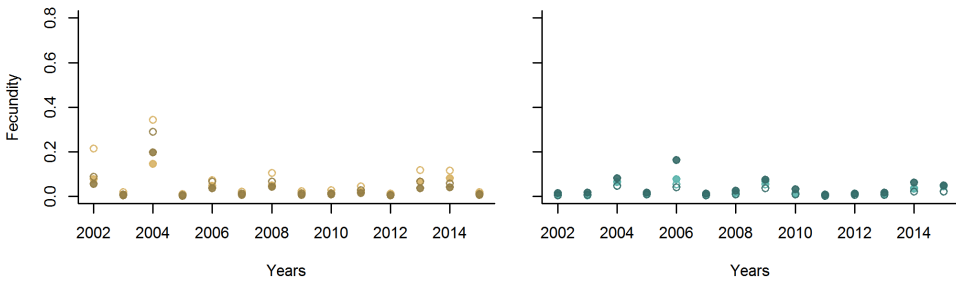
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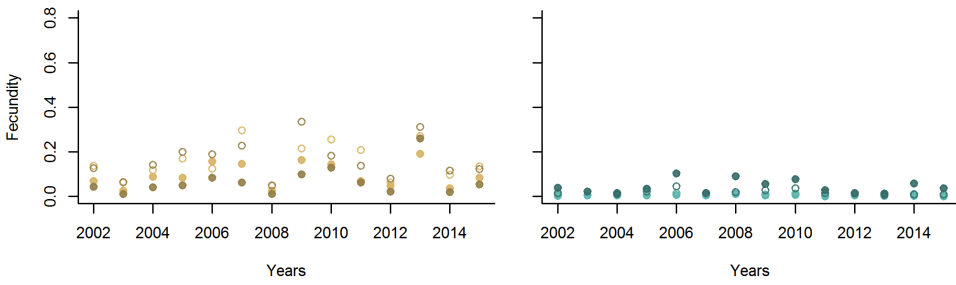
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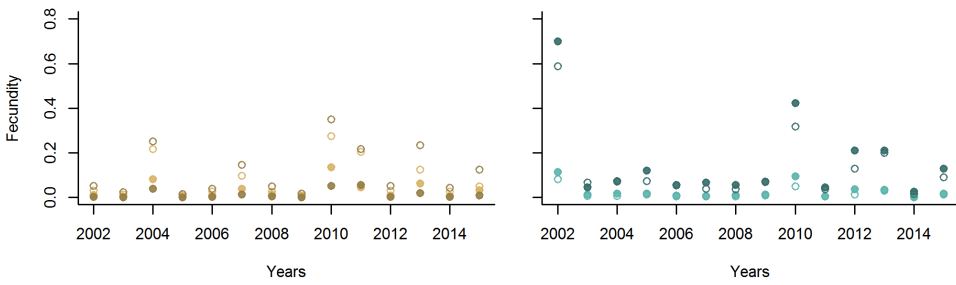
### Marley



### Marley Plantation



### Singing Way



**Supporting Information S5** Mean recapture probabilities  $P$  over the study period together with their 95% CRI estimated from the IPM in the great tit (GT) and blue tit (BT) populations in Belgium and the UK.

Study sites	Recapture probability GT	Recapture probability BT
Boshoek	0.96 [0.94; 0.97]	0.87 [0.83; 0.90]
Ghent	0.81 [0.72; 0.88]	0.49 [0.30; 0.68]
Peerdsbos	0.86 [0.81; 0.91]	0.83 [0.74; 0.90]
Bean Wood	0.88 [0.81; 0.94]	0.78 [0.60; 0.93]
Broad Oak	0.81 [0.73; 0.88]	0.72 [0.57; 0.86]
Common Piece	0.75 [0.61; 0.86]	0.70 [0.51; 0.85]
Extra	0.74 [0.67; 0.81]	0.79 [0.61; 0.93]
Great Wood	0.85 [0.77; 0.90]	0.59 [0.45; 0.74]
Marley	0.80 [0.72; 0.88]	0.78 [0.65; 0.88]
Marley Plantation	0.87 [0.79; 0.92]	0.83 [0.63; 0.97]
Singing Way	0.88 [0.80; 0.95]	0.69 [0.44; 0.88]



# Paper IV

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This paper is awaiting publication and is not included in NTNU Open



# Paper V

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This paper is awaiting publication and is not included in NTNU Open





**Doctoral theses in Biology**  
**Norwegian University of Science and Technology**  
**Department of Biology**

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos Zoology	Breeding events of birds in relation to spring temperature and environmental phenology
1978	Egil Sakshaug	Dr. philos Botany	The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton
1980	Arnfinn Langeland	Dr. philos Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of <i>Pisum sativum</i> and <i>Arabidopsis thaliana</i>
1982	Dag Dolmen	Dr. philos Zoology	Life aspects of two sympatric species of newts ( <i>Triturus</i> , <i>Amphibia</i> ) in Norway, with special emphasis on their ecological niche segregation
1984	Eivin Røskaft	Dr. philos Zoology	Sociobiological studies of the rook <i>Corvus frugilegus</i>
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinizing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exposed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos Zoology	Biochemical genetic studies in fish
1985	John Solem	Dr. philos Zoology	Taxonomy, distribution and ecology of caddisflies ( <i>Trichoptera</i> ) in the Dovrefjell mountains
1985	Randi E. Reinertsen	Dr. philos Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds
1986	Bernt-Erik Sæther	Dr. philos Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach
1986	Torleif Holthe	Dr. philos Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders <i>Oweniimorpha</i> and <i>Terebellomorpha</i> , with special reference to the Arctic and Scandinavian fauna
1987	Helene Lampe	Dr. scient Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires
1987	Olav Hogstad	Dr. philos Zoology	Winter survival strategies of the Willow tit <i>Parus montanus</i>
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coast-inland transect at Nord-Møre, Central Norway

