

# The causes and consequences of spatio-temporal variation in age structure in natural populations



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# Declaration

The work in this thesis was carried out at the University of Oxford between October 2020 and June 2024 under the supervision of Professor Ben Sheldon, Dr Josh Firth, and Dr Ella Cole. All research was undertaken primarily by the author, with the contributions of co-authors acknowledged for each chapter. No part of this thesis has previously been submitted for any other degree or professional qualification.

# Abstract

Age structure describes the distribution of age across time and space, which can exhibit substantial variation both within and between natural populations. While much research has identified how variation in the age structure and demographic rates of populations are tightly linked, we lack understanding of how age structure affects populations' ecological and behavioural dynamics other than those that strictly relate to demographic rates. However, given widespread age-specificity in individual traits relating to reproduction, physiology and behaviour, we might expect differences in the social and ecological properties of populations to depend on variation in age structure (Chapter 1). In this thesis, I examine the causes and consequences of variation in age structure at different social, spatial and temporal scales. I aim to broaden our understanding of how variability in the socio-ecology of wild populations relates to age structure.

First, I argue that variation in age structure has the capacity to shape the social organisation and operation of behavioural processes within populations (Chapter 2). I highlight the potential for using empirical data from wild populations to uncover pathways linking individual changes in social behaviour with age, population age structure, and societal functioning. From this foundational basis, I assess within-population behavioural dynamics in relation to age structure by evaluating the drivers of age-structuring within mated pairs, using two model species with contrasting life-histories (Chapter 3). I find that the structuring of age in breeding partners is linked to life history strategy, where fluctuations in overall population age structure determine levels of age-assortative pairing in short-lived great tits *Parus major*, but not longer-lived mute swans *Cygnus olor*.

I then develop a framework using the great tit model system to assess age structure at a larger socio-spatial scale, finding highly variable age assortment between individuals across breeding territories, suggesting that spatial variation in habitat features may be more important for generating spatially-variable demography than age structure (Chapter 4). Further, assessing the consequences of this variation in age structure across breeding territories, I find that fine-scale differences in local age structure can influence breeding timing (Chapter 5).

Finally, I used data from multiple populations spanning 3200km and 702 individual study-years to assess the drivers of variation in age structure, and quantify the spatial scale of their synchronous

fluctuations (Chapter 6). I demonstrate that synchrony is not controlled by spatial autocorrelation in climate, and yet is maintained over large scales, suggesting that the effects of age structure on population demography are likely to synchronously affect geographically-separated populations.

This thesis contributes to our understanding of the effects of age structure on wild population dynamics at various scales, as well as the mechanisms that drive its variation. Together, the frameworks I develop and predictions I make establish a foundation from which further work can advance our understanding of the causes and consequences of spatio-temporal variation in age structure in natural populations (Chapter 7).

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# Author contributions

## *Main contributors*

**Joe P. Woodman** had independent intellectual input into all chapters of this thesis; led data analysis for all projects; wrote first drafts; incorporated co-author comments; and contributed to three years of data collection for the Edward Grey Institute of Field Ornithology.

**Ella F. Cole** (supervisor, co-author of chapters 3, 4 and 6) provided intellectual input and guidance throughout the DPhil; advised on statistical approaches and provided detailed comments for contributed chapters.

**Josh A. Firth** (supervisor, co-author of chapters 2, 3, 4, 5 and 6) provided intellectual input and guidance throughout the DPhil; advised on statistical approaches and provided detailed comments for contributed chapters.

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## *Additional contributors*

**Samin Gokcekus** (co-author of chapter 2) contributed to the writing of the review.

**Kristina B. Beck** (co-author of chapter 2) helped with writing the section on human-impact on wild populations' social ageing.

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**Carys V. Jones** (co-author of chapter 5) contributed to analysis and writing of the chapter.

**Stefan J. G. Vriend** (co-author of chapter 6) provided general help in the original development, analysis and writing of the chapter.

Further author contributions accompany each chapter.

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# Chapter I

## Introduction



# Introduction

## Demography in the wild

Studying demographic variation in natural populations is challenging, requiring repeat observations over the lifespan of individually-identified organisms that might move freely over variable distances, disperse in and out of different habitats, recruit offspring, and die. All the while, such data must be collected without disturbing natural processes to obtain accurate estimates regarding the dynamics of demographic, behavioural, ecological, and evolutionary functioning in wild populations. Owing to technological advances in the tracking of wild organisms, and an increase in the number of long-term individual-based study populations, there is now great opportunity to study demography in the wild. Hence, it is possible to further our understanding on how fundamental population-level processes vary under natural conditions, the drivers of this variation, and its consequences for natural populations.

## Introduction to population age structure

Population age structure is a demographic property that describes the distribution of age across time and space. Age structure has the potential to exhibit profound spatio-temporal variation both within and between natural populations, due to natural or anthropogenic-driven non-stationarity which affects how many individuals are born, die, and migrate in and out of a population (Wolkovich et al. 2014; Koons et al. 2016; Hoy et al. 2020; Rollinson et al. 2021; Salguero-Gómez and Gamelon 2021). This might be generated by mechanisms that alter age structure directly, for example, age-specific disease epidemics (Härkönen et al. 2007; Pybus et al. 2012; Wood et al. 2013; Scheele et al. 2016; Ashby and Bruns 2018) or human activities such as harvesting (Langvatn and Loison 1999; Milner-Gulland et al. 2000; Wright et al. 2006; Milner et al. 2007; da Silva et al. 2016; Festa-Bianchet 2017; Knell and Martínez-Ruiz 2017; Audzijonyte and Pecl 2018; Valle et al. 2018). Alternatively, variation in intrinsic population dynamics can alter age structure, as changes in vital population rates affect how many individuals are born or die, and thus the overall distribution of age (Cole 1957; Preston and Coale 1982; Preston et al. 2001; Carey et al. 2012; Koons et al. 2016; Hoy

et al. 2020). In this sense, age structure and the demographic processes that determine its variation are intimately linked and can exert a reciprocal influence on one another. This is because while population rates can affect age structure, individual age-specificity in survival, reproduction and demographic sensitivity to density-dependence and environmental factors means that population demographic rates often depend on the proportion of individuals within each age cohort (Cole 1957; Coulson et al. 2001; Stenseth et al. 2002; Inaba 2017; Gamelon et al. 2019).

The role of population age structure and demographic rates in causing variation in each other is well-established. Quantitatively assessing this relationship stems from work in the 18th Century by Leonhard Euler, who first established the mathematical dependence of population growth rate on age-specific birth and death rates (Euler 1770), thus deriving the Euler-Lotka equation, which forms the base of demographic modelling in relation to age structure (Lotka 1907, 1922, 1931, 1937, 1939). From this, statistical methods to advance understanding regarding the relationship between variation in age structure and demographic rates has received much attention (Leslie 1945; Lefkovitch 1965; Caswell 2000; Sibly and Hone 2002; Salguero-Gómez and Gamelon 2021), and evidence for the synergistic dynamics of variation in age structure and demographic rates has been found in numerous wild populations (Fairall 1985; Jorgenson et al. 1997; Gaillard et al. 1998, 2003; Albon et al. 2000; Coulson et al. 2000, 2001, 2005; Festa-Bianchet et al. 2003; Gaillard and Yoccoz 2003; Gordon et al. 2004; Sandercock et al. 2005; Ezard et al. 2006; Haridas et al. 2009; Margalida et al. 2011; Pelletier et al. 2012; Koons et al. 2015; Gamelon et al. 2016b, 2016a, 2019; Gerber and Kendall 2016; Hoy et al. 2020; Guldmond et al. 2022).

However, research that demonstrates how age structure fluctuates rarely contextualises such variation in regard to what might be expected over spatio-temporal scales other than those specifically assessed within each study, often at the level of a single population. This means that fundamental understanding regarding the development of age structure at spatio-temporal scales smaller (within-population) or greater (between-population) than this, and the drivers of this variation (aside from those caused directly by recruitment and survival rates), is currently lacking. Further, a particularly understudied aspect of research into population age structure is the consequences its variation might have on population dynamics other than those that strictly relate to demographic growth rates. As previously described, due to individual age-specific rates of fecundity and sur-

vival, the age profile of a population affects overall population growth (Sibly and Hone 2002). Therefore, we might expect the effects of other traits that show age-specificity at the individual-level to propagate through a population, such that variation in age structure might affect how populations operate and vary across time and space.

Changes in individual-level traits with age are almost ubiquitous (Emlen 1970; Charlesworth 1994; Monaghan et al. 2008; Lemaître and Gaillard 2017; Korb and Heinze 2021; Paps 2021). The reason for this can be summarised through the framework of life-history theory, which posits that organisms have limited resources which are invested into traits and processes at different points throughout lifespan to maximise fitness (Stearns 1992). Thus, evidence of age-specificity in wild organisms has been found in multiple traits relating to reproduction and survival (Clutton-Brock 1988; Newton 1989; Sæther 1990; Forslund and Pärt 1995; Bouwhuis et al. 2012; Nussey et al. 2013; Warner et al. 2016; Froy et al. 2017; Lemaître and Gaillard 2017), physiology and morphology (Evans et al. 2011; Nussey et al. 2012; Jégo et al. 2014; Peters et al. 2019; Remot et al. 2022), and behaviour (Catry et al. 2006; Biondi et al. 2010; Lecomte et al. 2010; Farine et al. 2015; Machanda and Rosati 2020; Rosati et al. 2020; Rathke and Fischer 2021; Albery et al. 2022; Siracusa et al. 2022a, 2022b, 2023). Therefore, given widespread age-specificity in many individual-level characteristics, we should expect variation in age structure at the population-level to have an influence on the ecological and social functioning of natural populations.

For example, a general characteristic that shows age-specificity at the individual-level is social behaviour (Machanda and Rosati 2020; Siracusa et al. 2022a, 2023). Population-level sociality, in terms of the number, type and strength of social associations within a population, is often studied from the perspective of social structure. This is determined by interactions between individuals, from which relationships form and determine a group's overall organisation and stability (Hinde 1976). Therefore, properties that affect the social behaviour of individuals within a population will influence the overall population organisation and functioning. Thus, if there is age-specificity in social behaviour, this will affect how social interactions develop, and therefore the overall social structure of a population depending on age structure. Further, as well as influencing social structure through individual age-specificity in behaviour, variation in age structure might mediate population-level social processes more generally by affecting which individuals of a given age are

able to associate depending on whether the age distribution is skewed towards specific age-cohorts (i.e. certain age dyads are more or less likely to associate through passive mechanisms depending on the overall age composition of the population at that point in space or time).

Age-specificity related to an individual's movement in space is also widespread in animal taxa, with research suggesting age-specificity in territory selection (Austin 1949; Ferrer and Bisson 2003; Reitsma et al. 2008; Öst and Steele 2010; Delaney and Warner 2016; Camacho and Hendry 2020; Tao et al. 2021; Hüge et al. 2024) and dispersal patterns (Greenwood 1980; Greenwood and Harvey 1982; Morris 1984; Andreu and Barba 2006; Bowler and Benton 2009; Berry et al. 2012; Etezadifar et al. 2022). For example, Greenwood and Harvey (1982) reported that there are no philopatric bird species where adults disperse greater distances between breeding attempts than juveniles between their natal origin and first breeding. Therefore, given such age-specificity in dispersal and habitat choice, we might not only expect temporal variation in age structure to affect a population's overall use of and movement in space, but also for age structure to develop across space. Despite this, the relationship between age distribution and population-level movement patterns, rates of dispersal, and age-structured spatial arrangement has not received much attention (Ronce et al. 2000); which is particularly interesting given there is spatial variation in landscape quality, which might be associated with age and is known to affect output in natural populations (Andren 1994; Lambrechts et al. 2004).

Finally, as stated above, age-specificity in reproductive success is widespread across taxa (Sæther 1990; Forslund and Pärt 1995; Mauck et al. 2004; Descamps et al. 2008; Hayward et al. 2013; Rughetti et al. 2015; Lemaître and Gaillard 2017). In species with seasonal breeding, this success might be mediated by experience where older individuals better time their breeding attempts such that peak demand of raising young matches with peak resource availability (Perrins and Moss 1974; Harvey et al. 1979b; Jouventin et al. 1999; Auld et al. 2013; Bonamour et al. 2020; Saraux and Chiaradia 2022). Therefore, although much research has identified how variation in age structure influences population-level reproductive rates, the role of the relationship between age and phenological timing in producing this pattern is not known. Further, this is particularly interesting given there is potentially a social aspect to reproductive timing whereby individuals or pairs may adjust their timing depending on the timing of others in the population. This

process would be consistent with other reproductive behaviours which can be socially-dependent on decisions made by other members of the population (Losey et al. 1986; Dugatkin 1992; Gibson and Höglund 1992; Kirkpatrick and Dugatkin 1994; Jennions and Petrie 1997), and show age-specificity in the degree and direction of social copying (Pruett-Jones 1992; Dugatkin and Godin 1993; Höglund et al. 1995).

Therefore, considering widespread age-specificity in various individual-level characteristics, it is likely that a population's social and ecological functioning might depend on its age composition. The potential for between- or within-population differences to arise depending on age structure is a particularly interesting area of research given our current understanding of natural populations for two reasons. First, across a wide range of taxa, natural populations frequently show significant spatio-temporal variation in recruitment and survival (Sale et al. 1984; Cerqueira et al. 1993; Verboven and Visser 1998; Gaillard et al. 2000; Sæther et al. 2002; Gaillard and Yoccoz 2003; Muths et al. 2011), thus providing an opportunity to generate profound variation in the emergent age structure. Such spatio-temporal variation in age structure might therefore be partly responsible for the differences that arise in populations separated in time and space. Second, the significant impact of human activity on the natural world is likely to influence age structure in wild populations, either indirectly as anthropogenic-driven change impacts demography (Sandercock et al. 2005; Gaillard et al. 2013; McClure et al. 2017; Laughton and Knell 2019), or as a direct consequence of age-specific hunting and harvesting (Langvatn and Loison 1999; Berkeley et al. 2004; Hsieh et al. 2010; Hixon et al. 2014; Barnett et al. 2017; Audzijonyte and Pecl 2018). Therefore, through understanding the consequences of variation in age structure, we may deepen our knowledge of how humans are impacting natural populations by imposing changes to their age distribution. By studying population age structure, we will advance our understanding of the drivers of variation in the functioning and fitness of natural populations. Through considering the causes of its emergence and explicitly assessing the consequences that variation in age structure exhibits at different spatio-temporal scales, we can make predictions and address hypotheses regarding the differences we see in the social and ecological properties of wild populations.

## Study systems

Historically, studies of ageing have typically occurred in laboratory settings, generally using model insect species to assess age effects at the individual-level (Finch 1990; Partridge and Barton 1993; Kirkwood and Austad 2000). However, studies on captive animals may lead to conclusions that cannot be generalised to natural ecological contexts (Lambrechts et al. 1999; Partridge and Gems 2007; Kawasaki et al. 2008), which is particularly relevant if we want to attain the causes and consequences of age structure at the population-level. Therefore, the importance of studying ageing in wild populations is now widely acknowledged (Reznick and Ghalambor 2005; Partridge and Gems 2007; Nussey et al. 2013; Roach and Carey 2014; Fletcher and Selman 2015; Hayward et al. 2015; Kowald and Kirkwood 2015; Albery et al. 2023).

Considering this, natural bird populations offer particularly appropriate systems for research on population age structure, due to two primary reasons. First, many previous wild bird studies have repeatedly shown individual-level variation linked to ageing (Nol and Smith 1987; Desrochers and Magrath 1993; Pärt 2001; Ferrer and Bisson 2003; Catry et al. 2006; Balbontín et al. 2007; Jones et al. 2008; Bouwhuis et al. 2009, 2010a, 2010b, 2012, 2015; Péron et al. 2010; Evans et al. 2011, 2020; Hammers et al. 2012; Zhang et al. 2015; Bonamour et al. 2020; Dingemanse et al. 2020; Greggor et al. 2020; Etezadifar et al. 2022; Sparks et al. 2022; Hüge et al. 2024), thus providing *a priori* expectations that variation in age structure might be related to spatio-temporal differences in population dynamics. Second, bird populations provide highly suitable systems in which population processes can be monitored while retaining information of individual identity. This is largely due to bird ringing, which allows individuals to be marked with light-weight uniquely-numbered metal rings at the nestling stage and subsequently followed throughout their life history, through recapture during future breeding and foraging behaviour (Lack 1966; Lovette and Fitzpatrick 2016; Hackett and Hackett 2020). Further, birds often have long lifespans (Holmes and Austad 1995), providing a greater temporal opportunity to track individuals across their entire lifespan (Bouwhuis et al. 2009, 2010b, 2010a). This has led to many individual-based long-term study population of birds, perhaps most notably of the great tit *Parus major* (Lack 1966; Wooller et al. 1992; Clutton-Brock and Sheldon 2010; Culina et al. 2021; Sheldon et al. 2022).

Great tits are small cavity-nesting passerine birds found in mixed woodlands across much of the Western Palearctic (Perrins 1979; Gosler 1993). The species readily accepts nest-boxes for breeding, meaning entire populations can be monitored if an excess of boxes is provided (Perrins 1979), in addition to detailed data collection of reproductive behaviour, breeding metrics, and individual-level traits at the nest-box. Further, because most great tits are territorial and show limited breeding dispersal (Harvey et al. 1979a), it is possible to monitor individuals over their entire reproductive lifespan. Great tit populations therefore provide an ideal model system in which life-history variation under natural conditions can be studied, and have for this reason have been the focus of the first and longest running longitudinal studies of population ecology and evolution (Gibb 1950; Kluijver 1951; Lack 1952; Perrins 1965; Sheldon et al. 2022).

Great tits are seasonal breeders with socially monogamous mating systems, where pairs defend territories during annual breeding seasons (Hinde 1952; Krebs 1971; Perrins 1979). Their breeding ages range from 1 to 9, averaging 1.8 years and reproductive performance peaking at 2.8 years (Perrins and McCleery 1985; Bouwhuis et al. 2009). Throughout their lifespans, great tits show age-specificity in many traits relating to reproduction (Perrins 1965; Harvey et al. 1979b; Dhondt 1985, 1989; Perrins and McCleery 1985; McCleery and Perrins 1998; Bouwhuis et al. 2009, 2010b, 2012), survival (Clobert et al. 1988; Bouwhuis et al. 2009, 2010b, 2012), dispersal (Greenwood et al. 1979; Harvey et al. 1979a; Andreu and Barba 2006), physiology and morphology (Gosler 1986, 1996; Norte et al. 2009; Broggi et al. 2010; Evans et al. 2010; Vermeulen et al. 2017), and social behaviour (Sandell and Smith 1991; Barluenga et al. 2000; Naef-Daenzer et al. 2000; Carere et al. 2005; Rivera-Gutierrez et al. 2010; Aplin et al. 2012; Cole and Quinn 2012; Morand-Ferron et al. 2015; Recalde et al. 2023; Crouchet et al. 2024). Because of these age-specific characteristics, great tit populations with different age structures may be expected to vary in their dynamics. Additionally, juvenile survival and recruitment in great tits is highly dependent on their ecological and demographic environment. For example, seed masting cycles in European beech *Fagus sylvatica* are particularly influential for survival in juvenile great tits (Perrins 1965; Källander 1981; Perdeck et al. 2000), while density-dependent dynamics can greatly affect the number of individuals within certain age cohorts (Both et al. 1999; Gamelon et al. 2016b, 2019).

In summary, because great tit populations: (a) can be monitored over time with a high identi-



fication and recapture rate, thus tracking individuals across their entire lifespans; (b) consist of individuals which express age-specificity in a number of traits; and (c) have the potential to show profound spatio-temporal variation in age structure, they provide a powerful model system in which hypotheses regarding the causes and consequences of age structure might be explored.

This thesis primarily uses data from the long-term study site of Wytham Woods, Oxford, United Kingdom (51°46'N, 1°20'W), as part of a wider research agenda that studies the evolutionary ecology of wild passerine tit *Paridae* species. The study site is 385ha of mixed deciduous woodland surrounded mainly by farmland (Savill et al. 2010). Essential for studying aspects of breeding behaviour and ecology in great tits, the site contains 1209 nest-boxes (1020 of which are accessible to great tits) which are in fixed positions with known GPS coordinates (Krebs 1971; Wilkin et al. 2006). Approximately 60% of boxes are occupied each year by breeding birds throughout April–June, including great tits as well as other resident species such as blue tits *Cyanistes caeruleus*, marsh tits *Poecile palustris*, coal tits *Periparus ater* and nuthatches *Sitta europaea*. Great tit pairs breeding in these boxes make up the vast majority of the local breeding population, as the proportion of birds occupying natural cavities is very low (Greenwood et al. 1979; Kidd et al. 2015).

The breeding population has been monitored since 1947, and in a standardised format since the early 1960s, where the number and location of nest-boxes has remained constant. During the birds' breeding seasons, fieldworkers collect a range of reproductive data including lay date, clutch size, hatch date, number of chicks and number of fledglings. All nestlings are fitted with a unique British Trust for Ornithology (BTO) metal leg ring on day 15 post-hatching. Since 2007, individuals have also been marked with a plastic ring that contains a passive integrated transponder (PIT tag). These enclose a microchip that remains inactive until it passes through an electromagnetic field from a Radio Frequency Identification (RFID) antenna, at which point it transmits a unique alphanumeric code. These tags do not affect behaviour or fitness (Nicolaus et al. 2008; Schroeder et al. 2011) and allow individuals to be identified without physical capture at RFID-fitted nest-boxes and feeders. The BTO rings and PIT tags are crucial for research relating to age, as upon recapture they allow for exact calculation of age for all locally-hatched individuals. Breeding adults are also captured at the box and either identified by ring number or marked with a new ring and PIT tag if they have immigrated into the population (46.4% of breeding individuals).

Outside the breeding season, birds are regularly caught using mist nets to collect data on residents that have previously been marked, and to mark immigrant birds with a new ring. Individuals have their morphometrics recorded (wing length, maximum tarsus, weight, fat and muscle score, and moult score), in addition to their sex and age. Birds are aged using standard codes devised by The European Union for Bird Ringing (EURING, Table 1; Figure 1). Great tits undergo an annual moult from June to early-October, where new feathers are grown to replace old and poorer-quality feathers (Perrins, 1979). The first moult an individual completes in its lifespan is the post-juvenile moult, and all subsequent annual moults are post-breeding moults (Ginn and Melville, 1983; Jenni and Winkler, 1994). The post-juvenile moult is partial as primary coverts are retained in the wing (Perrins, 1979). Therefore, the contrast between feathers that are retained compared to those that are replaced following post-juvenile moult makes it possible to discern individuals that are in their first-year ('juveniles', Figure 1b), compared to older individuals which have completed a post-breeding moult and thus show less contrast between the primary and lesser coverts ('adults', Figure 1c; Svensson 1992; Demongin 2016).

Table 1 – EURING codes used when ageing great tits with their definitions (Svensson 1992). The final column shows the percentage of identified great tits found breeding in Wytham since 1965 that were given the respective age code when first marked. Note that all odd-numbered EURING age codes refer to individuals where exact year of hatching can be calculated (i.e. marked as a chick or within their first-year of life before their first post-breeding moult).

| EURING age code | Definition                                                                                                            | % of breeding birds |
|-----------------|-----------------------------------------------------------------------------------------------------------------------|---------------------|
| 0               | Age unknown – only to be used if data has been lost and the ringer has no idea if a bird was a nestling or full-grown | 0.0%                |
| 1               | Pullus in the nest                                                                                                    | 53.6%               |
| 1J              | Fledged, but flying so weakly that it is obviously incapable of having flown far from the nest                        | 0.0%                |
| 2               | Fully grown, year of hatching unknown (including current year)                                                        | <0.1%               |
| 3               | Hatched during current calendar year (e.g. first-years in autumn)                                                     | 9.8%                |
| 3J              | Hatched this calendar year and still has at least 90% juvenile body plumage (e.g. first-years in summer/early autumn) | 0.1%                |

| EURING age code | Definition                                                                             | % of breeding birds |
|-----------------|----------------------------------------------------------------------------------------|---------------------|
| 4               | Hatched before current calendar year – exact year unknown (e.g. many adults in autumn) | 3.0%                |
| 5               | Hatched during previous calendar year (e.g. first-years in early spring)               | 26.6%               |
| 6               | Hatched before last calendar year – exact year unknown (e.g. many adults in spring)    | 6.8%                |

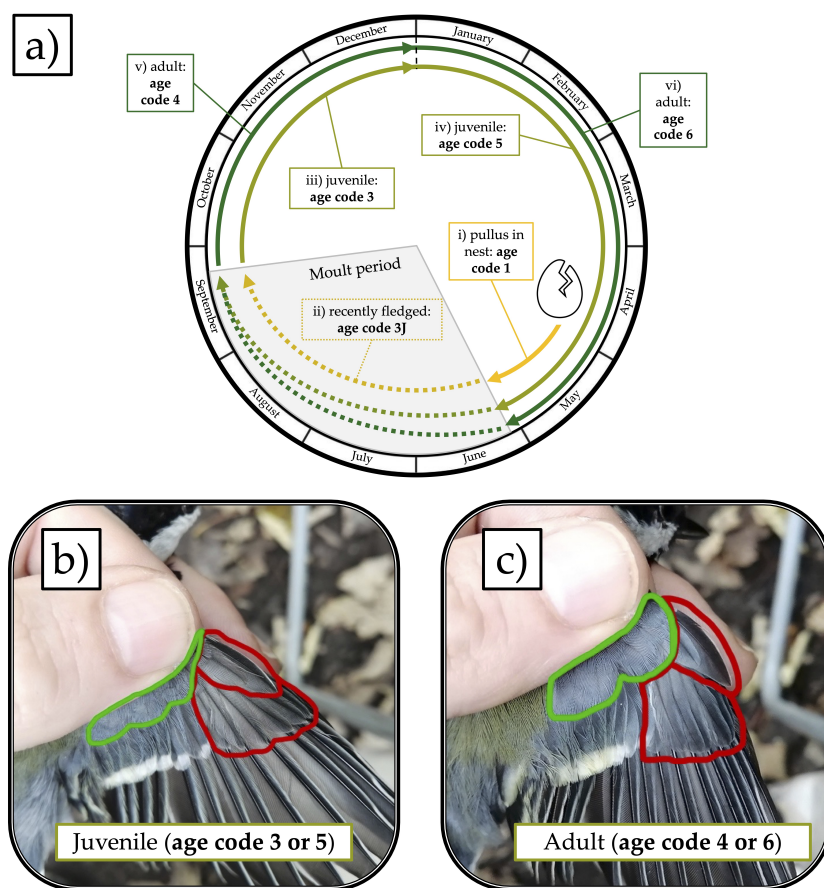


Figure 1 – Schematic showing how EURING ageing codes relate to calendar year and great tit life-history, and plumage differences in the field. (a) Shows a great tit's life-cycle in the context of using EURING age codes. (b) and (c) Show plumage differences between first-year ('juvenile')

and older ('adult') great tits respectively, used to age individuals in the field. Fringing of primary coverts (band of feathers in lower half of red-circled area) are a duller grey/green in juveniles compared to slightly brighter blue/slate grey in adult birds, thus juveniles show greater contrast between the primary and lesser coverts (green-circled area). Juveniles may also retain their alulas (upper two feathers in red-circled area), where adult upper alulas (A1) are a brighter blue/grey and lower alulas (A2) are a glossier black compared to juveniles (Svensson 1992; Demongin 2016).

By combining data from individuals that hatched in Wytham with ringing data of immigrant birds, it is possible to calculate the exact year of hatching for a very high proportion of individuals recorded in the study site (97.1% of 246,660 individual great tits, or 90.4% of 24,323 records of breeding adults, since 1965). Thus, the age structure and variation in this can be accurately calculated over various spatio-temporal scales (for example, see Figure 2).

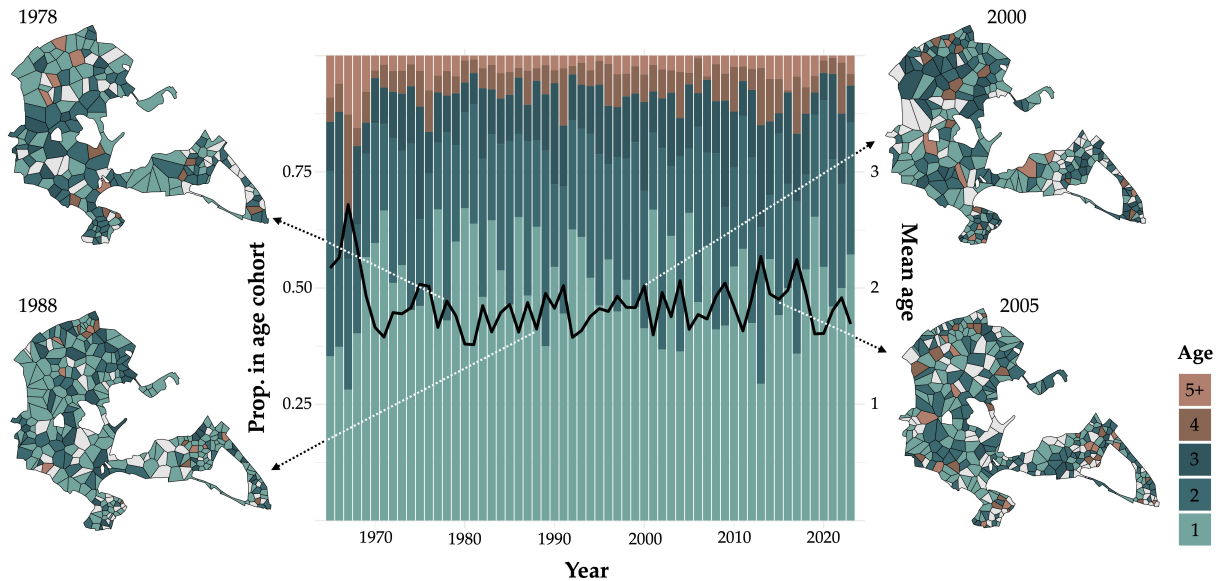


Figure 2 – Spatio-temporal variation in age structure within the great tit population at Wytham Woods. The central bar plot shows the annual age structure of great tit breeding populations 1965-2023; and the figures surrounding this show the spatial arrangement of differently-aged breeding female great tits in single years.

In addition to studying the great tit population in Wytham, this thesis also uses data from open-access databases that have demographic individual-level data on the study species at much greater spatial scales. This includes the Studies of Populations of Individual Birds (SPI-birds) Network & Database ([www.spibirds.org](http://www.spibirds.org)), an initiative which has collated data from various studies of wild birds across the globe. Using data from other populations makes it possible to calculate variation in age structure in contexts outside of the Wytham-specific study system, and to make comparisons at different spatial and temporal scales.

Insights regarding variation in age structure may also be gained through studying species with different age distributions. Mute swans *Cygnus olor* provide an appropriate model species in which age structure might be alternatively explored, because they also show age-specificity in individual-level traits (McCleery et al. 2002, 2008; Charmantier et al. 2006a, 2006b; Pybus et al. 2012; Auld et al. 2013; Włodarczyk and Minias 2020) and their populations can be studied while retaining information on individual identity (Perrins and Ogilvie 1981; Perrins et al. 1994; McCleery et al. 2002), but they are much longer-lived than great tits (annual survival rate ~85%, McCleery et al. 2002; compared to ~48% in great tits, Bouwhuis et al. 2012). This will lead to fundamental differences in their age structures compared to great tit populations, specifically in terms of how many age-cohorts there are and how age is distributed across the population.

Therefore, in addition to using great tit data from Wytham, this thesis utilises data collected from the study site at Abbotsbury Swannery and adjacent Chesil Fleet, Dorset, United Kingdom (50°35'N, 2°30'W) where swans have been breeding since at least the 14th Century (Perrins and Ogilvie 1981). Since 1977, all individuals that breed in the colony have been marked with unique BTO metal leg rings (Perrins and Ogilvie 1981; Perrins et al. 1994; Perrins 1996). Age is based either on date of hatching for resident birds, or colouration of plumage and beak at first capture for immigrant birds, which can discriminate between birds of 1-, 2- and 3-years or older (Auld et al. 2013). Most breeding individuals hatched in the swannery (80% males and 93% females), and therefore age is known. Additionally, of the 13% that immigrate and breed in the population, 57% do so at an age when they can still be aged accurately, thus 94% have their exact year of hatching known (McCleery et al. 2002; Auld et al. 2013).

## Objectives of thesis

The link between variation in age structure, ecology, and sociality is a key path to determining the consequences of age structure in natural populations. In **Chapter 2**, I review population age structure and sociality by synthesising how age is known to affect social processes at the individual-level, and suggest how variation in population age structure might thus be expected to influence social structure and functioning. I outline specific future directions, highlighting the potential for using empirical data from natural populations in combination with social network approaches to uncover pathways linking social ageing, population age structure and societal functioning. I then discuss the broader implications of the insights gained for understanding the social impacts of anthropogenic effects on wild population demography, and for building a deeper understanding of societal ageing in general.

From this foundational basis, I assess within-population behavioural and ecological dynamics and resolve how these relate to variation in age structure at various spatio-temporal scales. Perhaps one of the finest socio-spatial scales at which age structure arises is how age is structured within mated pairs. Such within-pair age structuring might be manifested as age-(dis)assortative mating, where individuals of either the same (or different) ages pair together. This can either magnify or mitigate the effects that age has on reproductive success depending on the age make-up of a pair. Despite this, in addition to evidence that age-assortment is widespread across taxa, the mechanisms that drive age-assortative mating are poorly understood, particularly the relative role of passive versus active mechanisms and whether this varies between species. In **Chapter 3**, I disentangle the roles of different mechanisms which might determine how age is structured within pairs, particularly focusing on the role of temporal variation in overall population age structure. To understand how this relates to between-species differences in population age structure, I take a comparative approach by comparing the role of the same mechanisms in species with contrasting demographic strategies and emergent age distributions (great tits and mute swans).

It is also important to assess how age is structured across greater socio-spatial scales when considering the consequences of variation in age structure on natural populations. This is because given that age relates to reproductive success at the individual and pair-level, spatial age structure across

territorial breeding populations might drive local age-related population dynamics. In **Chapter 4**, I use long-term great tit breeding data to assess the mechanisms that might generate spatial age structure across breeding territories through evaluating covariance between habitat quality and age, and suggest the relative contributions of spatial age structure and habitat quality in generating spatially-variable demography.

Variation in age structure across space might have several consequences which affect ecological functioning in natural populations. In seasonally breeding species, age effects on reproductive success might be mediated by previous experience and more accurate matching to local temporally-variable resource distributions. Thus, in **Chapter 5**, building from the evaluation of how age structure in breeding populations develops across space, and how this relates to spatially-variable demography, I assess the link between individual age and reproductive timing, and how local breeding age structure relates to phenological timing across breeding neighbourhoods.

Given the findings of how age is structured within breeding populations, and the consequences this can have on reproductive and ecological functioning, it is important to understand the spatial scale at which we should expect age structure to similarly fluctuate over time. Understanding the spatial scale at which temporal variation in age structure remains synchronised in natural populations would provide insight into the scale at which the consequences of this variation are likely to operate at. In **Chapter 6**, I quantify the role of reproductive and environmental stochasticity in generating variation in age structure across 32 great tit populations spanning 3200km and >109,000 birds across 702 study-years. Further, I assess the spatial synchrony of temporal variation in age structure across these populations, and whether accounting for variation in reproductive or environmental variables affects the observed levels of spatial synchrony.

Finally, I summarise my research findings in **Chapter 7**. This chapter synthesises my results to assess what general conclusions can be made regarding new insights gained into the causes and consequences of spatio-temporal variation in age structure in natural populations, and I discuss the implications for the broader fields of ecology.

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# Chapter II

## **The ecology of ageing in wild societies: linking age structure and social behaviour**

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# The ecology of ageing in wild societies: linking age structure and social behaviour

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## ABSTRACT

The age of individuals has consequences not only for their fitness and behaviour, but also for the functioning of the groups they form. Because social behaviour often changes with age, population age structure is expected to shape the social organisation, the social environments individuals experience, and the operation of social processes within populations. Although research has explored changes in individual social behaviour with age, particularly in controlled settings, there is limited understanding of how age structure governs sociality in wild populations. Here, we synthesise previous research into age-related effects on social processes in natural populations, and discuss the links between age structure, sociality and ecology, specifically focusing on how population age structure might influence social structure and functioning. We highlight the potential for using empirical data from natural populations in combination with social network approaches to uncover pathways linking individual social ageing, population age structure and societal functioning. We discuss the broader implications of these insights for understanding the social impacts of anthropogenic effects on animal population demography, and for building a deeper understanding of societal ageing in general.

panied by many other changes in an individual's biology in addition to physiological senescence in late life, such as sexual maturation, the accumulation of resources and social experience, or a changing social environment due to cohort effects and selective disappearance resulting from natural selection acting within a generation. Therefore, patterns of age-specificity in individual characteristics can be complex, but are evidenced in reproduction and survival probability [14–20], physiology and morphology [21–25], and behaviour [26–35]. Much previous research has studied ageing in laboratory settings, particularly using insects and other short-lived animals as models [9,10,36–38]. However, studies on captive animals may lead to conclusions that cannot be generalised to natural ecological contexts [39]. Therefore, the importance of studying ageing in wild populations is widely acknowledged [18,40–44].

An individual's age can have consequences not only for its own survival and behaviour, but also for the functioning of the population of which it is part. Recent work highlights that individual social behaviour can change with age [26–35], for example in terms of how many associates an individual has. This might be driven by a number of mechanisms [34] such as age-related changes in experience [45–48], space-use [26], cognitive physiology [49–51], or phenotypic plasticity [52,53]. Much of the research that has assessed age-related differences in sociality does so through comparing individual social behaviour among different age classes, as opposed to using longitudinal studies which measure how ageing relates to changing sociality within individuals across their lifetime. Thus, age-related differences in social behaviour may not be a direct result of within-individual ageing, but also between-individual processes such as cohort effects or selective disappearance [54–56]. Crucially, where age relates to social behaviour through whichever of the discussed mechanisms, and thus variation in the number, type and strength of relationships formed, the age profile of the population as a whole might be expected to influence the overall social organisation and functioning, and the consequences that depend on this. This can be conceptualised using the perspective of social structure, which is a synthesis of all social relationships between members of a group. It is determined by social inter-

## 1 INTRODUCTION

Age determines many aspects of life, underpinning variation in individual-level characteristics across species [1–4]. This is summarised through the framework of life-history theory, which posits that organisms have limited resources which are invested in traits and processes at different points throughout their lifespan to maximise fitness [5]. Ageing in late-life is generally associated with senescence i.e. a decline in physiological functioning that leads to a loss of organismal function, decreased fecundity and increased probability of death [6–13]. However, ageing itself broadly reflects a temporal parameter that measures the amount of time since birth, and therefore may be accom-

actions among individuals, from which relationships form, and thus govern the overall social structure of a group or population [57,58]. Hence, though frequently overlooked, the age structure is thus likely to be an important driver of variation in social structure across populations.

Age structure is a demographic property that describes the distribution of age within a population, determined by variation in processes that affect how many individuals are born, die, and migrate in and out of a population. It is well established that variation in age structure plays an important role in the demographic functioning of populations. This is because individual age-specificity in survival and reproduction means that fluctuations in age structure influence population vital rates [59,60]. Additionally, age groups differ in their demographic sensitivity to density-dependence and environmental factors [61–63]. Thus, variation in age structure influences overall population growth rate, which itself will cause a change to age structure as more or fewer individuals are recruited into the population or die [64–70]. Therefore, age structure and the demographic processes that determine it are highly interrelated and exert a reciprocal influence on one another (Fig. 1). As already explained, however, age structure will not only influence demographic rates but may also affect the social structure of populations and the operation of social processes within them. The interplay between age and society is of primary significance in a range of biological disciplines: to behavioural ecologists interested in the causes and consequences of social processes, and how this is shaped by age [31,54,71–75]; to evolutionary biologists concerned with the evolution of social behaviour and ageing, and how evolution influences social structure over generations [1,8,16,76–78]; and to gerontologists interested in ageing human societies [79–82]. However, our general understanding of how population age structure affects sociality in the wild is limited.

In this paper, we assess previous research into age-related effects on social processes with the aim to better understand the link between age structure and sociality in the wild (Section 2). While it is clear that age structure, sociality and the ageing process can profoundly influence the evolutionary dynamics of each other [3,83–90], this review is primarily focussed on the ecological perspective of the link between age and sociality in wild populations. Finally, we highlight the potential for using empirical data from natural populations in concert with a social network approach to uncover the causes and consequences of the relationship between age structure and sociality, and discuss future directions for the research field (Section 3).

## 2 POPULATION AGE STRUCTURE AND SOCIALITY

Existing work on natural populations identifies the potential for age structure and demographic rates to be tied to one another in various ways (Fig. 1). For example, for many European bird species, variation in masting events (e.g. in beech *Fagus* spp.) affects juvenile survival and recruitment [91,92]. As a consequence, considerable temporal variation in age structure is generated: in great tits (*Parus major*), for example, the proportion of the population consisting of yearlings can vary from 27–68% [93]. Age-specificity in reproduction and response to density dependence in this species [94–99] means that such changes in age structure will affect population growth rate. What remains to be understood is the role sociality plays in the determination of age structure and demographic rates in natural populations.

The role that sociality plays in affecting variation in population age structure is currently not well understood, but may be significant. This is because the patterning of social relationships, which produce overall social structure, can mediate survival and reproduction, thus influencing birth and death rates and the resulting distribution of age in wild populations. For example, foals with a higher number of associates in a feral horse (*Equus caballus*) population had greater survival following a catastrophic event that caused a loss of 40% of individuals [100]. Benefits to health and survival as a result of social cohesion have also been evidenced in killer whales (*Orcinus orca* [101]); giraffes (*Giraffa camelopardalis* [102]); bighorn sheep (*Ovis canadensis* [103]); rock hyrax (*Procavia capensis* [104]), yellow-bellied marmots (*Marmota flaviventris* [105,106]), Barbary macaques (*Macaca sylvanus* [107,108]), rhesus macaques (*Macaca mulatta* [109–111]); baboons (*Papio cynocephalus* [112–114]) and humans (*Homo sapiens* [115–118]). Indeed, such benefits may help to explain why individuals increase their social connections after major disturbances [119–121]. Conversely, in some contexts, increased sociality may reduce survival or reproduction [122–126], for instance, when social contact increases infection risk [127–132]. In these ways, social behaviour might directly influence vital rates and generate variation in the resulting age structure of wild populations.

While the social behaviour and resulting social structure of a population may influence its age structure, we can also conversely ask whether age structure might affect the social structure and functioning of social processes. Such social processes refer to behavioural interactions including two or more individuals, affected by age-specific tendencies to perform them, and the overall structure of the social network. Age-specific social behaviour has

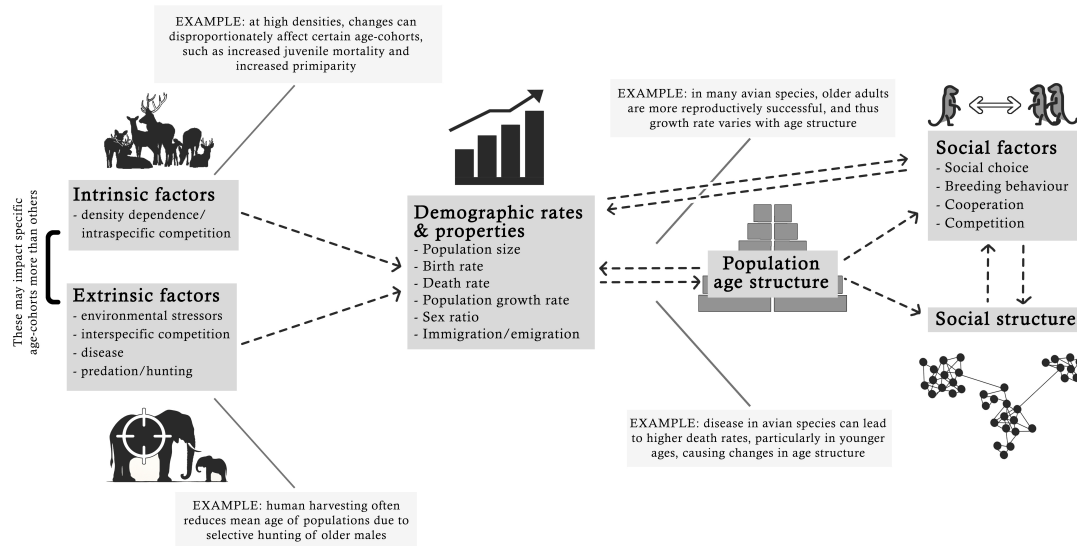


Fig. 1. A conceptual synthesis of how variation in demographic rates and properties, age structure, and sociality might mutually affect one another.

been demonstrated in many animal taxa from laboratory, domestic, and wild populations [26–35]. In some cases, changes in social behaviour with age are profound. For example, as male lions (*Panthera leo*) age, they move from their natal pride into coalitions with other older males [133], thus considerably altering their social associations. Therefore, age structure might be critical to the overall social structure of wild populations. Some research has considered age distribution in social networks, asking in particular whether groups exhibit assortment with respect to age. Age-assortment in social networks, whereby association between same- or similar-age individuals is stronger than that expected from chance, has been observed in birds [29,134,135], primates [136] (including humans [137]), yellow-bellied marmots [75], sea lions (*Zalophus wollebaeki* [138]) and potentially bottlenose dolphins (*Tursiops* spp. [139]). Such age-assortment may interact with the influence of age on social behaviour at the individual-level to provide a mechanism whereby overall age structure influences the emergent social structure, and the operation of social processes within the social network. Despite this, the causal effect of age structure on the functioning of social processes is relatively understudied, and few studies have explicitly considered the mechanisms through which age structure determines social behaviour and structuring in wild populations. Here, we explore this by assessing how age is known to affect the relationship that population age structure holds with four key social processes: (i) social choice; (ii) breeding behaviour; (iii) cooperation; & (iv) competition.

## 2.1 Social choice

Social preferences and relationships can influence survival and life-history outcomes in social species [89–105], as the choices made in terms of who to associate with and for how long can influence success in various contexts such as mating, cooperation, competition, and social learning. It is well established that physiological characteristics can change with age, and senescence in such traits with old age is a widespread phenomenon [8,18]. The neurological and hormonal mechanisms that underpin social choice have been studied extensively in laboratory settings [140–144]. For example, the neuropeptide oxytocin is particularly important in mediating social choice in humans, such as that involved in parent-offspring bonds [145,146]. However, senescence in the physiological properties that underpin social behaviour and its relation to social changes associated with ageing in wild populations is understudied, and we lack a general cross-species understanding on patterns of social senescence (see Future Directions).

In the context of social choice, humans become more selective with age, as individuals invest in fewer but stronger relationships [147–150]. Evidence is now emerging for similar patterns of social selectivity with increased age in non-human animals including: chimpanzees (*Pan troglodytes* [33]); macaques [32,151–153]; yellow-bellied marmots [75,154]; red deer (*Cervus elaphus* [26]) and killer whales [155]. In marmots, for example, fewer attempts are made to interact with old individuals, which consequently exert less social influence [154]. Observed patterns

of increasing social selectivity with age might emerge from different, and potentially simpler processes, in wild populations compared to human societies, for example through increased mortality of older social partners or changes in space-use and associated social interactions. For example, in red deer, older individuals are less socially-connected which may stem from changes in space-use, with older deer having smaller home ranges in areas of lower quality and density [26].

It is likely that these age-related changes in social choice will play a role in the relationship between population age structure and other social processes. For example, if strong mutual bonds between older individuals promote prosocial behaviour, the presence of older individuals within a population may contribute to higher average rates of cooperation. Overall, age-related changes in social choice may influence social structure through changing which, and with how many, associates an individual chooses to interact with depending on age. This therefore provides a mechanism by which variation in age structure may affect overall societal structure and functioning.

## 2.2 Breeding behaviour

Breeding behaviour is a well-studied aspect of social behaviour, and age-related changes might mean that variation in age structure will alter patterns of breeding across a population. Here, we review the implications of age-specificity for breeding processes that depend on social interactions, through mate choice and subsequent decisions of whether to form a long-term partner social bond, divorce or commit extra-pair copulations. We assess how these might affect population-level breeding behaviour given variation in age structure.

The choice of mate can be an important determinant of reproductive success [156–162]. It has been demonstrated that some females adjust mating preferences based on previous experience, known as the ‘previous male effect’ [160–173]. Because refinement of mating preferences occurs in response to previous mating behaviour, as older females will have undergone more breeding attempts, they may then be expected to show more refined mating preferences than younger females. This effect captures how age relates to mate choice, since females with greater experience must have undergone more breeding attempts, and therefore older individuals may be better at choosing mates [45]. Conversely, in some cases older females might be less choosy, which may be caused by delayed mating in senescent females resulting in reduced choosiness, or decreased ability to discriminate male quality due to deterioration

of sensory capacity with senescence [177–179]. As well as previous experience, mate preferences can be learnt socially, a process known as mate copying [180–184]. In some species, younger individuals are more likely to copy the mate choice of others [185–187], and thus age structure might influence the overall levels of mate copying, which could have considerable effects on population-level breeding behaviour through affecting which males are chosen. Further, as well as influencing population-level breeding behaviour through individual age-specificity, population age structure might mediate mate choice by determining which individuals of a given age mate together if the age distribution is skewed towards specific age-cohorts. For example, recent work demonstrates that in species with high mortality rates, a large proportion of the population exists in a single age-cohort, and thus fluctuations in age structure largely determine variation in levels of age-assortative mating [93,188].

In socially monogamous species, once a mate is chosen, individuals may remate with the same partner to increase breeding success [189–191]. Such remating results in pair-bonding behaviour, where a long-term relationship forms [192–195]. Pair-bonds require that partners sustain their relationship beyond a single or multiple mating attempts [192,196,197], and when individuals elect to remate based on previous success [198,199], we may expect to see a higher proportion of older individuals pair-bonded than younger ones, due to age-specific breeding success in many species where performance is lower in young breeders [15,19,200]. Age structure might therefore influence pair-bonding in populations, which may have important consequences as pair-bonding can be adaptive independent of age and reproductive experience [201], thus potentially affecting population productivity. However, this relationship is complicated by the fact that, as pairs age, there is an increasing likelihood that one partner will die between breeding attempts, leading to widowing [190,202]. Moreover, in short-lived species where mortality between breeding attempts is high, costs of waiting to remate with a partner that has died have been hypothesised to select for divorce and partner-switching [203]. The strength and direction of the relationship between individual age and pair-bonding behaviour is thus likely to be mediated by mortality and lifespan, with the prediction that population age structure should most strongly predict pair-bonding across populations in long-lived species with low extrinsic mortality.

In addition to avoiding costs associated with delayed breeding, an individual may divorce if it fails to reach opti-

imum reproductive potential with a partner of low quality [202–205]. Within a population, the proportion of prime-age individuals (those in the age class with the highest reproductive and survival rates [61,206–208]) may affect divorce rates, as partners choose to divorce to mate with individuals of higher reproductive value. For example, divorce rates in barnacle geese (*Branta leucopsis*) increase when there is a greater proportion of older, more experienced individuals among unpaired birds [189,190]. In some cases, rather than divorcing their partner, individuals may seek extra-pair copulations (EPCs) [209,210]. The likelihood of performing EPCs can be influenced by age, with meta-analyses pointing to a positive correlation between male age and extra-pair paternity gained from EPCs [211,212]. Thus, population age structure is likely to influence rates of both divorce and EPCs, which may in turn have a significant influence on population-level breeding behaviour depending on the distribution of age within the population.

### 2.3 Cooperation

There is emerging evidence for a close relationship between age and cooperation across multiple ecological contexts, and in some cases, there is a clear association between age structure and population-level measures of cooperation. For example, a study of 16 populations in a small-scale horticulturalist human society has demonstrated that demographic factors influence resource-sharing [213]. Age in particular had a positive effect on resource-sharing, with older individuals contributing more to the “group pot”. Further, villages with more adult sisters had higher inequality in resource distribution, suggesting an interplay between age structure, sex distribution, and kinship in explaining rates of cooperation. Some empirical evidence also demonstrates ecological links between cooperation and age in non-human animals [214–216] and bacteria [217], but the influence of variation in population age structure has not been explicitly considered.

Levels of tolerance and willingness to cooperate may be expected to vary over an individual’s lifespan, related to changes in payoffs, partner-choice, competitiveness, and the learning of heuristics that allow individuals to benefit from cooperative interactions. Older individuals may have more familiar associates and stronger bonds, allowing for more frequent cooperation with their social associates. For example, great tits are more likely to cooperate with familiar neighbours [218], and older individuals are more likely to be familiar with their neighbours [219]. Therefore, in such cases, populations with many older individuals may have higher rates of cooperation overall. Furthermore,

cooperation may increase with age if individuals learn to cooperate through their experiences with other cooperators. However, as individuals age, the number of social partners may dwindle if partners are not replaced upon their death, potentially leading to lower levels of cooperation through loss of opportunity [26]. Alternatively, the number of social partners may be reduced due to the previously discussed potential increases in social selectivity with age. Even if age is not directly related to the propensity to cooperate, it is possible, for example, that if individuals of a particular age are more likely to engage in policing of cheaters, the age structure of the population may influence rates of cooperation versus defection [220]. Furthermore, if cooperation confers survival or reproductive benefits to cooperators, individuals may cooperate more as they age in order to mitigate the potential negative effects of senescence [221–223] (see Future Directions).

An extreme form of cooperation seen in animals is cooperative breeding, where individuals provide care to young that are not their own (alloparental care). From an ecological perspective, cooperative breeding is considered to most commonly arise when individuals delay or forego natal dispersal and instead remain in their natal territory caring for the offspring of breeders [224]. In such systems, age-dependent plasticity in the provision of alloparental care may allow individuals to adjust their helping strategies to changes in social and environmental conditions that occur over their lifetime. Recent work shows that local relatedness to other group members can change systematically through the lifespan of an individual, known as kinship dynamics [78,216,225,226]. In cooperative breeders, relatedness between helpers and breeders commonly declines as helpers age, due to time-dependent breeder replacement and dispersal dynamics [216,227]. In these cases, individuals may reduce investment in help as they age [216,228], as lower relatedness often predicts decreased helping efforts in cooperative breeders [229–234]. In Damaraland mole-rats (*Fukomys damarensis*), for example, investment in alloparental care declines with age [235], although this effect may be due to more general age-related declines in performance. Moreover, a decline in relatedness with age, and with it the indirect fitness payoffs of helping, might provoke dispersal attempts by older helpers which then seek to boost inclusive fitness through reproduction outside of the natal group [236]. In other species, however, the prospect of territory inheritance and associated reproductive benefits may favour continued philopatry. This occurs, for example in primitively eusocial hover wasps (*Liostenogaster flavolineata*), where females form an

age-based queue in which only the oldest female reproduces [237–240]. In this and other species that queue for inheritance, individuals are observed to reduce investment in alloparental care as they ascend rank, which can be interpreted as an attempt by older and thus higher-ranking individuals to reduce the mortality risk associated with foraging off the nest in an attempt to survive to inherit the nest [241]. Such a selfish strategy therefore leads to a similar negative relationship between age and helping effort, but in this case the relationship is mediated by the prospect of direct fitness gains through future reproduction rather than the concurrent decline in relatedness and indirect fitness payoffs of help. Multiple ecological processes can shape age-specificity in cooperative breeding, which may therefore in turn generate relationships between age structure and cooperation at the population-level.

## 2.4 Competition

Competition for mates, breeding sites and food is a fundamental ecological process in wild populations [242], including in social species where individuals face local competition with group members. As with cooperative behaviours, an individual's ability to perform, and investment in, competitive behaviours can be sensitive to age [243,244]. In some taxa, older individuals are dominant in competitive interactions [245–251], allowing them to monopolise resources [252]. Age too is observed to confer competitive dominance in species where males form reproductive alliances with the aim of monopolising access to females. In bottlenose dolphins, for example, alliances comprising old males are more successful in competition against alliances of young males, despite typically comprising fewer individuals [253]. In some social species, costs of competition among group members favour the formation of dominance hierarchies, with differences in competitive ability reinforced through ritualised threat behaviours rather than escalated fighting [254,255]. Because competitive ability commonly increases with age, the age structure of populations can strongly influence the formation of hierarchies [256]. In *Polistes* wasps, for example, age structure is an important determinant of hierarchy formation due to an age-based system of queen replacement [257].

Variation in competitive ability with age will also have important consequences for density-dependence in age-structured populations. The effect of age distribution on both inter- and intra-specific competition has been explored through the use of density-dependence models that mathematically estimate the outcomes of competition de-

pending on age structure [61,258–262]. The use of such models alongside empirical data gives an indication of how age structure influences density dependence by mediating levels of competition. For example, in great tits, young individuals constitute the critical age-class for density regulation, whereby the youngest birds have the strongest competitive effect on other breeding females of the same age or older [263]. Expanding these initial findings, it has been shown that including age-specific effects in density-dependence models improves the predictions of population size fluctuations by up to three times in a great and blue tit (*Cyanistes caeruleus*) population [264], indicating the importance of age structure in determining population-level competition.

Variation in age structure will also affect the probability that certain individuals win competitive encounters and which competitive strategies are adopted. For example, the competitive environment is strengthened in mixed-age *Plodia interpunctella* and *Ephestia cautella* moth cohorts compared to uniform-aged cohorts [265]. Further, changes in age structure and the levels of competition might be mutually reinforcing, in that competition may also lead to fluctuations in age structure through its effect on death or dispersal rates. For example, it has been shown that competition for breeding patches, mediated by the presence of predators, induces changes in age structure through age-specific dispersal away from the breeding site in Audouin's gulls (*Ichthyophaga audouinii* [266]).

## 3 FUTURE DIRECTIONS

We have sought to highlight the potential for variation in age structure to govern sociality in wild populations through its impact on social behaviour. However, discussion of the effects of age structure on sociality at the population-level is largely conjectural based on predictions from age-dependence in behaviour mostly at the individual-level. We argue that wild animal populations provide a unique opportunity to advance knowledge regarding the relationship between age structure and sociality as it manifests explicitly at the population-level. This is because natural populations often show considerable variation in age composition across space and time in well-monitored systems; and also provide a useful setting for the fine-scale tracking of individuals over their entire lifetime, and the monitoring of their social networks (and associated social processes) over many generations. Below, we discuss future emerging directions for this area.

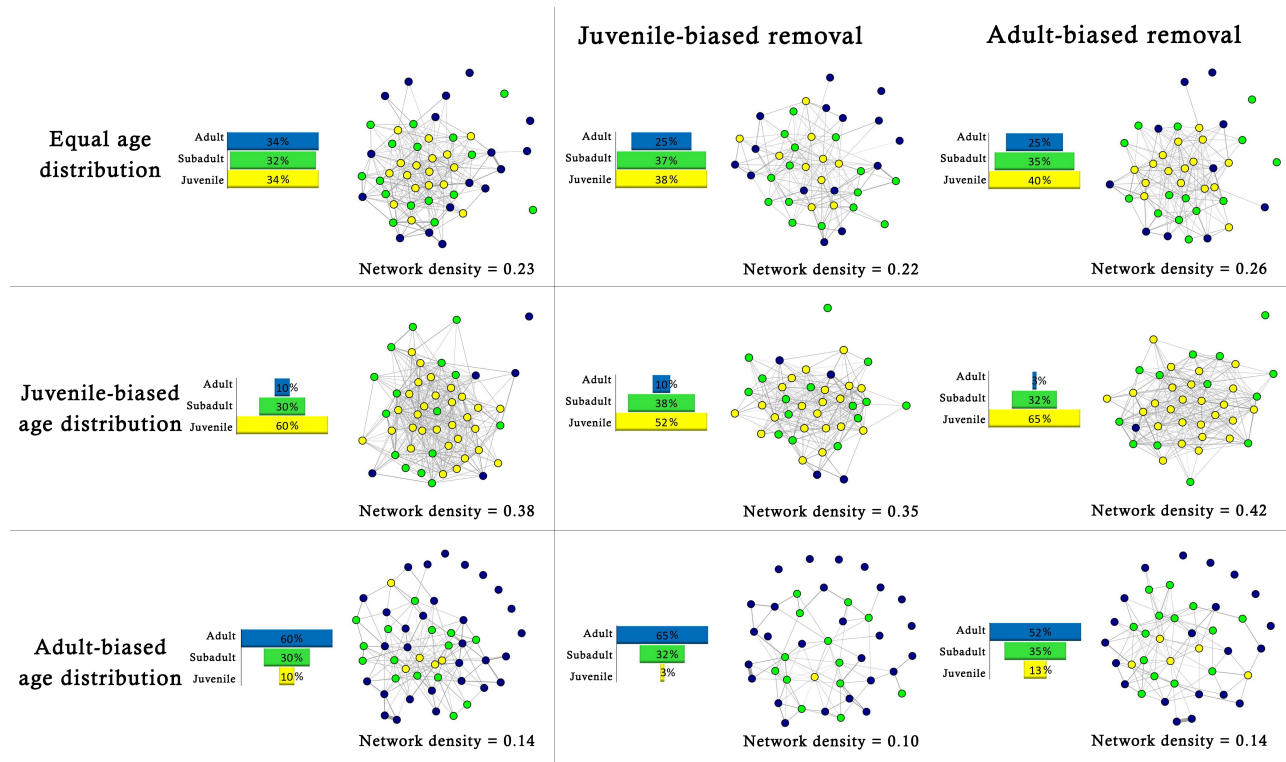


Fig. 2. Social networks of hypothetical populations with different age structures following juvenile- or adult-biased removal, demonstrating the potential shifts in social structure as age structure is altered. The left column shows three initial social networks of 50 individuals with an equal (top), juvenile-biased (middle), and adult-biased (bottom) age distribution. Adults are shown in blue, subadults in green, and juveniles in yellow. In these networks, we assume that the tendency to socialise decreases with age, i.e. juveniles are about six times more likely to socialise than adults. Underneath each social network, we present the network density (the number of existing connections divided by all possible connections), which gives a measure of how well individuals are connected. The right columns illustrate the hypothetical changes in network structure following juvenile-biased (left) or adult-biased (right) removal, i.e. under the juvenile-biased removal, juveniles had an 80% chance of being removed compared to adults and subadults (10% chance of removal each). In each case, 10 individuals were removed. Such effects of age distribution on social network structure should be assessed using empirical data from wild populations (see recent work [54,275]).

### 3.1 Advancing social network approaches in relation to ageing in wild populations

Recent advances have established social network analysis (SNA) as an increasingly powerful tool for understanding the causes and consequences of sociality in a range of evolutionary and ecological contexts [267–271]. By using SNA, individuals are studied as ‘nodes’ in a network, that are connected by ‘edges’ defined by social interactions [58,272,273]. Through this, the diverse range of associations between individuals are quantitatively assessed, such that hypotheses on the patterning of social processes and overall social structure can be tested in a generalised manner, providing insight into population-level behaviour. This allows examination of how individuals affect social processes and the emergent sociality of a group, such as social transmission of behaviour, information, or disease. Further, including individual-level phenotypes (such as sex, size etc.) in SNA allows for the quantitative link between such phenotypes, their associated social network metrics, and group-level sociality. Although age itself is not

a phenotype but rather represents a temporal parameter, it is associated with biological variance in various individual-level phenotypes and has a quantitative value which can be used in SNA. Specifically, due to the previously discussed effects of age on individual sociality, it is likely that age structure will influence interactions and relationships, thus necessarily shaping the overall social network and processes operating within it [54,274,275] (Fig. 2). For example, recent work by Siracusa et al. [54] assesses how changes in social behaviour in free-roaming rhesus macaques affect emergent social structure using SNA on empirical data. The results revealed that ageing female macaques became less indirectly connected for some, but not all, network measures. Further, the authors use agent-based models to understand the extent at which age-based social differences and certain age distributions would result in changes to the overall social network structure (similar to that presented in Fig. 2), but also reveal that variation in age structure does not relate to the structure of the network in this species. Such research is encouraging in that it shows the

applicability of SNA in uncovering links between age, individual social behaviour and overall social structure.

Here, we suggest the wider use of SNA to study how age influences societies through three main routes. Firstly, there are many detailed social networks that have been collected across numerous animal populations globally, which could be collated to test for relationships between age, social interactions, and the emergent social structure. Secondly, by combining datasets that describe life-history attributes within animal populations [276] with their associated network datasets, it can be established how key demographic factors (such as birth and death rates) interact with individual ageing to affect how societies change with time. Finally, simulation modelling techniques could be applied to empirical data to assess how selection for particular age-related phenotypes, together with trans-generational processes such as inheritance and vertical transmission, shape inter-generational social structure.

Further, an advantage of non-human animal populations is that they present several options to experimentally manipulate individual social behaviour, the social network, or age structure to test proposed hypotheses using SNA. For instance, previous social network studies in wild great tits have used experimental removals to examine the effects of the loss conspecifics on social behaviour and network structure [120] and used automated selective feeding stations to apply individual-level treatments to manipulate social structure. This has allowed researchers to experimentally impose social segregation of groups [277], alter the pathways of social information flow [278], assign foraging locations based on individuals' age [279], and manipulate individuals' social centrality [280]. In the future, such manipulations could be used to specifically manipulate local age structure and examine the direct consequences for social behaviour and arising social processes, which has recently been achieved using captive populations of forked fungus beetle (*Bolitotherus cornutus* [275]). Conversely, manipulations could be used to alter wild populations' social structure and assess the impact this has on group demographic rates and resulting age structure, which similarly was recently explored using experimental populations of forked fungus beetle to evaluate multilevel selection as variation in group network structure interacts with demographic rates [281].

The use of SNA to study effects of age structure in wild populations begs the question of how best to quantify this demographic property. In the literature, age structure is often used as a qualitative term, with little emphasis on how to examine it quantitatively. This may be because

it is challenging for a scalar index to convey all information contained in a vector – in this case the relative composition of individuals in every age-cohort [65]. This differs to many other demographic characteristics that can be captured in a single statistic, such as population size, growth rate or sex ratio. Typically, animal population age structure is quantified as either the mean or median age of a population [65,282–284], or as the proportion in a given age-cohort, such as prime-aged or juvenile individuals [61,65,93,206,207,266,282,285–290]. While these statistics contain information regarding the central tendency and aspects of skew, we suggest future research should re-establish quantitative definitions of age structure such that maximum information on the distribution of age can be captured, upon which hypotheses can then be tested. This could be done through greater application of research from human population ageing [80,82,291,292]. For example, the aged-child ratio is the ratio of the number of elderly persons to the number of children, thus considering both ends of the age structure simultaneously. It is represented by the formula

$$\frac{P^{65+}}{P^{0-14}} \times 100$$

where  $P^{65+}$  is the proportion of over 65-year-olds in the population, and  $P^{0-14}$  is the proportion of children 0–14-years-old [291]. Adapting the aged-child ratio may be a useful way of quantifying animal population age structure, for example, by substituting the proportion of 65+-year-olds with the proportion of senescent individuals, and the proportion of 0–14-year-olds with the proportion of juveniles or sexually-immature individuals.

In addition to suggesting the application of human ageing studies to inspire quantitative definitions of age structure, we also identify that explicit methodological studies can be used to define quantitative measures of ecological and evolutionary mechanisms or characteristics. For example, much research has been devoted to developing quantitative definitions of reproductive skew in populations, such that it can be studied in statistical terms with greater biological relevance [293–295]. We therefore suggest that future research should endeavour to determine new mathematical estimations of animal population age structure. This would improve studies of age structure and sociality by optimising the amount of information on the distribution of age across a population, allowing the incorporation of age structure in the use of statistical approaches (such as SNA) and permitting direct comparison of age structure and related processes between populations, even of different species.



### 3.2 Social contagions in relation to age structure

Age structure is expected to affect how information, behaviours, and diseases spread through populations by influencing social connections between individuals. Of these, the transmission of disease has received most attention. For example, morbidity and mortality in wild bird influenza outbreaks are age-specific, where the youngest mute swans (*Cygnus olor*) die 16.8 times more frequently than birds of other ages [296–298]. As a result of this age-specificity in infection, individuals of separate ages differ in their likelihood of transmitting disease [299–301]. Such effects may be exacerbated by social structure, because of age-related variation in social association [302–305]. However, age structure may also influence the transmission of information or behaviours, as well as disease. This may not be apparent if considered as a ‘simple contagion’, whereby the likelihood of learning is assumed to be determined by the total number of network connections to informed individuals [72,306–308]. However, instead, age-specificity in social learning means that behaviours may spread as ‘complex contagions’, whereby transmission is not only determined by the number of connections, but also by specific rules governed by age that affect uptake of the behaviour [72,73]. Thus, when considering complex patterns of transmission through SNA, age effects on social contagions might be detected.

Such age effects exist because the age composition of dyads that make up groups influences whether an individual learns from another, and how quickly information is transmitted [309–314]. Further, the age of individuals in such dyads will affect how long behavioural change will persist [315], influencing the likelihood that a behaviour will continue to spread through a population. This is caused by age-specific abilities to acquire, process, utilise and transmit information [74,316]. On a population-level, this means that age structure might influence if and how quickly behaviour spreads, dependent on the probability of transmission between different age-classes, or due to critical periods in development where social learning is easier [71]. For example, in troops of Japanese macaques (*Macaca fuscata*) with missing age-classes (and therefore an abnormal age structure), stone-handling behaviours are less likely to spread and are performed less frequently [317]. Similarly, when novel or invented behaviours are restricted to one age-class, they may be less likely to spread or be maintained within a population [318,319]. The causal effects of age on social transmission of behaviour should receive more attention and is an example of how SNA could be used to assess the effects of age structure on

sociality.

### 3.3 Human-impact on wild populations’ social ageing

Generating a better understanding of the link between age structure and social behaviour is crucial because human activities are increasingly modifying wild population demographics [290,320–324]. Human-induced environmental changes are diverse, ranging from structural modifications to the physical environment, such as landscape fragmentation, pollution, and anthropogenic food subsidies [325–327], to changes of the social environment by influencing population size, composition, and social interactions [328,329]. Importantly, changes in animal sociality can be mediated by human-induced changes in population age structure. Here, we briefly review two human activities – supplemental feeding, and the selective harvesting of wild animals – and their potential impact on population age structure and sociality.

Supplemental feeding, such as bird feeding stations, can affect age structure by artificially increasing survival rates in certain age-cohorts [330,331]. For example, adult tit species (*Paridae*) often have higher winter survival than yearlings, presumably because of more foraging experience and higher dominance [332,333]. Supplemental feeding increases survival of yearlings [332] and may thus lead to a bias in population age structure towards younger age classes. Further, food supplies can impact age structure if age-classes respond differently to anthropogenic food. For example, the provisioning of food is often used in the conservation of scavenger populations such as the bearded vulture (*Gypaetus barbatus*). Contrary to expectation, anthropogenic feeding sites have been found to increase the survival of sub-adults but not adults in this species, presumably because adult birds foraged less frequently on these food types, leading to on average younger populations [334]. By increasing the survival of younger cohorts, supplemental feeding thus has the potential to drive changes in emergent social structure and functioning by promoting social processes which are performed to a greater extent in younger age cohorts.

One of the best documented cases of human activities impacting wild populations’ age structure is selective harvesting. Hunting and fishing often target individuals with specific phenotypic traits [335–339]. Unsustainable trophy hunting selects individuals with the most attractive ornamental traits such as horns, antlers, plumage, and body size, which often correlates with age, thus often leading to age-specific removal of individuals [337]. For example, human hunters select on average younger female elks

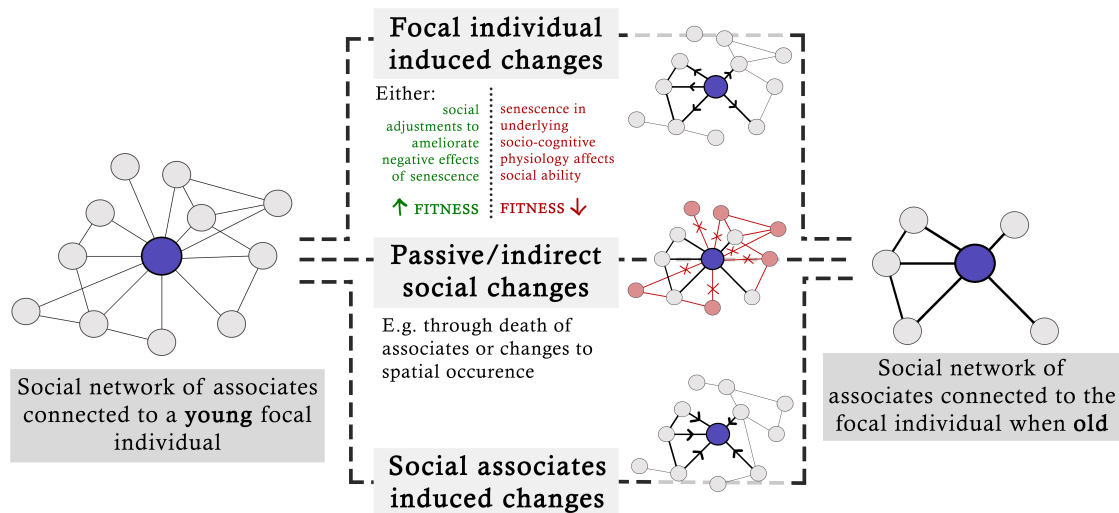


Fig. 3. Different mechanisms that could result in the same late-life changes in social selectivity with age. In each network, the focal individual is represented by the dark blue node.

(6.5 years) with greater reproductive value compared to those selected by natural grey wolf (*Canis lupus*) predators (13.9 years). Therefore, by primarily removing prime-aged females, humans may have a strong impact on the future population viability and emergent age structure of elks [340]. Age-specific harvesting is particularly evident in fish populations, where larger and older fish which contribute disproportionately to spawning and population growth are often the same cohort which are removed the most through commercial harvesting, thus causing truncations in the age structure and damaging future resilience of populations [341–348]. Related, illegal wildlife trade can result in age-biased removal of individuals [349,350]. For instance, poaching of various parrot species (order *Psittaciformes*) is biased towards the extraction of fledglings because they are easier to locate and catch than adult birds [350]. Hence, in addition to decreases in population size, certain harvesting practises can alter population age structure, which may have consequences for population social structure and functioning (for example, see effects of juvenile-biased removal on network density in Fig. 2).

### 3.4 Advancing our understanding of social senescence

Finally, we briefly highlight the importance to advance our understanding of social senescence. In this review, we have considered social ageing as a process of general age-related changes in social behaviour as individuals progress through time, and have discussed patterns that are likely to emerge in population-level sociality given variation in age

structure. We hope this may also provide an initial base from which further research can assess and build a cross-species understanding of social senescence specifically.

Senescence is the decline in organismal functioning with old age, and thus is associated with decreased fitness as selection is weakened in late-life [6–13]. Such senescence is evidenced in wild populations, with old age-related changes in survival probability, reproduction and other, typically physiological, traits [18]. However, while physiological senescence is evident, our understanding of social senescence remains considerably less clear. Specifically, while age-related changes in social behaviour occur with old age, the process behind such changes are ambiguous. Indeed, there is currently limited knowledge on whether age-related changes in social behaviour are generally as a result of senescence (i.e. declining physiological health) or other mechanisms, and whether old-age-related changes in social behaviour hold negative outcomes for the organism. For example, changes in social selectivity with age (where older individuals have fewer but stronger relationships, as discussed previously) could be generated by several different mechanisms while producing similar patterns, and may have positive or negative effects (Fig. 3). First, late-life-related social change might be induced by the focal individual, but this could either be associated with increasing fitness if they are adjustments in social behaviour to ameliorate the negative effects of senescence; or decreasing fitness if mediated by senescence in underlying socio-cognitive physiology. Second, old age social change may be unrelated to active changes in social behaviour but instead as a result

of other processes with old age, such as changes in spatial occurrence or death of conspecifics. Finally, social traits are influenced not only by genes carried by focal individuals (direct genetic effects), but also by social partners (indirect genetic effects) as dyadic relationships are as a result of more than one individual [90,269,351–353]. Therefore, late-life social change might be primarily mediated by changes in social behaviour of associates. Work has begun to assess the role of social senescence in driving late-life changes in social behaviour versus other mechanisms [34], along with the consequences of this for individuals' fitness, but more research is needed to gain a generalised understanding of social senescence and its role in natural populations.

#### 4 CONCLUDING REMARKS

We have highlighted the roles that population age structure and sociality each play in influencing variation in the other. However, the relationship between these variables remains little studied in the wild. We have further highlighted the opportunities to be gained by using SNA in combination with data from natural populations, and we hope that this inspires future research that uses SNA to examine the causal links between variation in age structure and the social functioning of wild populations. Understanding the consequences of variation in age structure on population-level processes is timely, given the increasing impact of anthropogenic activity on population age structure, both indirectly as environmental change impacts the demography and emergent age structure of populations, and directly as age structure is altered through hunting and harvesting. Further, human populations are rapidly ageing for the first time in history. Through advancements in our understanding of age structure in natural populations, greater insights into whether there are fundamental rules of how societies age and the potential social implications of this across systems may be possible. Our hope is that future research will provide new understanding of how age shapes social behaviour and emerging societal structure, the ecological and evolutionary forces that mediate these effects, and the consequences in turn of variation in age structure for fundamental social processes.

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## Chapter III

### **Disentangling the causes of age-assortative mating in bird populations with contrasting life-history strategies**

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## RESEARCH ARTICLE

# Disentangling the causes of age-assortative mating in bird populations with contrasting life-history strategies

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## Abstract

1. Age shapes fundamental processes related to behaviour, survival and reproduction, where age influences reproductive success, non-random mating with respect to age can magnify or mitigate such effects. Consequently, the correlation in partners' age across a population may influence its productivity. Despite widespread evidence for age-assortative mating, little is known about what drives this assortment and its variation. Specifically, the relative importance of active (same-age mate preference) and passive processes (assortment as a consequence of other spatial or temporal effects) in driving age assortment is not well understood.
2. In this paper, we compare breeding data from a great tit and mute swan population (51- and 31-year datasets, respectively) to tease apart the contributions of pair retention, cohort age structure and active age-related mate selection to age assortment in species with contrasting life histories.
3. Both species show age-assortative mating and variable assortment between years. However, we demonstrate that the drivers of age assortment differ between the species, as expected from their life histories and resultant demographic differences. In great tits, pair fidelity has a weak effect on age-assortative mating through pair retention; variation in age assortment is primarily driven by fluctuations in age structure from variable juvenile recruitment. Age-assortative mating is, therefore, largely passive, with no evidence consistent with active age-related mate selection. In mute swans, age assortment is partly explained by pair retention, but not population age structure, and evidence exists for active age-assortative pairing.
4. This difference is likely to result from shorter life-spans in great tits compared with mute swans, leading to fundamental differences in their population age structure, whereby a larger proportion of great tit populations consist of a single age cohort. In mute swans, age-assortative pairing through mate selection may also be driven by greater age-dependent variation in fitness.

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5. The study highlights the importance of considering how different life histories and demographic differences arising from these affect population processes that appear congruent across species. We suggest that future research should focus on uncovering the proximate mechanisms that lead to variation in active age-assortative mate selection (as seen in mute swans); and the consequences of variation in age structure on the ecological and social functioning of wild populations.

#### KEYWORDS

age-assortative mating, assortative mating, *Cygnus olor*, mate choice, natural populations, pair fidelity, *Parus major*, population age structure

## 1 | INTRODUCTION

An individual's age is instrumental in shaping many aspects of life, influencing processes relating to behaviour, survival and reproduction. This is because organisms have limited resources, which are allocated to processes and traits at different points throughout their lifespan to maximise fitness (Stearns, 1992), thus leading to variation in individual-level processes as an organism ages. Evidence demonstrates that individuals show age specificity in reproductive performance (Forslund & Pärt, 1995; Nussey et al., 2013; Sæther, 1990), survival probability (Bouwhuis et al., 2012; Kirkwood & Rose, 1991; Loison et al., 1999), physiology and morphology (Angelier et al., 2007; Jégo et al., 2014; Torres & Velando, 2007) and behaviour (Biondi et al., 2010; Kroeger et al., 2021; Rathke & Fischer, 2021). For example, the decline in physiological functioning with old age can lead to reduced survival and reproductive performance, referred to as senescence (Clutton-Brock, 1988; Medawar, 1952; Shefferson et al., 2017). In groups of individuals, the properties of the group are affected by the age of the component parts within it due to such age specificity (Albery et al., 2022; Albon et al., 2000; Cole, 1957; Gamelon et al., 2016). A dyad of individuals is the simplest case of this, where age-specific effects might be particularly expected with respect to reproduction and related processes. Specifically, the effects of age in a mated pair might be amplified, or mitigated, depending on whether they are the same or dissimilar ages (e.g. Auld et al., 2013; Bowers et al., 2017; Catry et al., 2006; Fasola et al., 2001; Perrins & McCleery, 1985). Furthermore, we might then expect population-level productivity and fitness to be influenced by the overall strength of correlation in age within pairs.

Age-assortative mating, where pairs consist of two partners of the same age, occurs in many animal systems (reviewed by Jiang et al., 2013), and particularly in birds (reviewed by Reid, 1988; Wang et al., 2019). Avian populations are useful models for the study of age assortment due to their long life-span compared with other vertebrates of the same size (Holmes & Austad, 1995). Additionally, 95% of bird species have socially monogamous mating systems (Bennett & Owens, 2002), compared with, for example, only 9% of mammal species (Lukas & Clutton-Brock, 2013), and thus partner choice is easily observable. Furthermore, the effects of age-assortative mating on

reproductive success and offspring fitness has been widely studied in birds (e.g. Auld et al., 2013; Bowers et al., 2017; Brown & Roth, 2009; Perrins & McCleery, 1985). Despite this, little is known about the underlying drivers of age assortment in natural populations, namely whether such patterns are driven by active mechanisms due to the fitness advantages that age assortment might confer, or whether it occurs as an incidental pattern that develops as a result of other processes that are operating. Younger individuals have lower reproductive success in birds (Forslund & Pärt, 1995; Martin, 1995; Sæther, 1990); thus, previous studies have hypothesised that selection favours a directional preference for older individuals, leading to active age assortment (Fasola et al., 2001; Perrins & McCleery, 1985; Reid, 1988; Shaw, 1985). Some tests for age-assortative mating have been performed by considering display or pairing behaviour, and whether this suggests an active preference for individuals of the same age (Cézilly et al., 1997; Jouventin et al., 1999). But evidence for active age-related mate choice is unclear, for example, due to uncertainty surrounding the proximate cues that might be used to determine age (Cézilly et al., 1997), as well as contrasting results between species (Reid, 1988).

Other research suggests that age-assortative mating occurs incidentally through the effect of pair fidelity in socially monogamous populations (Barbraud & Barbraud, 1999; Mills & Shaw, 1980). Due to a range of mechanisms that enhance breeding success, individuals may remate with the same partner across multiple years (Black, 1996). For example, the 'mate familiarity effect' can lead to increased reproductive success through improved parent co-operation (Sánchez-Macouzet et al., 2014; Tinbergen, 1959; Weiß et al., 2010). Pair-bonded individuals may also experience benefits of breeding earlier, as they do not need to allocate time into establishing a new pair (Lifjeld & Slagsvold, 1988; McGraw & Hill, 2004; Pampus et al., 2005), as well as improving their survival (Culina, Lachish, et al., 2015; Nicolai et al., 2012). Age assortment might, therefore, arise when individuals enter a breeding population at the same age, pair with each other, and then consecutively remate when they will continue to be assorted by age. A further consequence of this remating is that it may drive an age bias in the pool of potential non-paired partners. Because older individuals are more likely to be pair-bonded (Jouventin et al., 1999), it may mean that the mates

available for individuals breeding for the first time primarily includes other first-time breeders, which could lead to passive age assortment if the age at first breeding is similar.

An additional mechanism by which age-assortative mating might develop is as an incidental process due to spatial or temporal clustering of same-age individuals (Jiang et al., 2013; Lewontin et al., 1968; Moura et al., 2021). If there are many individuals of a specific age in time or space, high rates of age assortment can result. For example, age-assortative mating may occur due to temporal clustering of younger individuals resulting from age differences in arrival times at breeding territories following migration (Potti, 2000; Village, 1985), as well as spatial clustering of young breeders related to age specificity in territory quality (Ferrer & Penteriani, 2003). Furthermore, individuals of the same age may be clustered simply as a result of the fact that they occupy a large proportion of the population, that is, if the age structure of a population is skewed towards a certain age due to species' life history. This might be expected in short-lived species that exist at the 'fast' end of the fast-slow continuum of life history, whereby individuals die earlier (Stearns, 1983), and, therefore, high proportions of their populations may occupy younger age cohorts. The dependence of age assortment on overall age structure is relatively unrecognised in previous research given the large role it might play.

Here, we use long-term population data to assess variation in age-assortative mating and relate this variation to the processes that might drive it. We tease apart the relative contributions of passive and active age assortment using statistical approaches that assess for assortment above what would be expected through chance. We present analyses on age-assortative mating in two species with contrasting life-history strategies and resulting demographic structures using datasets that span 51 and 31 years of breeding in a passerine and waterfowl species, respectively. First, we identify evidence for age assortment in breeding pairs and assess the temporal variation in this which might be driven by variation in the underlying active or passive processes. Second, we evaluate the potential causes of age assortment and its variation by considering the effect of pair fidelity; assortment beyond what would be expected by chance given within-year population age composition; and active age-related mate choice. Finally, we discuss the implications of our findings in the context of life history and demographic structure.

## 2 | MATERIALS AND METHODS

### 2.1 | Study systems and data collection

The great tit *Parus major* is a passerine in mixed woodlands across much of Europe. They have relatively short lifespans, with breeding ages ranging from 1 to 9, averaging 1.8 years, and reproductive performance peaking at 2.8 years (Bouwhuis et al., 2009). They, therefore, exist at the 'fast' end of the fast-slow continuum of life history, whereby they start breeding early with relatively high fecundity, but die earlier (Stearns, 1983). Data used here are from a

long-term study population of great tits in Wytham Woods, Oxford (51°46'N, 1°20'W). This population has been monitored since 1947, where breeding adults and their chicks have been marked with unique British Trust for Ornithology (BTO) rings since the 1960s (Perrins, 1965). All chicks reared in nest-boxes are ringed at 14-days of age, while adults are trapped at boxes during the nestling phase, and identified by ring number or marked with a new ring if they are immigrant birds. Parent age is based on year of hatching for local birds, or plumage characteristics (Svensson, 1994) for immigrants. Although immigration rates are high (53%), most are first caught as yearlings (76%) and, therefore, can be aged accurately.

The mute swan *Cygnus olor* is a longer-lived bird, with breeding ages ranging from 2 to 24, averaging 7.6 years (Birkhead & Perrins, 1986; Perrins et al., 1994), thus existing at the 'slower' end of the fast-slow continuum of life history. Mute swans similarly show age-specific reproductive fitness, where individuals tend to improve performance up to age 6 or 7, and decline after age 12 (McCleery et al., 2008). Data used here are from Abbotsbury Swannery and Chesil Fleet (50°35'N, 2°30'W), where swans have been breeding since at least the fourteenth century. Since 1977, all individuals that breed and hatch at the colony have been marked with a unique BTO ring. Additionally, since 1989, a roundup occurs every 2-years after the breeding season, where all birds in the colony are captured and marked, thus identifying non-breeding individuals present in the population (Perrins et al., 1994). Age is based either on date of hatching for resident birds, or colouration of plumage and beak for immigrant birds, which can discriminate between birds of 1, 2 and 3 years or older (Auld et al., 2013). Most breeding individuals hatched in the swannery (80% males and 93% females), and, therefore, age is known. Additionally, of the 13% that immigrate and breed in the population, 57% do so at an age when they can still be aged accurately.

Data collection from both populations adhered to local guidelines for the use of animals in research, and all fieldworkers involved over the many years of fieldwork have held BTO ringing licences (author BTO permit number: C/6987). Additionally, the long-term monitoring in Wytham has been subject to review by the University of Oxford Department of Zoology Animal Welfare and Ethical Review Board (approval reference number: APA/1/5/ZOO/NASPA/Sheldon/TitBreedingEcology).

### 2.2 | Data selection

We constructed a dataset that assigns year of birth to all great tits between 1950 and 2020, in which exact age was calculated for 97.3% of 118,872 individuals, and 88.8% of 44,532 adults. Birds that entered the population with adult plumage were assigned a minimum age of 2, and subsequent age estimates were based on this (12.6% and 8.8% of breeding males and females). We assessed birds that attempted to breed between 1970 and 2020, for which data were more complete compared with earlier dates. Pairs were included no more than once per year, such that the representation of partner

age differences across the population were not inflated by repeated breeding attempts within a year between the same individuals. This was achieved by removing second broods from analysis, which are rare in this study system (Perrins, 1965). Exact age was calculated for both sexes in 67% of breeding attempts where at least one egg was laid (due to a combination of nests failing prior to adult trapping and unsuccessful trapping attempts, there were many cases where the identity of both parents was not known).

Since 1990, all resident swans breeding at Abbotsbury had hatched after the start of the individual monitoring programme, and their year of birth recorded. We, therefore, calculated exact age for 94.1% of 1745 breeding individuals between 1990 and 2020. The remaining 5.9% of birds—immigrants that entered the population with adult plumage—were removed from analysis due to uncertainty regarding their age. Additionally, we calculated exact age for 1755 non-breeding individuals that were caught at 15 biennial roundups at Abbotsbury 1991–2019.

## 2.3 | Statistical analyses

We assessed evidence for, and contributors to, age-assortative mating and its variation in the populations in two ways. First, we calculated the correlation of age in mates using a Spearman's rank correlation as a nonparametric test of association that calculates the direction and strength of correlation in partner ages. We also did this per year, as well as calculating the proportion of individuals per year assorted by age, to assess whether population-level age assortment shows temporal variation (see also Supp. Methods a).

Second, we compared the observed number of age-assorted pairs against a distribution expected from random pairing with respect to age. We created this distribution through permutation analysis by randomly assigning partners together, depending on individuals breeding in a given year, and calculating the frequency of absolute age differences in these randomly paired populations. This was repeated 1000 times. From 1000 iterations, we constructed a frequency distribution of the number of age-assorted pairs, against which we compared the observed number, to evaluate whether the number of pairs assorted by age would be expected through random pairing. In the case of the mute swan, we ran an additional parallel analysis for the 15 years where a roundup occurred (see Supp. Methods b).

## 2.4 | Disentangling the causes of age-assortative mating

### 2.4.1 | Does pair fidelity drive age-assortative mating?

We assessed whether the effect of pair fidelity drives age-assortative mating. This has the potential to influence age assortment because birds may pair at first breeding at the same age, and then remain

together in future years when they will continue to be assorted. We assessed the effect of pair fidelity in the two populations using the same above methods. We compared the frequency of the number of age-assorted pairs in 1000 permuted datasets with the observed number, but restricted the data so that it included only newly formed pairs, thus removing any assortative effect of pair fidelity.

### 2.4.2 | Does population age structure drive age-assortative mating?

Second, we evaluated whether age-assortative mating is age-dependent and driven by assortative pairing within certain age cohorts. If the age at first breeding is similar for most individuals, then they may consequently pair at this age as older individuals have already established pairs from previous breeding. Furthermore, if the age structure in such populations is skewed towards the age at which individuals first breed, then we may expect more assortment and thus variation in age structure to affect population-wide age assortment.

To preliminarily assess whether a greater number of individuals breeding for the first time in their life history, regardless of their age (hereafter 'first-time breeders'), might be related to population-level age assortment, we calculated the within-year proportion of the population consisting of first-time breeders and the proportion assorted by age in both species. We then ran a Spearman's rank correlation between these two variables. To explicitly test how this relates to whether variation in age structure affects age-assortative mating, we defined age cohorts within both populations that include the most first-time breeders (hereafter 'young breeders'). The median age at first breeding in great tits and mute swans is 1 and 4, respectively (Figure S1). Therefore, in great tits we defined yearlings (1-year-olds) as young breeders, whereas in mute swans we defined 2–4-year-olds as young breeders (yearling swans do not breed). The proportion of the population that are first-time breeders and the proportion consisting of these age cohorts were strongly correlated in both species (Figure S2). We then ran a Spearman's rank correlation between the proportion of young breeders and the proportion of age-assorted pairs in both populations. Furthermore, we used permutation analysis to assess whether the relationship we see between these two variables would exist if the population were to pair randomly. We assigned partners randomly, depending on those breeding in the given year, and calculated the relationship between the proportion of young breeders and age-assorted pairs. We repeated this 1000 times, yielding a distribution of 1000 Spearman's rank correlation coefficients when within-year pairing is random.

### 2.4.3 | Is there any evidence consistent with age-related mate selection?

Third, we partitioned our datasets to only include pairs where both partners had attempted to breed in a previous year, but with

a different individual to the current year, therefore representing pairs that did not form at either partners' first breeding (hereafter 'newly formed experienced pairs'). If age-assortative mating occurs within this subset of pairs, then it would be consistent with age-related mate selection, as individuals will not be age-assorted as a consequence of being the same age at first breeding, or through subsequent pair retention. We used a Spearman's rank correlation to assess the relationship between the within-year proportion of the population that consists of newly formed experienced pairs, and the proportion of the population assorted by age. Finally, we tested for age-assortative pairing in this subset of the population, thus removing any assortative effect of pair retention and assortment through similarity in age at first-breeding. We compared the observed number of age-assorted newly formed experienced pairs with a distribution obtained from 1000 permuted datasets where pairing is random.

### 3 | RESULTS

A total of 10,279 pairs involving 13,573 individuals were recorded in our great tit population with ages 1–9. Over the entire 51-year dataset, we found a moderate positive correlation between the age of mates (Spearman's correlation:  $r = 0.321$ ,  $p < 0.001$ ; Figure 1a). The strength of correlation is positive and statistically significant in 45 of the 51 years, with only a very weak positive relationship in some years (Table S1a; Figure S3a). There is temporal variation in age assortment, with the annual proportion of age-assorted pairs varying from 34.9% to 63.0%. A total of 3223 pairs involving 1520 individuals were recorded in our mute swan population with ages 2–24. In the 31-year dataset, there is a strong positive correlation in age between mated partners across all time (Spearman's correlation:  $r = 0.887$ ,

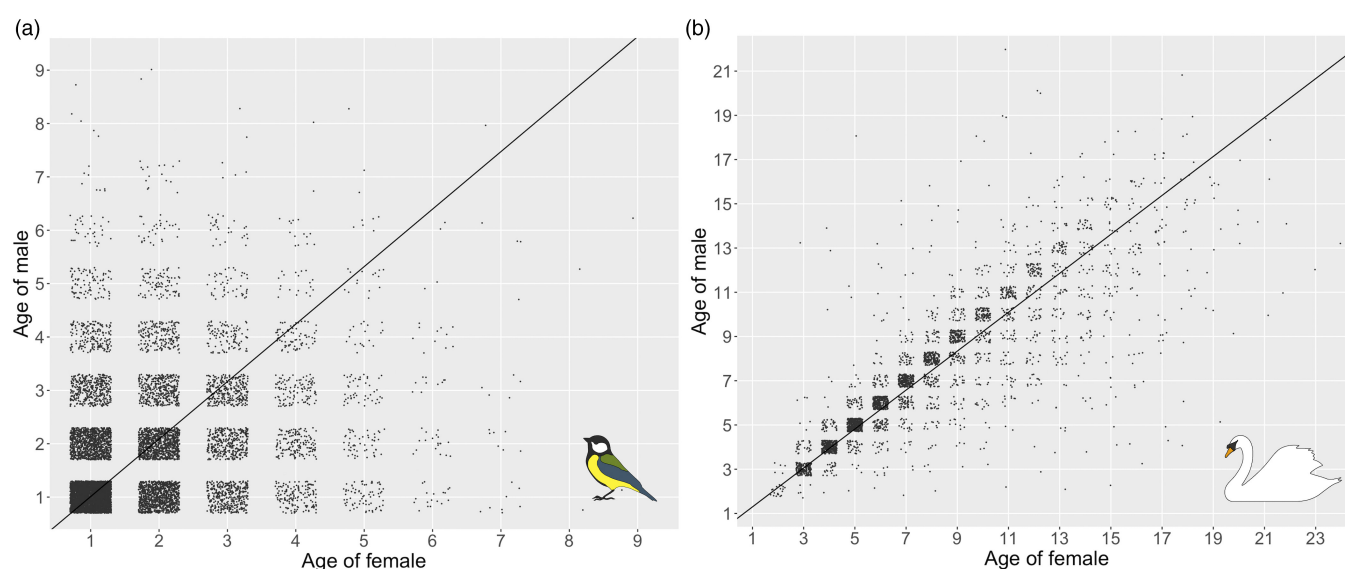
$p < 0.001$ ; Figure 1b) and also in each individual year (Table S1b; Figure S3b). Despite consistently high levels of age-assortative mating, the proportion of pairs assorted by age in the population varies from 38.1% to 73.0% between years.

These correlations in age are supported by the comparison of the observed number of age-assorted pairs with the frequency distribution obtained from 1000 permutations of random pairing with respect to age. The observed number of 4982 age-assorted great tit pairs is greater than expected from the null distribution (2.5th–97.5th percentiles: 3778–3941;  $p = 0$ ; observed value 29.1% greater than mean of null distribution; Figure 2a: first violin), indicating that we see greater age assortment than expected from random pairing. In mute swans, we see an even more marked difference between the observed number of 1888 age-assorted pairs and the null distribution (2.5th–97.5th percentiles: 334–401;  $p = 0$ ; observed value 412.6% greater than mean of null distribution; Figure 2b: first violin). We also see this difference when allowing non-breeding individuals from the roundup to pair (Figure S4; Table S3).

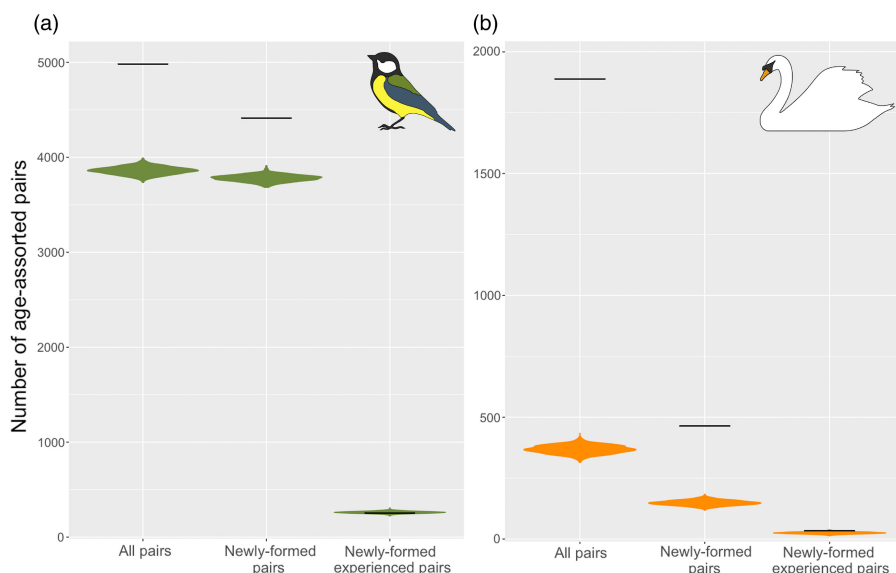
#### 3.1 | Disentangling the causes of age-assortative mating

##### 3.1.1 | Does pair fidelity drive age-assortative mating?

We tested whether pair fidelity affects age-assortative mating by subsetting the data to only include newly formed pairs, thus removing any age-assortative effect of pair retention. In great tits, the number of 4413 age-assorted pairs is greater than null distribution, indicating greater assortment than expected through random pairing (2.5th–97.5th percentiles: 3708–3845;  $p = 0$ ;



**FIGURE 1** Relationship between female and male partner age within mated pairs of (a) great tits 1970–2020 and (b) mute swans 1990–2020. Each point represents a pair with given female and male ages; points are jittered by 0.3 along both axes to avoid over-plotting at the same location. The line is a reduced major axis regression, which models the relationship between the age of partners (Table S2).



**FIGURE 2** The frequency of the number of age-assorted pairs in 1000 permutations where partners are randomly paired with respect to age in (a) all great tit pairs; newly formed great tit pairs; and newly formed experienced great tit pairs; and (b) all mute swan pairs; newly formed mute swan pairs; and newly formed experienced mute swan pairs. The black lines show the observed numbers of age-assorted pairs for each subset of the populations; all violins have the same maximum width to aid visualisation.

observed value 16.7% greater than mean of null distribution; [Figure 2a](#): second violin); this difference is less pronounced compared with when pair-bonded partnerships are included. In mute swans, the number of 464 age-assorted pairs is also greater than the null distribution, but this difference is even less marked compared with when pair-bonds are included (2.5th–97.5th percentiles: 129–170;  $p = 0$ ; observed value 148.6% greater than mean of null distribution; [Figure 2b](#): second violin). We see a similar pattern of a greater number of age-assorted pairs than expected through random pairing when including non-breeding individuals from the roundup ([Figure S4](#); [Table S3](#)).

### 3.1.2 | Does population age structure drive age-assortative mating?

We found a positive relationship between within-year proportion of first-time great tit breeders and proportion of age-assorted pairs (Spearman's correlation:  $r = 0.594$ ,  $p < 0.001$ ; [Figure S5](#)); the relationship between the proportion of first-time breeders and proportion of age-assorted pairs was much weaker in the mute swan population (Spearman's correlation:  $r = 0.206$ ,  $p = 0.266$ ; [Figure S5](#)). Furthermore, explicitly assessing how this relates to whether age structure affects assortative mating, the proportion of young breeders (yearlings) in the great tit population and the proportion of age-assorted pairs strongly correlate (Spearman's correlation:  $r = 0.784$ ,  $p < 0.001$ ; [Figure 3a](#)). This correlation coefficient is within a null distribution constructed from 1000 permutations of random pairing (2.5th–97.5th percentiles: 0.755–0.893;  $p = 0.210$ ; [Figure S6](#)), denoting that the relationship between proportion of yearlings and age-assorted pairs is consistent with random pairing. However, as expected from the previous analyses using proportion of first-time breeders, there was no relationship between the proportion of young breeders and age-assorted pairs in mute swans (Spearman's correlation:  $r = 0.086$ ,  $p = 0.645$ ; [Figure 3a](#)); and this correlation

coefficient is within a null distribution of coefficients from 1000 permutations of random pairing (2.5th–97.5th percentiles:  $-0.176$ – $0.441$ ;  $p = 0.740$ ; [Figure S7](#)). Additionally, there was little evidence for a relationship between proportion of 1–4-year-olds and population age assortment in roundup years (Spearman's correlation:  $r = 0.068$ ,  $p = 0.810$ ; [Figure S8](#)).