1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of <i>Nicotiana sanderae</i> and <i>Chrysanthemum morifolium</i>
1987	Bjørn Åge Tømmerås	Dr. scient Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction
1988	Hans Christian Pedersen	Dr. philos Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care
1988	Tor G. Heggberget	Dr. philos Zoology	Reproduction in Atlantic Salmon ( <i>Salmo salar</i> ): Aspects of spawning, incubation, early life history and population structure
1988	Marianne V. Nielsen	Dr. scient Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels ( <i>Mytilus edulis</i> )
1988	Ole Kristian Berg	Dr. scient Zoology	The formation of landlocked Atlantic salmon ( <i>Salmo salar</i> L.)
1989	John W. Jensen	Dr. philos Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth
1989	Helga J. Vivås	Dr. scient Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose <i>Alces alces</i>
1989	Reidar Andersen	Dr. scient Zoology	Interactions between a generalist herbivore, the moose <i>Alces alces</i> , and its winter food resources: a study of behavioural variation
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture
1990	Bengt Finstad	Dr. scient Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season
1990	Hege Johannesen	Dr. scient Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmon ( <i>Salmo salar</i> ) and brown trout ( <i>Salmo trutta</i> ): A summary of studies in Norwegian streams
1990	Tor Jørgen Almaas	Dr. scient Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues
1990	Magne Husby	Dr. scient Zoology	Breeding strategies in birds: Experiments with the Magpie <i>Pica pica</i>
1991	Tor Kvam	Dr. scient Zoology	Population biology of the European lynx ( <i>Lynx lynx</i> ) in Norway
1991	Jan Henning L'Abêe Lund	Dr. philos Zoology	Reproductive biology in freshwater fish, brown trout <i>Salmo trutta</i> and roach <i>Rutilus rutilus</i> in particular
1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient Zoology	Reflectometric studies of photomechanical adaptation in superposition eyes of arthropods
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway

1991	Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera <i>Coregonus</i> and <i>Salvelinus</i> : Ontogenic niche shifts and polymorphism
1991	Nina Jonsson	Dr. philos Zoology	Aspects of migration and spawning in salmonids
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torggrim Breiehagen	Dr. scient Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy ( <i>Phleum pratense</i> L.)
1992	Tycho Anker-Nilssen	Dr. scient Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins <i>Fratercula arctica</i>
1992	Bjørn Munro Jenssen	Dr. philos Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks
1992	Arne Vollan Aarset	Dr. philos Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O <sup>6</sup> -methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient Zoology	Cortisol dynamics in Atlantic salmon, <i>Salmo salar</i> L.: Basal and stressor-induced variations in plasma levels and some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter <i>Lutra lutra</i> .
1993	Kjetil Bevanger	Dr. scient Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Botany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient Zoology	Sexual selection in the lekking great snipe ( <i>Gallinago media</i> ): Male mating success and female behaviour at the lek
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant <i>Phalacrocorax carbo carbo</i>
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry ( <i>Rubus idaeus</i> L.)
1994	Inga Elise Bruteig	Dr. scient Botany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses

1994	Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, <i>Vulpes vulpes</i>
1994	Arne Moksnes	Dr. philos Zoology	Host adaptations towards brood parasitism by the Cuckoo
1994	Solveig Bakken	Dr. scient Botany	Growth and nitrogen status in the moss <i>Dicranum majus</i> Sm. as influenced by nitrogen supply
1994	Torbjørn Forseth	Dr. scient Zoology	Bioenergetics in ecological and life history studies of fishes.
1995	Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions
1995	Hanne Christensen	Dr. scient Zoology	Determinants of Otter <i>Lutra lutra</i> distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink <i>Mustela vison</i>
1995	Svein Håkon Lorentsen	Dr. scient Zoology	Reproductive effort in the Antarctic Petrel <i>Thalassoica antarctica</i> ; the effect of parental body size and condition
1995	Chris Jørgen Jensen	Dr. scient Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995	Martha Kold Bakkevig	Dr. scient Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport
1995	Vidar Moen	Dr. scient Zoology	Distribution patterns and adaptations to light in newly introduced populations of <i>Mysis relicta</i> and constraints on Cladoceran and Char populations
1995	Hans Haavardsholm Blom	Dr. philos Botany	A revision of the <i>Schistidium apocarpum</i> complex in Norway and Sweden
1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; impact fish-bacterial interactions on growth and survival of larvae
1996	Ola Ugedal	Dr. scient Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjörg Einarsdottir	Dr. scient Zoology	Production of Atlantic salmon ( <i>Salmo salar</i> ) and Arctic charr ( <i>Salvelinus alpinus</i> ): A study of some physiological and immunological responses to rearing routines
1996	Christina M. S. Pereira	Dr. scient Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation
1996	Jan Fredrik Børseth	Dr. scient Zoology	The sodium energy gradients in muscle cells of <i>Mytilus edulis</i> and the effects of organic xenobiotics
1996	Gunnar Henriksen	Dr. scient Zoology	Status of Grey seal <i>Halichoerus grypus</i> and Harbour seal <i>Phoca vitulina</i> in the Barents sea region
1997	Gunvor Øie	Dr. scient Botany	Evaluation of rotifer <i>Brachionus plicatilis</i> quality in early first feeding of turbot <i>Scophthalmus maximus</i> L. larvae
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spruce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters
1997	Ole Reitan	Dr. scient Zoology	Responses of birds to habitat disturbance due to damming
1997	Jon Arne Grøttum	Dr. scient Zoology	Physiological effects of reduced water quality on fish in aquaculture