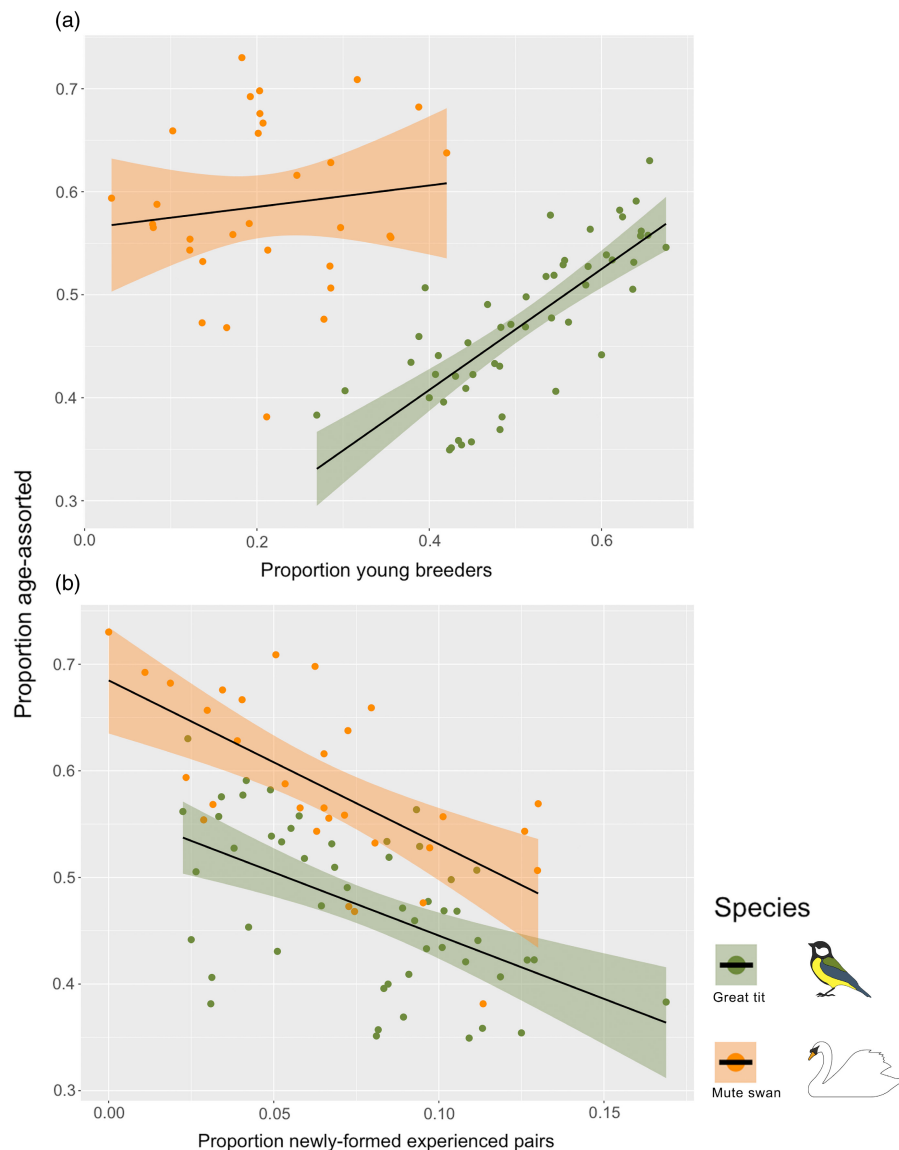
### 3.1.3 | Is there any evidence consistent with age-related mate selection?

We found a negative relationship between the proportion of newly formed experienced pairs and age-assorted pairs in both great tits (Spearman's correlation:  $r = -0.510$ ,  $p < 0.001$ ; [Figure 3b](#)) and mute swans (Spearman's correlation:  $r = -0.671$ ,  $p < 0.001$ ; [Figure 3b](#)). This means that in years where there are more pairs forming a new partnership, despite breeding with different individuals in previous years, less age assortment was observed.

In great tits, we found that among these 774 pairs, the observed number of 254 age-assorted pairs is within the null distribution obtained from the permuted datasets, suggesting that we do not see more newly formed experienced pairs assorted by age than if they were to pair randomly (2.5th–97.5th percentiles: 240–284;  $p = 0.578$ ; observed value 2.6% lower than mean of null distribution; [Figure 2a](#): third violin). However, in mute swans, among the 204 newly formed experienced pairs, there is evidence that the observed number of 34 age-assorted is greater than the null distribution based on random pairing (2.5th–97.5th percentiles: 18–33;  $p = 0.032$ ; observed value 33.7% greater than mean of null distribution; [Figure 2b](#): third violin). When including non-breeding individuals in analysis, we similarly find that the observed number of age-assorted pairs is greater than the mean of the null distribution ([Figure S4](#); [Table S3](#)). These results suggest that we may see more age-assorted newly formed experienced pairs than expected through random partner choice.



**FIGURE 3** Relationship between the within-year proportion of age-assorted pairs in great tits and mute swans and (a) the proportion of young breeders (where 'young breeder' is defined as being a yearling, or 4-years or younger, in the two species, respectively); (b) the proportion of newly formed experienced pairs. In both plots, the lines indicate a linear regression, which models the relationship between the two variables, and the shading around this shows the 0.95 confidence intervals.



## 4 | DISCUSSION

In this study, we assess mechanisms contributing to age-assortative pairing in two long-term studies of wild bird populations. We demonstrate that the processes driving age-assortative mating in the two populations do so to different extents. The amount of age-assortative mating varies between years in both species, which may be explained by different underlying mechanisms related to their different life histories and resulting demographic structures.

In both species, we found that pair fidelity contributes to age-assortative mating, but to a greater extent in mute swans. However, the process of pair retention is not the only contributor to the process, as we still observe age assortment when pair-bonded individuals are discounted. In great tits, the degree of population-level age assortment is largely driven by fluctuations in the population's age structure: when the proportion of yearlings in the population is higher, we see more age-assortative mating. We demonstrate that this relationship would be expected if pairing behaviour was random with respect to age, and thus that age assortment among yearlings occurs because they occupy a large cohort within the population and are, therefore, likely to pair with each

other through chance. We reveal that there is no age assortment above what would be expected through random pairing among newly formed experienced great tit pairs, supporting that age assortment in this population is passive and related to the age composition of available mates, as opposed to active age-based mate selection. In contrast, in mute swans, we see much weaker association between variation in population age structure and age-assortative mating. In years with a greater proportion of newly formed experienced pairs, there is less population-level age-assortative mating. However, even among these individuals, we find evidence of age-assortative mating above what might be expected through random pairing. This, therefore, suggests that a process of age-related mate selection may contribute to age-assortative pairing in this species.

### 4.1 | Does pair fidelity drive age-assortative mating?

Our study reveals that pair fidelity contributes to the process of age assortment in both species, but to different extents. In great tits, the number of age-assorted pairs across all individuals is greater

than the mean of a null distribution based on random pairing, but when we account for pair fidelity, this difference is less pronounced. In mute swans, the number of age-assorted pairs is considerably greater than the mean of the null distribution. However, when the effect of pair fidelity is removed, the difference between the observed and expected number of age-assorted pairs decreases markedly, yet there is still greater age assortment than expected from random pairing (Figure 2).

Two effects may partly explain why pair fidelity does not solely drive patterns of age-assortative mating in these two species, and why it appears to be a greater contributor in mute swans. First, pair-bonds must be sustained beyond the duration of a single reproductive event or mating season (Bales et al., 2021), and thus pair-bonded individuals are older (Jouventin et al., 1999). This means they potentially constitute a smaller proportion of the population - especially in species that are at the 'fast' end of the slow-fast continuum of life history—and hence are unlikely to have considerable effects on assortative behaviour at a population-level. This could lead to a weaker effect of pair fidelity in species with high mortality rates compared with longer-lived species. Indeed, in our great tit population, the annual proportion of first-time breeders is high (annual range: 46%–83%) while the proportion of the population made from pair-bonded partnerships is low (annual range: 3%–22%). In contrast, in mute swans a smaller proportion of the population consists of first-time breeders (annual range: 12%–45%) and pair-bonded partnerships are retained for a greater period of time as individuals survive for longer, making up a larger proportion of the population (annual range: 42%–86%). This may explain why, upon removing the effect of pair fidelity in our two populations, we see a much greater relative decrease in the observed number of age-assorted pairs towards to the frequency distribution obtained from random pairing in the swan population, compared with great tits.

Second, although pair-bonded individuals will continue to have the same age-difference in all years they remate, they will not necessarily be assorted by age, as this assumes that they first bond at equal age. Pair-bonds generally form at first reproduction (Black, 1996), but individuals may start breeding at different ages. Variability in age at first breeding is likely to be linked to species life history, as demonstrated in our study systems. Great tits have relatively short lifespans and most birds start breeding in their first year (Culina et al., 2020); thus, there is little variability in age at first breeding (median age at first breeding: 1; 10th–90th percentiles: 1–2). In contrast, longer-lived mute swans show deferred sexual maturity and greater variability in age at first breeding (Charmantier et al., 2006a; Minton, 1968; median age at first breeding: 4; 10th–90th percentiles: 3–7). Therefore, pair fidelity might not lead to age assortment as pairs retained from first breeding may be individuals of different ages, particularly in species with greater variability in age at onset of reproduction.

Pair-bonded mates may also be different ages in populations with high mortality and increased widowing (Black, 1996; Culina, Radersma, et al., 2015), whereby individuals change their partner following mate loss. This is particularly relevant in our great

tit population, which has high rates of annual mortality (~52%, Bouwhuis et al., 2012; compared with ~15% in mute swans, McCleery et al., 2002), and subsequently a high degree of widowing and re-pairing between years. Additionally, individuals may 'divorce' their partner and form a new partnership if they gain reproductive advantages in doing so (Choudhury, 1995; Culina, Radersma, et al., 2015). In these cases, a new pair-bond may be established where either one, or both, partners have previously bred and are of different ages. Indeed, in our great tit system, only 53% of pair-bonds are established at both partners' first reproduction, and 54% of pair-bonded partnerships are individuals of a different age. In the mute swan population, 64% of pair-bonds form at both partners' first reproduction, and 42% of pair-bonded individuals are of different age. Therefore, the strength of pair fidelity in a population does not necessarily relate to the amount of age-assortative mating as pair-bonds can exist between mates of different age, driven by variability in age at first reproduction, and remating due to widowing or divorce.

## 4.2 | Does population age structure drive age-assortative mating?

Our study reveals that temporal fluctuations in population age structure strongly correlate with variation in population-level age-assortative mating in great tits but not mute swans (Figure 3a). Moreover, we demonstrate that this relationship in great tits is consistent with pairing being random with respect to age (Figure S6). This indicates that age structure drives age-assortative mating, but as an incidental process whereby yearlings passively pair with each other to a greater degree in years where they occupy a larger proportion of the population. Such incidental age assortment is possible due to the life history of tits, in that high annual mortality rates mean that yearlings often occupy the majority of the breeding population (Figure S9a), especially when discounting established pairs that retain their partner from previous years. However, due to the life history and lower mortality rates of mute swans, younger age cohorts do not dominate the age structure (Figure S9b), and thus, we do not see the same incidental age assortment. It might then be expected that age assortment in species with comparable life histories to great tits, and thus similar demographic structures, might also be driven by fluctuations in age structure. Such species where age-assortative pairing has been demonstrated includes the house wren *Troglodytes aedon* (Bowers et al., 2017), wood thrush *Hylocichla mustelina* (Brown & Roth, 2009), pied flycatchers *Ficedula hypoleuca* (Potti, 2000) and pinyon jays *Gymnorhinus cyanoceph* (Marzluff & Balda, 1988). Future research should apply parallel methods used in our study to breeding data in such passerine populations that have similar demographic structures to determine whether age assortment occurs as a passive process, and even in non-avian systems with comparable life histories with regard to demographic structure.

It has been speculated that age-assortative mating in *Paridae* populations might be generated through older females selecting males whose age is greater than the population average before the

formation of spring territories, thus driven by a mechanism of active age-related mate choice. A period of activity among older birds in the winter might lead to experienced individuals pairing with each other, forcing first-time breeders to associate and mate with each other (Perrins & McCleery, 1985). Furthermore, Farine et al. (2015) show that age is non-randomly assorted in social networks that measure the associations between individuals in winter feeding flocks, potentially suggesting active age-related association during social activity. Winter social associations are known to carry-over into future breeding (Firth & Sheldon, 2016). However, we demonstrate that age-assortative associations between breeding yearlings would be expected through random pairing given the within-year age structure. Furthermore, research should focus on uncovering the link between age assortment as an incidental process among young breeding individuals that occupy large cohorts within populations, and non-random age-assortative association during behaviour prior to breeding. This would further our understanding of the processes driving age-assortative mating on a population level.

#### 4.3 | Is there any evidence consistent with age-related mate selection?

We find no evidence consistent with active age-related mate selection leading to age assortment in great tits. When there is a greater proportion of newly formed experienced pairs, we observe less population-level age-assortative mating (Figure 3b), however, these pairs cannot include yearlings. Therefore, this relationship is likely seen as a consequence of the fact that years in which such pairs occupy a greater proportion of the population have fewer juveniles (Figure S10), which we suggest drives population age assortment. When only assessing newly formed experienced pairs, we report a very similar number of age-assorted pairs as would be expected through random pairing (Figure 2a). This suggests no evidence that individuals are actively choosing to mate with individuals of a similar age. Furthermore, as explained, patterns of age-assortative mating observed across the entire population would be expected through random pairing considering fluctuations in age structure (Figure S6). Hence, despite age specificity in breeding success in great tits (Harvey et al., 1979), and indeed many other short-lived passerines (Forslund & Pärt, 1995; Sæther, 1990), there is no evidence consistent with a process whereby older and more experienced great tits actively mate assortatively.

In contrast, in our mute swan population, we find evidence consistent with active age-related mate selection. When assessing newly formed experienced pairs, we found evidence for age assortment, with the observed number of age-assorted pairs being marginally greater than the mean of a null distribution based on random pairing (Figure 2b), with similar results found when including non-breeding individuals (Figure S4; Table S3). The similarity in age within these pairs (Figure S11), above what would be expected if pairing was random, reveals that individuals may actively chose to mate with individuals of a similar age. This might be driven by greater

age-dependent variation in fitness in mute swans (Charmantier et al., 2006b; McCleery et al., 2008), where a directional mating preference for prime-age individuals may select for active age-assortative pairing.

Despite this, we report temporal variation in mute swan population-level age assortment. Furthermore, we demonstrate that in years where there is a greater proportion of newly formed experienced pairs, less population-level age-assortative mating is observed (Figure 3b). In contrast to our tit system, this relationship will not be driven by fluctuations in age structure because there is no relationship between the proportion of newly formed experienced pairs and the proportion of young breeders (Figure S10), neither is there a relationship between age structure and population-level age assortment (Figure 3a; Figure S8). Therefore, the correlation we find between proportion of newly formed experienced pairs and proportion of age-assorted pairs may suggest individual variation in age-related mate selection, whereby individuals forming a partnership with a new mate, either following divorce or widowhood, may not mate as assortatively compared with others in the population. Future research should investigate this to determine the proximate drivers behind individual-level variation in active age-assortative mating in long-lived species that exhibit age-related mate selection.

## 5 | CONCLUSIONS

In this study, we have demonstrated that age-assortative mating in a long-term natural great tit population is driven by variation in population age structure and influenced by pair fidelity, but there is no evidence for active age-based mate selection. In contrast, we find an apparent stronger effect of pair fidelity on age assortment in mute swans and provide evidence consistent with active age-related mate selection. We suggest that the differences between the drivers of age assortment in the two species are linked to their distinct life histories and consequent demographic structures. High mortality rates in great tits allow for a process of passive age-assortative pairing, which is not the case in longer-lived mute swans. However, the presence of temporal variation in age assortment in mute swans implies individual-level variation in age-related mate choice, which we suggest future work should focus on through identifying mechanisms that lead to such variation in swans and other species that mate assortatively by age. Primarily, our study reveals how demographic properties and life histories affect population-level mating processes, and how this differs between species. Furthermore, we highlight the importance of considering population age structure as a crucial demographic attribute of populations that has great potential to influence fundamental population-level processes, in this case relating to reproductive behaviour. Future research should, therefore, attempt to uncover the ecological and evolutionary forces that lead to fluctuations in age structure, whether this variation is adaptive, and other potential consequences it may have on the social and ecological functioning of populations.



## AUTHOR CONTRIBUTIONS

Joe P. Woodman conceived the idea for this work through discussion with Ben C. Sheldon. Joe P. Woodman designed and conducted analyses and led the writing of the manuscript; Ella F. Cole, Josh A. Firth, Christopher M. Perrins and Ben C. Sheldon provided detailed feedback on methodology, and contributed critically to drafts. All authors have participated in data collection.

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## CONFLICT OF INTEREST

No competing interests.

## DATA AVAILABILITY STATEMENT

Breeding data and code for analyses available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.m63xsj44s> (Woodman et al., 2022).

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## SUPPORTING INFORMATION

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

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# Disentangling the causes of age-assortative mating in bird populations with contrasting life-history strategies - SUPPORTING INFORMATION

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## 1 SUPPLEMENTARY METHODS

### 1.1 Linear models of age-assortative mating

In addition to a Spearman's rank correlation as a nonparametric test of association, we also ran linear models to assess the average relationship between partner age, with male age as the response variable. We ran such linear models in both species across all time, as well as each year individually (see results in Table S4).

### 1.2 Mute swan roundup analysis

During the 15 years where a roundup occurred in the mute swan population, we ran the same permutation analyses as in the main text, but additionally included the non-breeding birds present in the population, not including recently fledged cygnets. We randomly assigned partners together and calculated the frequency of age-differences in these randomly-paired populations; this was repeated 1000 times. From these 1000 permutations, we constructed a frequency distribution of the number of age-assorted pairs, against which we compared our observed number of age-assorted pairs to evaluate whether the number of pairs assorted by age would be expected through random pairing. Due to slight unequal sex ratios within years, we performed the analysis separately for each sex: first assessing all breeding individuals in addition to non-breeding males from the roundup; and then all breeding individuals and non-breeding females from the roundup. This resulted in a group of unpaired males and females, respectively, per permutation, and a pool of breeding individuals equal to the size of the actual breeding population for each given year. We undertook this analysis in two ways with regard to which individuals from the roundup are 'allowed' to pair: first, we allowed all individuals of the given sex to pair in each permutation; and second, we allowed a subset of birds per age to breed, equivalent to age-specific breeding probability calculated from the long-term data (see results in Fig. S4 and Table S3).

We also assessed whether the age structure of the non-breeding population affected population-level age-assortment, using a Spearman's rank between the proportion of 1–4-year-olds and the proportion of the breeding population assorted by age (Fig. S8).

## 2 SUPPLEMENTARY FIGURES

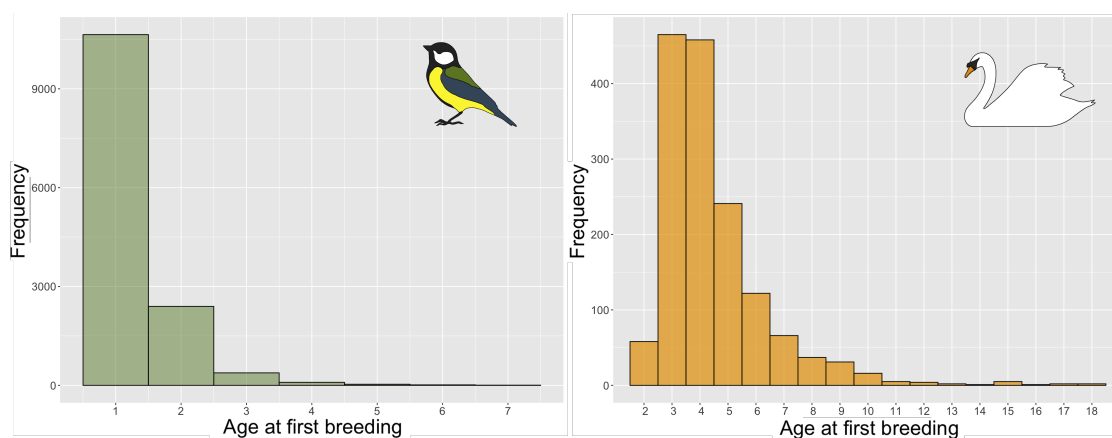


Fig. S1 - Distributions of the age at first reproduction for (a) great tits between 1970–2020 and (b) mute swans between 1990–2020. The median age at first reproduction is 1 for great tits, and 4 for mute swans.

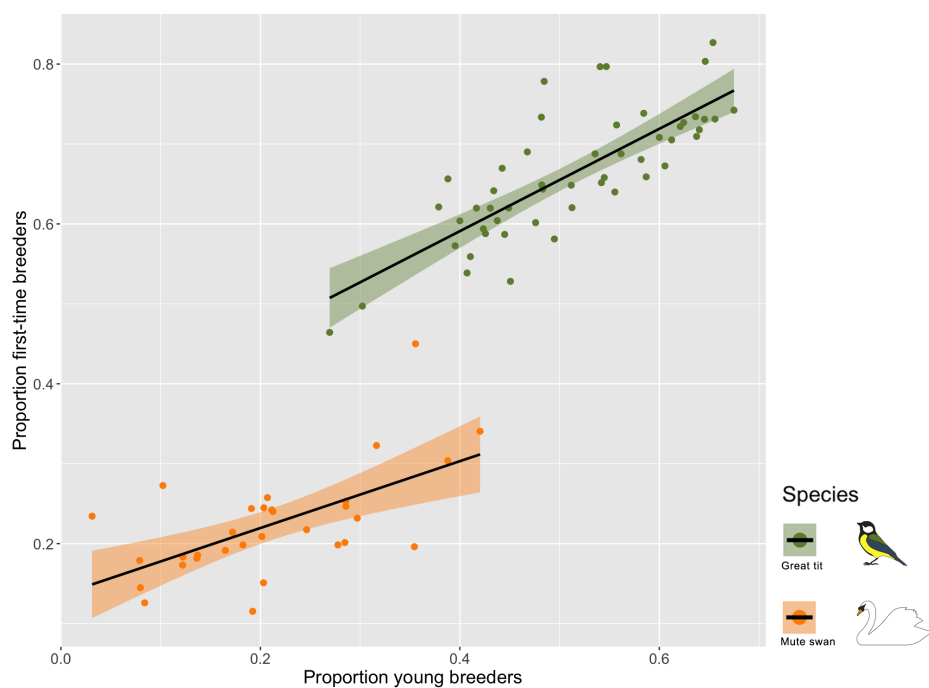
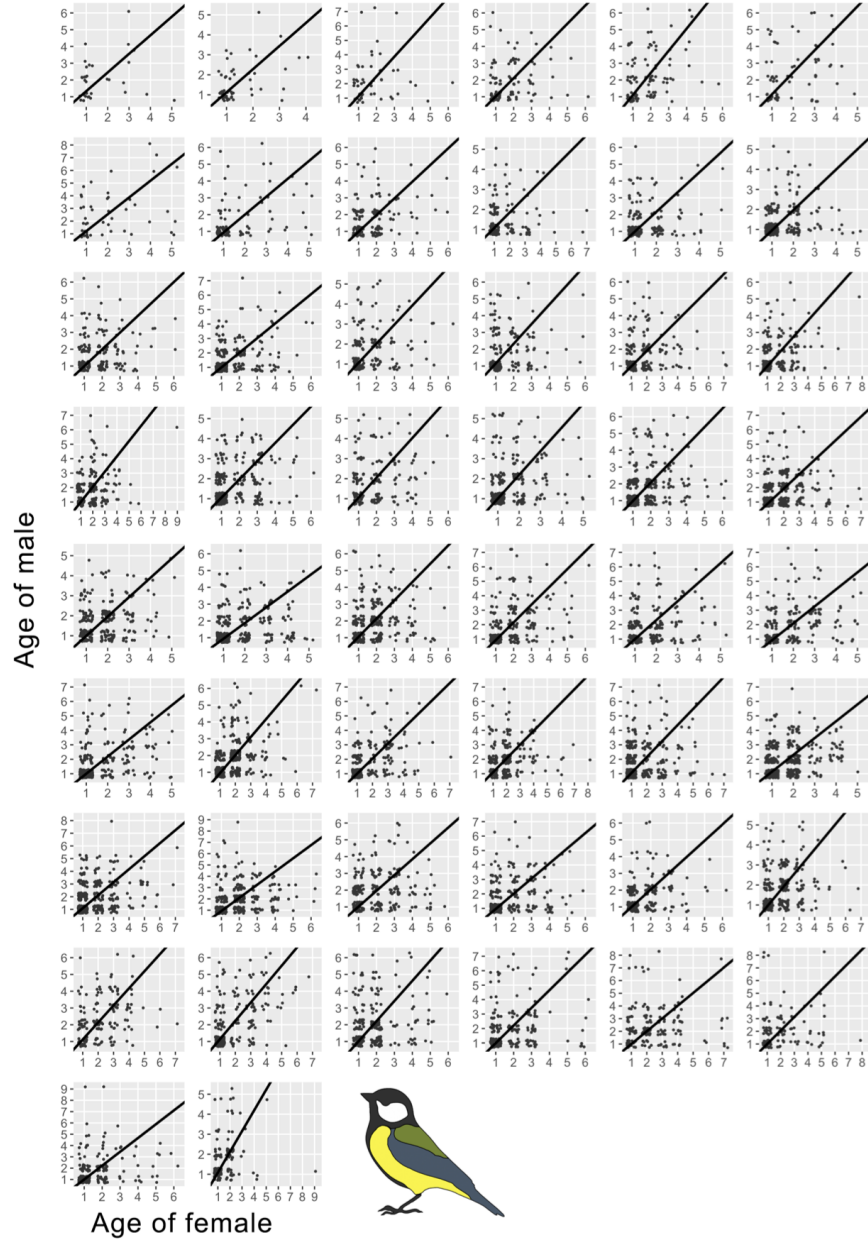


Fig. S2 - Relationship between the within-year proportion of young breeders and proportion of first-time breeders in great tits & mute swans (where ‘young breeder’ is defined as being a yearling, or 4-years or younger, in the two species respectively). The lines indicate a linear regression which models the relationship between these two variables, and the shading around this shows the 0.95 confidence intervals. The relationship is significant and positive in both great tits (Spearman’s correlation:  $r = 0.787$ ,  $p < 0.001$ ) and mute swans (Spearman’s correlation:  $r = 0.615$ ,  $p < 0.001$ ).

**a**



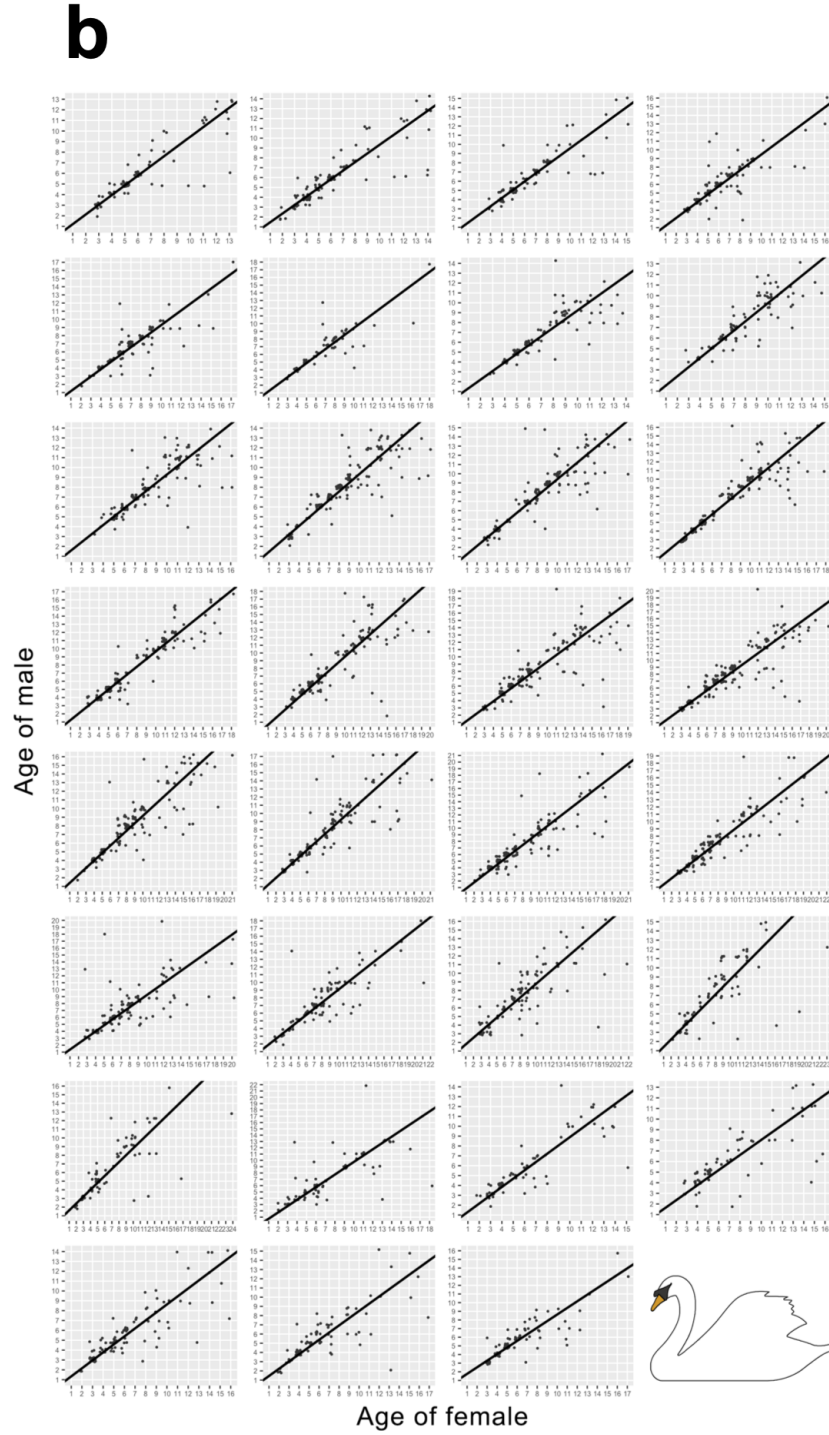


Fig. S3 - Relationship between female and male partner age per year within mated pairs of (a) great tits in Wytham between 1970–2020 and (b) mute swans in Abbotsbury between 1990–2020. Each point represents a pair with given female and male ages; points are jittered to avoid overplotting at the same location by 0.3 along both axes. The line indicates a reduced major axis regression which models the relationship between the age of males and females in breeding pairs.

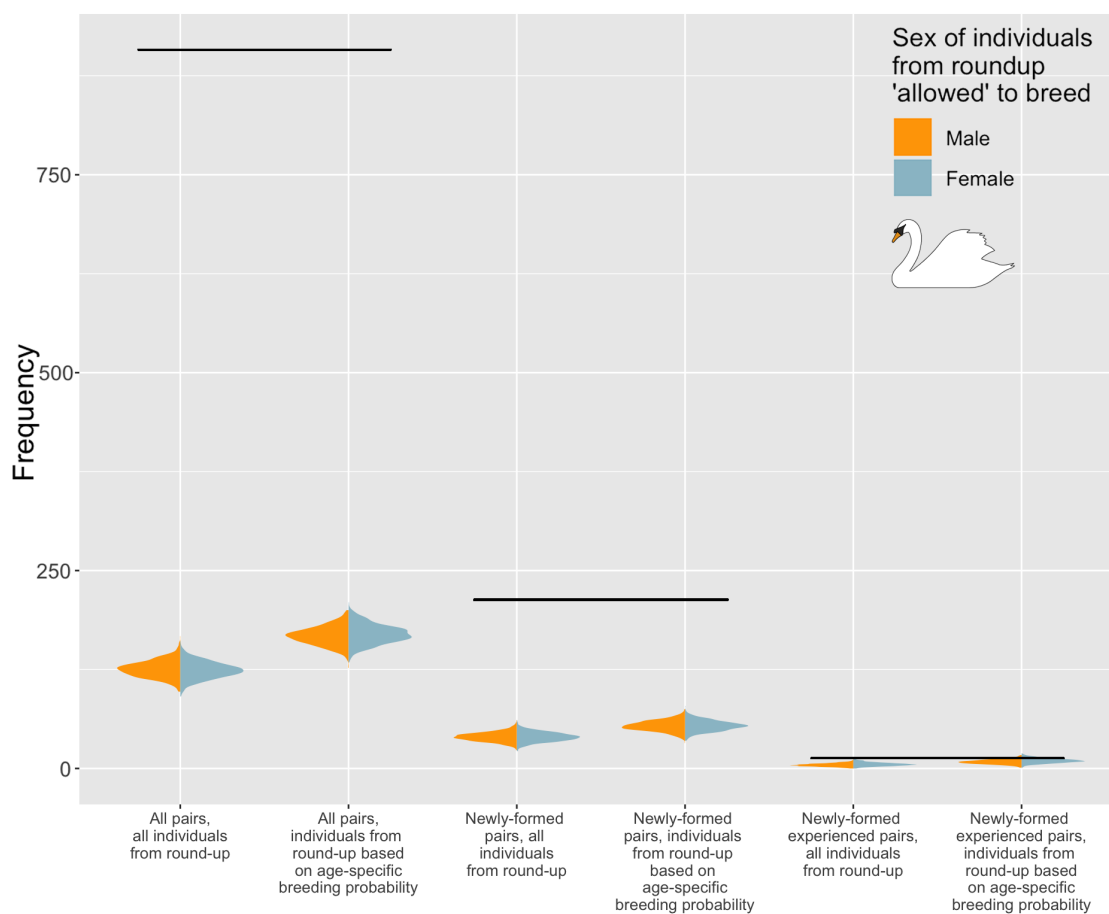


Fig. S4 - The frequency of the number of mute swan pairs assorted by age in roundup years in 1000 permutations where partners are randomly paired with respect to age. In order, the violins refer to permutations including: all pairs where all individuals of the given sex from the roundup are 'allowed' to breed; all pairs where the number of individuals of the given sex from the roundup allowed to breed is determined by age-specific breeding probabilities; newly-formed pairs where all individuals from the roundup are allowed to breed; newly-formed pairs where the number of individuals allowed to breed is determined by age-specific breeding probabilities; newly-formed experienced pairs where all individuals from the roundup are allowed to breed; and newly-formed experienced pairs where the number of individuals allowed to breed is determined by age-specific breeding probabilities. Orange half-violins are frequency distributions obtained when the males from the roundup are allowed to breed, while light-blue half-violins are when females are allowed to breed. The black lines show the observed numbers of age-assorted pairs for each subset of the mute swan populations across the assessed years; all violins have the same maximum width to aid visualisation.



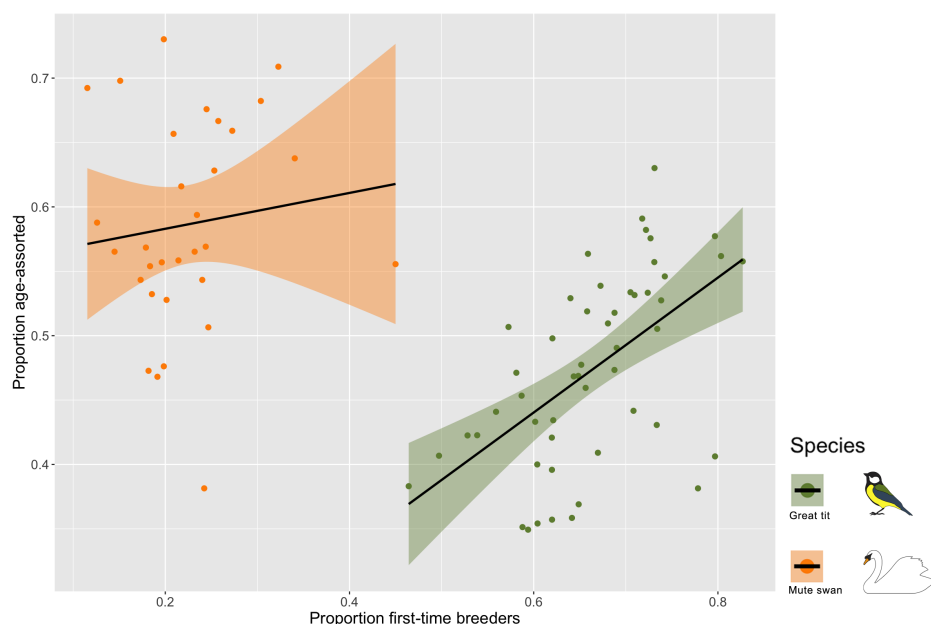


Fig. S5 - Relationship between the within-year proportion of first-time breeders and proportion of pairs assorted by age in great tits & mute swans. The lines indicate a linear regression which models the relationship between these two variables, and the shading around this shows the 0.95 confidence intervals. The relationship is significant and positive in great tits (Spearman's correlation:  $r = 0.594$ ,  $p < 0.001$ ), but there is a lack of evidence of any significant relationship in mute swans (Spearman's correlation:  $r = 0.206$ ,  $p = 0.266$ ).

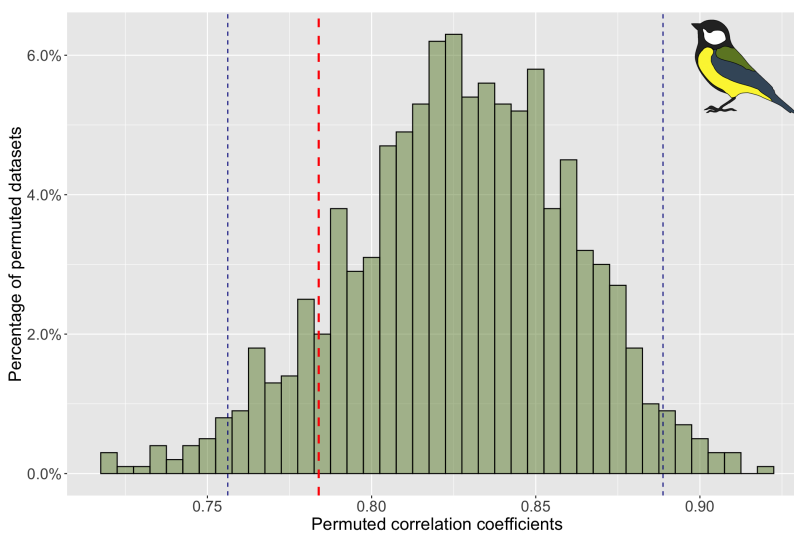


Fig. S6 - Distribution of correlation coefficients between the within-year proportion of great tit young breeders (yearlings) and proportion of individuals assorted by age obtained from 1000 permutations where pairing is random with respect to age; the red-dashed line shows the observed coefficient, which falls between the 2.5th to 97.5th percentiles of the distribution from the permutated datasets indicated by the blue-dashed lines.

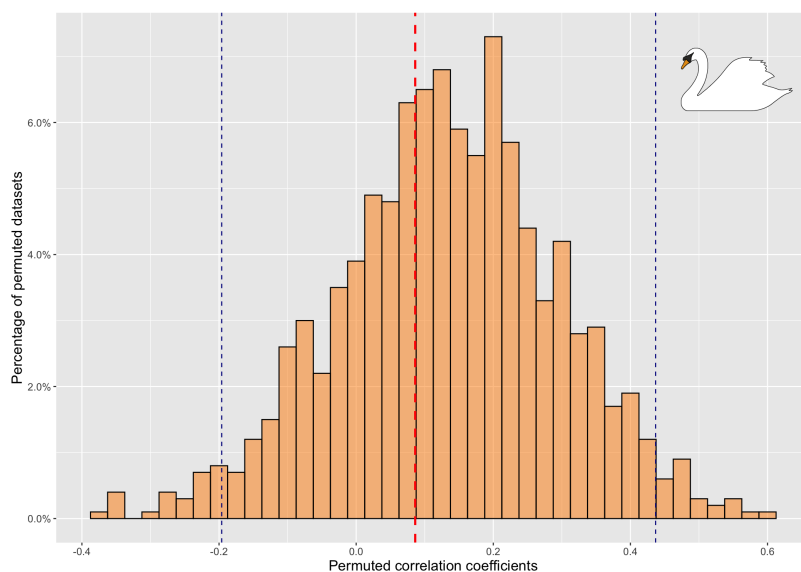


Fig. S7 - Distribution of correlation coefficients between the within-year proportion of mute swan young breeders (2–4-year-olds) and proportion of individuals assorted by age obtained from 1000 permutations where pairing is random with respect to age; the red-dashed line shows the observed coefficient, which falls between the 2.5th to 97.5th percentiles of the distribution from the permuted datasets indicated by the blue-dashed lines.

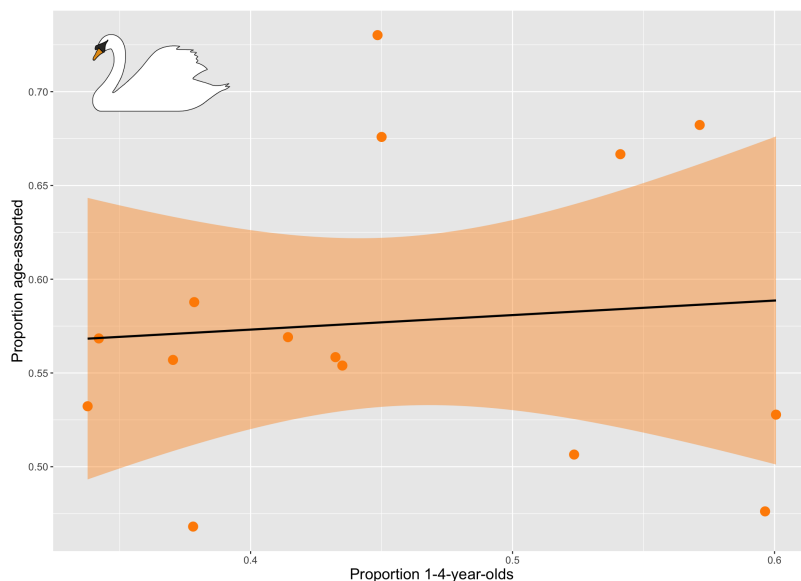


Fig. S8 - Relationship between within-year proportion of 1–4-year-olds present in the entire population and proportion of pairs assorted by age in mute swans during years where a roundup took place; the line indicates a linear regression which models the relationship between the two variables, and the shading around this shows the 0.95 confidence intervals. There is little evidence for any relationship between these two variables (Spearman's correlation:  $r = 0.068$ ,  $p = 0.810$ ).

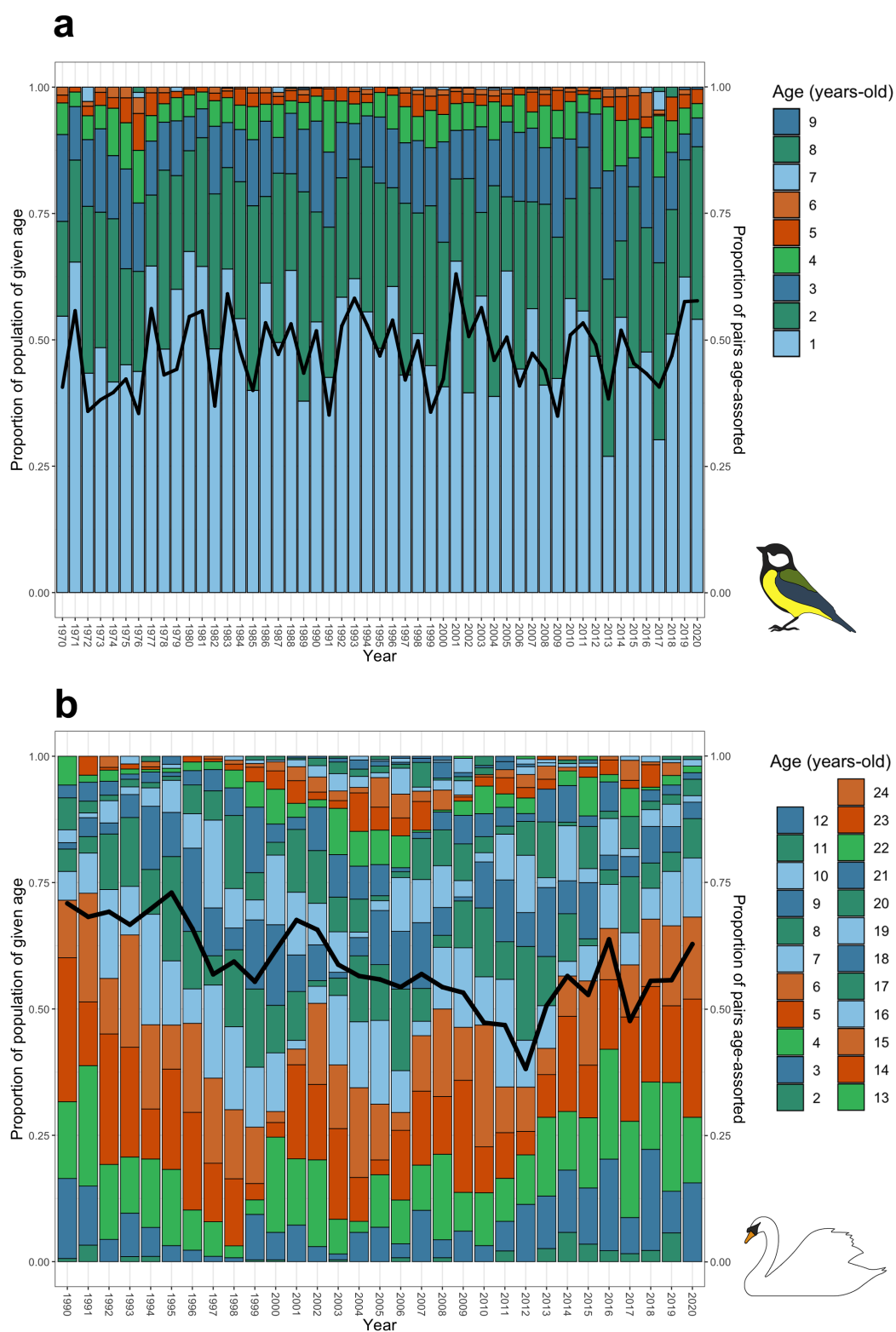


Fig. S9 - Age-structure of the breeding population of (a) great tits in Wytham between 1970–2020 and (b) mute swans in Abbotsbury between 1990–2020, and the proportion of the breeding population assorted by age.

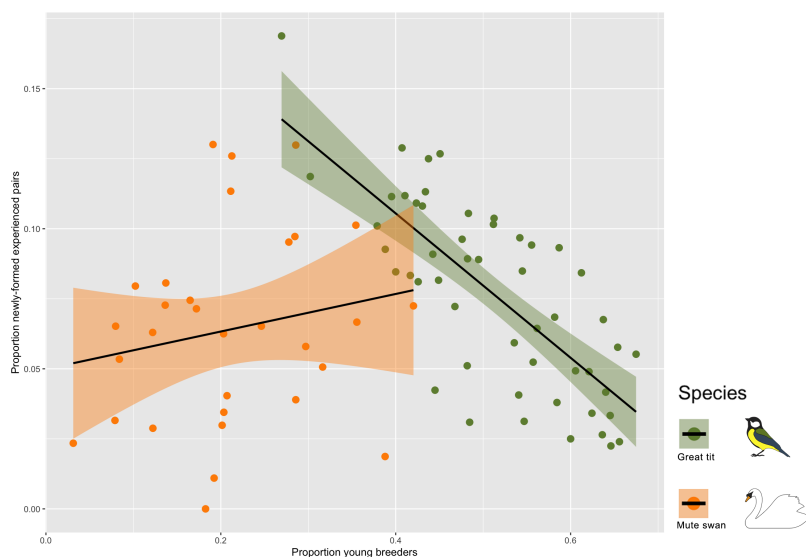


Fig. S10 - Relationship between the within-year proportion of young breeders and proportion of newly-formed experienced pairs in great tits & mute swans (where 'young breeder' is defined as being a yearling, or 4-years or younger, in the two species respectively). The lines indicate a linear regression which models the relationship between these two variables, and the shading around this shows the 0.95 confidence intervals. The relationship is significant and negative in great tits (Spearman's correlation:  $r = -0.713$ ,  $p < 0.001$ ), but there is a lack of evidence of any significant relationship in mute swans (Spearman's correlation:  $r = 0.197$ ,  $p = 0.286$ ).

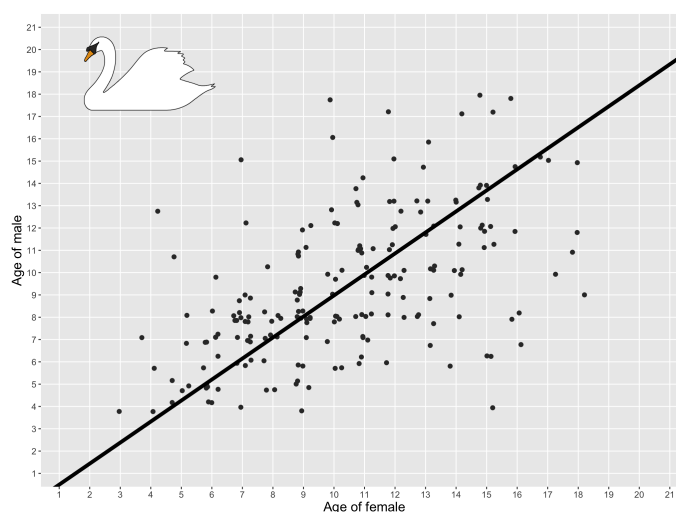


Fig. S11 - Relationship between female and male age in newly-formed experienced pairs of mute swans. Each point represents a pair with given female and male age; points are jittered to avoid overplotting at the same location by 0.3 along both axes. The line indicates a reduced major axis regression which models the relationship between the age of males and females in breeding pairs. Using a Spearman's rank correlation, we also found a moderate to strong positive correlation in partner age among this subset of pairs (Spearman's correlation:  $r = 0.568$ ,  $p < 0.001$ ).

### 3 SUPPLEMENTARY TABLES

Table S1 - Within-year Spearman's rank correlation results between male and female partner age in mated pairs of (a) great tits 1970–2020 and (b) mute swans 1990–2020. Cells with light red shading indicate non-significant test results (p value > 0.05).

| Year                  | <i>r</i> statistic | p value |
|-----------------------|--------------------|---------|
| <b>(a) Great tits</b> |                    |         |
| 1970                  | 0.180              | 0.325   |
| 1971                  | 0.405              | 0.003   |
| 1972                  | 0.208              | 0.135   |
| 1973                  | 0.213              | 0.036   |
| 1974                  | 0.370              | < 0.001 |
| 1975                  | 0.384              | 0.001   |
| 1976                  | 0.278              | 0.056   |
| 1977                  | 0.395              | < 0.001 |
| 1978                  | 0.303              | < 0.001 |
| 1979                  | 0.075              | 0.419   |
| 1980                  | 0.181              | 0.021   |
| 1981                  | 0.221              | 0.001   |
| 1982                  | 0.157              | 0.042   |
| 1983                  | 0.327              | < 0.001 |
| 1984                  | 0.230              | 0.004   |
| 1985                  | 0.326              | < 0.001 |
| 1986                  | 0.274              | < 0.001 |
| 1987                  | 0.255              | < 0.001 |
| 1988                  | 0.305              | < 0.001 |
| 1989                  | 0.250              | < 0.001 |
| 1990                  | 0.359              | < 0.001 |
| 1991                  | 0.137              | 0.097   |
| 1992                  | 0.312              | < 0.001 |
| 1993                  | 0.402              | < 0.001 |
| 1994                  | 0.327              | < 0.001 |
| 1995                  | 0.233              | < 0.001 |
| 1996                  | 0.314              | < 0.001 |
| 1997                  | 0.235              | < 0.001 |
| 1998                  | 0.460              | < 0.001 |
| 1999                  | 0.119              | 0.096   |
| 2000                  | 0.360              | < 0.001 |
| 2001                  | 0.455              | < 0.001 |
| 2002                  | 0.389              | < 0.001 |
| 2003                  | 0.467              | < 0.001 |
| 2004                  | 0.281              | < 0.001 |
| 2005                  | 0.217              | < 0.001 |
| 2006                  | 0.252              | < 0.001 |
| 2007                  | 0.342              | < 0.001 |
| 2008                  | 0.288              | < 0.001 |
| 2009                  | 0.200              | 0.002   |
| 2010                  | 0.311              | < 0.001 |

| Year                  | <i>r</i> statistic | p value |
|-----------------------|--------------------|---------|
| 2011                  | 0.304              | < 0.001 |
| 2012                  | 0.298              | < 0.001 |
| 2013                  | 0.339              | < 0.001 |
| 2014                  | 0.536              | < 0.001 |
| 2015                  | 0.220              | 0.001   |
| 2016                  | 0.227              | 0.002   |
| 2017                  | 0.197              | 0.009   |
| 2018                  | 0.273              | 0.002   |
| 2019                  | 0.333              | < 0.001 |
| 2020                  | 0.330              | < 0.001 |
| <b>(b) Mute swans</b> |                    |         |
| 1990                  | 0.923              | < 0.001 |
| 1991                  | 0.931              | < 0.001 |
| 1992                  | 0.909              | < 0.001 |
| 1993                  | 0.806              | < 0.001 |
| 1994                  | 0.836              | < 0.001 |
| 1995                  | 0.837              | < 0.001 |
| 1996                  | 0.875              | < 0.001 |
| 1997                  | 0.892              | < 0.001 |
| 1998                  | 0.865              | < 0.001 |
| 1999                  | 0.881              | < 0.001 |
| 2000                  | 0.893              | < 0.001 |
| 2001                  | 0.931              | < 0.001 |
| 2002                  | 0.953              | < 0.001 |
| 2003                  | 0.841              | < 0.001 |
| 2004                  | 0.865              | < 0.001 |
| 2005                  | 0.866              | < 0.001 |
| 2006                  | 0.861              | < 0.001 |
| 2007                  | 0.914              | < 0.001 |
| 2008                  | 0.920              | < 0.001 |
| 2009                  | 0.926              | < 0.001 |
| 2010                  | 0.746              | < 0.001 |
| 2011                  | 0.827              | < 0.001 |
| 2012                  | 0.803              | < 0.001 |
| 2013                  | 0.788              | < 0.001 |
| 2014                  | 0.813              | < 0.001 |
| 2015                  | 0.797              | < 0.001 |
| 2016                  | 0.898              | < 0.001 |
| 2017                  | 0.788              | < 0.001 |
| 2018                  | 0.865              | < 0.001 |
| 2019                  | 0.814              | < 0.001 |
| 2020                  | 0.849              | < 0.001 |

Table S2 - Reduced major axis (RMA) regression parameters between male and female partner age in mated pairs of great tits and mute swans across all time. RMA regressions model the relationship between two variables that are measured with error and are expected to have a symmetrical relationship.

|                  | Estimate | 95% confidence intervals |
|------------------|----------|--------------------------|
| <b>Great tit</b> |          |                          |
| $\beta_0$        | -0.067   | -0.113 – -0.022          |
| $\beta_1$        | 1.077    | 1.057 – 1.098            |
| <b>Mute swan</b> |          |                          |
| $\beta_0$        | 0.417    | 0.272 – 0.562            |
| $\beta_1$        | 0.880    | 0.864 – 0.897            |

Table S3 - Model results for permutation analyses assessing expected levels of age-assortative mating through random pairing during biennial roundup years 1991–2019. In each analyses, all breeding males and females were included in the permutations that met the assumptions of each model (either assessing across all pairs; newly-formed pairs; or newly-formed experienced pairs), in addition to either the non-breeding males or females caught at the roundup each year (excluding recently fledged cygnets; referred to in column “Sex ‘allowed’ to pair”). When including non-breeding individuals from the roundup in permutation analyses, either all individuals of the given sex were allowed to pair, or a subset of these individuals per age each year, equivalent to age-specific breeding probability calculated from the long-term data (referred to in column “Allowed’ to pair”). The result for each permutation model is shown in Fig. S4 (frequency distribution represented by a violin referred to in column “Violin in Fig. S4”; the 2.5<sup>th</sup>–97.5<sup>th</sup> percentiles of this frequency distribution referred to in column “2.5<sup>th</sup>–97.5<sup>th</sup> percentiles”; and the observed number of age-assorted pairs referred to in column “Number of age-assorted pairs”).

| Model              | Sex ‘allowed’ to pair | ‘Allowed’ to pair                                      | Violin in Fig. S4          | 2.5 <sup>th</sup> –97.5 <sup>th</sup> per-centiles | Number of age-assorted pairs |
|--------------------|-----------------------|--------------------------------------------------------|----------------------------|----------------------------------------------------|------------------------------|
| All pairs          | Male                  | All individuals                                        | First violin, first half   | 106–146                                            | 908                          |
| All pairs          | Female                | All individuals                                        | First violin, second half  | 104–145                                            | 908                          |
| All pairs          | Male                  | Subset equivalent to age-specific breeding probability | Second violin, first half  | 147–191                                            | 908                          |
| All pairs          | Female                | Subset equivalent to age-specific breeding probability | Second violin, second half | 147–194                                            | 908                          |
| Newly-formed pairs | Male                  | All individuals                                        | Third violin, first half   | 29–51                                              | 213                          |
| Newly-formed pairs | Female                | All individuals                                        | Third violin, second half  | 29–51                                              | 213                          |
| Newly-formed pairs | Male                  | Subset equivalent to age-specific breeding probability | Fourth violin, first half  | 41–67                                              | 213                          |
| Newly-formed pairs | Female                | Subset equivalent to age-specific breeding probability | Fourth violin, second half | 41–67                                              | 213                          |

| Model                          | Sex 'allowed' to pair | 'Allowed' to pair                                      | Violin in Fig. S4         | 2.5 <sup>th</sup> –97.5 <sup>th</sup> per-centiles | Number of age-assorted pairs |
|--------------------------------|-----------------------|--------------------------------------------------------|---------------------------|----------------------------------------------------|------------------------------|
| Newly-formed experienced pairs | Male                  | All individuals                                        | Fifth violin, first half  | 1–8                                                | 13                           |
| Newly-formed experienced pairs | Female                | All individuals                                        | Fifth violin, second half | 1–10                                               | 13                           |
| Newly-formed experienced pairs | Male                  | Subset equivalent to age-specific breeding probability | Sixth violin, first half  | 3–14                                               | 13                           |
| Newly-formed experienced pairs | Female                | Subset equivalent to age-specific breeding probability | Sixth violin, second half | 5–16                                               | 13                           |

Table S4 - Linear regression model outputs where male age is predicted by female age in mated pairs of (a) great tits across all time, and within-years 1970–2020 and (b) mute swans across all time, and within-years 1990–2020. As seen, the slope is positive in both species in all years; and is statistically significant in 43 out of 51 years in great tits, and in all years in mute swans. In great tits, despite being positive, the slope is often considerably lower than 1, which might imply much weaker assortative mating by age in great tits than mute swans. However, solely using linear model results might not be a robust method for assessing age-assortative mating in this system, as many data points exist in one category (across all time 34.6% of all great tit pairs consist of two yearlings, and in some years, such as 2001, this is as high as 52.7%). Additionally, linear models take into account the relationship in age in partners that are not age-assorted, so the lower slope values in great tits might reflect lower similarity in age in pairs that are not precisely age-assorted compared to mute swans. Further, in general, as indicated by the  $R^2$  values, a greater amount of the variation in mute swan male age can be explained by the age of females compared to great tits. However, in this paper, we are concerned specifically with assessing what drives age-assortative mating in terms of pairing between two individuals of the exact same age, as opposed to similarity in age between partners of different ages. Therefore, we predominantly use permutation analyses to quantify the extent of age-assortative mating (as seen in the main text).

| Year(s)               | Parameter      | Estimate | Standard error | p value |
|-----------------------|----------------|----------|----------------|---------|
| <b>(a) Great tits</b> |                |          |                |         |
| <b>1970–2020</b>      | $\beta_0$      | 1.365    | 0.022          | < 0.001 |
|                       | $\beta_1$      | 0.282    | 0.010          | < 0.001 |
|                       | $R^2$          | 0.068    |                |         |
|                       | $F_{1, 10277}$ | 754.87   |                | < 0.001 |
| <b>1970</b>           | $\beta_0$      | 1.72     | 0.394          | < 0.001 |
|                       | $\beta_1$      | 0.207    | 0.199          | 0.308   |
|                       | $R^2$          | 0.035    |                |         |
|                       | $F_{1, 30}$    | 1.076    |                | 0.308   |
| <b>1971</b>           | $\beta_0$      | 0.914    | 0.243          | < 0.001 |
|                       | $\beta_1$      | 0.500    | 0.148          | 0.001   |



| Year(s) | Parameter   | Estimate | Standard error | p value |
|---------|-------------|----------|----------------|---------|
| 1972    | $R^2$       | 0.186    |                |         |
|         | $F_{1,50}$  | 11.429   |                | 0.001   |
|         | $\beta_0$   | 2.035    | 0.404          | < 0.001 |
|         | $\beta_1$   | 0.116    | 0.191          | 0.545   |
|         | $R^2$       | 0.01     |                |         |
| 1973    | $F_{1,51}$  | 0.372    |                | 0.545   |
|         | $\beta_0$   | 1.699    | 0.235          | < 0.001 |
|         | $\beta_1$   | 0.130    | 0.110          | 0.244   |
|         | $R^2$       | 0.014    |                |         |
|         | $F_{1,95}$  | 1.376    |                | 0.244   |
| 1974    | $\beta_0$   | 1.374    | 0.270          | < 0.001 |
|         | $\beta_1$   | 0.462    | 0.128          | < 0.001 |
|         | $R^2$       | 0.122    |                |         |
|         | $F_{1,94}$  | 13.066   |                | < 0.001 |
|         | $\beta_0$   | 1.546    | 0.335          | < 0.001 |
| 1975    | $\beta_1$   | 0.429    | 0.149          | 0.005   |
|         | $R^2$       | 0.107    |                |         |
|         | $F_{1,69}$  | 8.252    |                | 0.005   |
|         | $\beta_0$   | 1.800    | 0.463          | < 0.001 |
|         | $\beta_1$   | 0.406    | 0.186          | 0.034   |
| 1976    | $R^2$       | 0.094    |                |         |
|         | $F_{1,46}$  | 4.785    |                | 0.034   |
|         | $\beta_0$   | 1.086    | 0.227          | < 0.001 |
|         | $\beta_1$   | 0.368    | 0.107          | < 0.001 |
|         | $R^2$       | 0.119    |                |         |
| 1977    | $F_{1,87}$  | 11.726   |                | < 0.001 |
|         | $\beta_0$   | 1.266    | 0.171          | < 0.001 |
|         | $\beta_1$   | 0.285    | 0.082          | < 0.001 |
|         | $R^2$       | 0.082    |                |         |
|         | $F_{1,135}$ | 12.059   |                | < 0.001 |
| 1978    | $\beta_0$   | 1.510    | 0.148          | < 0.001 |
|         | $\beta_1$   | 0.072    | 0.071          | 0.315   |
|         | $R^2$       | 0.009    |                |         |
|         | $F_{1,118}$ | 1.017    |                | 0.315   |
|         | $\beta_0$   | 1.183    | 0.154          | < 0.001 |
| 1979    | $\beta_1$   | 0.256    | 0.090          | 0.005   |
|         | $R^2$       | 0.048    |                |         |
|         | $F_{1,161}$ | 8.059    |                | 0.005   |
|         | $\beta_0$   | 1.267    | 0.121          | < 0.001 |
|         | $\beta_1$   | 1.143    | 0.070          | 0.041   |
| 1980    | $R^2$       | 0.020    |                |         |
|         | $F_{1,208}$ | 4.224    |                | 0.041   |
|         | $\beta_0$   | 1.543    | 0.164          | < 0.001 |
|         | $\beta_1$   | 0.160    | 0.077          | 0.039   |
|         | $R^2$       | 0.025    |                |         |
| 1981    | $F_{1,166}$ | 4.334    |                | 0.039   |
|         | $\beta_0$   | 1.066    | 0.113          | < 0.001 |

| Year(s) | Parameter    | Estimate | Standard error | p value |
|---------|--------------|----------|----------------|---------|
| 1984    | $\beta_1$    | 0.343    | 0.059          | < 0.001 |
|         | $R^2$        | 0.114    |                |         |
|         | $F_{1, 262}$ | 33.841   |                | < 0.001 |
|         | $\beta_0$    | 1.486    | 0.157          | < 0.001 |
|         | $\beta_1$    | 0.168    | 0.076          | 0.029   |
| 1985    | $R^2$        | 0.031    |                |         |
|         | $F_{1, 153}$ | 4.879    |                | 0.029   |
|         | $\beta_0$    | 1.685    | 0.199          | < 0.001 |
|         | $\beta_1$    | 0.247    | 0.094          | 0.010   |
|         | $R^2$        | 0.508    |                |         |
| 1986    | $F_{1, 128}$ | 6.845    |                | 0.010   |
|         | $\beta_0$    | 1.452    | 0.162          | < 0.001 |
|         | $\beta_1$    | 0.246    | 0.086          | 0.005   |
|         | $R^2$        | 0.044    |                |         |
|         | $F_{1, 176}$ | 8.082    |                | 0.005   |
| 1987    | $\beta_0$    | 1.480    | 0.147          | < 0.001 |
|         | $\beta_1$    | 0.165    | 0.066          | 0.013   |
|         | $R^2$        | 0.032    |                |         |
|         | $F_{1, 189}$ | 6.307    |                | 0.013   |
|         | $\beta_0$    | 1.099    | 0.114          | < 0.001 |
| 1988    | $\beta_1$    | 0.293    | 0.058          | < 0.001 |
|         | $R^2$        | 0.105    |                |         |
|         | $F_{1, 220}$ | 25.702   |                | < 0.001 |
|         | $\beta_0$    | 1.462    | 0.162          | < 0.001 |
|         | $\beta_1$    | 0.271    | 0.073          | < 0.001 |
| 1989    | $R^2$        | 0.066    |                |         |
|         | $F_{1, 196}$ | 13.872   |                | < 0.001 |
|         | $\beta_0$    | 1.268    | 0.115          | < 0.001 |
|         | $\beta_1$    | 0.286    | 0.055          | < 0.001 |
|         | $R^2$        | 0.099    |                |         |
| 1990    | $F_{1, 251}$ | 27.449   |                | < 0.001 |
|         | $\beta_0$    | 1.734    | 0.185          | < 0.001 |
|         | $\beta_1$    | 0.151    | 0.081          | 0.065   |
|         | $R^2$        | 0.023    |                |         |
|         | $F_{1, 146}$ | 3.463    |                | 0.065   |
| 1991    | $\beta_0$    | 1.313    | 0.141          | < 0.001 |
|         | $\beta_1$    | 0.268    | 0.075          | < 0.001 |
|         | $R^2$        | 0.051    |                |         |
|         | $F_{1, 235}$ | 12.627   |                | < 0.001 |
|         | $\beta_0$    | 1.110    | 0.107          | < 0.001 |
| 1992    | $\beta_1$    | 0.336    | 0.057          | < 0.001 |
|         | $R^2$        | 0.093    |                |         |
|         | $F_{1, 345}$ | 35.389   |                | < 0.001 |
|         | $\beta_0$    | 1.334    | 0.105          | < 0.001 |
|         | $\beta_1$    | 0.193    | 0.052          | < 0.001 |
| 1993    | $R^2$        | 0.037    |                |         |
|         | $F_{1, 359}$ | 13.958   |                | < 0.001 |
|         |              |          |                |         |

| Year(s) | Parameter    | Estimate | Standard error | p value |
|---------|--------------|----------|----------------|---------|
| 1995    | $\beta_0$    | 1.303    | 0.123          | < 0.001 |
|         | $\beta_1$    | 0.255    | 0.061          | < 0.001 |
|         | $R^2$        | 0.069    |                |         |
|         | $F_{1, 235}$ | 17.532   |                | < 0.001 |
| 1996    | $\beta_0$    | 1.233    | 0.110          | < 0.001 |
|         | $\beta_1$    | 0.231    | 0.054          | < 0.001 |
|         | $R^2$        | 0.061    |                |         |
|         | $F_{1, 282}$ | 18.292   |                | < 0.001 |
| 1997    | $\beta_0$    | 1.657    | 0.146          | < 0.001 |
|         | $\beta_1$    | 0.193    | 0.067          | 0.004   |
|         | $R^2$        | 0.031    |                |         |
|         | $F_{1, 257}$ | 8.351    |                | 0.004   |
| 1998    | $\beta_0$    | 1.132    | 0.159          | < 0.001 |
|         | $\beta_1$    | 0.458    | 0.074          | < 0.001 |
|         | $R^2$        | 0.139    |                |         |
|         | $F_{1, 239}$ | 38.579   |                | < 0.001 |
| 1999    | $\beta_0$    | 1.782    | 0.196          | < 0.001 |
|         | $\beta_1$    | 0.174    | 0.093          | 0.064   |
|         | $R^2$        | 0.018    |                |         |
|         | $F_{1, 194}$ | 3.472    |                | 0.064   |
| 2000    | $\beta_0$    | 1.47     | 0.189          | < 0.001 |
|         | $\beta_1$    | 0.326    | 0.082          | < 0.001 |
|         | $R^2$        | 0.077    |                |         |
|         | $F_{1, 192}$ | 15.927   |                | < 0.001 |
| 2001    | $\beta_0$    | 0.970    | 0.121          | < 0.001 |
|         | $\beta_1$    | 0.462    | 0.064          | < 0.001 |
|         | $R^2$        | 0.152    |                |         |
|         | $F_{1, 290}$ | 52.147   |                | < 0.001 |
| 2002    | $\beta_0$    | 1.202    | 0.127          | < 0.001 |
|         | $\beta_1$    | 0.377    | 0.059          | < 0.001 |
|         | $R^2$        | 0.122    |                |         |
|         | $F_{1, 294}$ | 40.975   |                | < 0.001 |
| 2003    | $\beta_0$    | 1.078    | 0.133          | < 0.001 |
|         | $\beta_1$    | 0.411    | 0.063          | < 0.001 |
|         | $R^2$        | 0.155    |                |         |
|         | $F_{1, 234}$ | 42.776   |                | < 0.001 |
| 2004    | $\beta_0$    | 1.649    | 0.131          | < 0.001 |
|         | $\beta_1$    | 0.180    | 0.059          | 0.002   |
|         | $R^2$        | 0.035    |                |         |
|         | $F_{1, 257}$ | 9.397    |                | 0.002   |
| 2005    | $\beta_0$    | 1.376    | 0.110          | < 0.001 |
|         | $\beta_1$    | 0.233    | 0.056          | < 0.001 |
|         | $R^2$        | 0.044    |                |         |
|         | $F_{1, 376}$ | 17.260   |                | < 0.001 |
| 2006    | $\beta_0$    | 1.580    | 0.125          | < 0.001 |
|         | $\beta_1$    | 0.251    | 0.063          | < 0.001 |
|         | $R^2$        | 0.046    |                |         |

| Year(s) | Parameter    | Estimate | Standard error | p value |
|---------|--------------|----------|----------------|---------|
| 2007    | $F_{1, 328}$ | 15.906   |                | < 0.001 |
|         | $\beta_0$    | 1.279    | 0.108          | < 0.001 |
|         | $\beta_1$    | 0.334    | 0.051          | < 0.001 |
|         | $R^2$        | 0.106    |                |         |
| 2008    | $F_{1, 355}$ | 42.227   |                | < 0.001 |
|         | $\beta_0$    | 1.633    | 0.145          | < 0.001 |
|         | $\beta_1$    | 0.208    | 0.065          | 0.001   |
|         | $R^2$        | 0.032    |                |         |
| 2009    | $F_{1, 311}$ | 10.271   |                | 0.001   |
|         | $\beta_0$    | 1.692    | 0.146          | < 0.001 |
|         | $\beta_1$    | 0.152    | 0.062          | 0.014   |
|         | $R^2$        | 0.026    |                |         |
| 2010    | $F_{1, 227}$ | 6.109    |                | 0.014   |
|         | $\beta_0$    | 1.335    | 0.132          | < 0.001 |
|         | $\beta_1$    | 0.249    | 0.063          | < 0.001 |
|         | $R^2$        | 0.056    |                |         |
| 2011    | $F_{1, 261}$ | 15.613   |                | < 0.001 |
|         | $\beta_0$    | 1.256    | 0.120          | < 0.001 |
|         | $\beta_1$    | 0.249    | 0.065          | < 0.001 |
|         | $R^2$        | 0.066    |                |         |
| 2012    | $F_{1, 208}$ | 14.746   |                | < 0.001 |
|         | $\beta_0$    | 1.402    | 0.118          | < 0.001 |
|         | $\beta_1$    | 0.208    | 0.056          | < 0.001 |
|         | $R^2$        | 0.050    |                |         |
| 2013    | $F_{1, 261}$ | 13.824   |                | < 0.001 |
|         | $\beta_0$    | 1.792    | 0.203          | < 0.001 |
|         | $\beta_1$    | 0.272    | 0.079          | < 0.001 |
|         | $R^2$        | 0.072    |                |         |
| 2014    | $F_{1, 152}$ | 11.751   |                | < 0.001 |
|         | $\beta_0$    | 1.045    | 0.148          | < 0.001 |
|         | $\beta_1$    | 0.565    | 0.065          | < 0.001 |
|         | $R^2$        | 0.266    |                |         |
| 2015    | $F_{1, 210}$ | 76.098   |                | < 0.001 |
|         | $\beta_0$    | 1.663    | 0.168          | < 0.001 |
|         | $\beta_1$    | 0.216    | 0.077          | 0.006   |
|         | $R^2$        | 0.032    |                |         |
| 2016    | $F_{1, 234}$ | 7.785    |                | 0.006   |
|         | $\beta_0$    | 1.667    | 0.204          | < 0.001 |
|         | $\beta_1$    | 0.247    | 0.088          | 0.005   |
|         | $R^2$        | 0.041    |                |         |
| 2017    | $F_{1, 185}$ | 7.920    |                | 0.005   |
|         | $\beta_0$    | 2.127    | 0.212          | < 0.001 |
|         | $\beta_1$    | 0.110    | 0.0756         | 0.147   |
|         | $R^2$        | 0.012    |                |         |
| 2018    | $F_{1, 175}$ | 2.125    |                | 0.147   |
|         | $\beta_0$    | 1.689    | 0.225          | < 0.001 |
|         | $\beta_1$    | 0.167    | 0.094          | 0.077   |

| Year(s)               | Parameter    | Estimate | Standard error | p value |
|-----------------------|--------------|----------|----------------|---------|
| <b>2019</b>           | $R^2$        | 0.025    |                |         |
|                       | $F_{1,126}$  | 3.185    |                | 0.077   |
|                       | $\beta_0$    | 1.353    | 0.162          | < 0.001 |
|                       | $\beta_1$    | 0.247    | 0.084          | 0.004   |
| <b>2020</b>           | $R^2$        | 0.041    |                |         |
|                       | $F_{1,203}$  | 8.642    |                | 0.004   |
|                       | $\beta_0$    | 1.439    | 0.178          | < 0.001 |
|                       | $\beta_1$    | 0.184    | 0.093          | 0.049   |
| <b>(b) Mute swans</b> | $R^2$        | 0.032    |                |         |
|                       | $F_{1,121}$  | 3.949    |                | 0.049   |
|                       |              |          |                |         |
|                       |              |          |                |         |
| <b>1990–2020</b>      | $\beta_0$    | 1.531    | 0.073          | < 0.001 |
|                       | $\beta_1$    | 0.738    | 0.008          | < 0.001 |
|                       | $R^2$        | 0.704    |                |         |
|                       | $F_{1,3221}$ | 7642.244 |                | < 0.001 |
| <b>1990</b>           | $\beta_0$    | 0.980    | 0.342          | 0.005   |
|                       | $\beta_1$    | 0.805    | 0.050          | < 0.001 |
|                       | $R^2$        | 0.773    |                |         |
|                       | $F_{1,77}$   | 261.690  |                | < 0.001 |
| <b>1991</b>           | $\beta_0$    | 1.280    | 0.283          | < 0.001 |
|                       | $\beta_1$    | 0.789    | 0.042          | < 0.001 |
|                       | $R^2$        | 0.758    |                |         |
|                       | $F_{1,105}$  | 329.255  |                | < 0.001 |
| <b>1992</b>           | $\beta_0$    | 1.385    | 0.342          | < 0.001 |
|                       | $\beta_1$    | 0.776    | 0.048          | < 0.001 |
|                       | $R^2$        | 0.749    |                |         |
|                       | $F_{1,89}$   | 264.896  |                | < 0.001 |
| <b>1993</b>           | $\beta_0$    | 1.540    | 0.397          | < 0.001 |
|                       | $\beta_1$    | 0.720    | 0.058          | < 0.001 |
|                       | $R^2$        | 0.618    |                |         |
|                       | $F_{1,97}$   | 156.575  |                | < 0.001 |
| <b>1994</b>           | $\beta_0$    | 1.414    | 0.400          | < 0.001 |
|                       | $\beta_1$    | 0.738    | 0.053          | < 0.001 |
|                       | $R^2$        | 0.672    |                |         |
|                       | $F_{1,94}$   | 192.144  |                | < 0.001 |
| <b>1995</b>           | $\beta_0$    | 1.424    | 0.499          | 0.006   |
|                       | $\beta_1$    | 0.752    | 0.066          | < 0.001 |
|                       | $R^2$        | 0.681    |                |         |
|                       | $F_{1,61}$   | 129.904  |                | < 0.001 |
| <b>1996</b>           | $\beta_0$    | 1.705    | 0.443          | < 0.001 |
|                       | $\beta_1$    | 0.711    | 0.056          | < 0.001 |
|                       | $R^2$        | 0.656    |                |         |
|                       | $F_{1,86}$   | 163.813  |                | < 0.001 |
| <b>1997</b>           | $\beta_0$    | 1.620    | 0.379          | < 0.001 |
|                       | $\beta_1$    | 0.743    | 0.045          | < 0.001 |
|                       | $R^2$        | 0.743    |                |         |
|                       | $F_{1,93}$   | 269.044  |                | < 0.001 |

| Year(s) | Parameter    | Estimate | Standard error | p value |
|---------|--------------|----------|----------------|---------|
| 1998    | $\beta_0$    | 2.122    | 0.400          | < 0.001 |
|         | $\beta_1$    | 0.692    | 0.045          | < 0.001 |
|         | $R^2$        | 0.656    |                |         |
|         | $F_{1, 126}$ | 240.201  |                | < 0.001 |
| 1999    | $\beta_0$    | 1.681    | 0.362          | < 0.001 |
|         | $\beta_1$    | 0.747    | 0.039          | < 0.001 |
|         | $R^2$        | 0.731    |                |         |
|         | $F_{1, 137}$ | 372.313  |                | < 0.001 |
| 2000    | $\beta_0$    | 1.424    | 0.359          | < 0.001 |
|         | $\beta_1$    | 0.776    | 0.040          | < 0.001 |
|         | $R^2$        | 0.739    |                |         |
|         | $F_{1, 136}$ | 384.228  |                | < 0.001 |
| 2001    | $\beta_0$    | 1.282    | 0.301          | < 0.001 |
|         | $\beta_1$    | 0.810    | 0.033          | < 0.001 |
|         | $R^2$        | 0.804    |                |         |
|         | $F_{1, 143}$ | 587.144  |                | < 0.001 |
| 2002    | $\beta_0$    | 0.734    | 0.242          | 0.003   |
|         | $\beta_1$    | 0.882    | 0.027          | < 0.001 |
|         | $R^2$        | 0.889    |                |         |
|         | $F_{1, 132}$ | 1061.257 |                | < 0.001 |
| 2003    | $\beta_0$    | 1.327    | 0.490          | 0.008   |
|         | $\beta_1$    | 0.799    | 0.050          | < 0.001 |
|         | $R^2$        | 0.662    |                |         |
|         | $F_{1, 129}$ | 253.069  |                | < 0.001 |
| 2004    | $\beta_0$    | 1.692    | 0.431          | < 0.001 |
|         | $\beta_1$    | 0.750    | 0.043          | < 0.001 |
|         | $R^2$        | 0.688    |                |         |
|         | $F_{1, 136}$ | 300.356  |                | < 0.001 |
| 2005    | $\beta_0$    | 1.482    | 0.377          | < 0.001 |
|         | $\beta_1$    | 0.761    | 0.038          | < 0.001 |
|         | $R^2$        | 0.722    |                |         |
|         | $F_{1, 152}$ | 394.961  |                | < 0.001 |
| 2006    | $\beta_0$    | 1.740    | 0.411          | < 0.001 |
|         | $\beta_1$    | 0.731    | 0.041          | < 0.001 |
|         | $R^2$        | 0.719    |                |         |
|         | $F_{1, 125}$ | 320.495  |                | < 0.001 |
| 2007    | $\beta_0$    | 1.386    | 0.398          | < 0.001 |
|         | $\beta_1$    | 0.765    | 0.042          | < 0.001 |
|         | $R^2$        | 0.733    |                |         |
|         | $F_{1, 121}$ | 331.843  |                | < 0.001 |
| 2008    | $\beta_0$    | 0.877    | 0.378          | 0.022   |
|         | $\beta_1$    | 0.823    | 0.042          | < 0.001 |
|         | $R^2$        | 0.757    |                |         |
|         | $F_{1, 125}$ | 389.505  |                | < 0.001 |
| 2009    | $\beta_0$    | 1.436    | 0.342          | < 0.001 |
|         | $\beta_1$    | 0.723    | 0.037          | < 0.001 |
|         | $R^2$        | 0.760    |                |         |

| Year(s) | Parameter   | Estimate | Standard error | p value |
|---------|-------------|----------|----------------|---------|
| 2010    | $F_{1,122}$ | 386.412  |                | < 0.001 |
|         | $\beta_0$   | 2.887    | 0.558          | < 0.001 |
|         | $\beta_1$   | 0.575    | 0.063          | < 0.001 |
|         | $R^2$       | 0.434    |                |         |
| 2011    | $F_{1,108}$ | 82.774   |                | < 0.001 |
|         | $\beta_0$   | 2.237    | 0.435          | < 0.001 |
|         | $\beta_1$   | 0.644    | 0.048          | < 0.001 |
|         | $R^2$       | 0.658    |                |         |
| 2012    | $F_{1,92}$  | 177.248  |                | < 0.001 |
|         | $\beta_0$   | 2.589    | 0.486          | < 0.001 |
|         | $\beta_1$   | 0.585    | 0.052          | < 0.001 |
|         | $R^2$       | 0.573    |                |         |
| 2013    | $F_{1,95}$  | 127.507  |                | < 0.001 |
|         | $\beta_0$   | 2.438    | 0.587          | < 0.001 |
|         | $\beta_1$   | 0.584    | 0.066          | < 0.001 |
|         | $R^2$       | 0.514    |                |         |
| 2014    | $F_{1,75}$  | 79.319   |                | < 0.001 |
|         | $\beta_0$   | 2.203    | 0.523          | < 0.001 |
|         | $\beta_1$   | 0.605    | 0.064          | < 0.001 |
|         | $R^2$       | 0.575    |                |         |
| 2015    | $F_{1,67}$  | 90.594   |                | < 0.001 |
|         | $\beta_0$   | 1.908    | 0.696          | 0.008   |
|         | $\beta_1$   | 0.705    | 0.085          | < 0.001 |
|         | $R^2$       | 0.497    |                |         |
| 2016    | $F_{1,70}$  | 69.075   |                | < 0.001 |
|         | $\beta_0$   | 1.229    | 0.382          | 0.002   |
|         | $\beta_1$   | 0.725    | 0.053          | < 0.001 |
|         | $R^2$       | 0.739    |                |         |
| 2017    | $F_{1,67}$  | 189.975  |                | < 0.001 |
|         | $\beta_0$   | 2.218    | 0.499          | < 0.001 |
|         | $\beta_1$   | 0.539    | 0.059          | < 0.001 |
|         | $R^2$       | 0.576    |                |         |
| 2018    | $F_{1,61}$  | 82.695   |                | < 0.001 |
|         | $\beta_0$   | 1.370    | 0.345          | < 0.001 |
|         | $\beta_1$   | 0.681    | 0.047          | < 0.001 |
|         | $R^2$       | 0.706    |                |         |
| 2019    | $F_{1,88}$  | 211.173  |                | < 0.001 |
|         | $\beta_0$   | 1.798    | 0.414          | < 0.001 |
|         | $\beta_1$   | 0.610    | 0.056          | < 0.001 |
|         | $R^2$       | 0.606    |                |         |
| 2020    | $F_{1,77}$  | 118.330  |                | < 0.001 |
|         | $\beta_0$   | 1.674    | 0.313          | < 0.001 |
|         | $\beta_1$   | 0.654    | 0.045          | < 0.001 |
|         | $R^2$       | 0.735    |                |         |
|         | $F_{1,75}$  | 208.088  |                | < 0.001 |





# Chapter IV

## Age-specificity in territory quality and spatial structure in a wild bird population

*Submitted:*

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# Age-specificity in territory quality and spatial structure in a wild bird population

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## ABSTRACT

Age influences behaviour, survival, and reproduction; hence variation in population age structure can affect population-level processes. The extent of spatial age structure may be important in driving spatially-variable demography, particularly when space-use is linked to reproduction, yet it is not well understood. We use long-term data from a wild bird population to examine spatial age structure and quantify covariance between territory quality and age. We find associations between age and aspects of territory quality, but little evidence for spatial age structure compared to territory quality and reproductive structure. We also report little between-year repeatability of spatial age structure compared to structure in reproductive output. We suggest that high breeding site fidelity and frequent territory turnover by younger breeders, driven by high mortality and immigration rates, limits the association between age and territory quality and weakens overall spatial age structure. Greater spatial structure and repeatability in reproductive output compared to age suggests that habitat quality may be more important in driving spatially-variable demography than age in this system. We suggest that the framework developed here can be used in other taxa to assess spatial age structure, particularly in longer-lived species where we predict from our findings there may be greater structure.

but the way in which age structure varies across space seems to be much less well understood. Some work identifies spatial variation in age structure in fish populations, often linked to human harvesting of different age-cohorts in given areas (Fowler et al. 2000; McIlwain et al. 2005); and in ungulate and bird populations, associated with age-specificity in habitat use and social behaviour (Ferrer and Bisson 2003; Albery et al. 2022). Given that age is often important for individuals' fitness, spatial age structure is particularly interesting as it might drive local age-related population dynamics. For example, if there is covariance between habitat quality and the age of individuals occupying sites, both could lead to spatially-variable demography, thus potentially biasing estimates of the effects of age on reproduction or, conversely, estimates of environmental effects on trait variation.

One social system where covariance between age and habitat might lead to local age structure is where individuals defend breeding territories. Here, age structure might be particularly important in driving spatial age-related dynamics due to the tight association between breeding territories and reproductive output (Kerbiriou et al. 2006; Jones et al. 2014; Groenendijk et al. 2015). In many animal taxa, individuals undergo reproductive attempts while defending a territory in which resources are used for breeding (Reynolds 1996; Davies et al. 2012). This is particularly prevalent in socially monogamous bird species (Hinde 1956; Greenwood 1980). In such cases, spatial age structure could develop as non-randomness arises when individuals of either similar or dissimilar age breed in closer proximity to each other than expected from chance.

Several mechanisms might affect spatial age structure in territorial animals; we outline four mechanisms here. (1) First, temporal variation in overall population age structure might influence how age is arranged in space. Temporal variation in wild population age structure is common, particularly in short-lived species where the proportion of populations consisting of the youngest age-cohorts may vary greatly between breeding seasons (Gamelon et al. 2016; Woodman et al. 2022). Such variation might affect how age is arranged in space through passive mechanisms whereby clusters of territories occupied by same-age individuals will be more likely to arise when the age distribu-

## 1 INTRODUCTION

Age affects many aspects of life, as resources are allocated into processes and traits at different points throughout lifespan to maximise fitness (Stearns 1992) and individuals gain in experience as they age. Further, variation in population age structure may affect population dynamics, via effects on reproductive output and social organisation (Coulson et al. 2005; Gamelon et al. 2019; Siracusa et al. 2023; Woodman et al. 2024). There is widespread evidence of temporal variation in age structure in wild populations (Coulson et al. 2005; Gamelon et al. 2016; Hoy et al. 2020),

tion is skewed towards this age-cohort. For example, recent work demonstrates how fluctuations in population age structure determine how age is structured within breeding pairs, where there is greater age-assortative pairing when the proportion of yearlings is higher (Woodman et al. 2022). Thus, between-year age distribution is likely to passively affect spatial age structure as clusters of territories occupied by same-age individuals are more likely to arise when much of the population exists in a single age-cohort (Fig. 1a).

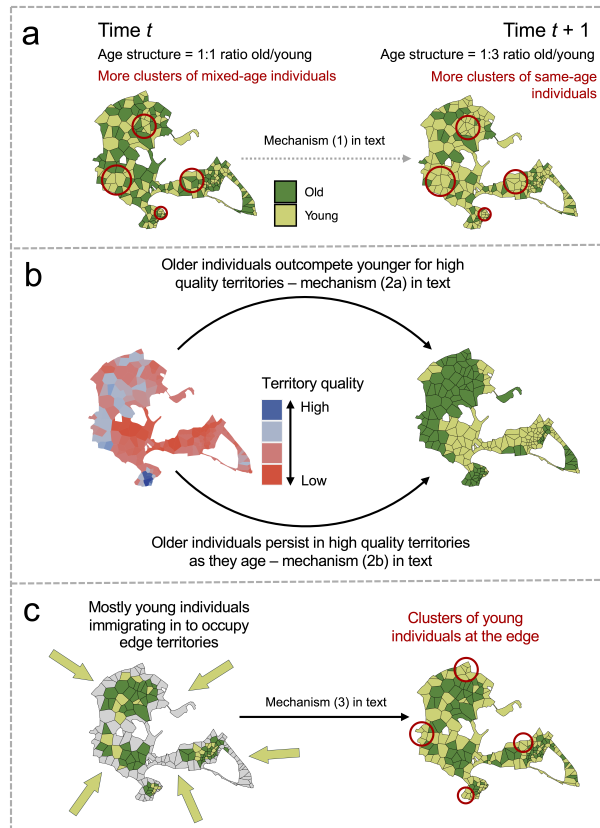


Fig. 1. Overview of mechanisms that might generate spatial age structure across territories referred to in the introduction. The theoretical populations consist of 200 individuals, each of which are associated with a territory, illustrated across Wytham Woods, Oxford, as an example. Yellow and green territories are occupied by 'young' and 'old' individuals respectively. In (a), individuals occupy territories randomly, but at time  $t$  the population consists of a 1:1 ratio of old/young individuals; and at time  $t+1$  a 1:3 ratio of old/young individuals. In (b), the population consists of a 1:1 ratio of old/young individuals, but older individuals occupy the territories of highest quality. In (c), territories which do not border the edge are occupied by a 3:1 ratio of old/young individuals, whereas territories with an edge boundary are occupied by a ratio 1:3 of old/young individuals.

However, age-specific biases in settlement may drive spatial age structure over-and-above that expected from temporal variation in age distribution alone. This may occur if there is spatial structure in territory quality (which may be generated for example through spatial clustering

of resources), and there is covariance between age and territory quality, which may arise through two mechanisms. (2a) In many species, older individuals are dominant (Piper 1997; Wilson 2000), thus potentially leading to age-specificity in territory use where older individuals out-compete younger ones to acquire higher quality territories (Ferrer and Bisson 2003; Garneau et al. 2008; Brewer et al. 2009; Stepanuk et al. 2021; Fig. 1b). (2b) Alternatively, covariance between age and territory quality might arise if higher quality territories elevate survival, and individuals therefore persist for longer in such territories over time (Kokko et al. 2006). Additionally, individuals might be more likely to remain on higher quality territories, which will generate a similar association between length of tenure and hence age (Fig. 1b). Therefore, if older individuals are more likely to occupy higher quality territories through either of these mechanisms, spatial structure in territory quality might drive spatial age structure and repeatability in this over time.

(3) Age-specific territory occupation might also be generated through mechanisms that do not directly link to how ageing affects territory acquisition. For example, if there is individual-specificity in territory acquisition mediated by states or phenotypes other than age, but there is covariance between these and age, then association may arise between age and the type of territory (despite no causal direct link between the two). For example, territory-specific occupation depending on prior dispersal is relatively common across taxa (Piper 2011). Specifically, in fragmented landscapes, sites have environmental 'edges', such as forest edges which provide an interface between internal woodland and the external environment (Saunders et al. 1991). In edge environments, there is often a higher incidence of individuals that disperse into the site (Krauss et al. 2003; Wilkin et al. 2007a). Dispersing between birth and first breeding, known as natal dispersal, generally involves greater distances than dispersal between two breeding attempts (Greenwood and Harvey 1982; Johst and Brandl 1999). Thus, individuals moving into a new environment are often younger (Greenwood 1980; Verhulst et al. 1997; Slagsvold and Wiebe 2018). In such cases, if edge territories are more commonly occupied by younger immigrant individuals, then this might provide a mechanism through which spatial age structure develops (Fig. 1c). Edge territories provide a particularly interesting mechanism by which spatial age structure is generated, not only because of immigrant-specific occupation, but also because they are often of poorer quality (Wilkin et al. 2007a; Purcell et al. 2012; Loveridge et al. 2017), thus they might also directly

generate spatial age structure if there is covariance between age and territory quality (mechanisms 2a and 2b).

These mechanisms lead to *a priori* expectations that spatial age structure might develop across breeding territories; however, empirical evidence of this is currently sparse. Additionally, although these mechanisms might act concurrently on individuals in time, the areas in space that bias age-specific settlement may differ from each other. For example, if different aspects of territory quality are independent then the relative strength of these resource distributions, if any, in influencing age-specific settlement is unknown. Further, how such mechanisms bias age-specific settlement might be influenced by sex given the different roles that males and females will often play in territory acquisition (Brown 1964; Greenwood 1980). In short, given the role that age structure might play in spatially-structured demography, it is important that we advance our understanding on the evidence for spatial age structure and the mechanisms that drive it.

Here, we outline processes and their consequences for generating spatial age structure on long-term breeding data from a natural population of great tits *Parus major* in Wytham Woods, Oxford. We first assess whether there is covariance between territory quality and the age of individuals in such territories. Second, we evaluate whether there is non-random spatial arrangement of age within breeding seasons. Finally, we assess evidence for age-biases in space that persist across time compared to spatial structure in territory quality and reproductive output. We discuss the relative roles of spatial age structure versus structure in territory quality for producing spatially-variable demography, and suggest that the framework presented here can be used across populations when considering spatial age structure.

## 2 METHODS

### 2.1 Study system and data collection

The great tit *Parus major* is a passerine bird found in woodlands across Europe, with breeding ages ranging 1–9, averaging 1.8 years (Perrins 1979; Gosler 1993; Bouwhuis et al. 2009). Although there are some continuous changes with age (Bouwhuis et al. 2009), the main age effects on many individual-level traits are captured by two age-classes: first-years (hereafter juveniles) and older (hereafter adults, Greenwood et al. 1979; Perrins 1979; Sandell and Smith 1991; Gosler 1993; Farine et al. 2015). The species is socially monogamous, with pairs defending territories during annual breeding seasons (Hinde 1952). Data used here are from a long-term study in Wytham Woods, Oxford

(51°46'N, 1°20'W), a 385ha mixed deciduous woodland surrounded by farmland (Savill et al. 2010). The tit population has been monitored since 1947, where breeding adults and their chicks have been marked with unique BTO (British Trust for Ornithology) rings since the 1960s; and standard reproductive metrics are collected (Perrins 1965). Individuals breed almost exclusively in the 1020 nest-boxes which are in fixed positions with known GPS coordinates (Krebs 1971; Wilkin et al. 2006). All chicks are ringed at 14 days of age, while adults are trapped at nest-boxes and identified by ring number, or marked with a new ring if they are immigrants. Age is based on year of hatching for local birds, or plumage characteristics for immigrants (Svensson 1992). Although immigration rates are high (46%), most are first caught as yearlings (78%) and can therefore be aged accurately.

### 2.2 Data selection

We constructed a dataset that assigns the year of hatching to all individuals between 1950–2022, across which exact age was calculated for 88.8% of 46062 identified breeding individuals. In this study, we included birds in analyses that attempted to breed between 1978–2022, for which data were more complete compared to earlier dates (Fig. S1). Individuals that were first caught post-fledging are assumed to be immigrants, as locally-hatched tits are marked as nestlings in nest-boxes and the proportion of birds hatched in natural cavities is very low (Kidd et al. 2015). Immigrants that entered the population with adult plumage were assigned a minimum age of 2, and subsequent age estimates were based on this (6.7% and 10.0% of breeding females and males). Age was therefore determined for 68.7% of breeding individuals where at least one egg was laid (due to a combination of nests failing prior to adult trapping and unsuccessful trapping attempts, there are cases where the identity of parents is unknown).

### 2.3 Statistical analyses

#### 2.3.1 Determining breeding territories

We defined annual breeding territories through a Dirichlet tessellation technique that forms Thiessen polygons (Rhynsburger 1973; Tanemura and Hasegawa 1980) around each occupied nest-box. The polygon includes all space within the habitat that is closer to the focal box than any other (with a boundary also imposed by the woodland edge). This metric of territory has been shown to be biologically meaningful in terms of territory size and territorial neighbours in tit species and is strongly related to other methods of calculating territories (Adams 2001;

Wilkin et al. 2006; Schlicht et al. 2014; Firth and Sheldon 2016; Gokcekus et al. 2023). However, a limitation is that unrealistically large polygons are formed in areas where nest-boxes are placed at great distances from each other. We therefore capped territories at 2ha, which is a more realistic maximum spatial scale at which individuals use territories, as supported in previous analytical and field studies (Krebs 1971; Both and Visser 2000; Wilkin et al. 2006, 2007a).

### 2.3.2 Age and territory quality

We first assessed covariance between the age of individuals and their territories' quality. We measured territory quality through four measures: the number of oak trees *Quercus* spp. within 75m of the nest-box; average territory density; the edge distance index; and the long-term nest-box popularity index. Each of these is justified below.

Great tits predominantly provision offspring with caterpillars collected close to their nests (Gosler 1993), thus variation in caterpillar availability is directly linked to reproductive success (Perrins 1991; Keller and van Noordwijk 1994; Rytönen and Krams 2003). Caterpillars are found most abundantly on oak trees (Perrins 1991; Gosler 1993), therefore oak proximity, health and abundance is important for breeding success (Wilkin et al. 2006, 2009; Cole et al. 2021; Gokcekus et al. 2023). A radius of 75m was chosen as the abundance of oaks within this distance has been shown to be particularly important for breeding (Wilkin et al. 2007b; Hinks et al. 2015).

The density of conspecifics breeding in proximity may influence resource availability if foraging ranges overlap, and therefore territory density may also represent an aspect of territory quality. Additionally, territory density may affect site quality through social mechanisms, such as increased competition and emergent need for territory defence leading to reduced foraging (Ydenberg and Krebs 1987), or conversely mutual benefits between familiar neighbours (Grabowska-Zhang et al. 2012b, 2012a; Gokcekus et al. 2023). We calculated average territory density directly from the Thiessen polygon area produced from tessellation by taking the reciprocal of the mean polygon area.

Territories at woodland edges are associated with lower reproductive success in great tits (Wilkin et al. 2007a). Following Wilkin et al. (2007a), we defined the edge distance index (EDI) for each nest-box by multiplying the distance to forest edge by the proportion of woodland habitat within a 75m radius of the box. Thus, boxes within 75m of the edge have an EDI value in proportion to the amount of woodland habitat within this radius, therefore considering

not only the distance to edge, but also the number and geometric arrangement of edges relative to nest-box.

Finally, the frequency a territory is occupied in the long-term may provide a measure of quality as individuals may choose sites that confer reproductive benefits more often, as evidenced in other species (Sergio and Newton 2003; Smith and Moore 2005; Johnson 2007; Steenhof and Newton 2007; Potti et al. 2018). There is evidence of this in Wytham, where the number of times a nest-box has been occupied positively correlates with the average number of offspring that fledge per breeding attempt (Fig. S2). We therefore calculated the number of times a nest-box has been occupied since 1965. However, this is related to the number of nest-boxes within close proximity to a focal box (Fig. S3), because in areas of high nest-box density there are multiple unoccupied boxes which would likely be associated with the same territorial range if they were occupied (thus, in regions of high box density, birds may re-occupy the same territory over multiple years, but not necessarily the exact same box). To correct for this, we ran a linear model between the number of boxes within 30m of a focal nest-box (supporting information) and the number of times said box has been occupied, and took the residuals as the long-term nest-box popularity index.

We constructed a generalised linear mixed-effects model assuming a binomial error distribution to analyse the association between these four measures of territory quality and the age of the breeding individual. We modelled age (juvenile/adult) as the response variable, with the territory quality measures as explanatory variables, which were z-transformed to compare their relative effects in predicting age. Individual ID, nest-box ID, and breeding year were included as random effects (Table S1). We ran three sets of these models: one with all individuals; one with only females; and one with only males, allowing us to assess potential sex-specific differences in the association between aspects of territory quality and age. These models were also run to test for covariance between territory quality and residency status (supporting information). All models were conducted in R statistical software (R Core Team 2021) using the *lme4* package (Bates et al. 2015).