1997	Per Gustav Thingstad	Dr. scient Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher
1997	Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as
1997	Signe Nybø	Dr. scient Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper <i>Cinclus cinclus</i> in southern Norway
1997	Atle Wibe	Dr. scient Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil ( <i>Hylobius abietis</i> ), analysed by gas chromatography linked to electrophysiology and to mass spectrometry
1997	Rolv Lundheim	Dr. scient Zoology	Adaptive and incidental biological ice nucleators
1997	Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to soil bacteria by studies of natural transformation in <i>Acinetobacter calcoaceticus</i>
1997	Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos Zoology	Population responses of Arctic charr ( <i>Salvelinus alpinus</i> (L.)) and brown trout ( <i>Salmo trutta</i> L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon ( <i>Salmo salar</i> ) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
1998	Thor Harald Ringsby	Dr. scient Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient Zoology	Variation in population dynamics and life history in a Norwegian moose ( <i>Alces alces</i> ) population: consequences of harvesting in a variable environment
1998	Sigurd Mjølven Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the <i>Sphagnum recurvum</i> complex (Bryophyta): genetic variation and phenotypic plasticity
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservation biological approach
1998	Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls <i>Strix aluco</i> : An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Botany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway

1999	Ingvar Stenberg	Dr. scient Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker <i>Dendrocopos leucotos</i>
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis
1999	Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod ( <i>Gadus morhua</i> L.) and Halibut ( <i>Hippoglossus hippoglossus</i> L.)
1999	Marianne Giæver	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting ( <i>Micromisistius poutassou</i> ), haddock ( <i>Melanogrammus aeglefinus</i> ) and cod ( <i>Gadus morhua</i> ) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes <i>Dicranum majus</i> , <i>Hylocomium splendens</i> , <i>Plagiochila asplenigides</i> , <i>Ptilium crista-castrensis</i> and <i>Rhytidiadelphus lukeus</i>
1999	Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon ( <i>Salmo salar</i> ) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from <i>Brassica napus</i> hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families:
1999	Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon ( <i>Salmo salar</i> L.) and Brown trout ( <i>Salmo trutta</i> L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient Zoology	Host specificity as a parameter in estimates of arthropod species richness
1999	Sonja Andersen	Dr. scient Zoology	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient Zoology	The Cuckoo ( <i>Cuculus canorus</i> ) and its host: adaptations and counteradaptations in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial control of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient Zoology	Sexual segregation in the African elephant ( <i>Loxodonta africana</i> )
2000	Odd A. Gulseth	Dr. philos Zoology	Seawater tolerance, migratory behaviour and growth of Charr, ( <i>Salvelinus alpinus</i> ), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout ( <i>Salmo trutta</i> ) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient Zoology	Production and nutritional adaptation of the brine shrimp <i>Artemia</i> sp. as live food organism for larvae of marine cold water fish species



2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forest systems
2001	Ingebrigt Uglem	Dr. scient Zoology	Male dimorphism and reproductive biology in corkwing wrasse ( <i>Symphodus melops</i> L.)
2001	Bård Gunnar Stokke	Dr. scient Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient Zoology	Spatio-temporal dynamics in Svalbard reindeer ( <i>Rangifer tarandus platyrhynchus</i> )
2002	Mariann Sandsund	Dr. scient Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient Zoology	The function of scent marking in beaver ( <i>Castor fiber</i> )
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A <sub>2</sub> in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr. philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in <i>Arabidopsis thaliana</i> and the Ral GTPase from <i>Drosophila melanogaster</i>
2002	Henrik Jensen	Dr. scient Biology	Causes and consequences of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback <i>Gasterosteus aculeatur</i> L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo ( <i>Syncerus caffer</i> ) in Chobe National Park, Botswana
2003	Marit Stranden	Dr. scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species ( <i>Helicoverpa armigera</i> , <i>Helicoverpa assulta</i> and <i>Heliothis virescens</i> )
2003	Kristian Hassel	Dr. scient Biology	Life history characteristics and genetic variation in an expanding species, <i>Pogonatum dentatum</i>
2003	David Alexander Rae	Dr. scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Arctic environments
2003	Åsa A Borg	Dr. scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr. scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon ( <i>Salmo salar</i> L.) parr and smolt
2004	Torkild Bakken	Dr. scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)