### 2.3.3 Spatial age structure

For each year's breeding population, we constructed an individual-by-individual matrix denoting breeding neighbours i.e. a network of breeding territories, where nodes represent individuals and edges represent the spatial connectivity of territories. Specifically, edges connected individuals if their territories share a boundary from the

tessellation technique and were weighted relative to the distance between nest-boxes of neighbouring territories.

We created three networks per year: one with all individuals (but removing edges within breeding pairs that occupy the same territory); one with only females; and one with only males. Edges connecting individuals of unknown identity were removed. Across these networks, we calculated the assortativity coefficient of age (juvenile/adult), which measures the correlation between individuals' age and that of their territorial neighbours accounting for edge weight (proximity of neighbouring nest-boxes) and the relative proportion of the two age classes across the network. Through this technique, the age-composition of neighbourhoods of birds that are likely to interact during territorial and foraging behaviour contribute to the emergent quantitative signal of spatial age structure to a greater degree than they would if spatial autocorrelation were calculated through pairwise distance of all individuals across the system. Thus, this method allows us to assess evidence for spatial age structure at a biologically relevant scale (analyses were also run treating age as a discrete and continuous trait, as well as calculating assortment of residency status; supporting information). We also ran analyses to compare spatial age structure with spatial structuring of territory quality and reproductive output. To calculate territory quality structure, we assigned the value from the previously described four measures of quality to each node (associated with an occupied nest-box) and calculated the territory quality assortativity coefficient across the network. For spatial reproductive output structure, we ran parallel analyses, but calculated the assortativity in clutch size, chick number, fledgling number, and binary success (where 0 is no fledglings and 1 is at least one fledgling) associated with each nest-box. These analyses were run using the *assortnet* package (Farine 2014).

### 2.3.4 Temporal repeatability of age structure

Finally, we tested whether spatial regions show temporal repeatability in age-composition, territory quality, and reproductive output. To assess this, within each year, we defined a radius around each occupied nest-box that corresponded to an area of 25, 50, 100, 150 and 200ha, representing neighbourhoods of breeding individuals of variable population sizes. Within each radius we calculated: the proportion of individuals that were adults; the mean number of oaks within 75m of the focal boxes; mean territory density; mean edge distance index; mean nest-box popularity index; mean clutch size; mean chick number; mean fledgling number; and proportion of boxes with binary success. We then calculated the same metrics for

all nest-boxes outside of the focal radius. From this, we calculated a ratio index of within versus outside radius for each calculated measure, where a value of one represents the same annual average measure within and outside the radius. We then tested the repeatability of the ratio index associated with each spatial scale across the 45 years of data by calculating the intraclass correlation coefficient (ICC) derived from a linear mixed-effects model, where the response variable is the ratio index, and year and radius area are fitted as categorical grouping variables.

## 3 RESULTS

### 3.1 Age and territory quality

Across 20121 breeding individuals, representing 11167 breeding attempts, we found that high density territories weakly predicted occupation by adults compared to juveniles (odds ratio [95% confidence intervals]: 1.108 [1.065, 1.153],  $p < 0.001$ ), in addition to territories with a greater long-term popularity index (1.084 [1.045, 1.124],  $p < 0.001$ ), with little evidence that the number of oaks within 75m or EDI were linked to age (Fig. 2; Table S2). When assessing the influence of territory quality on the age of individuals separately for both sexes, similar patterns were found, except territories that have a greater long-term popularity index more strongly predicted occupation by adult males (1.143 [1.092, 1.195],  $p < 0.001$ ), but were weakly if at all associated with female age (1.041 [0.997, 1.086],  $p = 0.066$ ).

### 3.2 Spatial age structure

Generally, we found weak positive age assortment across breeding territories, but there was temporal variation with many years having little evidence for spatial age structure and some having significant disassortment (i.e. birds of similar age less likely to be associated), whether considering the whole population (median  $r$  age assortativity coefficient = 0.014, 51% of annual standard errors overlap zero; Fig. 3), females (median  $r$  = 0.002; 58% SEs overlap zero), or males (median  $r$  = -0.004; 38% SEs overlap zero). In contrast, there was much greater spatial structure in territory quality (oak abundance median  $r$  = 0.782; territory density median  $r$  = 0.645; EDI median  $r$  = 0.817; and nest-box popularity index median  $r$  = 0.258, no annual SEs overlap zero). There is greater evidence for spatial reproductive output structure compared to age, but the signal of this structure is still relatively weak (clutch size median  $r$  = 0.059, 22% SEs overlap zero; chick number median  $r$  = 0.047, 29% SEs overlap zero; fledgling number median  $r$  = 0.075, 22% SEs overlap zero; binary success

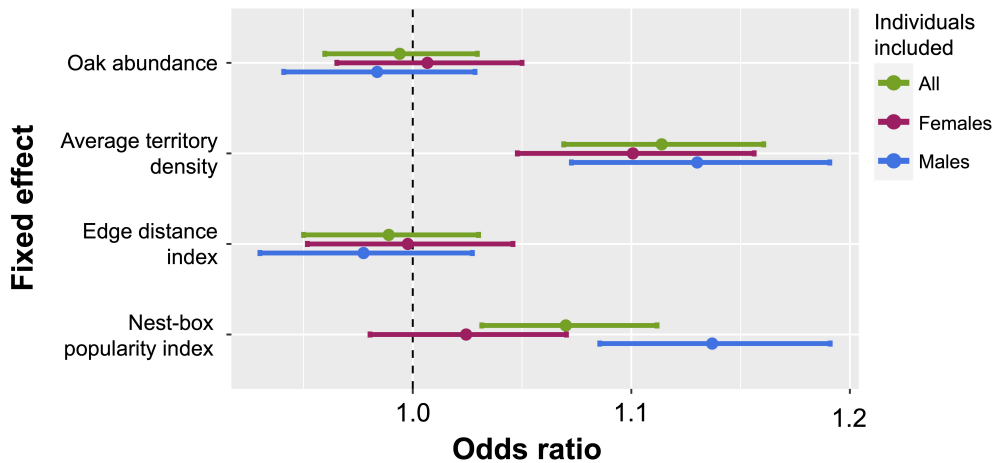


Fig. 2. Point estimates of odds ratios obtained from generalised linear mixed-effects models. The analysis examines the association between territory quality on the odds of the breeding individual being an adult. Each point corresponds to a specific level of the fixed effects (on the y-axis), and error bars denote 95% confidence intervals. Green points are from analysis assessing all individuals, purple are only females, and blue are only males.

median  $r = 0.057$ , 24% SEs overlap zero; Fig. 3; Table S3 for all results).

### 3.3 Temporal repeatability of spatial age structure

There was low temporal repeatability in the age-composition of spatial regions at all assessed scales 25–200ha (ICC range: 0.036–0.057; Fig. 4). In contrast, as would be expected, there is very high temporal repeatability in all assessed territory quality measures (Fig. 4). Compared to age-composition, there is higher temporal repeatability in average reproductive measures of neighbourhoods, with mean clutch size (ICC range: 0.234–0.447) displaying the highest repeatability (Fig. 4; Table S4 for all results).

## 4 DISCUSSION

We quantified the extent of spatial age structure in a large long-term study population of territorial birds, and tested several mechanisms that could generate assortment by age in space. We show that, in general, spatial age structure is weak, despite the occurrence of spatial structure in habitat features, some of which covary with age and could plausibly generate spatial age structure. We also find that there is little temporal repeatability of spatial regions which bias certain age structures, despite stronger evidence for repeatability in spatial structure of reproductive output and territory quality. Here, we discuss these findings, suggesting that spatial structure in territory quality might be a

greater contributor to spatially-variable demography and why there is not greater spatial age structure in this system.

### 4.1 Age and territory quality

Across all breeding individuals, we show that older individuals are more likely to acquire territories at higher densities that have a greater long-term popularity, while there is a lack of evidence for a relationship between age and the abundance of oak trees or distance to edge. Considering females and males separately, we find similar associations between age and territory quality, except that the popularity index of a nest-box more strongly predicts occupation by adult males than females.

It is interesting that territories at higher average densities are more likely to be occupied by adults than juveniles considering that this may result in reduced territory size, increased chance of encounter with conspecifics during chick-rearing behaviour, and has previously been linked to lower reproductive success (Wilkin et al. 2006). This may relate to evidence that adults have a weaker response to density dependence in great tit populations, where juvenile cohorts have a greater effect in reducing recruitment and survival, and more negatively respond to density dependence (Gamelon et al. 2016). Together with our results, this may reflect improved breeding competence of adults compared to juveniles leading to higher territorial densities. Specifically, older individuals may have increased foraging efficiency (Perrins and McCleery 1985), thus negating the need for large territories (indeed, individuals with smaller

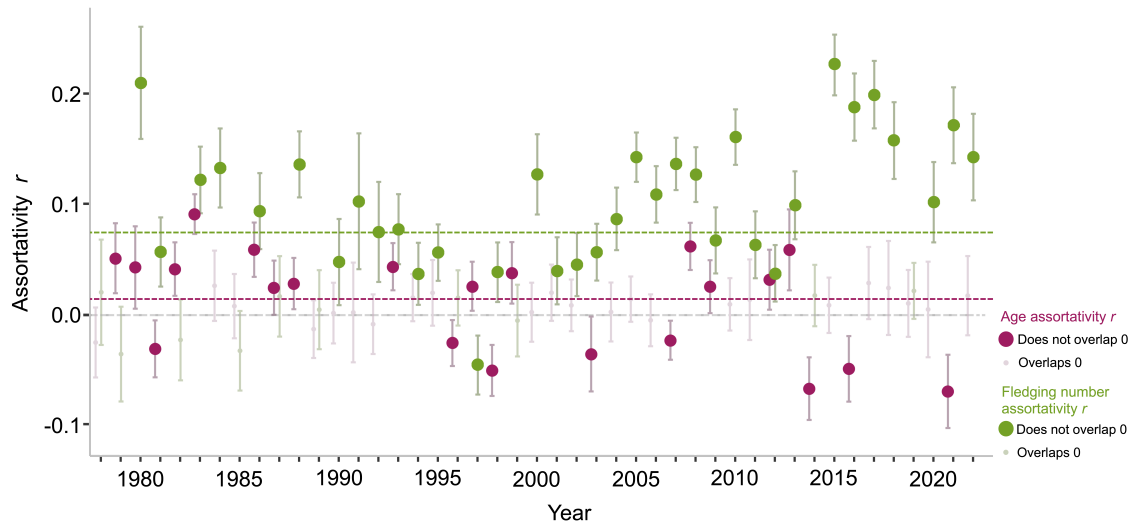


Fig. 3. Annual age and fledgling number assortativity  $r$  coefficients across territories. Large purple points represent age assortativity values where the standard error does not overlap zero, and large green points are fledgling number assortativity values where standard error does not overlap zero. The dotted purple line denotes the median age assortativity value, and the green line denotes the median fledgling number assortativity value.

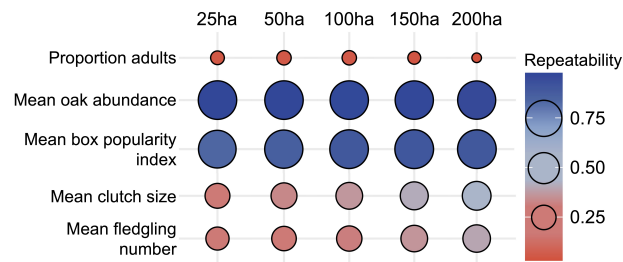


Fig. 4. Temporal repeatability of age-composition, territory quality and reproductive output of neighbourhoods at spatial scales of 25, 50, 100, 150 and 200ha. Repeatability was derived from the ICC from a linear mixed-effects model, where the ratio index of within versus outside the defined spatial scale of the average measure was the response variable, and year and spatial scale area categorical grouping variables. Circles are sized and coloured on a gradient from red to blue as repeatability increases.

foraging ranges can be more efficient with higher reproductive success, Cole et al. 2012), therefore generating higher breeding densities among adults and a weaker response to density dependence. Additionally, increased familiarity between adult territorial neighbours may reduce competition associated with foraging (Grabowska-Zhang et al. 2012b; Gokcekus et al. 2023), or even promote joint benefits such as nest defence (Grabowska-Zhang et al. 2012a), thus favouring closer breeding between adults. Recent advances in tracking technology of passerine foraging behaviour (Baldan and van Loon 2022) might advance insight into

whether competition is reduced among older familiar neighbours by assessing evidence for increased coordination during foraging compared to unfamiliar neighbours.

Territories that were more popular in the long-term were more likely to be occupied by adults than juveniles. The use of frequency of occupancy as a measure of territory quality is well-established in avian systems (Sergio and Newton 2003; Smith and Moore 2005; Johnson 2007; Steenhof and Newton 2007; Potti et al. 2018), and may capture information on cues of quality which individuals respond to in the long-term which cannot be directly measured. It is particularly interesting that the association between more popular territories and age is weakened when only assessing females, but strengthened in males. This may be explained by sex differences where male great tits are more important in initial acquisition and defence of territories (Krebs 1971, 1977; Perrins 1979; Björklund et al. 1989), which is widespread in other avian (Brown 1964; Stutchbury 1991; Beletsky 1992; Eikenaar et al. 2009) and taxonomic groups (Clutton-Brock 1989; López and Martín 2002; Milner et al. 2010). Thus, this could suggest that older males with greater competitive ability (Sandell and Smith 1991) outcompete younger individuals to occupy higher quality sites. This may be driven either by novel acquisition of high-quality territories, or by persistence and defence of a territory between years (Greenwood et al. 1979; Harvey



et al. 1979a). In the latter case, males may occupy a high-quality territory in their first breeding attempt, which supports successful breeding, and then retain this territory in future breeding. Thus, if survival is high between years, particularly among individuals in high-quality territories, then covariance between male age and territory quality may arise as younger first-year breeders are forced into low-quality territories.

There is little evidence that the abundance of oaks close to the nest predicts age. Oak abundance at this scale has been linked to great tit breeding success (Wilkin et al. 2006, 2007b, 2009; Hinks et al. 2015; Cole et al. 2021; Gokcekus et al. 2023), thus increased experience and competitive ability of adults (Sandell and Smith 1991) might lead to the assumption that older individuals will acquire territories with more oaks. However, although higher oak abundance might provide better quality territories when considering entire populations, little is known about how this interacts with phenological synchrony at the individual-level (Hinks et al. 2015) and how the degree of phenological matching depends on age. Specifically, older great tits typically breed earlier (Harvey et al. 1979b; McCleery and Perrins 1998), possibly due to improved breeding competence leading to greater synchrony between chick-rearing and peak caterpillar abundance. Further, the rate at which caterpillars are provisioned to chicks strongly correlates with the caterpillar biomass available (Naef-Daenzer et al. 2000). Thus, if a greater proportion of juveniles mistime their breeding compared to adults, then they may be unable to monopolise caterpillar resources even if in oak-rich territories due to temporal mismatch. In addition to greater phenological synchrony, older birds may improve their foraging ability in a broader sense through greater site familiarity from previous occupation (Perrins and McCleery 1985; Piper 2011; Slagsvold and Wiebe 2018), utilisation of a wider variety of food resources (Gosler 1993), and improved foraging coordination with pair-bonded partners (Mariette and Griffith 2015; Griffith 2019). In this sense, the overall abundance of oaks may not be a crucial cue when acquiring territories, rather there is stronger selection on phenological matching to the local environment (Hinks et al. 2015; Cole et al. 2021) and general foraging ability. Additionally, there is little evidence that the edge distance index is associated with age, which has been linked to reduced reproductive output (Wilkin et al. 2007a), and thus there is no apparent age-specificity in how edge effects mediate territory acquisition.

The lack of an effect of oak abundance and edge distance on age-specific territory occupation, as well as the

general weak association with other territory attributes, may suggest that territory acquisition in adults is predominantly driven by retaining previous territories in which they successfully bred, regardless of quality. This may be driven by a relative lack of available territories compared to overall population size, thus providing strong selection for the retention of a previously occupied territory (Clark 1994; Harts et al. 2016). High breeding site fidelity is evident in great tits (Harvey et al. 1979a). In this case, the cue which individuals respond to when acquiring a territory may be experience of previous breeding success, as opposed to current environmental quality cues. Consequently, any covariance between older age and high territory quality might break down through two mechanisms: either previous breeding occurred in a low-quality territory, but breeding was successful and thus the territory is retained as an adult; or previous breeding occurred in a high-quality territory, but the attempt was unsuccessful, and thus individuals move to new poorer quality territories in future years. Breeding success in poor quality territories can regularly occur, for example if intraspecific competition is low, or when individual or partner quality is high. In such cases, older individuals might utilise their higher competitive ability to defend territories in which they have had success regardless of quality (Harvey et al. 1979a; Yasukawa 1979; de Vos 1983). Conversely, unsuccessful breeding may happen in areas of high-quality, through stochastic environmental effects (such as extreme weather or predation), or low individual or partner quality. In these cases, despite being in high-quality territories, pairs may divorce in an attempt to improve future breeding (Culina et al. 2015) and disperse to new territories (Harvey et al. 1979a). Through this process, older individuals will not necessarily occupy the best quality territories, thus leaving unoccupied territories of higher quality for juveniles to acquire.

Given our findings, future research should aim to disentangle the relative effects of territory quality and previous reproductive success on site fidelity in territorial species, as well as assessing behavioural differences in the degree of territory defence in individuals that re-occupy sites of varying quality. Further, examining age-specific behaviour following divorce and acquisition of a new territory might shed light on how age relates to territory quality when removing the effect of site fidelity. For instance, there may be variation in territory quality across divorced individuals that newly settle depending on their own age and that of their new partner. Finally, more work should assess age-specificity in territory acquisition while considering non-

breeding individuals that fail to acquire a territory. For example, in great tit populations, there are often more individuals than available territories (Perrins 1979), leaving non-breeders in the population during the spring. In avian species, non-breeders tend to be younger (Stutchbury 1991; Sergio et al. 2009) and the ability to defend a territory against intrusions from non-breeders increases with age (Arcese 1987). Thus, experiments to identify non-breeders during territorial activity (Firth et al. 2018) and accounting for this cohort might reveal further age-specificity in territory quality.

## 4.2 Spatial age structure

Our study reveals more frequent positive annual spatial age structure, but this structure is weak and often absent, with no clear sex differences. In contrast, there is strong evidence for spatial territory quality structure, with particularly strong assortment in oak abundance, territory density and edge distance (the latter of which is spatially necessitated), and moderate assortment in the long-term popularity index of a nest-box. There is greater evidence for spatial structure in reproductive output compared to age, with fledgling number displaying the greatest structure.

It is interesting that there is not greater spatial age structure not only due to our evidence of covariance between some attributes of territory quality and age, and spatial structure in such territory quality, but also due to social mechanisms that might generate spatial age structure. Winter social associations in great tits are positively age-assorted, albeit fairly weakly (Farine et al. 2015), and social connections carryover into breeding as individuals establish territories closer to previous social associates (Firth and Sheldon 2016). This is likely because having familiar neighbours can reduce the need for territory defence, increase co-operation, and enhance reproductive success (Grabowska-Zhang et al. 2012b, 2012a; Gokcekus et al. 2023). Thus, because older individuals are more likely to be familiar with their neighbours than younger ones (Gokcekus et al. 2023), this might be expected to generate spatial age structure through clusters of older individuals breeding in proximity. However, although this mechanism provides direct benefits at the dyadic-level for closer breeding between adults, there is little overall spatial age structure. This may be partly explained by the species' life-history, where there is high annual mortality (~52%, Bouwhuis et al. 2009). Together with annual influxes of immigrant birds, this means that the breeding population is often composed of a large proportion of individuals that are first-time breeders (46–83%, Woodman et al. 2022), thus only making it possi-

ble for a small proportion of the population to have familiar neighbours. In short, despite benefits for older breeders to retain previous neighbours, high mortality rates lead to a high chance that at least some previous territorial associates will have died, and high competition for breeding sites mean these will be acquired by new and likely juvenile breeders (Krebs 1977; Perrins 1979; Björklund et al. 1989), thus reducing overall spatial age structure. This hypothesis should be tested through comparative analyses using the framework developed here by assessing whether there is greater spatial age structure in territorial species with lower mortality rates and thus a greater opportunity to retain previous neighbours, particularly considering familiarity between neighbours is adaptive in many taxonomic groups (Temeles 1994; Frostman and Sherman 2004; Siracusa et al. 2021).

Additionally, although there are benefits of retaining familiar neighbours, this is not necessarily underpinned by an active process where older individuals select territories based on closer breeding to previous associates. Instead, it may be underpinned by a passive process where individuals which survive between years occupy the same locality (Harvey et al. 1979a), leading to the incidental retention of familiar neighbours that also survive and have high site fidelity. Such a passive mechanism is consistent with recent findings that age-assortative mating within pairs of great tits, despite being adaptive (Harvey et al. 1979b), is underpinned by passive processes of pair retention and fluctuations in overall population age structure as opposed to active age-related selection (Woodman et al. 2022). Thus, even if there are direct advantages of retaining familiar neighbours, if it is not underpinned by active processes, then this might weaken its prevalence and therefore overall spatial age structure.

Finally, although there is temporal overlap in when territories are used, there is variation between pairs which will affect how neighbours interact depending on their breeding time synchrony, thus affecting spatial age structure at any single point in time. Firstly, there is spatial variation in the timing of food availability at a spatial scale relevant to individual territories, underpinned by variation in individual tree phenology (Cole and Sheldon 2017), and this local variation predicts breeding timing in individual pairs (Hinks et al. 2015). Thus, pairs with neighbouring territories may not interact much during chick-rearing behaviour if neighbouring phenology is highly asynchronous (although there is generally spatial structure in breeding phenology across Wytham, Wilkin et al. 2007b). Second, there might be even greater temporal mismatch in

occupation of neighbouring territories when considering initial acquisition and defence behaviour, which begins in January or even earlier, months before chick-rearing (Krebs 1977, 1978, 1982). Thus, interactions between individuals and competition associated with territory defence will be variable depending on the occupation status of neighbouring territories at the time of focal territory acquisition. For example, there may be extended periods of territorial activity pre-breeding where neighbouring pairs interact, but then a new pair may acquire a territory which bisects such breeding sites, thus breaking down the territorial boundary between the two original neighbouring pairs. Previous research in this system has assessed age-specificity in nest-site visitation patterns prior to breeding in terms of the number and spatial clustering of nest-boxes visited (Firth et al. 2018). Thus, future work could incorporate such techniques with advances in the tracking of movement (Levin et al. 2015; Baldan and van Loon 2022) and other defence behaviour (Merino Recalde 2023) to advance our understanding on the temporal scale at which individuals interact during territorial behaviour before breeding, how this is affected as territories are gradually occupied prior to the spring, and age-specific variation in this.

### 4.3 Temporal repeatability of spatial age structure

We find low repeatability in the age-composition of spatial regions between years compared to repeatability in spatial territory quality and reproductive output structure. High repeatability in spatial territory quality structure is expected, as annual variation in average quality measures across spatial regions is changed only depending on which nest-boxes are occupied (i.e. if the same boxes were occupied every year, there would be 100% repeatability). However, there is variation in which boxes are used each year. Thus, in conjunction with our previous finding of high within-year spatial territory quality structure, it is interesting then that we report a higher repeatability in the average reproductive output compared to the age-composition of spatial regions. This suggests that territory quality in this system may be more important in driving spatially-variable demography than local age structure. Additionally, the finding of low repeatability in spatial age-composition is consistent with our suggestion that adult occupation is likely largely driven by persistence in previous territories of varying quality as opposed to active acquisition of high-quality territories (the latter would lead to higher repeatability as older birds would frequently use higher quality sites independent of year).

## 5 CONCLUSIONS

Our study highlights association between age and aspects of territory quality in a territorial passerine species, specifically showing that older individuals breed at higher densities and in sites which are more popular in the long-term. However, we show limited evidence of spatial age structure. We suggest that age-specific occupation of territories is likely driven by persistence in territories across lifespan (largely irrespective of quality), leading to passive retention of some older neighbours which also survive between years. We emphasise the importance of exploring the operation of these mechanisms that might lead to spatial age structure in species with different life-histories. Specifically, it might be expected that in species with lower mortality rates, greater spatial age structure would be generated through passive mechanisms of territorial neighbour retention as more individuals survive between years. The observed patterns of higher spatial territory quality and reproductive output structure (compared to spatial age structure), in addition to greater temporal repeatability in these, contributes valuable insights into the drivers of spatially-variable demography. Namely, given these results, we suggest that spatial clustering of territory quality is likely to be more important in determining repeatable spatial structure in reproductive output compared to spatial age structure.

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# Age-specificity in territory quality and spatial structure in a wild bird population - SUPPORTING INFORMATION

Joe P. Woodman, Ella F. Cole, Josh A. Firth & Ben C. Sheldon

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## 1 SUPPLEMENTARY METHODS

### 1.1 Nest-box density and occupation

The number of times a nest-box has been occupied by a great tit since 1965 is likely affected by the density of nest-boxes placed in close proximity. This is because during the breeding season, in areas of high box density, there are multiple unoccupied boxes which would likely be associated with the same territorial range if they were occupied (Fig. S4), which is variable between individuals but estimated as approximately 2ha in area or within a 75m radius around a focal box (Krebs 1971; Barnes 1975; Both and Visser 2000; Wilkin et al. 2006, 2007b, 2007a; Hinks et al. 2015). Therefore, in areas of high nest-box density, birds may re-occupy effectively the same territory over multiple years, but not necessarily the exact same box, which is not the case in areas of low box density. To correct for this when using occupation rate as a measure of territory quality, we ran a linear model between the number of boxes within 30m of a focal nest-box and the number of times said box has been occupied, and took the residuals as the corrected long-term nest-box popularity index. 30m was chosen as territorial ranges (defined by a radius of 75m) around two focal points placed at 30m or less from each other overlap by ~75% or more (Fig. S4), thus largely representing the same territory. While it is currently unknown at which precise distance between neighbouring boxes an inter-annual switch represents retaining largely the same territory for breeding tits (as well as the fact that this is likely to be variable

depending on individual behaviour and local population size), previous analytical and field studies suggest that 30m is an appropriate distance to use based on our previous justification of territorial ranges. However, we additionally defined the nest-box popularity index by taking the residuals of a linear model between the number of boxes within 10, 20, 40, 50 and 75m of a focal nest-box and the number of times occupied. This did not substantially change the point estimates of our results when running a generalised linear mixed-effects model to test the association between our measures of territory quality and the age of the individual in a territory (Table S3).

## 1.2 Methods assessing residency status

### 1.2.1 *Residency status and territory quality*

Due to the association between residency status and age where a high proportion of immigrants are juveniles, in addition to well-established biological differences between residents and immigrants where residents are socially dominant (Sandell and Smith 1991; Farine and Sheldon 2015; Slagsvold and Wiebe 2018), have higher reproductive success (Dhondt et al. 1990; Wilkin et al. 2007a; Slagsvold and Wiebe 2018) and have greater site familiarity (Krebs 1982; Wilkin et al. 2007a; Slagsvold and Wiebe 2018), we ran parallel analyses to assess whether territory quality measures predict residency status. We define two types of residency status: immigration status (immigrant/local recruit: an individual-level trait that remains the same throughout life-history depending on whether the bird hatched within or outside of Wytham); and settled status (new/settled; an individual-level trait which may change across lifespan, where new birds refer to immigrants that are breeding for the first time, Fig. S5).

We therefore constructed a generalised linear mixed model assuming a binomial error distribution as in the main text to analyse the association between the four measures of territory quality and the immigration/settled status of the individual that acquires and breeds in a territory. Three models were run for each of these two binary traits: one with all individuals; one with only females; and one with only males.

### 1.2.2 *Spatial structure in residency status*

As in the main text, we assessed spatial structure in residency status by creating three networks per year: one with all individuals (but removing edges between breeding pairs that occupy the same territory); one with only females; and one with only males. Across these networks, we calculated the assortativity coefficient of immigration status (immigrant/local recruit) and settled status (new/settled).

### 1.2.3 *Temporal repeatability of spatial structure in residency status*

We tested the scale at which regions in space show repeatability in spatial structure in immigration and settled status. For each year, within each radius associated with a focal nest-box as outlined in the main text we calculated the proportion of breeding individuals that are local recruits and the proportion that are settled birds, and also calculated this for all nest-boxes outside the focal radius. We then tested the repeatability of the ratio index associated with each variably sized radius across the 45 years of data collection by calculating the intraclass correlation coefficient (ICC) derived from a mixed-effect model, where the response variable was the ratio index, and year and radius area were fitted as random categorical grouping variables.



## 2 SUPPLEMENTARY RESULTS

### 2.1 Territory quality and spatial structure in residency status

#### 2.1.1 Residency status and territory quality

Territories at lower densities significantly predicted occupation by local recruits compared to immigrants across all individuals (odds ratio [95% confidence intervals]: 0.662 [0.567, 0.773],  $p < 0.001$ ) and in females (0.624 [0.504, 0.773],  $p < 0.001$ ), but not in males (0.951 [0.748, 1.210],  $p = 0.683$ ; Fig. S6; Table S2). There is little evidence that the long-term popularity index or the abundance of oaks predicted the immigration status of the breeding individual, except some evidence that a slight reduction in the number of oaks within 75m predicted occupation by a local recruit (0.804 [0.687, 0.943],  $p = 0.007$ ) or a specifically a female local recruit (0.769 [0.617, 0.959],  $p = 0.020$ ). Greater EDI values (further from the edge) significantly predicted occupation by local recruits across all individuals (1.558 [1.295, 1.874],  $p < 0.001$ ) and females (1.484 [1.151, 1.913],  $p = 0.002$ ), but not males (1.098 [0.851, 1.416],  $p = 0.472$ ). There was little evidence that any territory quality attributes predict the settled status of breeding individuals (Fig. S7; Table S2), except territories with a greater long-term popularity index were more likely to be occupied by settled males (1.075 [1.024, 1.128],  $p = 0.003$ ), and territories with a higher EDI value were more likely to be acquired by settled individuals (1.047 [1.005, 1.089],  $p = 0.026$ ).

#### 2.1.2 Spatial structure in residency status

There is weak evidence for spatial structure in immigration status across breeding territories when considering the whole population (median  $r$  assortativity coefficient = 0.007; 51% of annual standard errors overlap zero), females (median  $r = 0.029$ ; 44% SEs overlap zero), or males (median  $r = -0.005$ ; 47% SEs overlap zero). Similar results are found for settled status when considering the entire population (median  $r = 0.008$ ; 51% SEs overlap zero), females (median  $r = 0.007$ ; 38% SEs overlap zero) or males (median  $r = -0.019$ ; 44% SEs overlap zero; Table S4 for all results).

#### 2.1.3 Temporal repeatability of spatial structure in residency status

There was low repeatability in the residency status composition of spatial regions across years at all assessed spatial scales 25–200 ha (immigration status ICC range: 0.076–0.173; settled status ICC range: 0.024–0.062; Table S5).

### 2.2 Spatial age structure as a continuous and discrete trait

As with binary age, we generally found weak positive age assortment across breeding territories when treating age as a discrete variable with five categories (1, 2, 3, 4, and 5 or more years-old) or as a continuous trait, whether considering the whole population (median discrete age  $r = 0.004$ , 58% SEs overlap zero; median continuous age  $r = 0.004$ , 58% SEs overlap zero), females (median discrete age  $r = -0.007$ , 60% SEs overlap zero; median continuous age  $r = -0.002$ , 53% SEs overlap zero), or males (median discrete age  $r = -0.013$ , 36% SEs overlap zero; median continuous age  $r = -0.012$ , 36% SEs overlap zero; Table S4 for all results).

## 3 SUPPLEMENTARY DISCUSSION

### 3.1 Residency status and territory quality

We reveal some covariance between territory quality and residency status. Specifically, locally-hatched females are more likely to occupy territories at lower densities and those that are further from the edge, but this effect is not

present in males. There is no association between the long-term popularity of a territory and the immigration status of the occupant in either sex, while there is weak evidence that immigrants may occupy territories with higher oak abundance. Interestingly, no territory quality attributes predict immigration status when considering males on their own. However, individuals that have newly dispersed into the woods are slightly more likely to occupy territories closer to the edge and newly immigrating males are very weakly associated with territories that have a lower long-term popularity index, while the settled status of females is not predicted by any territory quality attributes.

The strongest effects of lower territory density and greater distance from edge in predicting occupation by residents rather than immigrants, independent of age, might relate to greater site familiarity in locally-hatched individuals. Independent of the social advantages of high breeding density among adults as discussed in the main text, sites at lower density can provide better quality habitats if associated with greater foraging area (Wilkin et al. 2006), and edge sites often provide worse quality habitats due to overcrowding, increased predation and reduced foraging area (Paton 1994; Huhta et al. 1999; Batáry and Báldi 2004; Deng and Gao 2005; Wilkin et al. 2007a). Thus, residents with greater site familiarity (Krebs 1982; Wilkin et al. 2007a; Slagsvold and Wiebe 2018) and higher competitive ability (Sandell and Smith 1991) might be dominant over immigrants who settle in unoccupied areas of lower quality habitat. However, in this scenario we might expect relatively high assortment in how immigrants are spatially structured during breeding (Farine and Sheldon 2015, but see later discussion).

The effect of territory density and edge distance in predicting immigration status is not present when only assessing males, as with the other measures of territory quality. This may be related to sex-differences in dispersal dynamics in great tits, where females generally immigrate into sink populations such as Wytham from greater distances (Greenwood et al. 1979; Verhulst et al. 1997) and later in the year (Dhondt 1979; Hudde 1995; Verhulst et al. 1997). Therefore, immigrant males may be more familiar with the local environment compared to females, which is important given that males control initial territory acquisition (Krebs 1971, 1977; Harvey et al. 1979; Greenwood 1980; Clarke et al. 1997), thus potentially weakening the association between immigration status and territory quality in males compared to females. However, what then remains puzzling is the finding that new males (i.e. birds that have dispersed into the woods and are breeding for the first time) are more likely to occupy territories closer to the edge and those that have been occupied fewer times in the long-term. It would make sense that new males, and indeed all new individuals, are found closer to the edge considering that they might be expected to settle closer to their natal habitats, which are outside the main woodland (Wilkin et al. 2007a). However, by definition, all new birds are immigrants, but in their first year of breeding. Thus, our results suggest that the prediction that immigrants will occupy territories closer to the edge persists throughout lifespan when considering all individuals across the population, but this effect dissolves in males past the first breeding attempt. Related to discussion in the main text, this may be related to sex-differences in territory acquisition roles, where males initially acquire territories as the primary resource for obtaining a mate, whereas females assess and choose among males and their defended resources/territories (Krebs 1977; Greenwood 1980; Clarke et al. 1997). It might then be that immigrant males gain experience of the woods over time and move further from the edge past their first attempt to better quality territories that are less affected by negative edge effects (Wilkin et al. 2007a). This might also be mirrored in our results showing that new immigrant males are more likely to occupy territories which are less popular in the long-term, but this effect is not present when considering immigration status across lifespan.

### **3.2 Spatial structure in residency status**

We find similar results for spatial structure in immigration and settled status as with age structure, with a general pattern of slightly positive assortment, but still very weak. This might be indicative of the fact that despite some covariance in territory quality and these two traits, the association is not strong enough to generate overall spatial structure. Previous research in this population shows that immigration status is positively assorted across winter social behaviour both in terms of binary immigrant/resident status (Farine et al. 2015) and also arrival time into the woods (Farine and Sheldon 2015), but that this is mediated by spatial sorting rather than social decisions within

flocks. Seeing as residency is an important determinant of dominance in great tits (Sandell and Smith 1991), this likely represents a scenario where resident birds exclude immigrants from high-quality areas of winter foraging, or immigrants purposefully associate in areas of lower quality to reduce chances of future exclusion from breeding territories that are already well populated by residents (Farine and Sheldon 2015; Farine et al. 2015). However, the results of our analyses reveal that there is not strong evidence that immigrants are strongly partitioned into areas of lower quality.

#### 4 SUPPLEMENTARY FIGURES

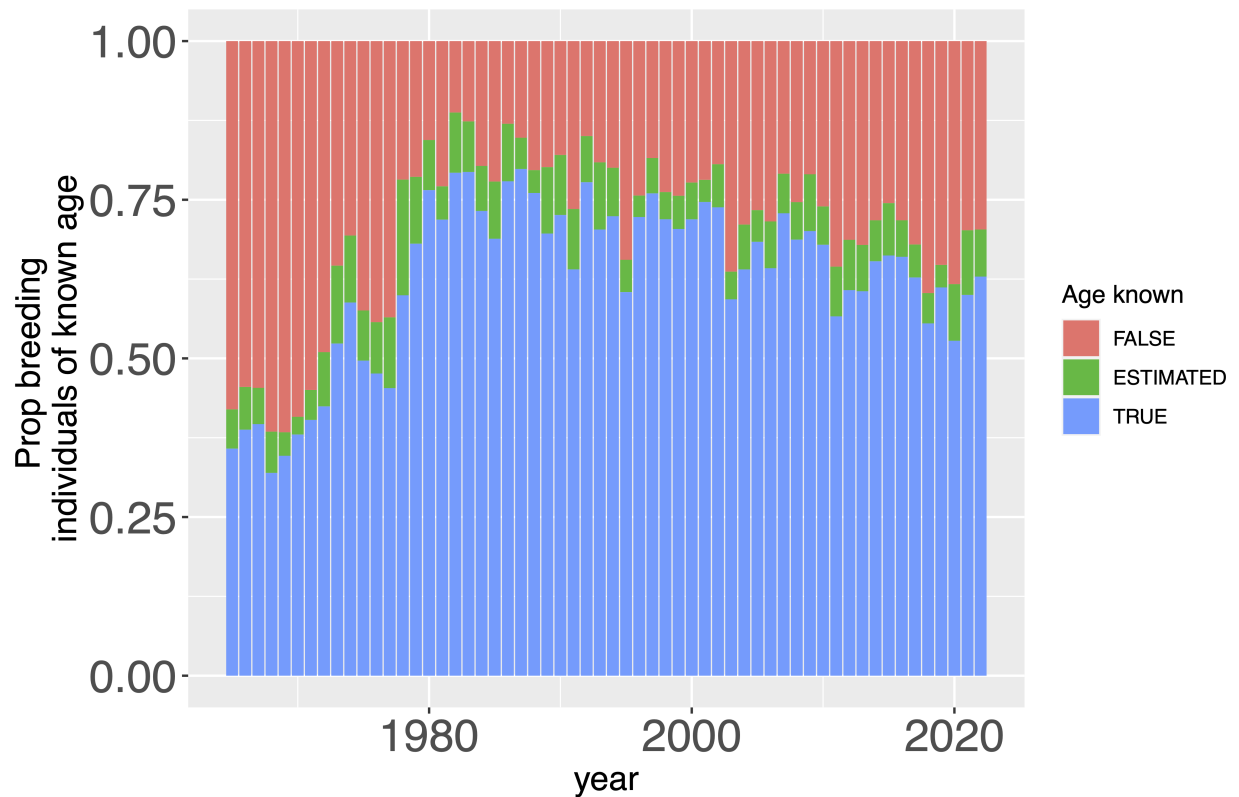


Fig. S1 - The annual proportion of breeding individuals where age is either unknown (individual not identified), estimated (individual first caught as an adult not in their first-year of life), or known (individual either first marked as a chick, or caught in their first-year of life) 1965–2022.

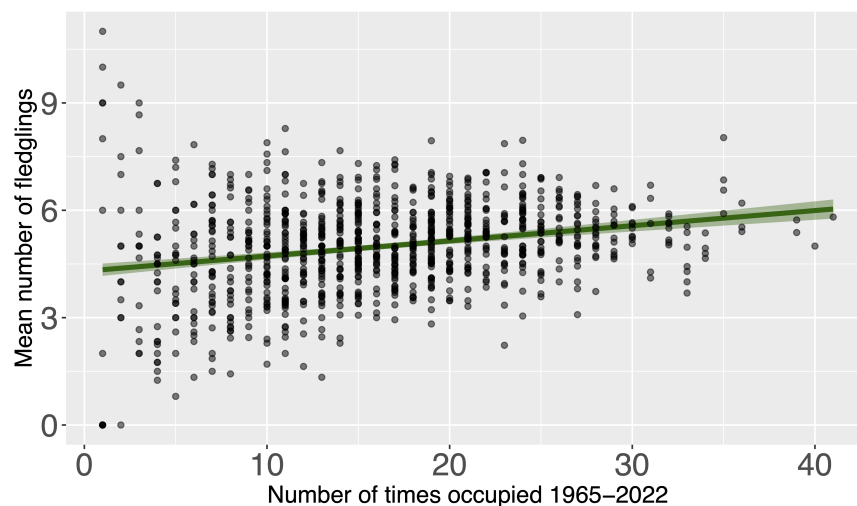


Fig. S2 - Relationship between the number of times a nest-box has been occupied 1965–2022 and the average number of chicks fledged from the box per breeding attempt. There is strong evidence for a weak to moderate relationship between these two variables (Spearman's correlation:  $r = 0.258$ ,  $p < 0.001$ ), therefore the frequency of occupation may provide a useful measure of quality.

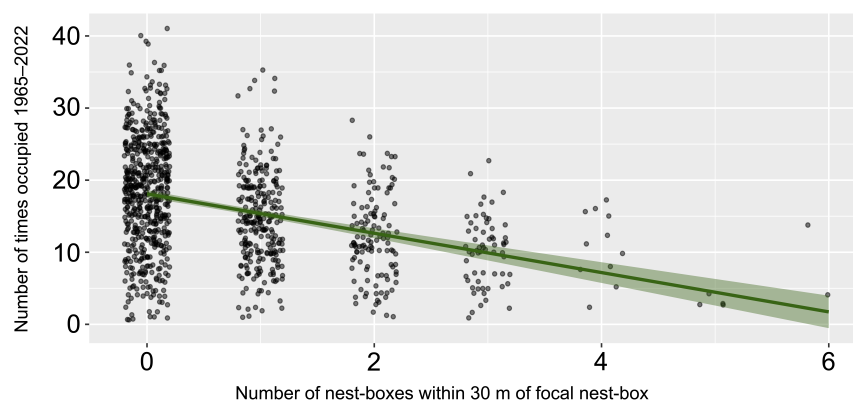


Fig. S3 - Relationship between the number of nest-boxes within a 30m radius of a focal box and the number of times it has been occupied 1965–2022. There is strong evidence for a weak to moderate negative relationship between these two variables (Spearman's correlation:  $r = -0.248$ ,  $p < 0.001$ ), therefore taking the residuals of a linear model between these two variables corrects for nest-box placing when calculating an index for long-term nest-box popularity. Points are jittered by 0.2 along the x-axis to avoid overplotting.

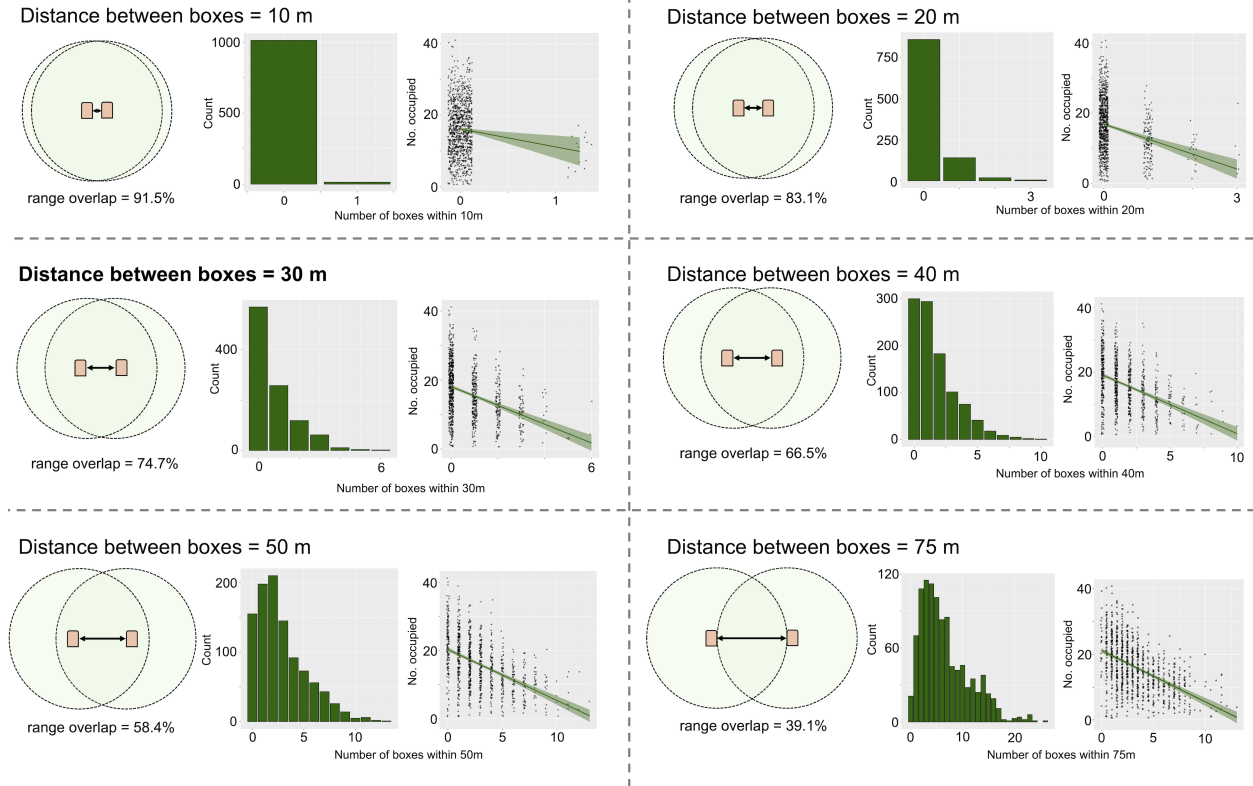


Fig. S4 - Overview of the different distances (10, 20, 30, 40, 50 and 75m) between a focal nest-box and neighbouring nest-boxes where, when placed at such densities, inter-annual switches between such boxes might result in largely similar territories regardless of which specific nest-box is occupied. For each focal distance: the Venn diagram displays the territorial range overlap (where territorial range is 75m); the histogram shows the number of nest-boxes across the study site which have a certain number of neighbouring boxes (on the x-axis) within the focal distance; and the plot on the right shows the relationship between the number of neighbouring boxes within the focal distance of a nest-box and the number of times said box has been occupied 1965–2022 (the green line indicates a linear regression between these two variables, the shading represents the 95% confidence intervals, and points are jittered by 0.1 along the x-axis to avoid overplotting).

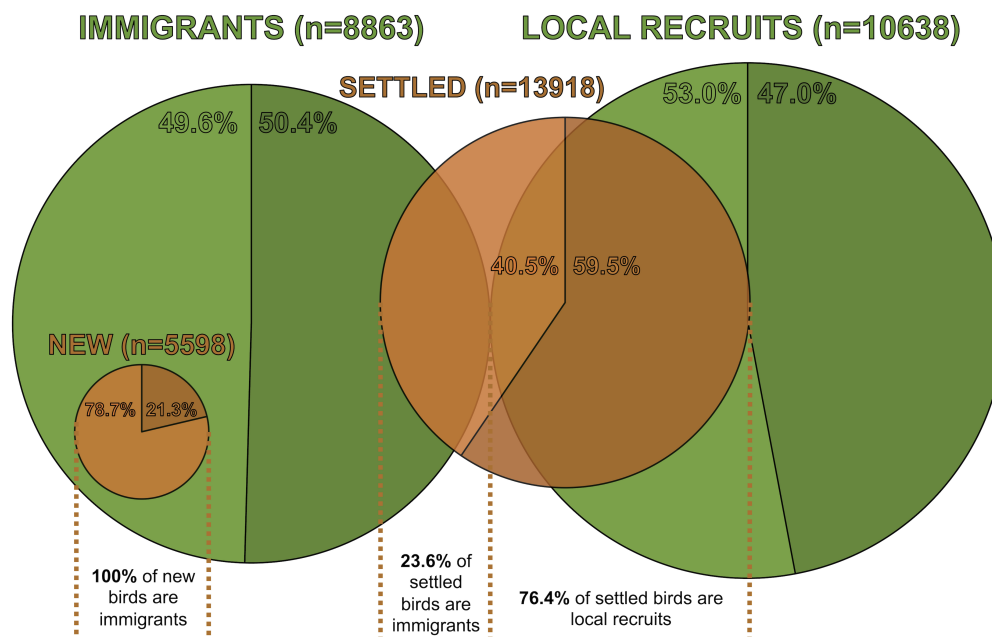


Fig. S5 - Synthesis of how different defined binary cohorts within the great tit population relate to one another. In all four pie charts, lighter colours represent the proportion of juveniles (yearlings), while the darker colours represent the proportion of adults (older than yearlings), with the proportion of each cohort fitting into these two age-classes expressed as a percentage in text. The green pie charts represent immigration status, where the two cohorts consist either of immigrants (hatched outside of Wytham Woods,  $n = 8863$ ) or local recruits (hatched within Wytham,  $n = 10638$ ). The two green pies' diameter is relative to the number of individuals found in these two cohorts. The orange pies represent settled status, where birds are either new (have arrived in Wytham within the last year,  $n = 5598$ ) or settled (either first-year local recruits that are breeding for the first time, or individuals breeding for at least the second time that have previously bred in Wytham,  $n = 13918$ ). The two orange pies' diameter is also relative to the number of individuals found in these two cohorts, but is not consistent with the scale used in the green pies. The overlap of orange with green pies represents the proportion of the respective settled status cohort that exists within the immigration status cohort (i.e. the entire orange pie representing new birds is within the green immigrants' pie as all new birds are immigrants, whereas there is only minimal overlap between the orange pie representing settled birds and the green immigrants pie as only 23.6% of settled birds originally immigrated into Wytham).

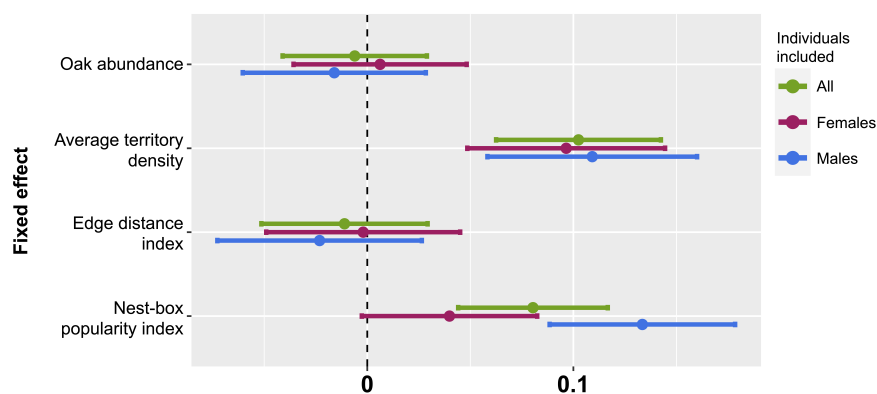


Fig. S6 - Point estimates of odds ratios obtained from generalised linear mixed-effects models. Each point corresponds to a specific level of the fixed effects (on the y-axis), and error bars denote 95% confidence intervals. The analysis examines the association between the four measures of territory quality on the odds of the breeding individual being a local recruit. Green points are from analysis assessing all individuals, purple are only females, and blue are only males.

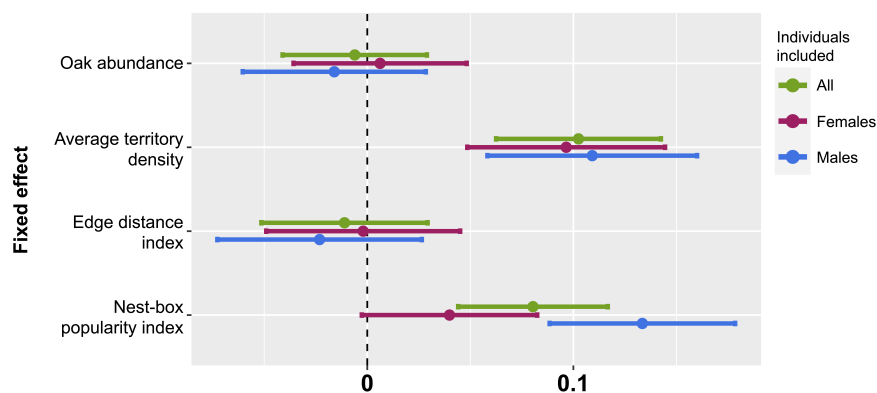


Fig. S7 - Point estimates of odds ratios obtained from generalised linear mixed-effects models. Each point corresponds to a specific level of the fixed effects (on the y-axis), and error bars denote 95% confidence intervals. The analysis examines the association between the four measures of territory quality on the odds of the breeding individual being a settled bird. Green points are from analysis assessing all individuals, purple are only females, and blue are only males.

## 5 SUPPLEMENTARY TABLES

Table S1 - Binomial generalised linear mixed-effects model structure. Each model was run with all individuals; only females; and only males.

| Response variables                                 | Fixed effects             | Random effects |
|----------------------------------------------------|---------------------------|----------------|
| Age (0/1 = juvenile/adult)                         | Oak abundance             | Individual ID  |
| Immigration status (0/1 = immigrant/local recruit) | Average territory density | Nest-box ID    |
| Settled status (0/1 = new/settled)                 | Edge distance index       | Year           |
|                                                    | Nest-box popularity index |                |

Table S2 - Binomial generalised linear mixed-effects model results for predictors of age, immigration status and settled status, for all individuals, females and males separately, with individual ID, nest-box ID, and year included as random effects. Cells with light green shading indicate significant test results where p value < 0.05.

| Response variable  | Individuals included | Fixed effect              | $\beta$ | Odds ratio | 95% confidence intervals | p value |
|--------------------|----------------------|---------------------------|---------|------------|--------------------------|---------|
| Age                | All                  | Oak abundance             | -0.006  | 0.994      | [0.960, 1.029]           | 0.734   |
|                    |                      | Average territory density | 0.102   | 1.108      | [1.065, 1.153]           | <0.001  |
|                    |                      | Edge distance index       | -0.011  | 0.989      | [0.950, 1.030]           | 0.591   |
|                    |                      | Nest-box popularity index | 0.080   | 1.084      | [1.045, 1.124]           | <0.001  |
|                    | Females              | Oak abundance             | 0.006   | 1.006      | [0.965, 1.049]           | 0.771   |
|                    |                      | Average territory density | 0.097   | 1.101      | [1.050, 1.155]           | <0.001  |
|                    |                      | Edge distance index       | -0.002  | 0.998      | [0.952, 1.046]           | 0.935   |
|                    |                      | Nest-box popularity index | 0.040   | 1.041      | [0.997, 1.086]           | 0.066   |
|                    | Males                | Oak abundance             | -0.016  | 0.984      | [0.941, 1.029]           | 0.480   |
|                    |                      | Average territory density | 0.109   | 1.115      | [1.060, 1.174]           | <0.001  |
|                    |                      | Edge distance index       | -0.023  | 0.977      | [0.930, 1.027]           | 0.361   |
|                    |                      | Nest-box popularity index | 0.133   | 1.143      | [1.092, 1.195]           | <0.001  |
| Immigration status | All                  | Oak abundance             | -0.218  | 0.804      | [0.687, 0.943]           | 0.007   |
|                    |                      | Average territory density | -0.413  | 0.662      | [0.567, 0.773]           | <0.001  |
|                    |                      | Edge distance index       | 0.443   | 1.558      | [1.295, 1.874]           | <0.001  |
|                    |                      | Nest-box popularity index | 0.014   | 1.014      | [0.899, 1.144]           | 0.817   |
|                    | Females              | Oak abundance             | -0.263  | 0.769      | [0.617, 0.959]           | 0.020   |
|                    |                      | Average territory density | -0.471  | 0.624      | [0.504, 0.773]           | <0.001  |
|                    |                      | Edge distance index       | 0.395   | 1.484      | [1.151, 1.913]           | 0.002   |
|                    |                      | Nest-box popularity index | -0.064  | 0.938      | [0.794, 1.108]           | 0.450   |
|                    | Males                | Oak abundance             | -0.008  | 0.992      | [0.796, 1.237]           | 0.945   |
|                    |                      | Average territory density | -0.050  | 0.951      | [0.748, 1.210]           | 0.683   |
|                    |                      | Edge distance index       | 0.093   | 1.098      | [0.851, 1.416]           | 0.472   |
|                    |                      | Nest-box popularity index | 0.045   | 1.046      | [0.846, 1.293]           | 0.680   |
| Settled status     | All                  | Oak abundance             | -0.024  | 0.976      | [0.943, 1.011]           | 0.179   |
|                    |                      | Average territory density | 0.008   | 1.008      | [0.968, 1.048]           | 0.711   |
|                    |                      | Edge distance index       | 0.045   | 1.047      | [1.005, 1.089]           | 0.026   |
|                    |                      | Nest-box popularity index | 0.027   | 1.028      | [0.992, 1.065]           | 0.132   |
|                    | Females              | Oak abundance             | -0.031  | 0.969      | [0.927, 1.013]           | 0.164   |
|                    |                      | Average territory density | -0.007  | 0.993      | [0.944, 1.044]           | 0.789   |
|                    |                      | Edge distance index       | 0.039   | 1.040      | [0.989, 1.093]           | 0.129   |
|                    |                      | Nest-box popularity index |         |            |                          |         |



| Response variable | Individuals included | Fixed effect              | $\beta$ | Odds ratio | 95% confidence intervals | p value |
|-------------------|----------------------|---------------------------|---------|------------|--------------------------|---------|
|                   | Males                | Nest-box popularity index | -0.012  | 0.988      | [0.945, 1.033]           | 0.600   |
|                   |                      | Oak abundance             | -0.016  | 0.985      | [0.939, 1.033]           | 0.521   |
|                   |                      | Average territory density | 0.022   | 1.022      | [0.968, 1.080]           | 0.425   |
|                   |                      | Edge distance index       | 0.053   | 1.055      | [0.999, 1.114]           | 0.054   |
|                   |                      | Nest-box popularity index | 0.072   | 1.075      | [1.024, 1.128]           | 0.003   |

Table S3 - Binomial generalised linear mixed-effects model results for predictors of age for all individuals. Nest-box popularity index was calculated by taking the residuals of a linear model between the number of boxes within 30m of a focal nest-box and the number of times occupied between 1965–2022 in the main text. Here, nest-box popularity index was calculated by alternatively taking the residuals of a linear model between the number of boxes within 10, 20, 40, 50 and 75m of a focal nest-box and the number of times occupied. Cells with light green shading indicate significant test results where p value < 0.05. Bold text face indicates the results for the 30m threshold used in the main text.

| Threshold distance between boxes | Fixed effect                     | $\beta$       | Odds ratio   | 95% confidence intervals | p value          |
|----------------------------------|----------------------------------|---------------|--------------|--------------------------|------------------|
| 10m                              | Oak abundance                    | -0.005        | 0.995        | [0.959, 1.030]           | 0.761            |
|                                  | Average territory density        | 0.107         | 1.113        | [1.072, 1.154]           | <0.001           |
|                                  | Edge distance index              | -0.011        | 0.989        | [0.949, 1.030]           | 0.594            |
|                                  | Nest-box popularity index        | 0.066         | 1.069        | [1.031, 1.106]           | <0.001           |
| 20m                              | Oak abundance                    | -0.006        | 0.994        | [0.959, 1.029]           | 0.738            |
|                                  | Average territory density        | 0.105         | 1.110        | [1.070, 1.151]           | <0.001           |
|                                  | Edge distance index              | -0.011        | 0.989        | [0.948, 1.029]           | 0.581            |
|                                  | Nest-box popularity index        | 0.071         | 1.073        | [1.036, 1.110]           | <0.001           |
| <b>30m</b>                       | <b>Oak abundance</b>             | <b>-0.006</b> | <b>0.994</b> | <b>[0.960, 1.029]</b>    | <b>0.734</b>     |
|                                  | <b>Average territory density</b> | <b>0.102</b>  | <b>1.108</b> | <b>[1.065, 1.153]</b>    | <b>&lt;0.001</b> |
|                                  | <b>Edge distance index</b>       | <b>-0.011</b> | <b>0.989</b> | <b>[0.950, 1.030]</b>    | <b>0.591</b>     |
|                                  | <b>Nest-box popularity index</b> | <b>0.080</b>  | <b>1.084</b> | <b>[1.045, 1.124]</b>    | <b>&lt;0.001</b> |
| 40m                              | Oak abundance                    | -0.007        | 0.993        | [0.958, 1.028]           | 0.685            |
|                                  | Average territory density        | 0.100         | 1.105        | [1.066, 1.145]           | <0.001           |
|                                  | Edge distance index              | -0.011        | 0.989        | [0.949, 1.030]           | 0.604            |
|                                  | Nest-box popularity index        | 0.083         | 1.086        | [1.050, 1.112]           | <0.001           |
| 50m                              | Oak abundance                    | -0.008        | 0.992        | [0.957, 1.027]           | 0.651            |
|                                  | Average territory density        | 0.097         | 1.102        | [1.062, 1.141]           | <0.001           |
|                                  | Edge distance index              | -0.010        | 0.990        | [0.950, 1.030]           | 0.635            |
|                                  | Nest-box popularity index        | 0.088         | 1.092        | [1.057, 1.128]           | <0.001           |
| 75m                              | Oak abundance                    | -0.009        | 0.991        | [0.956, 1.027]           | 0.632            |
|                                  | Average territory density        | 0.094         | 1.099        | [1.059, 1.138]           | <0.001           |
|                                  | Edge distance index              | -0.011        | 0.989        | [0.949, 1.030]           | 0.605            |
|                                  | Nest-box popularity index        | 0.077         | 1.080        | [1.044, 1.116]           | <0.001           |

Table S4 – Annual network  $r$  assortativity results and standard error intervals across breeding territories for: binary, discrete, and continuous age; immigration status, and settled status (assessed either across all individuals, just females, or just males); number of oaks within 75m of nest-box, mean territory density, edge distance index, and long-term occupancy rate of the nest-box; clutch size, number of chicks, number of fledglings, and binary success. Cells with light green shading indicate significant positive assortment where standard error does not overlap with 0, and light red shading indicates significant negative assortment.

| Year | Focal trait type  | Focal trait               | Individuals | $r$     | SE intervals     |
|------|-------------------|---------------------------|-------------|---------|------------------|
| 1978 | Age               | Binary age                | All         | -0.0247 | [-0.056, 0.007]  |
|      |                   |                           | Females     | 0.0159  | [-0.043, 0.075]  |
|      |                   |                           | Males       | -0.0736 | [-0.142, -0.005] |
|      |                   | Discrete age              | All         | -0.0230 | [-0.045, -0.001] |
|      |                   |                           | Females     | 0.0268  | [-0.015, 0.068]  |
|      |                   |                           | Males       | -0.0478 | [-0.094, -0.001] |
|      |                   | Continuous age            | All         | -0.0347 | [-0.062, -0.007] |
|      |                   |                           | Females     | 0.0441  | [-0.008, 0.096]  |
|      |                   |                           | Males       | -0.1502 | [-0.202, -0.098] |
|      | Residency status  | Immigration status        | All         | -0.0230 | [-0.054, 0.008]  |
|      |                   |                           | Females     | -0.1012 | [-0.160, -0.042] |
|      |                   |                           | Males       | 0.0622  | [-0.006, 0.130]  |
|      |                   | Settled status            | All         | -0.0289 | [-0.059, 0.001]  |
|      |                   |                           | Females     | -0.0922 | [-0.151, -0.034] |
|      |                   |                           | Males       | -0.0189 | [-0.090, 0.052]  |
|      | Territory quality | Oak abundance             | NA          | 0.7783  | [0.757, 0.799]   |
|      |                   | Average territory density | NA          | 0.6523  | [0.626, 0.678]   |
|      |                   | Edge distance index       | NA          | 0.7709  | [0.756, 0.786]   |
|      |                   | Nest-box popularity index | NA          | 0.3226  | [0.287, 0.359]   |
|      | Reproductive      | Clutch size               | NA          | -0.0072 | [-0.049, 0.035]  |
|      |                   | Number of chicks          | NA          | 0.0308  | [-0.019, 0.080]  |
|      |                   | Number of fledglings      | NA          | 0.0206  | [-0.027, 0.068]  |
|      |                   | Binary success            | NA          | -0.0604 | [-0.091, -0.030] |
| 1979 | Age               | Binary age                | All         | 0.0513  | [0.020, 0.083]   |
|      |                   |                           | Females     | -0.0940 | [-0.152, -0.036] |
|      |                   |                           | Males       | -0.0085 | [-0.073, 0.056]  |
|      |                   | Discrete age              | All         | 0.0343  | [0.013, 0.055]   |
|      |                   |                           | Females     | -0.0902 | [-0.121, -0.059] |
|      |                   |                           | Males       | -0.0234 | [-0.069, 0.022]  |
|      |                   | Continuous age            | All         | 0.0471  | [0.016, 0.078]   |
|      |                   |                           | Females     | -0.0219 | [-0.073, 0.029]  |
|      |                   |                           | Males       | 0.0548  | [-0.016, 0.125]  |
|      | Residency status  | Immigration status        | All         | -0.0005 | [-0.033, 0.032]  |
|      |                   |                           | Females     | 0.0196  | [-0.041, 0.081]  |
|      |                   |                           | Males       | 0.0536  | [-0.011, 0.118]  |
|      |                   | Settled status            | All         | -0.0549 | [-0.087, -0.023] |
|      |                   |                           | Females     | -0.0068 | [-0.065, 0.052]  |
|      |                   |                           | Males       | 0.0686  | [-0.001, 0.138]  |
|      | Territory quality | Oak abundance             | NA          | 0.7871  | [0.760, 0.814]   |
|      |                   | Average territory density | NA          | 0.7081  | [0.681, 0.736]   |

| Year | Focal trait type  | Focal trait               | Individuals | <i>r</i> | SE intervals     |
|------|-------------------|---------------------------|-------------|----------|------------------|
| 1980 | Reproductive      | Edge distance index       | NA          | 0.7163   | [0.698, 0.735]   |
|      |                   | Nest-box popularity index | NA          | 0.2655   | [0.227, 0.304]   |
|      |                   | Clutch size               | NA          | 0.0938   | [0.052, 0.135]   |
|      |                   | Number of chicks          | NA          | -0.0150  | [-0.049, 0.019]  |
|      |                   | Number of fledglings      | NA          | -0.0351  | [-0.078, 0.008]  |
|      |                   | Binary success            | NA          | -0.0573  | [-0.094, -0.020] |
|      | Age               | Binary age                | All         | 0.0429   | [0.006, 0.08]    |
|      |                   |                           | Females     | 0.0156   | [-0.050, 0.081]  |
|      |                   |                           | Males       | 0.0706   | [-0.010, 0.152]  |
|      |                   | Discrete age              | All         | 0.0434   | [0.018, 0.069]   |
|      |                   |                           | Females     | -0.0237  | [-0.067, 0.020]  |
|      |                   |                           | Males       | 0.0878   | [0.025, 0.151]   |
|      |                   | Continuous age            | All         | -0.0027  | [-0.035, 0.029]  |
|      |                   |                           | Females     | -0.0051  | [-0.056, 0.046]  |
|      |                   |                           | Males       | -0.0076  | [-0.081, 0.066]  |
|      | Residency status  | Immigration status        | All         | 0.0349   | [-0.001, 0.070]  |
|      |                   |                           | Females     | 0.0153   | [-0.049, 0.080]  |
|      |                   |                           | Males       | -0.0820  | [-0.161, -0.003] |
|      |                   | Settled status            | All         | 0.0104   | [-0.026, 0.047]  |
|      |                   |                           | Females     | 0.0762   | [0.011, 0.141]   |
|      |                   |                           | Males       | -0.1042  | [-0.183, -0.025] |
|      | Territory quality | Oak abundance             | NA          | 0.6970   | [0.668, 0.726]   |
|      |                   | Average territory density | NA          | 0.4360   | [0.399, 0.473]   |
|      |                   | Edge distance index       | NA          | 0.7193   | [0.698, 0.740]   |
|      |                   | Nest-box popularity index | NA          | 0.2980   | [0.255, 0.341]   |
| 1981 | Reproductive      | Clutch size               | NA          | -0.0180  | [-0.055, 0.019]  |
|      |                   | Number of chicks          | NA          | 0.2434   | [0.193, 0.294]   |
|      |                   | Number of fledglings      | NA          | 0.2094   | [0.159, 0.260]   |
|      |                   | Binary success            | NA          | 0.2822   | [0.231, 0.333]   |
|      | Age               | Binary age                | All         | -0.0304  | [-0.056, -0.005] |
|      |                   |                           | Females     | -0.0479  | [-0.096, 0.000]  |
|      |                   |                           | Males       | 0.0541   | [-0.005, 0.113]  |
|      |                   | Discrete age              | All         | -0.0160  | [-0.034, 0.002]  |
|      |                   |                           | Females     | -0.0094  | [-0.046, 0.027]  |
|      |                   |                           | Males       | 0.0847   | [0.036, 0.133]   |
|      |                   | Continuous age            | All         | -0.0279  | [-0.055, -0.001] |
|      |                   |                           | Females     | -0.0094  | [-0.065, 0.046]  |
|      |                   |                           | Males       | 0.1165   | [0.039, 0.194]   |
|      | Residency status  | Immigration status        | All         | 0.0195   | [-0.006, 0.045]  |
|      |                   |                           | Females     | 0.1335   | [0.086, 0.180]   |
|      |                   |                           | Males       | -0.0056  | [-0.062, 0.050]  |
|      |                   | Settled status            | All         | -0.0390  | [-0.064, -0.014] |
|      |                   |                           | Females     | 0.0479   | [0.000, 0.096]   |
|      |                   |                           | Males       | 0.0434   | [-0.018, 0.104]  |
|      | Territory quality | Oak abundance             | NA          | 0.7781   | [0.763, 0.794]   |
|      |                   | Average territory density | NA          | 0.6394   | [0.610, 0.669]   |
|      |                   | Edge distance index       | NA          | 0.8526   | [0.844, 0.861]   |

| Year | Focal trait type  | Focal trait               | Individuals | <i>r</i> | SE intervals     |
|------|-------------------|---------------------------|-------------|----------|------------------|
| 1982 | Reproductive      | Nest-box popularity index | NA          | 0.2931   | [0.265, 0.321]   |
|      |                   | Clutch size               | NA          | 0.0447   | [0.014, 0.075]   |
|      |                   | Number of chicks          | NA          | 0.0534   | [0.022, 0.085]   |
|      |                   | Number of fledglings      | NA          | 0.0569   | [0.026, 0.088]   |
|      | Age               | Binary success            | NA          | 0.0728   | [0.041, 0.105]   |
|      |                   | Binary age                | All         | 0.0415   | [0.017, 0.066]   |
|      |                   |                           | Females     | 0.0903   | [0.046, 0.135]   |
|      |                   |                           | Males       | 0.0503   | [0.001, 0.100]   |
|      |                   | Discrete age              | All         | 0.0274   | [0.012, 0.043]   |
|      |                   |                           | Females     | 0.0487   | [0.019, 0.079]   |
|      |                   |                           | Males       | 0.0489   | [0.014, 0.084]   |
|      |                   | Continuous age            | All         | 0.0016   | [-0.019, 0.023]  |
|      |                   |                           | Females     | 0.0290   | [-0.008, 0.066]  |
|      |                   |                           | Males       | 0.0622   | [0.014, 0.111]   |
|      | Residency status  | Immigration status        | All         | -0.0301  | [-0.054, -0.006] |
|      |                   |                           | Females     | 0.1412   | [0.097, 0.186]   |
|      |                   |                           | Males       | -0.0201  | [-0.071, 0.030]  |
|      |                   | Settled status            | All         | 0.0071   | [-0.017, 0.031]  |
|      |                   |                           | Females     | 0.1559   | [0.108, 0.204]   |
|      |                   |                           | Males       | -0.0460  | [-0.092, -0.001] |
|      | Territory quality | Oak abundance             | NA          | 0.7354   | [0.710, 0.761]   |
|      |                   | Average territory density | NA          | 0.6014   | [0.570, 0.633]   |
|      |                   | Edge distance index       | NA          | 0.7634   | [0.748, 0.779]   |
|      |                   | Nest-box popularity index | NA          | 0.2106   | [0.174, 0.247]   |
| 1983 | Reproductive      | Clutch size               | NA          | 0.1464   | [0.112, 0.181]   |
|      |                   | Number of chicks          | NA          | 0.0012   | [-0.038, 0.040]  |
|      |                   | Number of fledglings      | NA          | -0.0224  | [-0.059, 0.014]  |
|      |                   | Binary success            | NA          | -0.0580  | [-0.092, -0.024] |
|      | Age               | Binary age                | All         | 0.0911   | [0.073, 0.109]   |
|      |                   |                           | Females     | -0.0316  | [-0.065, 0.002]  |
|      |                   |                           | Males       | -0.0333  | [-0.070, 0.004]  |
|      |                   | Discrete age              | All         | 0.0618   | [0.049, 0.074]   |
|      |                   |                           | Females     | -0.0070  | [-0.031, 0.017]  |
|      |                   |                           | Males       | -0.0337  | [-0.057, -0.011] |
|      |                   | Continuous age            | All         | 0.0759   | [0.057, 0.094]   |
|      |                   |                           | Females     | -0.0219  | [-0.052, 0.008]  |
|      |                   |                           | Males       | -0.0228  | [-0.054, 0.008]  |
|      | Residency status  | Immigration status        | All         | -0.0224  | [-0.040, -0.004] |
|      |                   |                           | Females     | -0.0069  | [-0.040, 0.027]  |
|      |                   |                           | Males       | -0.0383  | [-0.077, 0.000]  |
|      |                   | Settled status            | All         | 0.0238   | [0.006, 0.042]   |
|      |                   |                           | Females     | 0.0075   | [-0.026, 0.041]  |
|      |                   |                           | Males       | -0.0766  | [-0.115, -0.038] |
|      | Territory quality | Oak abundance             | NA          | 0.7889   | [0.776, 0.802]   |
|      |                   | Average territory density | NA          | 0.5873   | [0.556, 0.619]   |
|      |                   | Edge distance index       | NA          | 0.8664   | [0.860, 0.873]   |
|      |                   | Nest-box popularity index | NA          | 0.2899   | [0.266, 0.314]   |

| Year | Focal trait type  | Focal trait               | Individuals | $r$     | SE intervals     |
|------|-------------------|---------------------------|-------------|---------|------------------|
| 1984 | Reproductive      | Clutch size               | NA          | 0.1671  | [0.140, 0.194]   |
|      |                   | Number of chicks          | NA          | 0.0931  | [0.065, 0.121]   |
|      |                   | Number of fledglings      | NA          | 0.1219  | [0.092, 0.152]   |
|      |                   | Binary success            | NA          | 0.1020  | [0.068, 0.136]   |
|      | Age               | Binary age                | All         | 0.0265  | [-0.005, 0.058]  |
|      |                   |                           | Females     | -0.0490 | [-0.104, 0.006]  |
|      |                   |                           | Males       | -0.0030 | [-0.076, 0.070]  |
|      |                   | Discrete age              | All         | 0.0111  | [-0.009, 0.031]  |
|      |                   |                           | Females     | 0.0006  | [-0.040, 0.041]  |
|      |                   |                           | Males       | 0.0161  | [-0.035, 0.067]  |
|      |                   | Continuous age            | All         | 0.0156  | [-0.015, 0.046]  |
|      |                   |                           | Females     | -0.0978 | [-0.140, -0.056] |
|      |                   |                           | Males       | 0.0756  | [0.000, 0.151]   |
|      | Residency status  | Immigration status        | All         | -0.0177 | [-0.050, 0.014]  |
|      |                   |                           | Females     | 0.0325  | [-0.023, 0.088]  |
|      |                   |                           | Males       | -0.1831 | [-0.244, -0.122] |
|      |                   | Settled status            | All         | -0.0445 | [-0.077, -0.012] |
|      |                   |                           | Females     | -0.0736 | [-0.123, -0.024] |
|      |                   |                           | Males       | -0.1622 | [-0.202, -0.122] |
|      | Territory quality | Oak abundance             | NA          | 0.7746  | [0.759, 0.790]   |
|      |                   | Average territory density | NA          | 0.6586  | [0.637, 0.680]   |
|      |                   | Edge distance index       | NA          | 0.7714  | [0.758, 0.785]   |
|      |                   | Nest-box popularity index | NA          | 0.1574  | [0.121, 0.193]   |
| 1985 | Reproductive      | Clutch size               | NA          | 0.1128  | [0.078, 0.147]   |
|      |                   | Number of chicks          | NA          | 0.1639  | [0.130, 0.198]   |
|      |                   | Number of fledglings      | NA          | 0.1327  | [0.097, 0.168]   |
|      |                   | Binary success            | NA          | 0.1139  | [0.077, 0.151]   |
|      | Age               | Binary age                | All         | 0.0081  | [-0.021, 0.037]  |
|      |                   |                           | Females     | 0.0187  | [-0.038, 0.075]  |
|      |                   |                           | Males       | -0.0562 | [-0.114, 0.002]  |
|      |                   | Discrete age              | All         | -0.0063 | [-0.026, 0.013]  |
|      |                   |                           | Females     | 0.0057  | [-0.036, 0.048]  |
|      |                   |                           | Males       | -0.0818 | [-0.114, -0.049] |
|      |                   | Continuous age            | All         | -0.0191 | [-0.046, 0.008]  |
|      |                   |                           | Females     | 0.0049  | [-0.048, 0.058]  |
|      |                   |                           | Males       | -0.0406 | [-0.088, 0.007]  |
|      | Residency status  | Immigration status        | All         | 0.0103  | [-0.020, 0.040]  |
|      |                   |                           | Females     | 0.0745  | [0.016, 0.133]   |
|      |                   |                           | Males       | -0.1155 | [-0.172, -0.059] |
|      |                   | Settled status            | All         | 0.0292  | [-0.001, 0.060]  |
|      |                   |                           | Females     | 0.1209  | [0.062, 0.180]   |
|      |                   |                           | Males       | -0.0715 | [-0.126, -0.017] |
|      | Territory quality | Oak abundance             | NA          | 0.6730  | [0.648, 0.698]   |
|      |                   | Average territory density | NA          | 0.7026  | [0.681, 0.724]   |
|      |                   | Edge distance index       | NA          | 0.7621  | [0.748, 0.777]   |
|      |                   | Nest-box popularity index | NA          | 0.2792  | [0.242, 0.317]   |
|      | Reproductive      | Clutch size               | NA          | 0.0420  | [0.003, 0.081]   |

| Year | Focal trait type  | Focal trait               | Individuals | <i>r</i> | SE intervals     |
|------|-------------------|---------------------------|-------------|----------|------------------|
| 1986 | Age               | Number of chicks          | NA          | 0.0453   | [0.005, 0.086]   |
|      |                   | Number of fledglings      | NA          | -0.0321  | [-0.068, 0.004]  |
|      |                   | Binary success            | NA          | -0.0506  | [-0.085, -0.017] |
|      |                   | Binary age                | All         | 0.0590   | [0.034, 0.083]   |
|      |                   |                           | Females     | 0.0627   | [0.012, 0.113]   |
|      |                   |                           | Males       | 0.0949   | [0.045, 0.144]   |
|      |                   | Discrete age              | All         | 0.0440   | [0.028, 0.060]   |
|      |                   |                           | Females     | 0.0403   | [0.007, 0.074]   |
|      |                   |                           | Males       | 0.0644   | [0.032, 0.097]   |
|      |                   | Continuous age            | All         | 0.0143   | [-0.010, 0.038]  |
|      |                   |                           | Females     | 0.0883   | [0.032, 0.145]   |
|      |                   |                           | Males       | -0.0227  | [-0.065, 0.020]  |
|      | Residency status  | Immigration status        | All         | 0.0669   | [0.043, 0.091]   |
|      |                   |                           | Females     | 0.0504   | [0.002, 0.099]   |
|      |                   |                           | Males       | 0.0364   | [-0.013, 0.086]  |
|      |                   | Settled status            | All         | 0.0144   | [-0.009, 0.038]  |
|      |                   |                           | Females     | 0.1035   | [0.055, 0.152]   |
|      |                   |                           | Males       | -0.0920  | [-0.139, -0.045] |
|      | Territory quality | Oak abundance             | NA          | 0.7713   | [0.750, 0.793]   |
|      |                   | Average territory density | NA          | 0.6548   | [0.625, 0.685]   |
|      |                   | Edge distance index       | NA          | 0.8038   | [0.791, 0.817]   |
|      |                   | Nest-box popularity index | NA          | 0.3357   | [0.304, 0.368]   |
|      | Reproductive      | Clutch size               | NA          | 0.0836   | [0.054, 0.113]   |
|      |                   | Number of chicks          | NA          | 0.0646   | [0.032, 0.097]   |
|      |                   | Number of fledglings      | NA          | 0.0938   | [0.060, 0.128]   |
|      |                   | Binary success            | NA          | 0.0297   | [-0.008, 0.068]  |
|      |                   | Binary age                | All         | 0.0247   | [0.000, 0.049]   |
|      |                   |                           | Females     | 0.0016   | [-0.042, 0.045]  |
|      |                   |                           | Males       | -0.1140  | [-0.171, -0.057] |
| 1987 | Age               | Discrete age              | All         | 0.0416   | [0.023, 0.060]   |
|      |                   |                           | Females     | 0.0049   | [-0.026, 0.036]  |
|      |                   |                           | Males       | -0.0959  | [-0.134, -0.058] |
|      |                   | Continuous age            | All         | 0.0798   | [0.038, 0.121]   |
|      |                   |                           | Females     | -0.0191  | [-0.063, 0.025]  |
|      |                   |                           | Males       | -0.1377  | [-0.176, -0.099] |
|      | Residency status  | Immigration status        | All         | 0.0282   | [0.004, 0.053]   |
|      |                   |                           | Females     | 0.1845   | [0.141, 0.228]   |
|      |                   |                           | Males       | -0.0516  | [-0.108, 0.005]  |
|      |                   | Settled status            | All         | -0.0057  | [-0.029, 0.018]  |
|      |                   |                           | Females     | 0.0547   | [-0.005, 0.114]  |
|      |                   |                           | Males       | -0.1820  | [-0.218, -0.146] |
|      | Territory quality | Oak abundance             | NA          | 0.7816   | [0.764, 0.799]   |
|      |                   | Average territory density | NA          | 0.7054   | [0.689, 0.722]   |
|      |                   | Edge distance index       | NA          | 0.8135   | [0.802, 0.825]   |
|      |                   | Nest-box popularity index | NA          | 0.2417   | [0.211, 0.272]   |
|      | Reproductive      | Clutch size               | NA          | 0.0751   | [0.044, 0.106]   |
|      |                   | Number of chicks          | NA          | 0.1020   | [0.055, 0.149]   |

| Year | Focal trait type  | Focal trait               | Individuals | <i>r</i> | SE intervals     |
|------|-------------------|---------------------------|-------------|----------|------------------|
| 1988 | Age               | Number of fledglings      | NA          | 0.0169   | [-0.019, 0.053]  |
|      |                   | Binary success            | NA          | 0.0267   | [-0.013, 0.067]  |
|      |                   | Binary age                | All         | 0.0285   | [0.005, 0.052]   |
|      |                   |                           | Females     | 0.0388   | [-0.004, 0.082]  |
|      |                   |                           | Males       | -0.1148  | [-0.162, -0.067] |
|      |                   | Discrete age              | All         | 0.0268   | [0.011, 0.042]   |
|      |                   |                           | Females     | 0.0115   | [-0.015, 0.038]  |
|      |                   |                           | Males       | -0.0927  | [-0.120, -0.066] |
|      |                   | Continuous age            | All         | 0.0206   | [-0.008, 0.049]  |
|      |                   |                           | Females     | -0.0366  | [-0.075, 0.001]  |
|      |                   |                           | Males       | -0.0747  | [-0.116, -0.033] |
|      | Residency status  | Immigration status        | All         | 0.0266   | [0.003, 0.050]   |
|      |                   |                           | Females     | 0.0409   | [-0.002, 0.084]  |
|      |                   |                           | Males       | 0.0632   | [0.010, 0.116]   |
|      |                   | Settled status            | All         | -0.0271  | [-0.051, -0.004] |
|      |                   |                           | Females     | -0.0620  | [-0.103, -0.021] |
|      |                   |                           | Males       | -0.0178  | [-0.068, 0.033]  |
|      | Territory quality | Oak abundance             | NA          | 0.8245   | [0.811, 0.838]   |
|      |                   | Average territory density | NA          | 0.5981   | [0.567, 0.629]   |
|      |                   | Edge distance index       | NA          | 0.8207   | [0.810, 0.832]   |
|      |                   | Nest-box popularity index | NA          | 0.3522   | [0.328, 0.377]   |
|      | Reproductive      | Clutch size               | NA          | 0.0823   | [0.048, 0.117]   |
|      |                   | Number of chicks          | NA          | 0.0505   | [0.022, 0.08]    |
|      |                   | Number of fledglings      | NA          | 0.1359   | [0.106, 0.166]   |
|      |                   | Binary success            | NA          | 0.0599   | [0.026, 0.094]   |
| 1989 | Age               | Binary age                | All         | -0.0126  | [-0.039, 0.013]  |
|      |                   |                           | Females     | 0.0459   | [0.002, 0.089]   |
|      |                   |                           | Males       | 0.1221   | [0.064, 0.180]   |
|      |                   | Discrete age              | All         | -0.0068  | [-0.023, 0.010]  |
|      |                   |                           | Females     | 0.0587   | [0.028, 0.089]   |
|      |                   |                           | Males       | 0.0456   | [0.011, 0.080]   |
|      |                   | Continuous age            | All         | -0.0223  | [-0.045, 0.000]  |
|      |                   |                           | Females     | -0.0163  | [-0.046, 0.013]  |
|      |                   |                           | Males       | 0.1862   | [0.141, 0.231]   |
|      | Residency status  | Immigration status        | All         | 0.0150   | [-0.011, 0.041]  |
|      |                   |                           | Females     | 0.1168   | [0.072, 0.161]   |
|      |                   |                           | Males       | -0.1679  | [-0.224, -0.111] |
|      |                   | Settled status            | All         | 0.0076   | [-0.019, 0.034]  |
|      |                   |                           | Females     | 0.0677   | [0.024, 0.112]   |
|      |                   |                           | Males       | -0.0808  | [-0.134, -0.027] |
|      | Territory quality | Oak abundance             | NA          | 0.7541   | [0.729, 0.780]   |
|      |                   | Average territory density | NA          | 0.6372   | [0.618, 0.657]   |
|      |                   | Edge distance index       | NA          | 0.8271   | [0.816, 0.838]   |
|      |                   | Nest-box popularity index | NA          | 0.2444   | [0.214, 0.275]   |
|      | Reproductive      | Clutch size               | NA          | 0.0916   | [0.060, 0.123]   |
|      |                   | Number of chicks          | NA          | 0.1124   | [0.073, 0.152]   |
|      |                   | Number of fledglings      | NA          | 0.0049   | [-0.031, 0.041]  |

| Year | Focal trait type  | Focal trait               | Individuals | <i>r</i> | SE intervals     |
|------|-------------------|---------------------------|-------------|----------|------------------|
| 1990 | Age               | Binary success            | NA          | 0.0370   | [-0.001, 0.075]  |
|      |                   | Binary age                | All         | 0.0018   | [-0.026, 0.029]  |
|      |                   |                           | Females     | 0.0114   | [-0.044, 0.067]  |
|      |                   |                           | Males       | 0.0256   | [-0.029, 0.080]  |
|      |                   | Discrete age              | All         | 0.0140   | [-0.003, 0.031]  |
|      |                   |                           | Females     | 0.0465   | [0.010, 0.083]   |
|      |                   |                           | Males       | -0.0128  | [-0.044, 0.018]  |
|      |                   | Continuous age            | All         | 0.0020   | [-0.027, 0.031]  |
|      |                   |                           | Females     | 0.0577   | [0.007, 0.109]   |
|      |                   |                           | Males       | 0.0272   | [-0.035, 0.090]  |
|      | Residency status  | Immigration status        | All         | -0.0206  | [-0.048, 0.007]  |
|      |                   |                           | Females     | -0.0686  | [-0.125, -0.012] |
|      |                   |                           | Males       | 0.1045   | [0.050, 0.159]   |
|      |                   | Settled status            | All         | -0.0037  | [-0.032, 0.024]  |
|      |                   |                           | Females     | -0.0957  | [-0.152, -0.039] |
|      |                   |                           | Males       | 0.1242   | [0.061, 0.187]   |
|      | Territory quality | Oak abundance             | NA          | 0.8162   | [0.796, 0.836]   |
|      |                   | Average territory density | NA          | 0.6706   | [0.632, 0.709]   |
|      |                   | Edge distance index       | NA          | 0.7964   | [0.783, 0.810]   |
|      |                   | Nest-box popularity index | NA          | 0.4233   | [0.392, 0.454]   |
|      | Reproductive      | Clutch size               | NA          | 0.0399   | [0.007, 0.073]   |
|      |                   | Number of chicks          | NA          | 0.0502   | [0.013, 0.087]   |
|      |                   | Number of fledglings      | NA          | 0.0478   | [0.009, 0.087]   |
|      |                   | Binary success            | NA          | 0.0606   | [0.020, 0.101]   |
| 1991 | Age               | Binary age                | All         | 0.0024   | [-0.043, 0.047]  |
|      |                   |                           | Females     | 0.0080   | [-0.074, 0.09]   |
|      |                   |                           | Males       | 0.0412   | [-0.064, 0.147]  |
|      |                   | Discrete age              | All         | 0.0091   | [-0.017, 0.035]  |
|      |                   |                           | Females     | -0.0159  | [-0.063, 0.032]  |
|      |                   |                           | Males       | 0.0022   | [-0.055, 0.059]  |
|      |                   | Continuous age            | All         | 0.0608   | [0.016, 0.106]   |
|      |                   |                           | Females     | 0.0423   | [-0.044, 0.128]  |
|      |                   |                           | Males       | -0.0065  | [-0.104, 0.091]  |
|      | Residency status  | Immigration status        | All         | -0.0403  | [-0.086, 0.005]  |
|      |                   |                           | Females     | 0.2058   | [0.119, 0.292]   |
|      |                   |                           | Males       | 0.0929   | [-0.004, 0.189]  |
|      |                   | Settled status            | All         | 0.0717   | [0.015, 0.129]   |
|      |                   |                           | Females     | 0.1599   | [0.057, 0.263]   |
|      |                   |                           | Males       | 0.2198   | [0.095, 0.344]   |
|      | Territory quality | Oak abundance             | NA          | 0.6776   | [0.643, 0.713]   |
|      |                   | Average territory density | NA          | 0.5689   | [0.523, 0.615]   |
|      |                   | Edge distance index       | NA          | 0.5780   | [0.540, 0.616]   |
|      |                   | Nest-box popularity index | NA          | 0.1270   | [0.071, 0.183]   |
|      | Reproductive      | Clutch size               | NA          | -0.0391  | [-0.094, 0.016]  |
|      |                   | Number of chicks          | NA          | 0.1191   | [0.034, 0.205]   |
|      |                   | Number of fledglings      | NA          | 0.1026   | [0.041, 0.164]   |
|      |                   | Binary success            | NA          | 0.2290   | [0.165, 0.293]   |



| Year | Focal trait type  | Focal trait               | Individuals | <i>r</i> | SE intervals     |
|------|-------------------|---------------------------|-------------|----------|------------------|
| 1992 | Age               | Binary age                | All         | -0.0082  | [-0.035, 0.019]  |
|      |                   |                           | Females     | -0.0394  | [-0.091, 0.012]  |
|      |                   |                           | Males       | -0.0893  | [-0.145, -0.034] |
|      |                   | Discrete age              | All         | 0.0033   | [-0.015, 0.021]  |
|      |                   |                           | Females     | -0.0020  | [-0.045, 0.041]  |
|      |                   |                           | Males       | -0.0520  | [-0.085, -0.019] |
|      |                   | Continuous age            | All         | -0.0118  | [-0.038, 0.015]  |
|      |                   |                           | Females     | 0.0779   | [0.017, 0.138]   |
|      |                   |                           | Males       | -0.0517  | [-0.102, -0.001] |
|      | Residency status  | Immigration status        | All         | -0.0302  | [-0.057, -0.003] |
|      |                   |                           | Females     | -0.0617  | [-0.114, -0.009] |
|      |                   |                           | Males       | -0.0048  | [-0.059, 0.050]  |
|      |                   | Settled status            | All         | -0.0405  | [-0.067, -0.014] |
|      |                   |                           | Females     | -0.0259  | [-0.079, 0.027]  |
|      |                   |                           | Males       | -0.0329  | [-0.086, 0.020]  |
|      | Territory quality | Oak abundance             | NA          | 0.6877   | [0.663, 0.712]   |
|      |                   | Average territory density | NA          | 0.5633   | [0.538, 0.589]   |
|      |                   | Edge distance index       | NA          | 0.7447   | [0.729, 0.760]   |
|      |                   | Nest-box popularity index | NA          | 0.2762   | [0.242, 0.311]   |
|      | Reproductive      | Clutch size               | NA          | -0.0220  | [-0.058, 0.014]  |
|      |                   | Number of chicks          | NA          | 0.0550   | [0.003, 0.107]   |
|      |                   | Number of fledglings      | NA          | 0.0750   | [0.030, 0.120]   |
|      |                   | Binary success            | NA          | 0.0988   | [0.053, 0.144]   |
| 1993 | Age               | Binary age                | All         | 0.0437   | [0.022, 0.065]   |
|      |                   |                           | Females     | 0.0260   | [-0.014, 0.066]  |
|      |                   |                           | Males       | -0.0439  | [-0.088, 0.000]  |
|      |                   | Discrete age              | All         | 0.0364   | [0.020, 0.053]   |
|      |                   |                           | Females     | -0.0019  | [-0.030, 0.026]  |
|      |                   |                           | Males       | -0.0452  | [-0.074, -0.016] |
|      |                   | Continuous age            | All         | 0.0161   | [-0.002, 0.035]  |
|      |                   |                           | Females     | 0.0145   | [-0.023, 0.052]  |
|      |                   |                           | Males       | -0.0420  | [-0.078, -0.006] |
|      | Residency status  | Immigration status        | All         | 0.0580   | [0.037, 0.079]   |
|      |                   |                           | Females     | 0.0205   | [-0.018, 0.060]  |
|      |                   |                           | Males       | -0.0111  | [-0.056, 0.034]  |
|      |                   | Settled status            | All         | 0.0551   | [0.034, 0.076]   |
|      |                   |                           | Females     | -0.0246  | [-0.062, 0.013]  |
|      |                   |                           | Males       | 0.0490   | [0.004, 0.094]   |
|      | Territory quality | Oak abundance             | NA          | 0.7931   | [0.774, 0.812]   |
|      |                   | Average territory density | NA          | 0.6147   | [0.592, 0.637]   |
|      |                   | Edge distance index       | NA          | 0.8310   | [0.822, 0.840]   |
|      |                   | Nest-box popularity index | NA          | 0.3054   | [0.280, 0.331]   |
|      | Reproductive      | Clutch size               | NA          | 0.0716   | [0.044, 0.100]   |
|      |                   | Number of chicks          | NA          | 0.0290   | [-0.003, 0.061]  |
|      |                   | Number of fledglings      | NA          | 0.0775   | [0.046, 0.109]   |
|      |                   | Binary success            | NA          | 0.0297   | [-0.001, 0.061]  |
| 1994 | Age               | Binary age                | All         | 0.0158   | [-0.005, 0.037]  |

| Year | Focal trait type  | Focal trait               | Individuals | <i>r</i> | SE intervals     |
|------|-------------------|---------------------------|-------------|----------|------------------|
| 1995 | Residency status  | Discrete age              | Females     | 0.0901   | [0.050, 0.130]   |
|      |                   |                           | Males       | -0.0931  | [-0.139, -0.047] |
|      |                   |                           | All         | 0.0189   | [0.004, 0.034]   |
|      |                   | Continuous age            | Females     | 0.0289   | [-0.001, 0.059]  |
|      |                   |                           | Males       | -0.0614  | [-0.091, -0.032] |
|      |                   |                           | All         | 0.0118   | [-0.012, 0.035]  |
|      |                   | Immigration status        | Females     | 0.1016   | [0.068, 0.136]   |
|      |                   |                           | Males       | -0.0907  | [-0.133, -0.049] |
|      |                   |                           | All         | 0.0026   | [-0.019, 0.024]  |
|      |                   | Settled status            | Females     | 0.0258   | [-0.014, 0.066]  |
|      |                   |                           | Males       | 0.0639   | [0.018, 0.110]   |
|      |                   |                           | All         | 0.0074   | [-0.014, 0.029]  |
|      | Territory quality | Oak abundance             | All         | 0.0375   | [-0.002, 0.077]  |
|      |                   |                           | Males       | 0.0276   | [-0.015, 0.071]  |
|      |                   |                           | NA          | 0.7981   | [0.784, 0.812]   |
|      |                   |                           | NA          | 0.6940   | [0.677, 0.711]   |
|      |                   | Average territory density | NA          | 0.8370   | [0.829, 0.845]   |
|      |                   |                           | NA          | 0.2398   | [0.210, 0.270]   |
|      | Reproductive      | Nest-box popularity index | NA          | 0.0600   | [0.026, 0.094]   |
|      |                   |                           | NA          | 0.0320   | [-0.002, 0.066]  |
|      |                   | Clutch size               | NA          | 0.0372   | [0.009, 0.065]   |
|      |                   |                           | NA          | -0.0026  | [-0.031, 0.026]  |
|      | Age               | Number of chicks          | All         | 0.0201   | [-0.010, 0.050]  |
|      |                   |                           | Females     | -0.0427  | [-0.097, 0.012]  |
|      |                   | Number of fledglings      | Males       | -0.0521  | [-0.113, 0.009]  |
|      |                   |                           | All         | 0.0006   | [-0.020, 0.021]  |
|      |                   | Binary success            | Females     | -0.0178  | [-0.055, 0.020]  |
|      |                   |                           | Males       | -0.0644  | [-0.108, -0.020] |
|      |                   | Binary age                | All         | -0.0196  | [-0.047, 0.008]  |
|      |                   |                           | Females     | -0.0017  | [-0.056, 0.052]  |
|      | Residency status  | Discrete age              | Males       | 0.0037   | [-0.053, 0.060]  |
|      |                   |                           | All         | 0.0318   | [0.003, 0.061]   |
|      |                   |                           | Females     | -0.0564  | [-0.111, -0.002] |
|      |                   | Continuous age            | Males       | -0.0636  | [-0.124, -0.003] |
|      |                   |                           | All         | 0.0404   | [0.010, 0.071]   |
|      |                   |                           | Females     | -0.0255  | [-0.080, 0.029]  |
|      |                   | Immigration status        | Males       | 0.0220   | [-0.045, 0.089]  |
|      |                   |                           | All         | 0.7852   | [0.773, 0.798]   |
|      |                   |                           | NA          | 0.6551   | [0.638, 0.673]   |
|      | Territory quality | Oak abundance             | NA          | 0.8579   | [0.852, 0.864]   |
|      |                   |                           | NA          | 0.2155   | [0.191, 0.240]   |
|      |                   |                           | NA          | 0.0504   | [0.025, 0.076]   |
|      |                   |                           | NA          | 0.0043   | [-0.022, 0.030]  |
|      | Reproductive      | Nest-box popularity index | NA          | 0.0564   | [0.031, 0.082]   |
|      |                   |                           | NA          | 0.0104   | [-0.015, 0.036]  |
|      |                   | Clutch size               | All         | -0.0252  | [-0.046, -0.004] |
|      |                   |                           | Females     | -0.0880  | [-0.125, -0.051] |
|      | Age               | Number of chicks          | NA          | 0.0104   | [-0.015, 0.036]  |
|      |                   |                           | NA          | -0.0252  | [-0.046, -0.004] |
|      |                   | Number of fledglings      | NA          | -0.0880  | [-0.125, -0.051] |
|      |                   |                           | NA          | 0.0104   | [-0.015, 0.036]  |
|      |                   | Binary success            | NA          | -0.0252  | [-0.046, -0.004] |
|      |                   |                           | NA          | -0.0880  | [-0.125, -0.051] |
|      | Age               | Binary age                | All         | -0.0252  | [-0.046, -0.004] |
|      |                   |                           | Females     | -0.0880  | [-0.125, -0.051] |
|      |                   | Clutch size               | NA          | 0.0104   | [-0.015, 0.036]  |
|      |                   |                           | NA          | -0.0252  | [-0.046, -0.004] |
|      |                   | Number of chicks          | NA          | -0.0880  | [-0.125, -0.051] |
|      |                   |                           | NA          | 0.0104   | [-0.015, 0.036]  |