2004	Ingar Pareliussen	Dr. scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr. scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in <i>Arabidopsis thaliana</i>
2004	Liv S. Nilsen	Dr. scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr. scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species ( <i>Heliothis virescens</i> , <i>Helicoverpa armigera</i> and <i>Helicoverpa assulta</i> )
2004	Lene Østby	Dr. scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr. scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004	Lisbeth Mehli	Dr. scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry ( <i>Fragaria x ananassa</i> ): characterisation and induction of the gene following fruit infection by <i>Botrytis cinerea</i>
2004	Børge Moe	Dr. scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr. scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr. scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr. scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	PhD Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr. scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr. scient Biology	Organochlorine pollutants in grey seal ( <i>Halichoerus grypus</i> ) pups and their impact on plasma thyroid hormone and vitamin A concentrations
2005	Christian Westad	Dr. scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	PhD Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	PhD Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	PhD Biology	Investigation of the biological activities and chemical constituents of selected <i>Echinops</i> spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	PhD Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	PhD Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr. scient Biology	The European whitefish <i>Coregonus lavaretus</i> (L.) species complex: historical contingency and adaptive radiation



2006	Kari Mette Murvoll	PhD Biology	Levels and effects of persistent organic pollutants (POPs) in seabirds, Retinoids and $\alpha$ -tocopherol – potential biomarkers of POPs in birds?
2006	Ivar Herfindal	Dr. scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	PhD Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on <i>Calanus finmarchicus</i>
2006	Jan Ove Gjershaug	Dr. philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr. scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	PhD Biology	<i>Acesta oophaga</i> and <i>Acesta excavata</i> – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	PhD Biology	Metal-mediated oxidative stress responses in brown trout ( <i>Salmo trutta</i> ) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	PhD Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	PhD Biology	Wildlife conservation and local land use conflicts in Western Serengeti Corridor, Tanzania
2006	Anna Maria Billing	PhD Biology	Reproductive decisions in the sex role reversed pipefish <i>Syngnathus typhle</i> : when and how to invest in reproduction
2006	Henrik Pärn	PhD Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	PhD Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	PhD Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	PhD Biology	Metal binding proteins and antifreeze proteins in the beetle <i>Tenebrio molitor</i> - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	PhD Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	PhD Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	PhD Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth <i>Heliothis virescens</i>
2007	Stig Ulland	PhD Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, ( <i>Mamestra brassicae</i> L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	PhD Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	PhD Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	PhD Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
2007	Julius William Nyahongo	PhD Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania

2007	Shombe Ntaraluka Hassan	PhD Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	PhD Biology	Functional development and response to dietary treatment in larval Atlantic cod ( <i>Gadus morhua</i> L.) Focus on formulated diets and early weaning
2007	Anne Skjetne Mortensen	PhD Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	PhD Biology	The Svalbard reindeer ( <i>Rangifer tarandus platyrhynchus</i> ) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	PhD Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	PhD Biology	The ecology and behaviour of the Masai Ostrich ( <i>Struthio camelus massaicus</i> ) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	PhD Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, <i>Taeniopygia guttata</i>
2008	Sølvi Wehn	PhD Biology	Biodiversity dynamics in semi-natural mountain landscapes - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	PhD Biology	The Role of Androgens on previtellogenic oocyte growth in Atlantic cod ( <i>Gadus morhua</i> ): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations
2008	Katarina Mariann Jørgensen	Dr. scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008	Tommy Jørstad	PhD Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	PhD Biology	<i>Arabidopsis thaliana</i> Responses to Aphid Infestation
2008	Jussi Evertsen	PhD Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	PhD Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008	Ragnhild Lyngved	PhD Biology	Somatic embryogenesis in <i>Cyclamen persicum</i> . Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	PhD Biology	Cost of rapid growth in salmonid fishes
2008	Line Johansen	PhD Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	PhD Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease
2009	Pål Kvello	PhD Biology	Neurons forming the network involved in gustatory coding and learning in the moth <i>Heliothis virescens</i> : Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	PhD Biology	Extreme Frost Tolerance in Boreal Conifers
2009	Johan Reinert Vikan	PhD Biology	Coevolutionary interactions between common cuckoos <i>Cuculus canorus</i> and <i>Fringilla</i> finches