| Year | Focal trait type  | Focal trait               | Individuals | <i>r</i> | SE intervals     |
|------|-------------------|---------------------------|-------------|----------|------------------|
| 1997 | Residency status  | Discrete age              | Males       | -0.1207  | [-0.166, -0.075] |
|      |                   |                           | All         | -0.0114  | [-0.025, 0.002]  |
|      |                   |                           | Females     | -0.0624  | [-0.084, -0.040] |
|      |                   | Continuous age            | Males       | -0.0471  | [-0.078, -0.016] |
|      |                   |                           | All         | -0.0258  | [-0.046, -0.006] |
|      |                   |                           | Females     | -0.0339  | [-0.070, 0.002]  |
|      |                   | Immigration status        | Males       | -0.0906  | [-0.134, -0.048] |
|      |                   |                           | All         | -0.0066  | [-0.027, 0.014]  |
|      |                   |                           | Females     | 0.0446   | [0.006, 0.083]   |
|      |                   | Settled status            | Males       | 0.1154   | [0.065, 0.165]   |
|      |                   |                           | All         | 0.0086   | [-0.012, 0.029]  |
|      |                   |                           | Females     | 0.0713   | [0.032, 0.111]   |
|      | Territory quality | Oak abundance             | Males       | 0.0296   | [-0.018, 0.077]  |
|      |                   |                           | NA          | 0.7980   | [0.787, 0.809]   |
|      |                   |                           | NA          | 0.5983   | [0.573, 0.624]   |
|      |                   |                           | NA          | 0.8811   | [0.876, 0.886]   |
|      | Reproductive      | Nest-box popularity index | NA          | 0.2756   | [0.253, 0.298]   |
|      |                   |                           | NA          | 0.2008   | [0.179, 0.223]   |
|      |                   |                           | NA          | 0.0867   | [0.062, 0.112]   |
|      |                   |                           | NA          | 0.0155   | [-0.009, 0.040]  |
|      |                   |                           | NA          | -0.0215  | [-0.047, 0.004]  |
|      |                   |                           | NA          | -0.0215  | [-0.047, 0.004]  |
|      | Age               | Binary age                | All         | 0.0260   | [0.004, 0.048]   |
|      |                   |                           | Females     | -0.0296  | [-0.070, 0.011]  |
|      |                   |                           | Males       | 0.0635   | [0.017, 0.110]   |
|      |                   | Discrete age              | All         | 0.0130   | [-0.002, 0.028]  |
|      |                   |                           | Females     | -0.0004  | [-0.027, 0.026]  |
|      |                   |                           | Males       | 0.0432   | [0.017, 0.069]   |
|      |                   | Continuous age            | All         | 0.0382   | [0.017, 0.059]   |
|      |                   |                           | Females     | -0.0792  | [-0.113, -0.046] |
|      |                   |                           | Males       | -0.0529  | [-0.097, -0.009] |
|      |                   | Immigration status        | All         | 0.0387   | [0.017, 0.061]   |
|      |                   |                           | Females     | 0.0579   | [0.015, 0.101]   |
|      |                   |                           | Males       | 0.0434   | [-0.004, 0.091]  |
|      |                   | Settled status            | All         | 0.0365   | [0.013, 0.060]   |
|      |                   |                           | Females     | 0.1001   | [0.051, 0.149]   |
|      |                   |                           | Males       | -0.0660  | [-0.103, -0.029] |
| 1998 | Territory quality | Oak abundance             | NA          | 0.8111   | [0.799, 0.823]   |
|      |                   |                           | NA          | 0.6738   | [0.653, 0.694]   |
|      |                   |                           | NA          | 0.8426   | [0.835, 0.850]   |
|      |                   |                           | NA          | 0.3552   | [0.332, 0.378]   |
|      | Reproductive      | Nest-box popularity index | NA          | 0.0502   | [0.019, 0.081]   |
|      |                   |                           | NA          | -0.0105  | [-0.036, 0.015]  |
|      |                   |                           | NA          | -0.0450  | [-0.072, -0.018] |
|      |                   |                           | NA          | -0.0309  | [-0.055, -0.007] |
|      | Age               | Binary age                | All         | -0.0499  | [-0.073, -0.027] |
|      |                   |                           | Females     | -0.0989  | [-0.138, -0.059] |
|      |                   |                           | Males       | 0.0632   | [0.009, 0.117]   |

| Year | Focal trait type  | Focal trait               | Individuals | <i>r</i> | SE intervals     |
|------|-------------------|---------------------------|-------------|----------|------------------|
| 1999 | Residency status  | Discrete age              | All         | -0.0202  | [-0.034, -0.007] |
|      |                   |                           | Females     | -0.0728  | [-0.096, -0.050] |
|      |                   |                           | Males       | -0.0139  | [-0.041, 0.014]  |
|      |                   | Continuous age            | All         | -0.0836  | [-0.104, -0.063] |
|      |                   |                           | Females     | -0.0532  | [-0.096, -0.011] |
|      |                   |                           | Males       | 0.0635   | [-0.012, 0.139]  |
|      |                   | Immigration status        | All         | 0.0019   | [-0.021, 0.025]  |
|      |                   |                           | Females     | -0.0105  | [-0.051, 0.031]  |
|      |                   |                           | Males       | 0.0565   | [0.002, 0.111]   |
|      |                   | Settled status            | All         | 0.0284   | [0.004, 0.052]   |
|      |                   |                           | Females     | -0.0266  | [-0.064, 0.011]  |
|      |                   |                           | Males       | -0.0372  | [-0.085, 0.011]  |
|      | Territory quality | Oak abundance             | NA          | 0.7732   | [0.759, 0.788]   |
|      |                   | Average territory density | NA          | 0.6634   | [0.643, 0.684]   |
|      |                   | Edge distance index       | NA          | 0.8631   | [0.856, 0.870]   |
|      |                   | Nest-box popularity index | NA          | 0.2128   | [0.188, 0.238]   |
|      | Reproductive      | Clutch size               | NA          | 0.0402   | [0.015, 0.066]   |
|      |                   | Number of chicks          | NA          | -0.0023  | [-0.028, 0.024]  |
|      |                   | Number of fledglings      | NA          | 0.0387   | [0.012, 0.066]   |
|      |                   | Binary success            | NA          | -0.0288  | [-0.056, -0.002] |
|      | Age               | Binary age                | All         | 0.0381   | [0.010, 0.066]   |
|      |                   |                           | Females     | 0.0090   | [-0.041, 0.059]  |
|      |                   |                           | Males       | -0.0576  | [-0.122, 0.007]  |
|      |                   | Discrete age              | All         | 0.0170   | [-0.001, 0.035]  |
|      |                   |                           | Females     | 0.0077   | [-0.023, 0.038]  |
|      |                   |                           | Males       | -0.0054  | [-0.051, 0.040]  |
|      |                   | Continuous age            | All         | 0.0405   | [0.014, 0.067]   |
|      |                   |                           | Females     | -0.0492  | [-0.098, -0.001] |
|      |                   |                           | Males       | 0.0838   | [0.026, 0.141]   |
|      |                   | Immigration status        | All         | -0.0128  | [-0.040, 0.015]  |
|      |                   |                           | Females     | 0.0617   | [0.012, 0.111]   |
|      |                   |                           | Males       | 0.0649   | [-0.001, 0.131]  |
|      |                   | Settled status            | All         | 0.0147   | [-0.013, 0.042]  |
|      |                   |                           | Females     | 0.0528   | [0.003, 0.103]   |
|      |                   |                           | Males       | 0.0065   | [-0.060, 0.073]  |
| 2000 | Territory quality | Oak abundance             | NA          | 0.7623   | [0.747, 0.778]   |
|      |                   | Average territory density | NA          | 0.6251   | [0.594, 0.656]   |
|      |                   | Edge distance index       | NA          | 0.8166   | [0.807, 0.826]   |
|      |                   | Nest-box popularity index | NA          | 0.1891   | [0.158, 0.220]   |
|      | Reproductive      | Clutch size               | NA          | 0.1081   | [0.078, 0.139]   |
|      |                   | Number of chicks          | NA          | 0.0489   | [0.017, 0.081]   |
|      |                   | Number of fledglings      | NA          | -0.0049  | [-0.037, 0.027]  |
|      |                   | Binary success            | NA          | -0.0716  | [-0.106, -0.037] |
|      | Age               | Binary age                | All         | 0.0026   | [-0.024, 0.029]  |
|      |                   |                           | Females     | 0.0015   | [-0.045, 0.048]  |
|      |                   |                           | Males       | -0.0879  | [-0.151, -0.025] |
|      |                   | Discrete age              | All         | -0.0122  | [-0.028, 0.004]  |

| Year | Focal trait type  | Focal trait               | Individuals | <i>r</i> | SE intervals     |
|------|-------------------|---------------------------|-------------|----------|------------------|
| 2001 | Residency status  | Continuous age            | Females     | 0.0278   | [-0.003, 0.059]  |
|      |                   |                           | Males       | -0.0996  | [-0.138, -0.062] |
|      |                   |                           | All         | -0.0123  | [-0.037, 0.012]  |
|      |                   | Immigration status        | Females     | -0.0161  | [-0.059, 0.027]  |
|      |                   |                           | Males       | -0.0353  | [-0.097, 0.026]  |
|      |                   |                           | All         | -0.0175  | [-0.044, 0.009]  |
|      |                   | Settled status            | Females     | -0.0830  | [-0.129, -0.037] |
|      |                   |                           | Males       | -0.0628  | [-0.127, 0.001]  |
|      |                   |                           | All         | 0.0595   | [0.032, 0.087]   |
|      | Territory quality | Oak abundance             | Females     | 0.0000   | [-0.048, 0.048]  |
|      |                   |                           | Males       | -0.0847  | [-0.144, -0.025] |
|      |                   |                           | NA          | 0.7968   | [0.782, 0.811]   |
|      |                   | Average territory density | NA          | 0.6278   | [0.602, 0.654]   |
|      |                   | Edge distance index       | NA          | 0.7887   | [0.777, 0.800]   |
|      |                   | Nest-box popularity index | NA          | 0.2575   | [0.226, 0.289]   |
|      | Reproductive      | Clutch size               | NA          | 0.0686   | [0.030, 0.107]   |
|      |                   | Number of chicks          | NA          | 0.0822   | [0.050, 0.114]   |
|      |                   | Number of fledglings      | NA          | 0.1269   | [0.091, 0.163]   |
|      |                   | Binary success            | NA          | 0.1001   | [0.061, 0.139]   |
|      | Age               | Binary age                | All         | 0.0202   | [-0.005, 0.046]  |
|      |                   |                           | Females     | 0.0782   | [0.035, 0.121]   |
|      |                   |                           | Males       | -0.0572  | [-0.125, 0.010]  |
|      |                   | Discrete age              | All         | 0.0151   | [-0.001, 0.031]  |
|      |                   |                           | Females     | 0.0141   | [-0.011, 0.039]  |
|      |                   |                           | Males       | 0.0345   | [-0.015, 0.084]  |
|      |                   | Continuous age            | All         | 0.0161   | [-0.009, 0.041]  |
|      |                   |                           | Females     | 0.1567   | [0.110, 0.204]   |
|      |                   |                           | Males       | -0.1855  | [-0.229, -0.142] |
|      | Residency status  | Immigration status        | All         | 0.0168   | [-0.009, 0.043]  |
|      |                   |                           | Females     | 0.1097   | [0.068, 0.152]   |
|      |                   |                           | Males       | 0.0529   | [-0.019, 0.125]  |
|      |                   | Settled status            | All         | 0.0014   | [-0.025, 0.028]  |
|      |                   |                           | Females     | 0.0607   | [0.020, 0.101]   |
|      |                   |                           | Males       | 0.1072   | [0.023, 0.192]   |
|      | Territory quality | Oak abundance             | NA          | 0.8620   | [0.851, 0.873]   |
|      |                   |                           | NA          | 0.6157   | [0.591, 0.640]   |
|      |                   |                           | NA          | 0.8234   | [0.814, 0.833]   |
|      |                   | Edge distance index       | NA          | 0.1715   | [0.144, 0.199]   |
|      |                   | Nest-box popularity index | NA          | 0.0831   | [0.045, 0.121]   |
|      |                   | Clutch size               | NA          | 0.0144   | [-0.018, 0.047]  |
| 2002 | Reproductive      | Number of chicks          | NA          | 0.0400   | [0.010, 0.070]   |
|      |                   | Number of fledglings      | NA          | -0.0192  | [-0.052, 0.013]  |
|      |                   | Binary success            | NA          | 0.0088   | [-0.014, 0.032]  |
|      |                   | Binary age                | All         | -0.0513  | [-0.090, -0.013] |
|      |                   |                           | Males       | -0.0038  | [-0.055, 0.047]  |
|      |                   |                           | All         | -0.0164  | [-0.032, -0.001] |
|      | Age               | Discrete age              | Females     | -0.0553  | [-0.080, -0.031] |
|      |                   |                           | All         | -0.0164  | [-0.032, -0.001] |
|      |                   |                           | Females     | -0.0553  | [-0.080, -0.031] |

| Year | Focal trait type  | Focal trait               | Individuals | <i>r</i> | SE intervals     |
|------|-------------------|---------------------------|-------------|----------|------------------|
| 2003 | Residency status  | Continuous age            | Males       | -0.0195  | [-0.055, 0.016]  |
|      |                   |                           | All         | 0.0825   | [0.056, 0.109]   |
|      |                   |                           | Females     | 0.1227   | [0.074, 0.171]   |
|      |                   |                           | Males       | 0.0935   | [0.045, 0.142]   |
|      |                   | Immigration status        | All         | -0.0176  | [-0.040, 0.005]  |
|      |                   |                           | Females     | 0.0514   | [0.012, 0.091]   |
|      |                   |                           | Males       | -0.0993  | [-0.151, -0.048] |
|      |                   | Settled status            | All         | 0.0122   | [-0.013, 0.037]  |
|      |                   |                           | Females     | -0.0351  | [-0.069, -0.002] |
|      | Territory quality | Oak abundance             | Males       | 0.0364   | [-0.029, 0.102]  |
|      |                   |                           | NA          | 0.8361   | [0.824, 0.849]   |
|      |                   |                           | NA          | 0.6655   | [0.639, 0.692]   |
|      |                   |                           | NA          | 0.8406   | [0.832, 0.849]   |
|      |                   | Average territory density | NA          | 0.3003   | [0.276, 0.325]   |
|      |                   |                           | NA          | 0.0567   | [0.029, 0.084]   |
|      |                   |                           | NA          | 0.0004   | [-0.025, 0.026]  |
|      |                   |                           | NA          | 0.0456   | [0.017, 0.074]   |
|      | Reproductive      | Edge distance index       | NA          | 0.0550   | [0.024, 0.086]   |
|      |                   |                           | NA          | -0.0351  | [-0.069, -0.001] |
|      |                   |                           | Females     | 0.1460   | [0.099, 0.194]   |
|      |                   |                           | Males       | -0.0014  | [-0.092, 0.089]  |
|      | Age               | Binary success            | All         | -0.0175  | [-0.038, 0.003]  |
|      |                   |                           | Females     | 0.0832   | [0.050, 0.116]   |
|      |                   |                           | Males       | -0.0585  | [-0.111, -0.006] |
|      |                   | Binary age                | All         | -0.0975  | [-0.124, -0.071] |
|      |                   |                           | Females     | 0.0787   | [0.034, 0.124]   |
|      |                   |                           | Males       | -0.0218  | [-0.091, 0.048]  |
|      | Residency status  | Immigration status        | All         | -0.0567  | [-0.089, -0.024] |
|      |                   |                           | Females     | 0.0470   | [-0.004, 0.098]  |
|      |                   |                           | Males       | -0.0386  | [-0.127, 0.049]  |
|      |                   |                           | All         | -0.0617  | [-0.094, -0.029] |
|      |                   | Settled status            | Females     | 0.1625   | [0.108, 0.217]   |
|      |                   |                           | Males       | -0.0014  | [-0.071, 0.069]  |
|      |                   |                           | NA          | 0.8597   | [0.848, 0.871]   |
|      | Territory quality | Oak abundance             | NA          | 0.6143   | [0.583, 0.646]   |
|      |                   |                           | NA          | 0.8303   | [0.822, 0.838]   |
|      |                   |                           | NA          | 0.3236   | [0.303, 0.344]   |
|      |                   |                           | NA          | 0.0579   | [0.034, 0.082]   |
|      | Reproductive      | Nest-box popularity index | NA          | -0.0374  | [-0.063, -0.011] |
|      |                   |                           | NA          | 0.0568   | [0.031, 0.082]   |
|      |                   |                           | NA          | -0.0193  | [-0.045, 0.007]  |
|      |                   |                           | All         | 0.0028   | [-0.024, 0.029]  |
| 2004 | Age               | Clutch size               | Females     | -0.1146  | [-0.162, -0.067] |
|      |                   |                           | Males       | 0.0816   | [0.018, 0.145]   |
|      |                   |                           | All         | -0.0261  | [-0.043, -0.009] |
|      |                   |                           | Females     | -0.0660  | [-0.096, -0.035] |
|      |                   | Number of chicks          | Males       | 0.0322   | [-0.008, 0.073]  |
|      |                   |                           | NA          |          |                  |
|      |                   |                           | NA          |          |                  |
|      |                   | Number of fledglings      | NA          |          |                  |
|      |                   |                           | NA          |          |                  |
|      |                   |                           | NA          |          |                  |

| Year | Focal trait type  | Focal trait               | Individuals | <i>r</i> | SE intervals     |
|------|-------------------|---------------------------|-------------|----------|------------------|
| 2005 | Residency status  | Continuous age            | All         | 0.0137   | [-0.011, 0.038]  |
|      |                   |                           | Females     | -0.0453  | [-0.099, 0.009]  |
|      |                   |                           | Males       | 0.0577   | [0.010, 0.105]   |
|      |                   | Immigration status        | All         | -0.0345  | [-0.062, -0.007] |
|      |                   |                           | Females     | -0.1067  | [-0.155, -0.058] |
|      |                   |                           | Males       | -0.1118  | [-0.168, -0.056] |
|      |                   | Settled status            | All         | 0.0245   | [-0.002, 0.051]  |
|      |                   |                           | Females     | -0.0077  | [-0.059, 0.043]  |
|      |                   |                           | Males       | -0.0119  | [-0.070, 0.047]  |
|      | Territory quality | Oak abundance             | NA          | 0.7954   | [0.780, 0.810]   |
|      |                   | Average territory density | NA          | 0.6033   | [0.581, 0.626]   |
|      |                   | Edge distance index       | NA          | 0.8286   | [0.820, 0.838]   |
|      |                   | Nest-box popularity index | NA          | 0.3120   | [0.290, 0.334]   |
|      | Reproductive      | Clutch size               | NA          | 0.1715   | [0.141, 0.202]   |
|      |                   | Number of chicks          | NA          | 0.0370   | [0.009, 0.065]   |
|      |                   | Number of fledglings      | NA          | 0.0868   | [0.059, 0.115]   |
|      |                   | Binary success            | NA          | 0.0633   | [0.033, 0.094]   |
|      | Age               | Binary age                | All         | 0.0144   | [-0.006, 0.035]  |
|      |                   |                           | Females     | 0.0889   | [0.052, 0.126]   |
|      |                   |                           | Males       | -0.0847  | [-0.129, -0.040] |
|      |                   | Discrete age              | All         | 0.0064   | [-0.008, 0.020]  |
|      |                   |                           | Females     | 0.0720   | [0.046, 0.098]   |
|      |                   |                           | Males       | -0.0575  | [-0.084, -0.031] |
|      |                   | Continuous age            | All         | -0.0032  | [-0.022, 0.015]  |
|      |                   |                           | Females     | 0.0316   | [0.001, 0.062]   |
|      |                   |                           | Males       | -0.0952  | [-0.130, -0.060] |
|      | Residency status  | Immigration status        | All         | 0.0127   | [-0.007, 0.033]  |
|      |                   |                           | Females     | 0.0631   | [0.027, 0.100]   |
|      |                   |                           | Males       | -0.0668  | [-0.114, -0.019] |
|      |                   | Settled status            | All         | -0.0146  | [-0.034, 0.005]  |
|      |                   |                           | Females     | 0.0861   | [0.049, 0.123]   |
|      |                   |                           | Males       | -0.0778  | [-0.124, -0.031] |
|      | Territory quality | Oak abundance             | NA          | 0.8316   | [0.822, 0.841]   |
|      |                   | Average territory density | NA          | 0.6622   | [0.646, 0.678]   |
|      |                   | Edge distance index       | NA          | 0.8660   | [0.860, 0.872]   |
|      |                   | Nest-box popularity index | NA          | 0.2309   | [0.209, 0.252]   |
|      | Reproductive      | Clutch size               | NA          | 0.1261   | [0.102, 0.150]   |
|      |                   | Number of chicks          | NA          | 0.0866   | [0.062, 0.111]   |
|      |                   | Number of fledglings      | NA          | 0.1424   | [0.120, 0.165]   |
|      |                   | Binary success            | NA          | 0.0944   | [0.071, 0.118]   |
| 2006 | Age               | Binary age                | All         | -0.0047  | [-0.028, 0.019]  |
|      |                   |                           | Females     | -0.0487  | [-0.090, -0.007] |
|      |                   |                           | Males       | 0.0687   | [0.015, 0.122]   |
|      |                   | Discrete age              | All         | -0.0041  | [-0.020, 0.012]  |
|      |                   |                           | Females     | 0.0344   | [0.002, 0.066]   |
|      |                   |                           | Males       | 0.0371   | [0.005, 0.069]   |
|      |                   | Continuous age            | All         | -0.0066  | [-0.030, 0.017]  |

| Year | Focal trait type  | Focal trait               | Individuals        | <i>r</i>         | SE intervals     |                  |
|------|-------------------|---------------------------|--------------------|------------------|------------------|------------------|
| 2007 | Residency status  | Immigration status        | Females            | -0.0378          | [-0.088, 0.012]  |                  |
|      |                   |                           | Males              | -0.0092          | [-0.063, 0.045]  |                  |
|      |                   |                           | All                | -0.0392          | [-0.063, -0.016] |                  |
|      |                   |                           | Females            | 0.0099           | [-0.032, 0.052]  |                  |
|      |                   | Males                     | -0.1358            | [-0.189, -0.083] |                  |                  |
|      |                   | All                       | -0.0417            | [-0.065, -0.019] |                  |                  |
|      |                   | Females                   | -0.0835            | [-0.125, -0.042] |                  |                  |
|      |                   | Males                     | -0.1245            | [-0.174, -0.075] |                  |                  |
|      | Territory quality | Oak abundance             | NA                 | 0.8257           | [0.815, 0.836]   |                  |
|      |                   | Average territory density | NA                 | 0.6453           | [0.616, 0.674]   |                  |
|      |                   | Edge distance index       | NA                 | 0.8591           | [0.853, 0.865]   |                  |
|      |                   | Nest-box popularity index | NA                 | 0.2990           | [0.275, 0.323]   |                  |
|      | Reproductive      | Clutch size               | NA                 | 0.0477           | [0.021, 0.074]   |                  |
|      |                   | Number of chicks          | NA                 | 0.0183           | [-0.005, 0.042]  |                  |
|      |                   | Number of fledglings      | NA                 | 0.1089           | [0.083, 0.134]   |                  |
|      |                   | Binary success            | NA                 | 0.0865           | [0.059, 0.114]   |                  |
|      | Age               | Binary age                | All                | -0.0226          | [-0.040, -0.005] |                  |
|      |                   |                           | Females            | -0.0136          | [-0.047, 0.019]  |                  |
|      |                   |                           | Males              | -0.0607          | [-0.102, -0.020] |                  |
|      |                   | Discrete age              | All                | -0.0062          | [-0.018, 0.006]  |                  |
|      |                   |                           | Females            | -0.0112          | [-0.035, 0.013]  |                  |
|      |                   |                           | Males              | -0.0124          | [-0.039, 0.014]  |                  |
|      |                   | Continuous age            | All                | -0.0166          | [-0.034, 0.001]  |                  |
|      |                   |                           | Females            | -0.0039          | [-0.033, 0.025]  |                  |
|      |                   |                           | Males              | -0.0993          | [-0.136, -0.063] |                  |
|      |                   | Residency status          | Immigration status | All              | -0.0296          | [-0.047, -0.012] |
|      |                   |                           |                    | Females          | -0.0118          | [-0.044, 0.020]  |
|      | Males             |                           |                    | 0.0603           | [0.020, 0.101]   |                  |
|      | Settled status    |                           | All                | -0.0459          | [-0.063, -0.028] |                  |
|      |                   |                           | Females            | -0.0723          | [-0.104, -0.041] |                  |
|      |                   |                           | Males              | 0.0424           | [0.000, 0.085]   |                  |
| 2008 | Territory quality | Oak abundance             | NA                 | 0.8105           | [0.801, 0.820]   |                  |
|      |                   | Average territory density | NA                 | 0.6211           | [0.597, 0.645]   |                  |
|      |                   | Edge distance index       | NA                 | 0.8904           | [0.886, 0.895]   |                  |
|      |                   | Nest-box popularity index | NA                 | 0.2454           | [0.224, 0.266]   |                  |
|      | Reproductive      | Clutch size               | NA                 | 0.0588           | [0.036, 0.081]   |                  |
|      |                   | Number of chicks          | NA                 | 0.0589           | [0.036, 0.082]   |                  |
|      |                   | Number of fledglings      | NA                 | 0.1363           | [0.113, 0.160]   |                  |
|      |                   | Binary success            | NA                 | 0.1090           | [0.084, 0.134]   |                  |
|      | Age               | Binary age                | All                | 0.0620           | [0.041, 0.083]   |                  |
|      |                   |                           | Females            | 0.0860           | [0.049, 0.123]   |                  |
|      |                   |                           | Males              | 0.1014           | [0.048, 0.155]   |                  |
|      |                   | Discrete age              | All                | 0.0478           | [0.034, 0.062]   |                  |
|      |                   |                           | Females            | 0.0517           | [0.026, 0.077]   |                  |
|      |                   |                           | Males              | 0.0588           | [0.025, 0.093]   |                  |
|      |                   | Continuous age            | All                | 0.0233           | [0.002, 0.045]   |                  |
|      |                   |                           | Females            | 0.0680           | [0.029, 0.108]   |                  |



| Year | Focal trait type  | Focal trait               | Individuals | <i>r</i> | SE intervals     |
|------|-------------------|---------------------------|-------------|----------|------------------|
| 2009 | Residency status  | Immigration status        | Males       | 0.1391   | [0.086, 0.192]   |
|      |                   |                           | All         | 0.0070   | [-0.014, 0.028]  |
|      |                   |                           | Females     | 0.0274   | [-0.009, 0.064]  |
|      |                   | Settled status            | Males       | -0.0880  | [-0.142, -0.034] |
|      |                   |                           | All         | -0.0036  | [-0.024, 0.017]  |
|      |                   |                           | Females     | 0.0232   | [-0.014, 0.060]  |
|      | Territory quality | Oak abundance             | Males       | -0.0699  | [-0.122, -0.018] |
|      |                   |                           | NA          | 0.8341   | [0.825, 0.843]   |
|      |                   |                           | NA          | 0.6573   | [0.626, 0.689]   |
|      |                   | Average territory density | NA          | 0.8791   | [0.874, 0.884]   |
|      |                   |                           | NA          | 0.2312   | [0.207, 0.255]   |
|      |                   |                           | NA          | 0.0543   | [0.013, 0.095]   |
|      | Reproductive      | Clutch size               | NA          | 0.0450   | [0.010, 0.08]    |
|      |                   |                           | NA          | 0.1267   | [0.102, 0.151]   |
|      |                   |                           | NA          | 0.1121   | [0.086, 0.138]   |
|      |                   | Number of chicks          | NA          | 0.0257   | [0.002, 0.050]   |
|      |                   |                           | All         | 0.0110   | [-0.029, 0.051]  |
|      |                   |                           | Males       | 0.0041   | [-0.053, 0.061]  |
|      | Age               | Discrete age              | All         | 0.0077   | [-0.007, 0.022]  |
|      |                   |                           | Females     | -0.0270  | [-0.050, -0.004] |
|      |                   |                           | Males       | 0.0036   | [-0.031, 0.038]  |
|      |                   | Continuous age            | All         | 0.0468   | [0.021, 0.073]   |
|      |                   |                           | Females     | -0.0090  | [-0.047, 0.029]  |
|      |                   |                           | Males       | -0.1442  | [-0.196, -0.092] |
| 2010 | Residency status  | Immigration status        | All         | 0.0006   | [-0.023, 0.024]  |
|      |                   |                           | Females     | 0.1482   | [0.109, 0.187]   |
|      |                   |                           | Males       | 0.0658   | [0.010, 0.122]   |
|      |                   | Settled status            | All         | 0.0203   | [-0.004, 0.044]  |
|      |                   |                           | Females     | 0.0710   | [0.030, 0.112]   |
|      |                   |                           | Males       | 0.0022   | [-0.055, 0.059]  |
|      | Territory quality | Oak abundance             | NA          | 0.7973   | [0.781, 0.814]   |
|      |                   |                           | NA          | 0.7075   | [0.692, 0.723]   |
|      |                   |                           | NA          | 0.8175   | [0.808, 0.827]   |
|      |                   | Average territory density | NA          | 0.2576   | [0.232, 0.283]   |
|      |                   |                           | NA          | 0.0611   | [0.019, 0.103]   |
|      |                   |                           | NA          | 0.0373   | [0.006, 0.069]   |
|      | Reproductive      | Clutch size               | NA          | 0.0674   | [0.038, 0.097]   |
|      |                   |                           | NA          | 0.0336   | [0.002, 0.065]   |
|      |                   |                           | NA          | 0.0097   | [-0.014, 0.033]  |
|      |                   | Number of chicks          | Females     | 0.0561   | [0.015, 0.098]   |
|      |                   |                           | Males       | 0.0030   | [-0.057, 0.063]  |
|      |                   |                           | All         | 0.0016   | [-0.013, 0.016]  |
|      | Age               | Discrete age              | Females     | 0.0441   | [0.016, 0.072]   |
|      |                   |                           | Males       | -0.0699  | [-0.099, -0.041] |
|      |                   |                           | All         | 0.0039   | [-0.021, 0.029]  |
|      |                   | Continuous age            | Females     | -0.0004  | [-0.040, 0.039]  |
|      |                   |                           | Males       | 0.0347   | [-0.023, 0.093]  |
|      |                   |                           |             |          |                  |

| Year | Focal trait type  | Focal trait               | Individuals | <i>r</i> | SE intervals     |
|------|-------------------|---------------------------|-------------|----------|------------------|
| 2011 | Residency status  | Immigration status        | All         | 0.0378   | [0.014, 0.061]   |
|      |                   |                           | Females     | -0.1072  | [-0.149, -0.065] |
|      |                   |                           | Males       | 0.0315   | [-0.027, 0.090]  |
|      |                   | Settled status            | All         | -0.0129  | [-0.036, 0.011]  |
|      |                   |                           | Females     | -0.0959  | [-0.136, -0.056] |
|      |                   |                           | Males       | -0.0453  | [-0.105, 0.014]  |
|      | Territory quality | Oak abundance             | NA          | 0.8335   | [0.821, 0.846]   |
|      |                   | Average territory density | NA          | 0.6586   | [0.641, 0.676]   |
|      |                   | Edge distance index       | NA          | 0.8159   | [0.808, 0.824]   |
|      |                   | Nest-box popularity index | NA          | 0.2606   | [0.238, 0.283]   |
|      | Reproductive      | Clutch size               | NA          | 0.0208   | [-0.004, 0.046]  |
|      |                   | Number of chicks          | NA          | 0.0371   | [0.008, 0.066]   |
|      |                   | Number of fledglings      | NA          | 0.1605   | [0.136, 0.186]   |
|      |                   | Binary success            | NA          | 0.0753   | [0.047, 0.103]   |
|      | Age               | Binary age                | All         | 0.0139   | [-0.022, 0.050]  |
|      |                   |                           | Females     | -0.0516  | [-0.112, 0.009]  |
|      |                   |                           | Males       | -0.2251  | [-0.307, -0.144] |
|      |                   | Discrete age              | All         | 0.0005   | [-0.027, 0.028]  |
|      |                   |                           | Females     | -0.0454  | [-0.088, -0.003] |
|      |                   |                           | Males       | -0.1563  | [-0.206, -0.106] |
|      |                   | Continuous age            | All         | -0.0166  | [-0.049, 0.016]  |
|      |                   |                           | Females     | -0.0993  | [-0.137, -0.061] |
|      |                   |                           | Males       | -0.1716  | [-0.252, -0.091] |
|      | Residency status  | Immigration status        | All         | -0.0129  | [-0.049, 0.023]  |
|      |                   |                           | Females     | -0.0081  | [-0.071, 0.055]  |
|      |                   |                           | Males       | 0.0861   | [0.000, 0.172]   |
|      |                   | Settled status            | All         | 0.0689   | [0.032, 0.105]   |
|      |                   |                           | Females     | 0.1009   | [0.032, 0.170]   |
|      |                   |                           | Males       | -0.1335  | [-0.215, -0.052] |
| 2012 | Territory quality | Oak abundance             | NA          | 0.7725   | [0.756, 0.789]   |
|      |                   | Average territory density | NA          | 0.6448   | [0.614, 0.676]   |
|      |                   | Edge distance index       | NA          | 0.8191   | [0.809, 0.829]   |
|      |                   | Nest-box popularity index | NA          | 0.1989   | [0.171, 0.227]   |
|      | Reproductive      | Clutch size               | NA          | 0.0116   | [-0.022, 0.046]  |
|      |                   | Number of chicks          | NA          | -0.0794  | [-0.107, -0.052] |
|      |                   | Number of fledglings      | NA          | 0.0634   | [0.033, 0.094]   |
|      |                   | Binary success            | NA          | 0.0859   | [0.054, 0.118]   |
|      | Age               | Binary age                | All         | 0.0319   | [0.005, 0.059]   |
|      |                   |                           | Females     | 0.0094   | [-0.030, 0.049]  |
|      |                   |                           | Males       | 0.1383   | [0.061, 0.215]   |
|      |                   | Discrete age              | All         | 0.0037   | [-0.013, 0.021]  |
|      |                   |                           | Females     | -0.0185  | [-0.043, 0.006]  |
|      |                   |                           | Males       | 0.1078   | [0.057, 0.159]   |
|      |                   | Continuous age            | All         | 0.0485   | [0.023, 0.074]   |
|      |                   |                           | Females     | 0.0344   | [-0.002, 0.071]  |
|      |                   |                           | Males       | 0.0821   | [0.012, 0.153]   |
|      | Residency status  | Immigration status        | All         | 0.0274   | [0.000, 0.055]   |

| Year | Focal trait type  | Focal trait               | Individuals | <i>r</i> | SE intervals     |
|------|-------------------|---------------------------|-------------|----------|------------------|
| 2013 | Territory quality | Settled status            | Females     | 0.0060   | [-0.032, 0.044]  |
|      |                   |                           | Males       | 0.2227   | [0.149, 0.297]   |
|      |                   |                           | All         | 0.0481   | [0.021, 0.075]   |
|      |                   | Oak abundance             | Females     | -0.0332  | [-0.075, 0.008]  |
|      |                   |                           | Males       | 0.0244   | [-0.053, 0.102]  |
|      |                   |                           | NA          | 0.8142   | [0.802, 0.827]   |
|      |                   | Average territory density | NA          | 0.6362   | [0.610, 0.662]   |
|      |                   |                           | NA          | 0.8513   | [0.844, 0.858]   |
|      |                   |                           | NA          | 0.2746   | [0.250, 0.299]   |
|      |                   | Edge distance index       | NA          | 0.0003   | [-0.024, 0.025]  |
|      |                   |                           | NA          | -0.0561  | [-0.081, -0.031] |
|      |                   |                           | NA          | 0.0377   | [0.012, 0.063]   |
| 2014 | Reproductive      | Nest-box popularity index | NA          | 0.0304   | [0.004, 0.057]   |
|      |                   |                           | NA          | 0.0588   | [0.022, 0.095]   |
|      |                   |                           | Females     | 0.0964   | [0.026, 0.167]   |
|      |                   | Clutch size               | Males       | -0.1308  | [-0.168, -0.093] |
|      |                   |                           | All         | 0.0154   | [-0.005, 0.036]  |
|      |                   |                           | Females     | -0.0151  | [-0.051, 0.021]  |
|      |                   | Number of chicks          | Males       | -0.0393  | [-0.072, -0.007] |
|      |                   |                           | All         | 0.0811   | [0.049, 0.114]   |
|      |                   |                           | Females     | 0.1041   | [0.031, 0.178]   |
|      |                   | Number of fledglings      | Males       | 0.1262   | [0.058, 0.194]   |
|      |                   |                           | All         | 0.1080   | [0.071, 0.145]   |
|      |                   |                           | Females     | 0.0706   | [0.002, 0.139]   |
| 2014 | Age               | Binary success            | Males       | 0.3344   | [0.258, 0.411]   |
|      |                   |                           | All         | 0.0683   | [0.031, 0.105]   |
|      |                   |                           | Females     | -0.0583  | [-0.128, 0.011]  |
|      |                   | Binary age                | Males       | 0.1747   | [0.095, 0.254]   |
|      |                   |                           | NA          | 0.7544   | [0.737, 0.772]   |
|      |                   |                           | NA          | 0.5966   | [0.573, 0.621]   |
|      |                   | Discrete age              | NA          | 0.7228   | [0.708, 0.738]   |
|      |                   |                           | NA          | 0.2183   | [0.188, 0.249]   |
|      |                   |                           | NA          | 0.0093   | [-0.022, 0.040]  |
|      |                   | Continuous age            | NA          | 0.0471   | [0.014, 0.080]   |
|      |                   |                           | NA          | 0.0990   | [0.068, 0.130]   |
|      |                   |                           | NA          | 0.0615   | [0.028, 0.095]   |
| 2014 | Residency status  | Immigration status        | All         | -0.0663  | [-0.095, -0.038] |
|      |                   |                           | Females     | -0.0246  | [-0.077, 0.028]  |
|      |                   |                           | Males       | -0.1372  | [-0.198, -0.076] |
|      |                   | Settled status            | All         | -0.0398  | [-0.055, -0.025] |
|      |                   |                           | Females     | -0.0273  | [-0.055, 0.001]  |
|      |                   |                           | Males       | -0.0167  | [-0.056, 0.023]  |
|      |                   | Continuous age            | All         | -0.0176  | [-0.045, 0.009]  |
|      |                   |                           | Females     | 0.0758   | [0.028, 0.123]   |
|      |                   |                           | Males       | -0.0010  | [-0.068, 0.066]  |
|      |                   | Immigration status        | All         | 0.0761   | [0.048, 0.104]   |
|      |                   |                           | Females     | 0.0423   | [-0.010, 0.095]  |

| Year | Focal trait type  | Focal trait               | Individuals | <i>r</i> | SE intervals     |
|------|-------------------|---------------------------|-------------|----------|------------------|
| 2015 | Territory quality | Settled status            | Males       | 0.0048   | [-0.058, 0.068]  |
|      |                   |                           | All         | -0.0190  | [-0.049, 0.011]  |
|      |                   |                           | Females     | 0.0772   | [0.025, 0.129]   |
|      |                   |                           | Males       | -0.1633  | [-0.212, -0.115] |
|      |                   | Oak abundance             | NA          | 0.8164   | [0.802, 0.830]   |
|      |                   |                           | NA          | 0.6610   | [0.646, 0.676]   |
|      |                   |                           | NA          | 0.7477   | [0.735, 0.760]   |
|      |                   |                           | NA          | 0.2316   | [0.206, 0.257]   |
|      |                   | Average territory density | NA          | 0.1034   | [0.073, 0.134]   |
|      |                   |                           | NA          | 0.0395   | [0.012, 0.067]   |
|      |                   |                           | NA          | 0.0177   | [-0.010, 0.045]  |
|      |                   |                           | NA          | -0.0130  | [-0.043, 0.017]  |
|      | Reproductive      | Edge distance index       | All         | 0.0089   | [-0.016, 0.034]  |
|      |                   |                           | Females     | -0.0628  | [-0.110, -0.016] |
|      |                   |                           | Males       | 0.1243   | [0.070, 0.179]   |
|      |                   |                           | All         | -0.0010  | [-0.017, 0.015]  |
|      |                   | Nest-box popularity index | Females     | -0.0292  | [-0.061, 0.003]  |
|      |                   |                           | Males       | 0.0416   | [0.007, 0.077]   |
|      |                   |                           | All         | 0.0188   | [-0.003, 0.041]  |
|      |                   |                           | Females     | -0.0484  | [-0.099, 0.002]  |
|      |                   | Clutch size               | Males       | 0.0700   | [0.028, 0.112]   |
|      |                   |                           | All         | 0.0128   | [-0.013, 0.038]  |
|      |                   |                           | Females     | -0.1064  | [-0.153, -0.059] |
|      |                   |                           | Males       | -0.1063  | [-0.162, -0.051] |
| 2016 | Age               | Discrete age              | All         | 0.0010   | [-0.025, 0.027]  |
|      |                   |                           | Females     | -0.0739  | [-0.120, -0.028] |
|      |                   |                           | Males       | -0.0742  | [-0.126, -0.023] |
|      |                   | Continuous age            | NA          | 0.7805   | [0.764, 0.797]   |
|      |                   |                           | NA          | 0.6561   | [0.635, 0.678]   |
|      |                   |                           | NA          | 0.8040   | [0.794, 0.814]   |
|      |                   |                           | NA          | 0.2880   | [0.264, 0.312]   |
|      |                   | Immigration status        | NA          | 0.1328   | [0.108, 0.158]   |
|      |                   |                           | NA          | 0.0142   | [-0.018, 0.047]  |
|      |                   |                           | NA          | 0.2255   | [0.198, 0.253]   |
|      |                   |                           | NA          | 0.0534   | [0.022, 0.085]   |
|      |                   | Settled status            | All         | -0.0484  | [-0.078, -0.019] |
|      |                   |                           | Females     | 0.0101   | [-0.045, 0.065]  |
|      |                   |                           | Males       | 0.1141   | [0.046, 0.182]   |
|      | Residency status  | Discrete age              | All         | -0.0153  | [-0.034, 0.003]  |
|      |                   |                           | Females     | -0.0246  | [-0.057, 0.008]  |
|      |                   |                           | Males       | 0.0364   | [-0.005, 0.078]  |
|      |                   | Continuous age            | All         | -0.0135  | [-0.043, 0.016]  |
|      |                   |                           | Females     | 0.0541   | [0.003, 0.105]   |
|      |                   |                           | Males       | -0.0696  | [-0.117, -0.022] |
|      |                   | Immigration status        | All         | -0.0543  | [-0.083, -0.025] |
|      |                   |                           | Females     | -0.1133  | [-0.168, -0.059] |
|      |                   |                           | Males       | 0.0277   | [-0.041, 0.097]  |

| Year | Focal trait type  | Focal trait               | Individuals | <i>r</i> | SE intervals     |
|------|-------------------|---------------------------|-------------|----------|------------------|
| 2017 | Territory quality | Settled status            | All         | -0.0477  | [-0.078, -0.017] |
|      |                   |                           | Females     | -0.0203  | [-0.073, 0.033]  |
|      |                   |                           | Males       | 0.0211   | [-0.049, 0.091]  |
|      |                   | Oak abundance             | NA          | 0.7478   | [0.726, 0.769]   |
|      |                   |                           | NA          | 0.6688   | [0.649, 0.688]   |
|      |                   |                           | NA          | 0.8021   | [0.790, 0.814]   |
|      |                   | Average territory density | NA          | 0.2097   | [0.178, 0.241]   |
|      |                   |                           | NA          | 0.1184   | [0.068, 0.169]   |
|      |                   |                           | NA          | 0.0529   | [0.016, 0.090]   |
|      |                   | Edge distance index       | NA          | 0.1876   | [0.157, 0.218]   |
|      |                   |                           | NA          | 0.1227   | [0.089, 0.156]   |
|      |                   |                           | NA          | 0.1227   | [0.089, 0.156]   |
|      | Reproductive      | Nest-box popularity index | All         | 0.0289   | [-0.004, 0.061]  |
|      |                   |                           | Females     | -0.0404  | [-0.100, 0.020]  |
|      |                   |                           | Males       | -0.0637  | [-0.127, -0.001] |
|      |                   | Clutch size               | All         | 0.0181   | [0.000, 0.036]   |
|      |                   |                           | Females     | -0.0186  | [-0.054, 0.016]  |
|      |                   |                           | Males       | -0.0124  | [-0.052, 0.027]  |
|      |                   | Number of chicks          | All         | 0.0395   | [0.006, 0.072]   |
|      |                   |                           | Females     | -0.0209  | [-0.075, 0.033]  |
|      |                   |                           | Males       | -0.0124  | [-0.083, 0.058]  |
|      |                   | Number of fledglings      | All         | 0.0607   | [0.029, 0.093]   |
|      |                   |                           | Females     | 0.0602   | [-0.001, 0.121]  |
|      |                   |                           | Males       | 0.0856   | [0.018, 0.153]   |
| 2018 | Age               | Binary success            | All         | 0.0359   | [0.002, 0.070]   |
|      |                   |                           | Females     | -0.0499  | [-0.109, 0.009]  |
|      |                   |                           | Males       | -0.0733  | [-0.128, -0.019] |
|      |                   | Binary age                | All         | 0.7128   | [0.695, 0.730]   |
|      |                   |                           | NA          | 0.6461   | [0.624, 0.668]   |
|      |                   |                           | NA          | 0.7817   | [0.770, 0.793]   |
|      |                   | Discrete age              | NA          | 0.2846   | [0.257, 0.312]   |
|      |                   |                           | NA          | 0.0744   | [0.042, 0.107]   |
|      |                   |                           | NA          | 0.1504   | [0.113, 0.187]   |
|      |                   | Continuous age            | NA          | 0.1988   | [0.168, 0.229]   |
|      |                   |                           | NA          | 0.1856   | [0.152, 0.219]   |
|      |                   |                           | NA          | 0.1856   | [0.152, 0.219]   |
|      | Residency status  | Immigration status        | All         | 0.0245   | [-0.018, 0.067]  |
|      |                   |                           | Females     | -0.0260  | [-0.100, 0.048]  |
|      |                   |                           | Males       | 0.0418   | [-0.085, 0.168]  |
|      |                   | Settled status            | All         | 0.0475   | [0.019, 0.076]   |
|      |                   |                           | Females     | -0.0779  | [-0.118, -0.038] |
|      |                   |                           | Males       | 0.0508   | [-0.022, 0.123]  |
|      |                   | Territory quality         | All         | -0.0142  | [-0.060, 0.032]  |
|      |                   |                           | Females     | 0.2417   | [0.141, 0.342]   |
|      |                   |                           | Males       | -0.0483  | [-0.179, 0.083]  |
|      |                   | Reproductive              | All         | 0.0373   | [-0.005, 0.079]  |
|      |                   |                           | Females     | 0.0290   | [-0.048, 0.106]  |
|      |                   |                           | Males       | -0.0951  | [-0.212, 0.021]  |
|      |                   | Age                       | All         | 0.0195   | [-0.022, 0.061]  |

| Year         | Focal trait type  | Focal trait               | Individuals               | <i>r</i>         | SE intervals     |                 |
|--------------|-------------------|---------------------------|---------------------------|------------------|------------------|-----------------|
| 2019         | Territory quality | Oak abundance             | Females                   | -0.0155          | [-0.089, 0.058]  |                 |
|              |                   |                           | Males                     | 0.0117           | [-0.116, 0.140]  |                 |
|              |                   |                           | NA                        | 0.7464           | [0.725, 0.767]   |                 |
|              |                   |                           | NA                        | 0.6708           | [0.651, 0.691]   |                 |
|              |                   | Average territory density | NA                        | 0.7854           | [0.774, 0.797]   |                 |
|              |                   |                           | NA                        | 0.2077           | [0.180, 0.236]   |                 |
|              |                   |                           | NA                        | 0.0436           | [0.016, 0.071]   |                 |
|              |                   |                           | NA                        | 0.1792           | [0.143, 0.216]   |                 |
|              | Reproductive      | Number of fledglings      | NA                        | 0.1574           | [0.123, 0.192]   |                 |
|              |                   |                           | NA                        | 0.1641           | [0.124, 0.204]   |                 |
|              |                   |                           | All                       | 0.0106           | [-0.020, 0.041]  |                 |
|              |                   |                           | Females                   | -0.0334          | [-0.095, 0.028]  |                 |
|              | Age               | Discrete age              | Males                     | 0.0261           | [-0.035, 0.087]  |                 |
|              |                   |                           | All                       | 0.0028           | [-0.018, 0.024]  |                 |
|              |                   |                           | Females                   | -0.0196          | [-0.058, 0.019]  |                 |
|              |                   |                           | Males                     | 0.0154           | [-0.026, 0.057]  |                 |
|              |                   | Continuous age            | All                       | 0.0404           | [0.012, 0.069]   |                 |
|              |                   |                           | Females                   | -0.0912          | [-0.137, -0.046] |                 |
|              |                   |                           | Males                     | 0.1849           | [0.098, 0.272]   |                 |
|              |                   |                           | All                       | 0.0515           | [0.021, 0.082]   |                 |
|              |                   | Residency status          | Immigration status        | Females          | 0.1250           | [0.065, 0.185]  |
|              |                   |                           |                           | Males            | -0.0398          | [-0.104, 0.024] |
|              |                   |                           |                           | All              | 0.0497           | [0.019, 0.080]  |
|              |                   |                           |                           | Females          | 0.0882           | [0.027, 0.149]  |
|              | Territory quality | Oak abundance             | Males                     | 0.0065           | [-0.058, 0.071]  |                 |
|              |                   |                           | NA                        | 0.7684           | [0.756, 0.781]   |                 |
|              |                   |                           | NA                        | 0.6372           | [0.618, 0.656]   |                 |
|              |                   |                           | NA                        | 0.8197           | [0.811, 0.829]   |                 |
|              |                   |                           | Average territory density | NA               | 0.2097           | [0.184, 0.236]  |
| NA           |                   |                           |                           | 0.0154           | [-0.010, 0.041]  |                 |
| NA           |                   |                           |                           | 0.0465           | [0.019, 0.074]   |                 |
| NA           |                   |                           |                           | 0.0219           | [-0.003, 0.047]  |                 |
| Reproductive |                   | Number of fledglings      | NA                        | 0.0068           | [-0.018, 0.032]  |                 |
|              |                   |                           | NA                        | 0.0051           | [-0.038, 0.048]  |                 |
|              |                   |                           | Females                   | -0.1136          | [-0.176, -0.051] |                 |
|              |                   |                           | Males                     | -0.4807          | [-0.605, -0.357] |                 |
| Age          | Discrete age      | All                       | 0.0032                    | [-0.031, 0.037]  |                  |                 |
|              |                   | Females                   | -0.0753                   | [-0.124, -0.026] |                  |                 |
|              |                   | Males                     | -0.2837                   | [-0.364, -0.203] |                  |                 |
|              |                   | All                       | 0.0102                    | [-0.027, 0.047]  |                  |                 |
|              | Continuous age    | Females                   | 0.0657                    | [0.000, 0.132]   |                  |                 |
|              |                   | Males                     | -0.2245                   | [-0.367, -0.082] |                  |                 |
|              |                   | All                       | 0.0631                    | [0.019, 0.107]   |                  |                 |
|              |                   | Females                   | -0.0319                   | [-0.093, 0.030]  |                  |                 |
|              | Residency status  | Immigration status        | Males                     | 0.0025           | [-0.157, 0.162]  |                 |
|              |                   |                           | All                       | -0.0184          | [-0.061, 0.025]  |                 |
|              |                   |                           | Females                   | -0.1451          | [-0.206, -0.084] |                 |

| Year | Focal trait type  | Focal trait               | Individuals | <i>r</i> | SE intervals     |
|------|-------------------|---------------------------|-------------|----------|------------------|
| 2021 | Territory quality | Oak abundance             | Males       | -0.2971  | [-0.435, -0.159] |
|      |                   | Average territory density | NA          | 0.7269   | [0.705, 0.749]   |
|      |                   | Edge distance index       | NA          | 0.6088   | [0.586, 0.632]   |
|      |                   | Nest-box popularity index | NA          | 0.7707   | [0.755, 0.786]   |
|      | Reproductive      | Clutch size               | NA          | 0.1573   | [0.127, 0.188]   |
|      |                   | Clutch size               | NA          | -0.0643  | [-0.099, -0.030] |
|      |                   | Number of chicks          | NA          | 0.0122   | [-0.020, 0.045]  |
|      |                   | Number of fledglings      | NA          | 0.1018   | [0.066, 0.138]   |
|      | Age               | Binary success            | NA          | 0.0570   | [0.018, 0.096]   |
|      |                   | Binary age                | All         | -0.0688  | [-0.102, -0.036] |
|      |                   |                           | Females     | -0.0361  | [-0.095, 0.023]  |
|      |                   |                           | Males       | 0.1431   | [0.056, 0.230]   |
|      | Discrete age      |                           | All         | -0.0361  | [-0.057, -0.016] |
|      |                   |                           | Females     | 0.0380   | [-0.004, 0.080]  |
|      |                   |                           | Males       | 0.1339   | [0.067, 0.200]   |
|      |                   | Continuous age            | All         | -0.0315  | [-0.070, 0.007]  |
|      | Residency status  |                           | Females     | -0.0896  | [-0.146, -0.033] |
|      |                   |                           | Males       | 0.3546   | [0.151, 0.558]   |
|      |                   | Immigration status        | All         | 0.0347   | [0.001, 0.068]   |
|      |                   |                           | Females     | 0.0551   | [-0.006, 0.116]  |
|      | Settled status    |                           | Males       | -0.1153  | [-0.202, -0.029] |
|      |                   |                           | All         | -0.0099  | [-0.043, 0.023]  |
|      |                   |                           | Females     | 0.0707   | [0.011, 0.130]   |
|      |                   |                           | Males       | -0.0861  | [-0.170, -0.003] |
| 2022 | Territory quality | Oak abundance             | NA          | 0.7820   | [0.762, 0.802]   |
|      |                   | Average territory density | NA          | 0.6958   | [0.680, 0.712]   |
|      |                   | Edge distance index       | NA          | 0.7398   | [0.726, 0.754]   |
|      |                   | Nest-box popularity index | NA          | 0.1864   | [0.152, 0.220]   |
|      | Reproductive      | Clutch size               | NA          | -0.0171  | [-0.051, 0.017]  |
|      |                   | Number of chicks          | NA          | 0.0712   | [0.036, 0.107]   |
|      |                   | Number of fledglings      | NA          | 0.1712   | [0.137, 0.205]   |
|      |                   | Binary success            | NA          | 0.2060   | [0.168, 0.244]   |
|      | Age               | Binary age                | All         | 0.0175   | [-0.018, 0.053]  |
|      |                   |                           | Females     | 0.0849   | [0.024, 0.146]   |
|      |                   |                           | Males       | -0.1108  | [-0.190, -0.032] |
|      | Discrete age      |                           | All         | 0.0319   | [0.008, 0.056]   |
|      |                   |                           | Females     | -0.0128  | [-0.048, 0.023]  |
|      |                   |                           | Males       | -0.0476  | [-0.092, -0.003] |
|      |                   | Continuous age            | All         | -0.0338  | [-0.069, 0.001]  |
|      |                   |                           | Females     | 0.1149   | [0.060, 0.170]   |
|      |                   |                           | Males       | -0.1203  | [-0.190, -0.050] |
|      | Residency status  | Immigration status        | All         | -0.0328  | [-0.068, 0.002]  |
|      |                   |                           | Females     | -0.0316  | [-0.090, 0.026]  |
|      |                   |                           | Males       | -0.0993  | [-0.178, -0.020] |
|      |                   | Settled status            | All         | 0.1053   | [0.068, 0.142]   |
|      |                   |                           | Females     | 0.0185   | [-0.045, 0.082]  |
|      |                   |                           | Males       | 0.2716   | [0.193, 0.350]   |

| Year | Focal trait type  | Focal trait               | Individuals | <i>r</i> | SE intervals   |
|------|-------------------|---------------------------|-------------|----------|----------------|
|      | Territory quality | Oak abundance             | NA          | 0.7450   | [0.724, 0.766] |
|      |                   | Average territory density | NA          | 0.5982   | [0.565, 0.631] |
|      |                   | Edge distance index       | NA          | 0.7330   | [0.718, 0.748] |
|      |                   | Nest-box popularity index | NA          | 0.2888   | [0.258, 0.319] |
|      | Reproductive      | Clutch size               | NA          | 0.1064   | [0.065, 0.148] |
|      |                   | Number of chicks          | NA          | 0.0889   | [0.050, 0.128] |
|      |                   | Number of fledglings      | NA          | 0.1425   | [0.103, 0.181] |
|      |                   | Binary success            | NA          | 0.1152   | [0.072, 0.159] |

Table S5 – Temporal repeatability of age composition, residency status composition, average territory quality and average reproductive output of neighbourhoods at spatial scales of 25, 50, 100, 150 and 200ha. Repeatability was derived from the intra-class correlation coefficient (ICC) from a linear mixed-effects model, where the ratio index of within versus outside the defined spatial scale of the average measure was the response variable, and year and spatial scale area categorical grouping variables.

| Trait                          | Repeatability at spatial scales: |       |       |       |       |
|--------------------------------|----------------------------------|-------|-------|-------|-------|
|                                | 25ha                             | 50ha  | 100ha | 150ha | 200ha |
| Proportion adults              | 0.036                            | 0.050 | 0.057 | 0.043 | 0.031 |
| Proportion local recruits      | 0.076                            | 0.102 | 0.135 | 0.157 | 0.173 |
| Proportion settled individuals | 0.024                            | 0.035 | 0.048 | 0.057 | 0.062 |
| Mean oak abundance             | 0.971                            | 0.973 | 0.969 | 0.962 | 0.955 |
| Mean territory density         | 0.968                            | 0.974 | 0.976 | 0.975 | 0.975 |
| Mean EDI                       | 0.965                            | 0.965 | 0.967 | 0.970 | 0.973 |
| Mean box popularity index      | 0.916                            | 0.939 | 0.959 | 0.967 | 0.971 |
| Mean clutch size               | 0.234                            | 0.294 | 0.364 | 0.412 | 0.447 |
| Mean chick number              | 0.090                            | 0.118 | 0.165 | 0.194 | 0.219 |
| Mean fledgling number          | 0.182                            | 0.240 | 0.314 | 0.361 | 0.398 |
| Proportion binary successes    | 0.084                            | 0.111 | 0.150 | 0.176 | 0.202 |

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# Chapter V

## **The influence of age and social interactions on plasticity in breeding phenology in a wild bird population**

*In preparation:*

Jones, C. V.\*, **Woodman, J. P.\***, Firth, J. A. & Sheldon, B. C. (2024). The influence of age and social interactions on plasticity in breeding phenology in a wild bird population.