2009	Zsolt Volent	PhD Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009	Lester Rocha	PhD Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009	Dennis Ikanda	PhD Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions ( <i>Panthera leo</i> ) in Tanzania
2010	Huy Quang Nguyen	PhD Biology	Egg characteristics and development of larval digestive function of cobia ( <i>Rachycentron canadum</i> ) in response to dietary treatments - Focus on formulated diets
2010	Eli Kvingedal	PhD Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010	Sverre Lundemo	PhD Biology	Molecular studies of genetic structuring and demography in <i>Arabidopsis</i> from Northern Europe
2010	Iddi Mihijai Mfunda	PhD Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. The Case of Serengeti Ecosystem, Tanzania
2010	Anton Tinchov Antonov	PhD Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010	Anders Lyngstad	PhD Biology	Population Ecology of <i>Eriophorum latifolium</i> , a Clonal Species in Rich Fen Vegetation
2010	Hilde Færevik	PhD Biology	Impact of protective clothing on thermal and cognitive responses
2010	Ingerid Brønne Arbo	PhD Medical technology	Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans
2010	Yngvild Vindenes	PhD Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010	Hans-Richard Brattbakk	PhD Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011	Geir Hysing Bolstad	PhD Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy
2011	Karen de Jong	PhD Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby ( <i>Gobiusculus flavescens</i> )
2011	Ann-Iren Kittang	PhD Biology	<i>Arabidopsis thaliana</i> L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS: The science of space experiment integration and adaptation to simulated microgravity
2011	Aline Magdalena Lee	PhD Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011	Christopher Gravingen Sørmo	PhD Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in <i>Arabidopsis thaliana</i>
2011	Grethe Robertsen	PhD Biology	Relative performance of salmonid phenotypes across environments and competitive intensities
2011	Line-Kristin Larsen	PhD Biology	Life-history trait dynamics in experimental populations of guppy ( <i>Poecilia reticulata</i> ): the role of breeding regime and captive environment
2011	Maxim A. K. Teichert	PhD Biology	Regulation in Atlantic salmon ( <i>Salmo salar</i> ): The interaction between habitat and density
2011	Torunn Beate Hancke	PhD Biology	Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology

2011	Sajeda Begum	PhD Biology	Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh
2011	Kari J. K. Attramadal	PhD Biology	Water treatment as an approach to increase microbial control in the culture of cold water marine larvae
2011	Camilla Kalvatn Egset	PhD Biology	The Evolvability of Static Allometry: A Case Study
2011	AHM Raihan Sarker	PhD Biology	Conflict over the conservation of the Asian elephant ( <i>Elephas maximus</i> ) in Bangladesh
2011	Gro Dehli Villanger	PhD Biology	Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals
2011	Kari Bjørneraas	PhD Biology	Spatiotemporal variation in resource utilisation by a large herbivore, the moose
2011	John Odden	PhD Biology	The ecology of a conflict: Eurasian lynx depredation on domestic sheep
2011	Simen Pedersen	PhD Biology	Effects of native and introduced cervids on small mammals and birds
2011	Mohsen Falahati-Anbaran	PhD Biology	Evolutionary consequences of seed banks and seed dispersal in <i>Arabidopsis</i>
2012	Jakob Hønborg Hansen	PhD Biology	Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance
2012	Elin Noreen	PhD Biology	Consequences of diet quality and age on life-history traits in a small passerine bird
2012	Irja Ida Ratikainen	PhD Biology	Foraging in a variable world: adaptations to stochasticity
2012	Aleksander Handå	PhD Biology	Cultivation of mussels ( <i>Mytilus edulis</i> ): Feed requirements, storage and integration with salmon ( <i>Salmo salar</i> ) farming
2012	Morten Kraabøl	PhD Biology	Reproductive and migratory challenges inflicted on migrant brown trout ( <i>Salmo trutta</i> L.) in a heavily modified river
2012	Jisca Huisman	PhD Biology	Gene flow and natural selection in Atlantic salmon
2012	Maria Bergvik	PhD Biology	Lipid and astaxanthin contents and biochemical post-harvest stability in <i>Calanus finmarchicus</i>
2012	Bjarte Bye Løfaldli	PhD Biology	Functional and morphological characterization of central olfactory neurons in the model insect <i>Heliothis virescens</i> .
2012	Karen Marie Hammer	PhD Biology	Acid-base regulation and metabolite responses in shallow- and deep-living marine invertebrates during environmental hypercapnia
2012	Øystein Nordrum Wiggen	PhD Biology	Optimal performance in the cold
2012	Robert Dominikus Fyumagwa	Dr. Philos Biology	Anthropogenic and natural influence on disease prevalence at the human –livestock-wildlife interface in the Serengeti ecosystem, Tanzania
2012	Jenny Bytingsvik	PhD Biology	Organohalogenated contaminants (OHCs) in polar bear mother-cub pairs from Svalbard, Norway. Maternal transfer, exposure assessment and thyroid hormone disruptive effects in polar bear cubs
2012	Christer Moe Rolandsen	PhD Biology	The ecological significance of space use and movement patterns of moose in a variable environment
2012	Erlend Kjeldsberg Hovland	PhD Biology	Bio-optics and Ecology in <i>Emiliania huxleyi</i> Blooms: Field and Remote Sensing Studies in Norwegian Waters

2012	Lise Cats Myhre	PhD Biology	Effects of the social and physical environment on mating behaviour in a marine fish
2012	Tonje Aronsen	PhD Biology	Demographic, environmental and evolutionary aspects of sexual selection
2012	Bin Liu	PhD Biology	Molecular genetic investigation of cell separation and cell death regulation in <i>Arabidopsis thaliana</i>
2013	Jørgen Rosvold	PhD Biology	Ungulates in a dynamic and increasingly human dominated landscape – A millennia-scale perspective
2013	Pankaj Barah	PhD Biology	Integrated Systems Approaches to Study Plant Stress Responses
2013	Marit Linnerud	PhD Biology	Patterns in spatial and temporal variation in population abundances of vertebrates
2013	Xinxin Wang	PhD Biology	Integrated multi-trophic aquaculture driven by nutrient wastes released from Atlantic salmon ( <i>Salmo salar</i> ) farming
2013	Ingrid Ertshus Mathisen	PhD Biology	Structure, dynamics, and regeneration capacity at the sub-arctic forest-tundra ecotone of northern Norway and Kola Peninsula, NW Russia
2013	Anders Foldvik	PhD Biology	Spatial distributions and productivity in salmonid populations
2013	Anna Marie Holand	PhD Biology	Statistical methods for estimating intra- and inter-population variation in genetic diversity
2013	Anna Solvang Båtnes	PhD Biology	Light in the dark – the role of irradiance in the high Arctic marine ecosystem during polar night
2013	Sebastian Wacker	PhD Biology	The dynamics of sexual selection: effects of OSR, density and resource competition in a fish
2013	Cecilie Miljeteig	PhD Biology	Phototaxis in <i>Calanus finmarchicus</i> – light sensitivity and the influence of energy reserves and oil exposure
2013	Ane Kjersti Vie	PhD Biology	Molecular and functional characterisation of the IDA family of signalling peptides in <i>Arabidopsis thaliana</i>
2013	Marianne Nymark	PhD Biology	Light responses in the marine diatom <i>Phaeodactylum tricorutum</i>
2014	Jannik Schultner	PhD Biology	Resource Allocation under Stress - Mechanisms and Strategies in a Long-Lived Bird
2014	Craig Ryan Jackson	PhD Biology	Factors influencing African wild dog ( <i>Lycaon pictus</i> ) habitat selection and ranging behaviour: conservation and management implications
2014	Aravind Venkatesan	PhD Biology	Application of Semantic Web Technology to establish knowledge management and discovery in the Life Sciences
2014	Kristin Collier Valle	PhD Biology	Photoacclimation mechanisms and light responses in marine micro- and macroalgae
2014	Michael Puffer	PhD Biology	Effects of rapidly fluctuating water levels on juvenile Atlantic salmon ( <i>Salmo salar</i> L.)
2014	Gundula S. Bartzke	PhD Biology	Effects of power lines on moose ( <i>Alces alces</i> ) habitat selection, movements and feeding activity
2014	Eirin Marie Bjørkvoll	PhD Biology	Life-history variation and stochastic population dynamics in vertebrates
2014	Håkon Holand	PhD Biology	The parasite <i>Syngamus trachea</i> in a metapopulation of house sparrows
2014	Randi Magnus Sommerfelt	PhD Biology	Molecular mechanisms of inflammation – a central role for cytosolic phospholipase A2
2014	Espen Lie Dahl	PhD Biology	Population demographics in white-tailed eagle at an on-shore wind farm area in coastal Norway

2014	Anders Øverby	PhD Biology	Functional analysis of the action of plant isothiocyanates: cellular mechanisms and in vivo role in plants, and anticancer activity
2014	Kamal Prasad Acharya	PhD Biology	Invasive species: Genetics, characteristics and trait variation along a latitudinal gradient.
2014	Ida Beathe Øverjordet	PhD Biology	Element accumulation and oxidative stress variables in Arctic pelagic food chains: <i>Calanus</i> , little auks ( <i>Alle alle</i> ) and black-legged kittiwakes ( <i>Rissa tridactyla</i> )
2014	Kristin Møller Gabrielsen	PhD Biology	Target tissue toxicity of the thyroid hormone system in two species of arctic mammals carrying high loads of organohalogen contaminants
2015	Gine Roll Skjervø	Dr. philos Biology	Testing behavioral ecology models with historical individual-based human demographic data from Norway
2015	Nils Erik Gustaf Forsberg	PhD Biology	Spatial and Temporal Genetic Structure in Landrace Cereals
2015	Leila Alipanah	PhD Biology	Integrated analyses of nitrogen and phosphorus deprivation in the diatoms <i>Phaeodactylum tricornutum</i> and <i>Seminavis robusta</i>
2015	Javad Najafi	PhD Biology	Molecular investigation of signaling components in sugar sensing and defense in <i>Arabidopsis thaliana</i>
2015	Bjørnar Sporsheim	PhD Biology	Quantitative confocal laser scanning microscopy: optimization of in vivo and in vitro analysis of intracellular transport
2015	Magni Olsen Kyrkjæide	PhD Biology	Genetic variation and structure in peatmosses ( <i>Sphagnum</i> )
2015	Keshuai Li	PhD Biology	Phospholipids in Atlantic cod ( <i>Gadus morhua</i> L.) larvae rearing: Incorporation of DHA in live feed and larval phospholipids and the metabolic capabilities of larvae for the de novo synthesis
2015	Ingvild Fladvad Størdal	PhD Biology	The role of the copepod <i>Calanus finmarchicus</i> in affecting the fate of marine oil spills
2016	Thomas Kvalnes	PhD Biology	Evolution by natural selection in age-structured populations in fluctuating environments
2016	Øystein Leiknes	PhD Biology	The effect of nutrition on important life-history traits in the marine copepod <i>Calanus finmarchicus</i>
2016	Johan Henrik Hårdensson Berntsen	PhD Biology	Individual variation in survival: The effect of incubation temperature on the rate of physiological ageing in a small passerine bird
2016	Marianne Opsahl Olufsen	PhD Biology	Multiple environmental stressors: Biological interactions between parameters of climate change and perfluorinated alkyl substances in fish
2016	Rebekka Varne	PhD Biology	Tracing the fate of escaped cod ( <i>Gadus morhua</i> L.) in a Norwegian fjord system
2016	Anette Antonsen Fenstad	PhD Biology	Pollutant Levels, Antioxidants and Potential Genotoxic Effects in Incubating Female Common Eiders ( <i>Somateria mollissima</i> )
2016	Wilfred Njama Marealle	PhD Biology	Ecology, Behaviour and Conservation Status of Masai Giraffe ( <i>Giraffa camelopardalis tippelskirchi</i> ) in Tanzania
2016	Ingunn Nilssen	PhD Biology	Integrated Environmental Mapping and Monitoring: A Methodological approach for end users.
2017	Konika Chawla	PhD Biology	Discovering, analysing and taking care of knowledge.
2017	Øystein Hjorthol Opedal	PhD Biology	The Evolution of Herkogamy: Pollinator Reliability, Natural Selection, and Trait Evolvability.



2017	Ane Marlene Myhre	PhD Biology	Effective size of density dependent populations in fluctuating environments
2017	Emmanuel Hosiana Masenga	PhD Biology	Behavioural Ecology of Free-ranging and Reintroduced African Wild Dog ( <i>Lycaon pictus</i> ) Packs in the Serengeti Ecosystem, Tanzania
2017	Xiaolong Lin	PhD Biology	Systematics and evolutionary history of <i>Tanytarsus</i> van der Wulp, 1874 (Diptera: Chironomidae)
2017	Emmanuel Clamsen Mmassy	PhD Biology	Ecology and Conservation Challenges of the Kori bustard in the Serengeti National Park
2017	Richard Daniel Lyamuya	PhD Biology	Depredation of Livestock by Wild Carnivores in the Eastern Serengeti Ecosystem, Tanzania
2017	Katrin Hoydal	PhD Biology	Levels and endocrine disruptive effects of legacy POPs and their metabolites in long-finned pilot whales of the Faroe Islands
2017	Berit Glomstad	PhD Biology	Adsorption of phenanthrene to carbon nanotubes and its influence on phenanthrene bioavailability/toxicity in aquatic organism
2017	Øystein Nordeide Kielland	PhD Biology	Sources of variation in metabolism of an aquatic ectotherm
2017	Narjes Yousefi	PhD Biology	Genetic divergence and speciation in northern peatmosses ( <i>Sphagnum</i> )
2018	Signe Christensen-Dalgaard	PhD Biology	Drivers of seabird spatial ecology - implications for development of offshore wind-power in Norway
2018	Janos Urbancsok	PhD Biology	Endogenous biological effects induced by externally supplemented glucosinolate hydrolysis products (GHPs) on <i>Arabidopsis thaliana</i>
2018	Alice Mühlroth	PhD Biology	The influence of phosphate depletion on lipid metabolism of microalgae
2018	Franco Peniel Mbise	PhD Biology	Human-Carnivore Coexistence and Conflict in the Eastern Serengeti, Tanzania
2018	Stine Svalheim Markussen	PhD Biology	Causes and consequences of intersexual life history variation in a harvested herbivore population
2018	Mia Vedel Sørensen	PhD Biology	Carbon budget consequences of deciduous shrub expansion in alpine tundra ecosystems
2018	Hanna Maria Kauko	PhD Biology	Light response and acclimation of microalgae in a changing Arctic
2018	Erlend I. F. Fossen	PhD Biology	Trait evolvability: effects of thermal plasticity and genetic correlations among traits
2019	Peter Sjolte Ranke	PhD Biology	Demographic and genetic and consequences of dispersal in house sparrows
2019	Mathilde Le Moullec	PhD Biology	Spatiotemporal variation in abundance of key tundra species: from local heterogeneity to large-scale synchrony
2019	Endre Grüner Ofstad	PhD Biology	Causes and consequences of variation in resource use and social structure in ungulates
2019	Yang Jin	PhD Biology	Development of lipid metabolism in early life stage of Atlantic salmon ( <i>Salmo salar</i> )
2019	Elena Albertsen	PhD Biology	Evolution of floral traits: from ecological context to functional integration
2019	Mominul Islam Nahid	PhD Biology	Interaction between two Asian cuckoos and their hosts in Bangladesh
2019	Knut Jørgen Egelie	PhD Biology	Management of intellectual property in university-industry collaborations – public access to and control of knowledge
2019	Thomas Ray Haaland	PhD Biology	Adaptive responses to environmental stochasticity on different evolutionary time-scales

2019	Kwaslema Malle Hariohay	PhD Biology	Human wildlife interactions in the Ruaha-Rungwa Ecosystem, Central Tanzania
2019	Mari Engvig Løseth	PhD Biology	Exposure and effects of emerging and legacy organic pollutants in white-tailed eagle ( <i>Haliaeetus albicilla</i> ) nestlings
2019	Joseph Mbyati Mukeka	PhD Biology	Human-Wildlife Conflicts and Compensation for Losses in Kenya: Dynamics, Characteristics and Correlates
2019	Helene Løvstrand Svarva	PhD Biology	Dendroclimatology in southern Norway: tree rings, demography and climate
2019	Nathalie Briels	PhD Biology	Exposure and effects of legacy and emerging organic pollutants in developing birds – Laboratory and field studies
2019	Anders L.Kolstad	PhD Biology	Moose browsing effects on boreal production forests – implications for ecosystems and human society
2019	Bart Peeters	PhD Biology	Population dynamics under climate change and harvesting: Results from the high Arctic Svalbard reindeer
2019	Alex Kojo Datsomor	PhD Biology	The molecular basis of long chain polyunsaturated fatty acid (LC-PUFA) biosynthesis in Atlantic salmon ( <i>Salmo salar L</i> ): In vivo functions, functional redundancy and transcriptional regulation of LC-PUFA biosynthetic enzymes
2020	Ingun Næve	PhD Biology	Development of non-invasive methods using ultrasound technology in monitoring of Atlantic salmon ( <i>Salmo salar</i> ) production and reproduction
2020	Rachael Morgan	PhD Biology	Physiological plasticity and evolution of thermal performance in zebrafish
2020	Mahsa Jalili	PhD Biology	Effects of different dietary ingredients on the immune responses and antioxidant status in Atlantic salmon ( <i>Salmo salar L.</i> ): possible nutrionomics approaches
2020	Haiqing Wang	PhD Biology	Utilization of the polychaete <i>Hediste diversicolor</i> (O.F. Millier, 1776) in recycling waste nutrients from land-based fish farms for value adding applications'
2020	Louis Hunninck	PhD Biology	Physiological and behavioral adaptations of impala to anthropogenic disturbances in the Serengeti ecosystems
2020	Kate Layton-Matthews	PhD Biology	Demographic consequences of rapid climate change and density dependence in migratory Arctic geese
2020	Amit Kumar Sharma	PhD Biology	Genome editing of marine algae: Technology development and use of the CRISPR/Cas9 system for studies of light harvesting complexes and regulation of phosphate homeostasis
2020	Lars Rød-Eriksen	PhD Biology	Drivers of change in meso-carnivore distributions in a northern ecosystem
2020	Lone Sunniva Jevne	PhD Biology	Development and dispersal of salmon lice ( <i>Lepeophtheirus salmonis</i> Krøyer, 1837) in commercial salmon farming localities
2020	Sindre Håvarstein Eldøy	PhD Biology	The influence of physiology, life history and environmental conditions on the marine migration patterns of sea trout
2020	Vasundra Touré	PhD Biology	Improving the FAIRness of causal interactions in systems biology: data curation and standardisation to support systems modelling applications
2020	Silje Forbord	PhD Biology	Cultivation of <i>Saccharina latissima</i> (Phaeophyceae) in temperate marine waters; nitrogen uptake kinetics, growth characteristics and chemical composition



2020	Jørn Olav Løkken	PhD Biology	Change in vegetation composition and growth in the forest-tundra ecotone – effects of climate warming and herbivory
2020	Kristin Odden Nystuen	PhD Biology	Drivers of plant recruitment in alpine vegetation
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2021	Semona Issa	PhD Biology	Combined effects of environmental variation and pollution on zooplankton life history and population dynamics
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2021	Håkon Austad Langberg	PhD Biology	Fate and transport of forever chemicals in the aquatic environment: Partitioning and biotransformation of mixtures of Per- and Polyfluoroalkyl Substances (PFAS) from different point sources and resulting concentrations in biota
2021	Julie Renberg	PhD Biology	Muscular and metabolic load and manual function when working in the cold
2021	Olena Meleshko	PhD Biology	Gene flow and genome evolution on peatmosses ( <i>Sphagnum</i> )
2021	Essa Ahsan Khan	PhD Biology	Systems toxicology approach for evaluating the effects of contaminants on fish ovarian development and reproductive endocrine physiology: A combination of field-, in vivo and ex vivo studies using Atlantic cod ( <i>Gadus morhua</i> )
2021	Tanja Kofod Petersen	PhD Biology	Biodiversity dynamics in urban areas under changing land-uses
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2021	Elise Skottene	PhD Biology	Lipid metabolism and diapause timing in <i>Calanus</i> copepods. The impact of predation risk, food availability and oil exposure
2021	Michael Le Pepke	PhD Biology	The ecological and evolutionary role of telomere length in house sparrows
2022	Niklas Erik Johansson	Dr. philos	On the taxonomy of Northern European Darwin wasps (Hymenoptera: Ichneumonidae)
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2022	Anne Mehlhoop	PhD Biology	Evaluating mitigation measures to reduce negative impacts of infrastructure construction on vegetation and wildlife.
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2022	Martin René Ellegaard	PhD Biology	Human Population Genomics in Northern Europe in the Past 2000 years
2022	Gaute Kjærstad	PhD Biology	The eradication of invasive species using rotenone and its impact on freshwater macroinvertebrates





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