# The influence of age and social interactions on plasticity in breeding phenology in a wild bird population

Carys V. Jones<sup>\*1</sup>, Joe P. Woodman<sup>\*1</sup>, Josh A. Firth<sup>1,2</sup> & Ben C. Sheldon<sup>1</sup>

## ABSTRACT

In seasonally-breeding species, selection is expected to favour parents timing reproduction so that peak energetic demand of offspring aligns with resource distribution. Phenotypic plasticity allows individuals to fine-tune their reproductive timing, but many factors might influence plasticity in timing, and drive spatio-temporal variation across populations. Age is likely to affect plasticity in timing as greater experience can shape breeding performance, of which phenological timing is a component. However, there is limited understanding of how age relates to breeding timing given spatial variation in local phenology across habitats, and the role of age-related social mechanisms in mediating this, such as density effects and social learning. We use data from >10,000 great tit breeding events to examine age-specific breeding timing and the effects of local age structure. We find that adult individuals breed earlier than juveniles even when accounting for local phenological variation, providing evidence of advanced breeding with age. We find no evidence that local age structure affects juvenile timing, but that adults breed relatively later when their neighbours are also old. This indicates that juveniles do not use social cues from older more experienced birds to time breeding, potentially due to limited phenotypic plasticity. We suggest that later breeding among adults in adult-biased neighbourhoods could be underpinned by both adaptive and non-adaptive mechanisms. Given that climate change affects phenology across trophic levels, our findings of age-related breeding timing at the individual- and neighbourhood-level are relevant for understanding the drivers of phenotypic plasticity in wild populations in changing environments.

itzman & Foster 2010; Schwartz 2003). As such, breeding phenology is under selection to coincide with time-varying resources, often from other trophic levels (Daan et al. 1989; Kharouba & Wolkovich 2020; Park & Post 2022). Phenotypic plasticity, where individuals with a given genotype express different phenotypes depending on environmental conditions (DeWitt & Scheiner 2004; Pigliucci 2001; Stager et al. 2024), allows individuals to fine-tune their reproductive timing such that it matches with temporal variation in resource availability (Charmantier et al. 2008; Nussey et al. 2007; Vedder et al. 2013). However, factors that might influence plasticity in reproductive timing within individuals, and mechanisms that generate spatio-temporal variation in breeding timing across populations, are often neglected when assessing the drivers of breeding phenology.

First (a), for phenotypic plasticity to improve the timing of breeding to better match to the local environment, individuals must be able to forecast the timing of environmental events (Lande 2009; Scheiner 1993). In seasonal environments, this is often achieved using indirect cues, such as temperature, photoperiod, phenological events that are indirectly related to resource availability, or the behaviour of conspecifics (Reed et al. 2010), meaning individuals that are better at recognising and responding to these cues will better time their breeding. Evidence across taxa suggests that breeding performance improves with age, leading to peak performance followed by a decrease in late-life through reproductive senescence (Charlesworth 1994; Clutton-Brock 1988, 1989; Heinze & Schrenpf 2008; Nussey et al. 2013). The constraint hypothesis states that this is underpinned by increasing competence mediated by a longer period of learning through previous breeding (Curio 1983; Nol & Smith 1987; Pärt 2001). With regards to phenological timing, the constraint hypothesis might lead to better matching to a local optimum with age as older individuals use previous experience to more effectively track cues related to resource phenology and adjust their breeding timing in response (Fig. 1a). Indeed, there are often repeatable age-related differences in the timing of seasonal breeding, with a general trend of older individuals breeding earlier, particularly in birds (Forslund & Pärt 1995; Martin 1995; Mills & Shaw 1980; Newton 1989; Nol &

## 1 INTRODUCTION

In species with seasonal breeding, selection favours parents timing reproduction so that peak energetic demand of young matches with greatest resource availability (Kre-

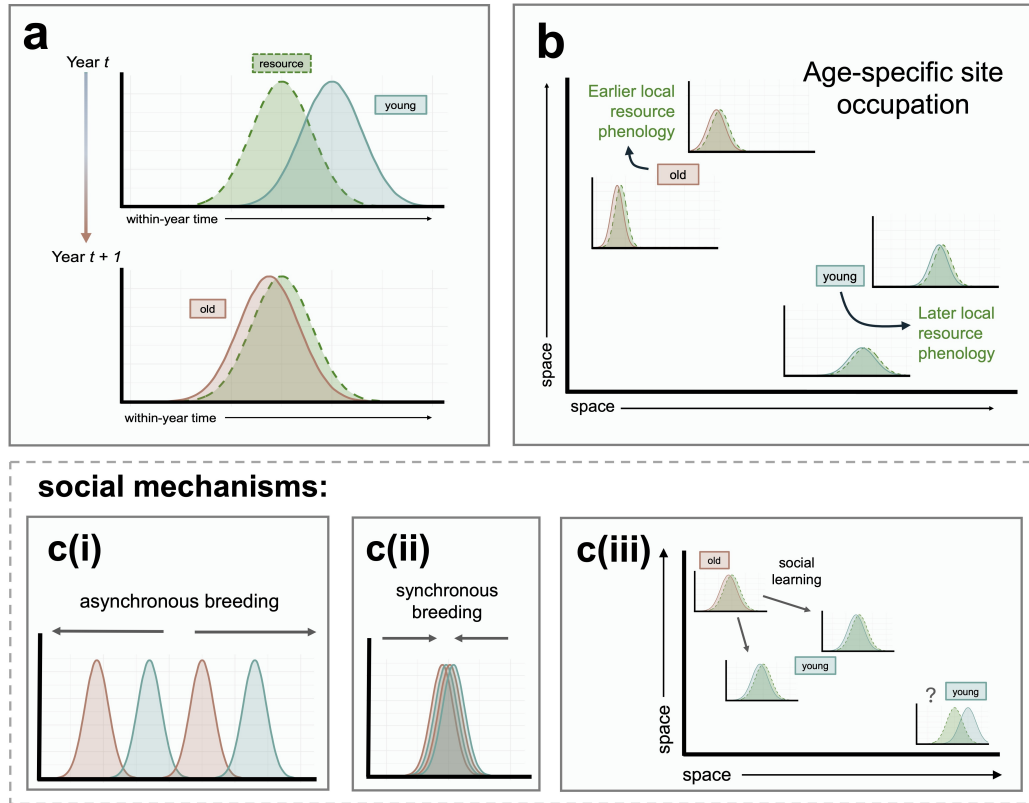


Fig. 1. Overview of mechanisms that might shape phenological timing within and between individuals referred to in the introduction. In all plots, green dashed distributions illustrate phenological timing of a resource, blue distributions refer to phenological timing of young individuals, and red distributions refer to phenological timing of old individuals. In a) phenological timing advances as individuals better match a local resource peak with age. In b) there is spatial variation in local resource phenology, and age-specific occupation of sites, but individuals match to their local phenology equally independent of age. In c(i) local breeding phenology is asynchronous between individuals, in c(ii) it is synchronous, and in c(iii) young individuals copy the breeding phenology of older individuals when in close spatial proximity.

Smith 1987; Sæther 1990).

Second (b), other factors might influence phenological timing where earlier breeding with age might not be driven by increased phenotypic plasticity in relation to matching to the local environment. In fact, plasticity in behavioural traits is often higher in younger individuals (Araya-Ajoy & Dingemanse 2017; Atwell & Wagner 2014; Ericsson et al. 2016). An understudied mechanism which could lead to age-related differences in breeding timing is age-specificity in breeding habitat choice, across which there is variation in the timing of local resource phenology. If older individuals breed in higher quality sites (Brewer et al. 2009; Ferrer & Bisson 2003; Garneau et al. 2008; Stepanuk et al. 2021) which have earlier local phenology compared to the population mean, but all individuals equally match to local resource optima regardless of age, then older individuals will breed earlier on average (Fig. 1b). Therefore, rather than plastically changing breeding timing given previous experience, timing might largely be driven by spatial variation in phenology across the environment, across which

there is age-specific occupation of sites. Indeed, recent work shows that accounting for environmental similarity across breeding sites decreases estimates of the heritability of reproductive timing (Jones et al. 2024), and in this way the same might be true not just for similarity in breeding timing between related individuals, but also for those of the same age.

Third (c), a neglected aspect that might influence breeding timing, and plasticity in this, is the operation of social mechanisms among individuals within the local breeding environment, and how these relate to age. We identify three potential social mechanisms here: (ci) effects due to density; (cii) effects due to selection favouring local synchrony within trophic levels; and (ciii) effects due to social learning of local optima.

(ci) At a proximate scale, breeding density of conspecifics in territorial species can negatively affect reproductive timing if there is higher competition, which may - for instance - hinder the rate at which critical resources are obtained, such as food or breeding sites (Wilkin et al.

2006). This might induce asynchronous breeding across neighbourhoods as some individuals' breeding attempts are delayed (Fig. 1ci). Further, the effects of density might be mediated by local age structure, because older individuals are generally of higher social dominance (Piper 1997; Poston 1997; Sol et al. 2000; Woodman et al. 2024b), thus enhancing the competitive landscape of local breeding environments.

(cii) On an ultimate scale, we might see selection for breeding asynchrony between conspecifics in local breeding environments, such that the negative effects of density-driven competition are avoided, including the need for territory defence, reduced foraging times or increased chance of mortality during aggressive interactions (Both & Visser 2000; Facka & Powell 2021; Goubault et al. 2005; Ward et al. 2006; Wilkin et al. 2006; Ydenberg & Krebs 1987). However, this might involve a trade-off between timing to best fit the social environment versus matching to a temporally-variable resource in the physical environment. Conversely, in some cases selection may favour breeding synchrony among territorial conspecifics if social familiarity is adaptive (Akçay et al. 2009; Frostman & Sherman 2004; Gokcekus et al. 2023; Grabowska-Zhang et al. 2012b; Siracusa et al. 2021; Temeles 1994). In such cases, social familiarity might promote mutual benefits during synchronised breeding such as relaxed competition allowing for coinciding optimal breeding timing to match the local environment, or increased cooperation such as joint predator defence between neighbours (Grabowska-Zhang et al. 2012a; Griffiths et al. 2003; Jungwirth et al. 2015; Rosell et al. 2008; Strodl & Schausberger 2012; Fig. 1cii).

(ciii) Finally, the adjustment of breeding timing may be mediated by social learning. Further, such social learning might be age-specific, as younger individuals may adjust their timing by copying older individuals who have greater familiarity of the local environment from previous breeding (Perrins & McCleery 1985; Piper 2011; Slagsvold & Wiebe 2018), and thus might better forecast the timing of phenological events (Fig. 1ciii). Social cues are important in other reproductive behaviours, such as mate choice (Dugatkin 1992; Gibson & Höglund 1992) and breeding habitat selection (Doligez et al. 2002; Pärt & Doligez 2003; Valone & Templeton 2002). These breeding behaviours often show age-specificity in the degree and direction of social copying, with a common pattern of young tending to learn from older individuals (Dugatkin & Godin 1993; Höglund et al. 1995; Valone 2007; Woodman et al. 2024b). Given that the constraint hypothesis predicts older individuals to better time their reproduction (mechanism 1), and

there is high potential for adjusting breeding timing based on social cues, we might expect that individuals breeding for the first time copy and therefore have similarly-timed reproduction to older individuals when exposed to a greater number of experienced breeders in their social environment. However, the operation of these mechanisms that link age-based phenological timing to age-related social mechanisms are currently unknown due to the difficulty of assessing this in wild populations.

In this study, we use 46 years of data from a natural population of great tits *Parus major* detailing individual-level breeding behaviour of 6,850 individuals to assess age-related breeding phenology and understand how the social environment shapes this. First, we assess whether breeding is differentially timed in juvenile and adult individuals, and if age-specific differences in reproductive timing are maintained when accounting for fine-scale phenological differences in the environment. Second, we determine how variation in the age structure of breeding social environments affects reproductive timing in juvenile and adult individuals.

## 2 METHODS

### 2.1 Study system and data collection

The great tit *Parus major* is a passerine bird found in woodlands across Europe, with breeding ages ranging 1–9, averaging 1.8 years (Perrins 1979; Woodman et al. 2022). Although there are some continuous changes with age (Bouwhuis et al. 2009), the main age effects on many individual-level traits linked to experience are captured by two age-classes: first-years (hereafter juveniles) and older (hereafter adults, Greenwood et al. 1979; Perrins 1979; Sandell and Smith 1991; Gosler 1993; Farine et al. 2015). The species is socially monogamous, with pairs defending territories during annual breeding seasons April–June (Hinde 1952). During breeding, great tits provision their young primarily with a local temporally-variable food supply of caterpillars (Gosler 1993). As such, peak energetic demand of young should be matched to the peak in caterpillar abundance, which itself depends on the leaf development of deciduous trees in the local environment (Hinks et al. 2015).

Data used here are from a long-term study in Wytham Woods, Oxford (51°46'N, 1°20'W), a 385ha mixed deciduous woodland (Savill et al. 2010). The great tit population has been monitored since 1947, where breeding adults and their chicks have been marked with unique British Trust for Ornithology (BTO) rings since the 1960s. Additionally, standard reproductive metrics are collected including clutch

size, lay date (the day the first egg of a clutch is laid), hatch date, number of chicks, and number of fledglings (Perrins 1965). Individuals breed almost exclusively in the 1020 nest-boxes which are in fixed positions with known GPS coordinates (Krebs 1971; Wilkin et al. 2006). All chicks are ringed at 14 days of age, while adults are trapped at nest-boxes and identified by ring number, or marked with a new ring if they are immigrants. Age is based on year of hatching for local birds, or plumage characteristics for immigrants which can discern between juveniles and those older than this (Svensson 1992). Although immigration rates are high (46%), most are first caught as juveniles (78%) and can therefore be aged accurately.

## 2.2 Data selection

We used a dataset that assigned the year of hatching to all individuals since 1950, across which exact year of hatching was known for 88.8% of 46,062 identified breeding individuals (Woodman et al. 2022). In this study, we included birds in analyses that attempted to breed between 1978–2023, for which individual identity data were more complete compared to earlier dates (nest-box design was also changed in 1973 from wood boxes that backed directly onto tree trunks to woodcrete boxes suspended by a wire, which changed predation regime, Dunn 1977). Individuals that were first caught post-fledging are assumed to be immigrants, as locally-hatched tits are marked as nestlings in nest-boxes and the proportion of great tits hatched in natural cavities is very low (Kidd et al. 2015). Immigrants that entered the population with adult plumage were assigned a minimum age of 2, and subsequent age estimates were based on this (6.7% and 10.0% of breeding females and males; in these cases, individuals can still be categorised into ‘juvenile’ and ‘adult’ categories with certainty). Age was therefore assigned to 80.8% and 71.5% of breeding females and males respectively where at least one egg was laid (due to nests failing prior to adult capture, and unsuccessful trapping attempts, parental identity was unknown in some cases).

## 2.3 Local age-related breeding timing

In order to capture breeding timing both relative to other individuals in an annual breeding population, and also given fine-scale phenological differences in local resource distributions, we calculated two measures of reproductive timing. First, we took each year and centred the lay dates of all breeding attempts such that the mean lay date was 0 for every year. This provides an absolute measure of breeding timing relative to the entire population while removing

between-year variability in population-level average breeding timing, which has advanced over time with climate change (Charmantier et al. 2008; Cole et al. 2021).

Second, we calculated a measure of breeding timing relative to fine-scale phenological differences across the study site (hereafter ‘local breeding timing mismatch’). Great tit lay dates are linked to local tree phenology, particularly in terms of bud-burst dates of oaks *Quercus* spp. within their foraging range. Individual timing of oak bud-burst is highly repeatable between years relative to other oaks in the population, but varies across small spatial scales (Cole & Sheldon 2017; Hinks et al. 2015). Therefore, we took every breeding attempt within each year, and calculated the difference between a focal female’s lay date and the lay date expected given the breeding locality, giving a measure of breeding timing relative to that of the average for a specific local environment. We calculated the average lay date for each locality by taking the median of all year-centred lay dates 1965–2023 associated with the focal nest-box in which the breeding attempt took place (additional years of data were used to calculate the long-term average because since 1978 data for individual identity is more complete, but before this date standardised and complete data collection of laying dates were still recorded). In the analysis we used a subset of boxes that had been occupied at least 10 times over the study period (leaving 80% of all boxes; Fig. S1) to ensure that the box-level median lay date was representative, as boxes with low occupancy over years are more likely to be skewed by individual breeding attempts. We also calculated average lay date for each locality at a coarser spatial scale (supporting information). The average lay date associated with a nest-box is not biased by age-specific occupation in the long-term, as this does not show temporal repeatability within this study system (Woodman et al. 2024a).

To assess the role of age-related social mechanisms on breeding timing, we considered how the age structure of breeding neighbourhoods interacts with lay date in terms of absolute breeding timing, and local breeding timing mismatch. Great tit lay dates are primarily considered a female trait, as the timing is principally controlled by the female, and heritability of the trait is less than a fifth in males compared to females (Evans et al. 2020; Jones et al. 2024; Perrins & McCleery 1989). Therefore, we considered how a female’s lay date varied depending on the age composition of its female neighbours. We defined neighbours as individuals that bred within 75m of each other. While there are alternative ways to determine neighbourhoods in territorial species (e.g. Thiessen polygons, Gokcekus et

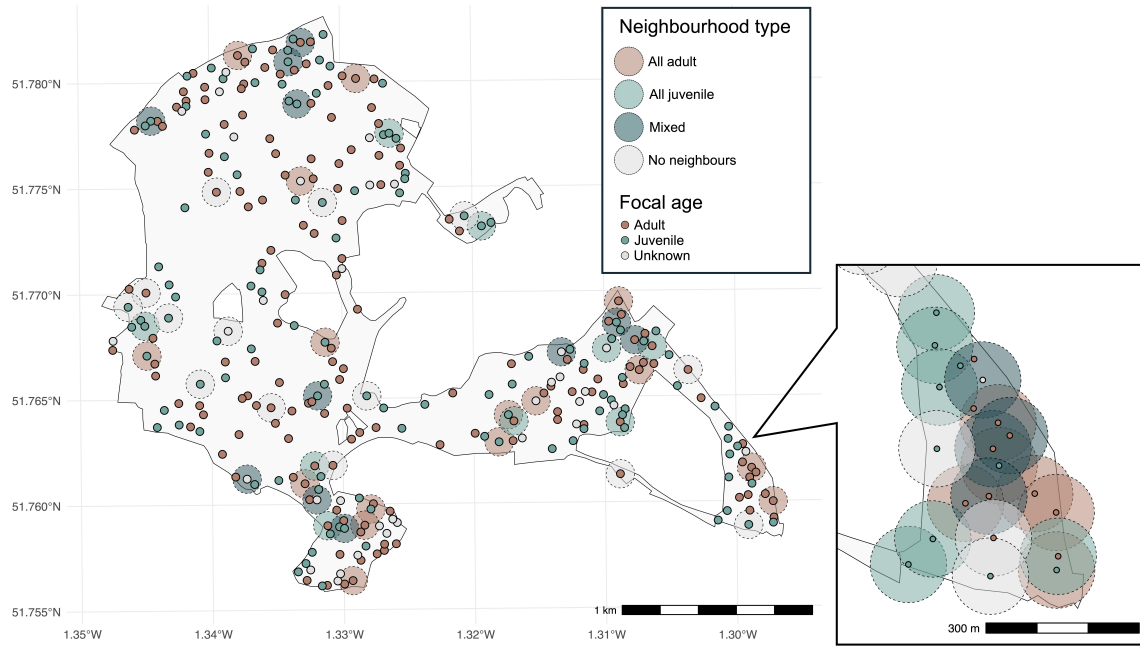


Fig. 2. Illustration of variation in neighbourhood age structures across Wytham within a single year (2009). We demonstrate the variation in age structure neighbourhood types by randomly sampling 50 occupied boxes in the plot of the entire study system, and provide an enlarged section on the right of all neighbourhoods within a specific subset of Wytham. Each point is a nest-box, occupied by either an adult (red), juvenile (blue) or unknown (grey) female. Around each box a 75m radius buffer was placed to calculate whether a focal female has all adult (red), all juvenile (light blue), mixed aged (dark blue), or no neighbours (grey).

al. 2023; Schlicht et al. 2014; Wilkin et al. 2006; Woodman et al. 2024a), these are more appropriate when considering neighbours during concurrent chick-rearing behaviour. Here, we are concerned with behaviour prior to egg-laying, which is the period during which social mechanisms might affect breeding timing between neighbours.

Although the precise spatial scale at which individuals interact during this period is not known, we chose 75m as an appropriate scale based on previous studies that assess space-use during pre-breeding behaviour in great tits (Both & Visser 2000; Firth et al. 2018; Krebs 1971). For every breeding female, we calculated the number of their female neighbours that were adults. We removed cases where a nest-box was used for a second time (0.30%) and females' second broods (0.75%) within years, as these occur much later (Perrins 1965, 1979) and it can be assumed that the timing of these attempts are not underpinned by the same mechanisms as first breeding events.

## 2.4 Statistical analyses

We used Bayesian regression models to assess the effect of neighbourhood age structure on lay date as (1) absolute breeding timing and (2) local breeding timing mismatch. Bayesian regression models were chosen due to their flexibility in handling complex hierarchical structures and the ability to incorporate prior information, which is

particularly useful in ecological studies such as this where data can be noisy. The models also provide full posterior distributions of the estimated parameters, allowing for nuanced interpretation of the results.

We constructed separate Gaussian models to estimate the marginal effects of local age structure on breeding timing defined by a categorised measure of neighbourhood type (either 'all juvenile', 'all adult', 'mixed', where both age classes exist within the neighbourhood, or 'no neighbours', where no birds bred within 75m of the focal female; Fig. 2). We chose a categorical instead of continuous measure to allow for a more biologically-meaningful interpretation of interactions between different age structures and breeding timing. Additionally, using a continuous measure would not allow for clear differentiation of the 'no neighbours' category, as 0% adult neighbours could either mean no neighbours at all or only juvenile neighbours (see also supporting information).

To account for between-year differences in breeding timing variance, and repeated measures of the same nest-box or female across years, we included year, nest-box and female ID as random effects. In all models, we included the age of the focal female as an interaction term to test for differences in the effect of neighbourhood age structure on breeding timing depending on the focal female's age (Table S1).



These models were run using *brms* version 2.21.0 (Bürkner 2017), an interface to the Hamilton Monte Carlo engine Stan (Stan Development Team 2024). Models were run using standard priors and the *marginaleffects* package was used to process posterior distributions (Arel-Bundock et al. forthcoming). Model convergence was checked using the effective number of samples and inspection of chain trace plots. We report posterior median estimates and their 95% credible intervals.

### 3 RESULTS

In total, we recorded 10,931 breeding attempts by 6,850 female great tits across 46 years. There was profound spatial variation in the average phenology of breeding sites, with the average year-centred lay date of nest-boxes ranging from -8.4 to 10.3 (i.e. approximately 19 days difference in the average lay date at nest-boxes accounting for between-year differences in breeding populations' overall timing). The number of neighbours found breeding within 75m of a focal female ranged from 0–9. Both annual population size and age structure showed marked temporal variation (proportion of juvenile females ranged from 29.7–67.8%; female population size ranged from 145–470), which together led to great spatio-temporal variation in the range of neighbourhood age structure types across the study system (Fig. S2).

Our results support previous studies showing average absolute breeding timing (laying date accounting for annual differences) of juvenile birds is a little more than 2 days later than adult birds (lay date difference in days posterior median [95% credible intervals]: 2.22 [1.73, 2.70]). Further, we find that when calculating local breeding timing mismatch, therefore accounting for spatial variation in local phenology, the average difference between adults and juveniles is also close to 2 days (2.09 [1.61, 2.57]).

Neighbourhood age structure had a stronger influence on adult birds' absolute laying date and local breeding timing mismatch compared to juveniles (Fig. 3). There was not a significant difference between the absolute laying date of juvenile birds depending on whether they are surrounded by all adult or all juvenile neighbours (all adult neighbours: 0.93 [0.63, 1.23], all juvenile neighbours: 0.67 [0.40, 0.92]). Adult birds with all adult neighbours had later absolute laying dates compared to those with all juvenile neighbours, but they still laid earlier than the mean within years (all adult neighbours: -1.21 [-1.50, -0.93], all juvenile neighbours: -1.81 [-2.08, -1.53]). Similar patterns were found assessing local breeding timing mismatch, in that adults showed slightly later average breeding when

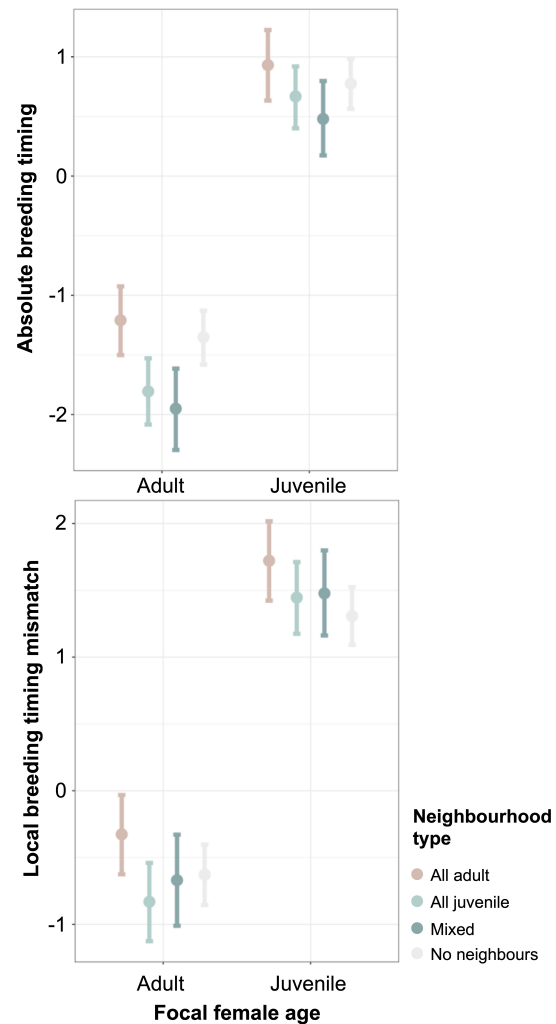


Fig. 3. Marginal predictions of breeding timing in adult and juvenile great tits depending on their neighbourhood age structure as defined by: a) absolute breeding timing; or b) local breeding timing mismatch.

surrounded by all adult neighbours compared to all juvenile neighbours (all adult neighbours: -0.33 [-0.63, -0.03], all juvenile neighbours: -0.83 [-1.13, -0.54]), whereas the same pattern was not seen as strongly in juvenile birds (all adult neighbours: 1.72 [1.42, 2.02], all juvenile neighbours: 1.45 [1.18, 1.71]).

Birds within mixed age-cohort neighbourhoods had very similar laying dates to birds with all juvenile neighbours regardless of the focal female's age, though there are minor differences depending on whether laying date is measured as absolute or local breeding timing mismatch (Fig. 3). Both absolute lay date and local breeding timing mismatch for individuals that have no neighbours varies across models (Table S2 for all results).

## 4 DISCUSSION

Using 10,931 records of breeding female great tits across 46 years, we quantified whether age-specific earlier breeding in adult great tits is maintained considering fine-scale variation in local phenology, and whether such timing is affected by the age structure of the social breeding environment. We find that adult females breed earlier than juveniles not only compared to the population-average, but also given local phenological variability, providing evidence of significant age-related differences in breeding behaviour, which is potentially consistent with the constraint hypothesis. Given persistent differences in breeding timing relative to local environmental variation between juvenile and older individuals, we find no evidence that the age structure of breeding neighbourhoods has an effect on the timing of juveniles' reproductive attempts, but that adults breed relatively later when their neighbours are also adults compared to when they have all juvenile neighbours.

Adult females had earlier lay dates not only relative to the breeding population within any year, but also considering local environmental differences in phenology. While it is well-established that there are often repeatable age-related differences in breeding timing across taxa (Forslund & Pärt 1995; Morgan et al. 2013; Newton 1989; Nussey et al. 2006; Sæther 1990), the role of age-specific habitat-use in phenologically-variable environments in driving this pattern is often overlooked. Our findings suggest that there is not covariation between age and average local resource phenology in breeding sites. If there was age-specific site occupation where adults breed in habitats with earlier local resource phenology, then given our findings that adults breed earlier than juveniles regardless of local phenology, we would expect an even greater difference between the absolute breeding timing of juveniles and adults at the population-level. Instead, the difference in average breeding timing between juveniles and adults is similar whether assessing local breeding timing mismatch or absolute breeding timing, suggesting earlier breeding in adults is driven by advancement relative to their local average phenology across which there is not age-specific occupation.

Given theories of increasing reproductive performance with age under the constraint hypothesis, this might suggest that adults with greater experience advance their lay dates to enhance breeding performance (Harvey et al. 1979b; Perrins & McCleery 1985, 1989), such as through better matching breeding with temporally-variable resource distributions, even when there is fine-scale phenological variation (Cole et al. 2021; Hinks et al. 2015). This is

consistent with findings in other age-related reproductive behaviours in closely-related blue tits *Cyanistes caeruleus*, where adults use knowledge from previous breeding of average patch reproductive success to make decisions regarding settlement, whereas juveniles are unable to do so as they lack breeding experience (Parejo et al. 2007). However, implicit in this suggestion would be that advancement of breeding timing leads to better precision of matching chick rearing behaviour with local resource phenology, whereas in fact advancement could represent cases where breeding occurs so early that there is a mismatch between peak energetic demand of offspring and resource availability. Future work could decouple age-related advancement of breeding timing with increasing precision to local resource phenology through more detailed data collection of phenological timing across multiple trophic levels at local scales across phenologically-variable environments.

Irrespective of their neighbourhood age structure, we find that juvenile great tits lay later relative to both the population average, and the average of its local environment. This suggests that birds undertaking their first reproductive attempts do not use social cues to adjust breeding timing. Adult great tits breed earlier on average (Harvey et al. 1979b; Perrins 1965; Sæther 1990), and as shown in the present study, earlier breeding exhibited by adults occurs even when accounting for fine-scale phenological variation across territories. Therefore, if juveniles were to use social cues from neighbours to adjust their own timing, we would expect differences among their lay dates depending on whether they are mainly exposed to adult or juvenile neighbours, or if they exist in areas of low density and thus have little social opportunity. However, despite the extent of the data used here, we find no evidence of social cues affecting breeding timing in juveniles.

The fact that there is no evidence of juveniles copying the breeding timing of conspecifics is interesting given the wider socio-ecology of great tits and other short-lived territorial species. This is because tit *Paridae* species often show age-specific trends where younger individuals rely more on copying conspecifics in behaviours associated with foraging (Aplin et al. 2017), and are more plastic in changing such behaviours in response to social cues (Aplin et al. 2012, 2013). However, we find no evidence that juveniles copy phenological timing behaviour in the same way. This suggests that juveniles instead predominantly use cues within their physical environment to time breeding, such as budburst in local tree species or increasing temperatures (Reed et al. 2010).

While it is expected that younger individuals have less

experience-based information of when to time breeding attempts, this does not explain why they show limited ability to use social cues from those in their breeding environment. This may be driven by lower phenotypic plasticity in juveniles. For example, recent work shows that juvenile blue tits show minimal phenotypic plasticity with regards to adjusting lay date to temperature (Bonamour et al. 2020). It is suggested that younger individuals may have not accumulated enough resources to adequately modulate laying date in response to temperature, which for example might require an earlier onset of egg production (Nilsson & Råberg 2001; Perrins 1996; Visser & Lessells 2001). Therefore, the same might be the case here, where juveniles are unable to adjust their laying date in response to the timing of more experienced neighbours due to the associated energetic cost.

We find a greater difference in breeding timing among adults depending on the age structure of their neighbourhoods compared to juveniles. Specifically, we find that breeding timing relative to the entire population is later in adults with either no or only adult neighbours. When breeding timing is calculated accounting for local phenological variability, adults with juvenile, mixed-age cohort or no neighbours breed earlier (and with a greater mismatch to the box-level average) compared to those with only adult neighbours (Fig. 3). The difference in breeding timing in adults with no neighbours depending on whether this is calculated accounting for local phenological variation or not highlights the potential for estimates of age-related breeding timing to be biased based on fine-scale phenological variability. Specifically, when comparing against a within-year population average, adults with no neighbours breed later than those in juvenile or mixed age-cohort neighbourhoods. However, accounting for average phenological variation across territories, adults with no neighbours are more similar in their relative breeding timing to those with juvenile neighbours. When assessing the relationship between the number of neighbours and the average phenological timing of nest-boxes in the long-term, we find that there is a relationship where boxes with fewer neighbours are timed slightly later on average (Fig. S3). This is likely driven by habitat heterogeneity within the study site, where areas of high nest-box density tend to be in regions with habitat features associated with earlier phenology (i.e. lower altitude and nearer the woodland edge, Fig. S4; Wilkin et al. 2007a, 2007b). It is unlikely that this relationship is confounded with age-biased use of territories over time, as there is no temporal repeatability in age-specific occupation of nest-boxes in this study system

(Woodman et al. 2024a).

Previous research has suggested that in seasonally-breeding species, selection might act to promote early breeding to increase reproductive success (Arnold et al. 2004; Perrins 1970; Verhulst & Tinbergen 1991). However, breeding later than this optimum is frequently observed, suggesting that there are either physiological constraints that prevent individuals breeding when reproductive output is maximised, or breeding time is the outcome of an optimisation process where there are sometimes fitness costs associated with early breeding (Arcese & Smith 1988; Brown & Brown 2000; Davies & Lundberg 1985; Nager & van Noordwijk 1992; Nilsson 1994; Perrins 1996). However, the proximate mechanisms that might induce trade-offs in breeding timing are still not well understood.

Our finding of differences in average breeding timing among adults depending on their neighbourhood age structure might provide initial evidence that social mechanisms are involved in the trade-off associated with breeding timing. One such social mechanism might be related to how familiarity among territorial neighbours can increase reproductive success during synchronised breeding events (Akçay et al. 2009; Frostman & Sherman 2004; Grabowska-Zhang et al. 2012b; Siracusa et al. 2021). Given that adults are more likely to be familiar with each other from previous breeding and winter flocking behaviour compared to juveniles or mixed age-cohorts (Gokcekus et al. 2023), we might expect their neighbourhoods to synchronise breeding to obtain mutual benefits, such as cooperative nest defence (Grabowska-Zhang et al. 2012a). Synchronised breeding among individuals might induce on average later breeding than the local optimum, where individuals which could breed earlier delay egg laying to match with their neighbours. Indeed, research using captive starlings *Sturnus vulgaris* found that adults housed next to experimentally-induced late breeders (through food rationing) delay their own laying to synchronise with the experimental birds, whereas a control group that was isolated from the rationed birds bred earlier (Meijer & Langer 1995). This finding, in combination with the suggestions made here, point to a potential socially adaptive mechanism that promotes on average later breeding to increase reproductive synchronisation among adults.

Alternatively, delayed breeding among adults with adult-biased breeding neighbourhoods might be driven by non-adaptive mechanisms. In this case, instead of later laying being a result of a trade-off between early and later breeding to maximise reproductive success, non-adaptive delayed breeding might occur due to age-specific social

mechanisms. For example, in many taxa, older individuals are dominant in competitive interactions, allowing them to monopolise resources (Piper 1997; Poston 1997; Sol et al. 2000; Woodman et al. 2024b), including in great tits (Krebs 1971, 1982; Sandell & Smith 1991). Therefore, adult great tits that either have no neighbours in areas of low density, or acquire territories near subdominant juvenile neighbours, might be able to breed earlier due to their social dominance or lack of competition. This might allow dominant adults to monopolise local food resources thus reaching the necessary energetic demands for egg laying at earlier dates (Nager & van Noordwijk 1992; Perrins 1996; Visser & Lessells 2001).

Alternatively, socially dominant adults might acquire breeding territories at earlier dates, particularly if this territory was occupied in previous years (Greenwood et al. 1979; Harvey et al. 1979a), allowing for earlier egg-laying compared to subdominant neighbouring individuals that take longer to acquire territories. In these cases, adults breeding in adult-biased breeding environments might experience greater competition, delaying the rate at which they can obtain critical breeding resources and leading to later average lay dates. This is consistent with findings that suggest higher breeding densities lead to greater competition, thus delaying lay dates in territorial species (Wilkin et al. 2006). Future research would ideally use experimental manipulations to disentangle the relative role of adaptive versus nonadaptive mechanisms in mediating breeding timing in territorial species depending on local age structure and familiarity among older individuals. Further, experiments could be used to separate out the roles of age *per se* versus familiarity (i.e. either social familiarity from previous association with neighbours, or environmental familiarity with the breeding location from prior reproduction) in driving differences in breeding timing among adults. However, these sorts of experiments are complex and may not be possible to carry out in wild systems such as the one used in this study.

The findings presented here may be relevant in the context of the effects of climate change on breeding phenology. Over recent decades, climate change has advanced the timing of phenological events due to earlier and warmer temperatures (Davis et al. 2005; Visser & Both 2005; Zettle-moyer & DeMarche 2022). In some cases, this has advanced interacting species' phenological events to different extents, leading to phenological asynchrony where seasonal breeding in one species occurs later than peak abundance of resources from another (Radchuk et al. 2019; Renner & Zohner 2018; Visser & Gienapp 2019). This poses a

considerable potential concern for birds in a deciduous tree–caterpillar–passerine–bird food chain, such as great tits, where there is evidence for an evolved response to climate-induced changes in phenology (Both et al. 2004, 2009; Burgess et al. 2018; Dunn et al. 2010; Marrot et al. 2018; Simmonds et al. 2020; Visser et al. 1998, 2004, 2006). Given large-scale climatic changes to phenology, it is important to understand potential drivers of plasticity in populations due to processes operating at various levels, such as the suggestions made here of persistent age-specific differences in the timing of breeding, reduced plasticity in juveniles manifested as an inability to copy experienced adults in their social environment, and differences among adult lay dates associated with local age structure.

Further, age effects on phenology at the individual- and neighbourhood-level might be relevant given our current understanding of the effects of climate on population demography. Short-lived seasonally-breeding species show profound fluctuations in population age structure (Gamelon et al. 2016; Woodman et al. 2022). For example, the age structure of breeding great tit populations in a given year can range from being almost entirely composed of adults to being almost 90% juvenile individuals, which appears to be linked to climatic variation affecting age-specific survival and recruitment (Woodman et al. 2024c). As such, climate change induced changes to population age structure might be synergistic in their effects on population reproductive output. This is because fluctuations in age structure affect output due to age-specific reproduction and density dependent dynamics (Bouwhuis et al. 2009, 2010; Gamelon et al. 2016; Perrins & McCleery 1985), but also because population-level matching to changes in phenology may be affected by the overall distribution of age and how age is spatially-structured within a population, given our findings presented here. Future work should further our understanding on how climatic induced changes to age structure in wild populations affects population-level reproductive output mediated by phenological synchrony, how this is influenced by within-population structuring of age, and whether the sensitivity of breeding timing given local age structure is affected by spatio-temporal environmental variability.

## 5 CONCLUSIONS

Using long-term data from a wild territorial bird species in which reproductive success is mediated by phenological timing, we show that adult individuals breed earlier than juveniles even when accounting for fine-scale local phenological variability, thus providing evidence of in-

creased phenotypic plasticity in adults consistent with the constraint hypothesis. We find no evidence that the age structure of breeding neighbourhoods affects the timing of reproduction in younger individuals breeding for the first-time in their life-history, suggesting that such individuals do not use social cues when timing breeding, possibly due to reduced phenotypic plasticity. In contrast, we find that local age structure relates to reproductive timing in adults, where relatively later breeding is observed when their neighbours consist of other older individuals. This could be underpinned either by adaptive mechanisms, where increased familiarity leads to synchronised later breeding to obtain joint benefits, or nonadaptive mechanisms, where greater competition delays breeding. Our study provides a framework to study how social mechanisms influence reproductive timing in territorial breeding populations, not just with regard to age, but other individual-level traits and site-level attributes. Finally, we highlight the potential for climate change to have complex synergistic effects on wild population dynamics, not just by altering average phenological timing across a population, but also because changes to overall population age structure induced by environmental change will influence within-population structuring of age and population-level phenological synchrony.

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# The influence of age and social interactions on plasticity in breeding phenology in a wild bird population - SUPPORTING INFORMATION

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## 1 SUPPLEMENTARY METHODS

In addition to calculating average lay date given local phenological variation by taking the median lay date at the box-level, we additionally defined local average breeding timing by taking the median of all year-centred lay dates 1965–2023 associated with all nest-boxes found within 75m of (and including) the focal nest-box. The foraging range of breeding great tits is estimated as 75m (Barnes 1975; Naef-Daenzer 2000; Wilkin et al. 2007). As such, within any year, there are unoccupied boxes in areas of high nest-box density which are largely associated with the same local environment when occupied in the long-term. Calculating average local breeding timing through this method, in addition to the individual box-level, therefore corrects for potential biases that are obtained at the box-level since boxes in areas of higher density are occupied less (Woodman et al. 2024), but retains local environmental differences in tree bud-burst phenology which are positively correlated within distances less than 100m (Hinks et al. 2015; Table S2 for all results; Fig. S5).

As well as modelling absolute lay date and breeding timing mismatch depending on the age type of a focal individual's neighbourhood (all juvenile, all adult, mixed, or no neighbours), we also constructed models to estimate the marginal effects of local age structure on breeding timing defined by the proportion of adult neighbours. We suggest that the methods used in the main text are more biologically meaningful in that it allows us to include focal individuals with no neighbours in the same model (whereas in this case, such individuals are removed, such that they are not treated the same as individuals with only juvenile neighbours, i.e. 0% adult neighbours; Table S3 for results; Fig. S6).

## 2 SUPPLEMENTARY TABLES

Table S1 – Model structure for predicting age-specific breeding timing depending on the age structure of a local breeding neighbourhood as used in the main text.

| Response variable                                                                            | Fixed effect                                                              | Interaction term                     | Random effects               |
|----------------------------------------------------------------------------------------------|---------------------------------------------------------------------------|--------------------------------------|------------------------------|
| (1) Absolute breeding timing                                                                 | Neighbourhood age type (all juvenile, all adult, mixed, or no neighbours) | Age of focal female (juvenile/adult) | Year, nest-box ID, female ID |
| (2) Breeding timing compared to average of focal nest-box ('local breeding timing mismatch') | Neighbourhood age type (all juvenile, all adult, mixed, or no neighbours) | Age of focal female (juvenile/adult) | Year, nest-box ID, female ID |

Table S2 - Posterior predictions from Bayesian regression models modelling breeding timing (either absolute breeding timing; local breeding timing mismatch at the box-level; or local breeding timing mismatch at the 75m radius level) by neighbourhood age structure (either all juveniles; all adults; mixed age-cohorts; or no neighbours) depending on focal female age (either juvenile or adult). We report the posterior median with 95% credible intervals.

| Model                                             | Focal female age | Neighbourhood age structure | Posterior median | 95% credible intervals |
|---------------------------------------------------|------------------|-----------------------------|------------------|------------------------|
| Absolute breeding timing                          | Adult            | All adult                   | -1.213           | [-1.495, -0.926]       |
|                                                   |                  | All juvenile                | -1.802           | [-2.078, -1.526]       |
|                                                   |                  | Mixed                       | -1.951           | [-2.283, -1.612]       |
|                                                   |                  | No neighbours               | -1.353           | [-1.578, -1.126]       |
|                                                   | Juvenile         | All adult                   | 0.929            | [0.638, 1.213]         |
|                                                   |                  | All juvenile                | 0.668            | [0.402, 0.924]         |
|                                                   |                  | Mixed                       | 0.481            | [0.160, 0.797]         |
|                                                   |                  | No neighbours               | 0.780            | [0.569, 0.986]         |
| Local breeding timing mismatch (box-level)        | Adult            | All adult                   | -0.331           | [-0.628, -0.004]       |
|                                                   |                  | All juvenile                | -0.831           | [-1.118, -0.536]       |
|                                                   |                  | Mixed                       | -0.667           | [-1.008, -0.335]       |
|                                                   |                  | No neighbours               | -0.629           | [-0.857, 0.407]        |
|                                                   | Juvenile         | All adult                   | 1.723            | [1.429, 2.019]         |
|                                                   |                  | All juvenile                | 1.450            | [1.1183, 1.718]        |
|                                                   |                  | Mixed                       | 1.477            | [1.146, 1.800]         |
|                                                   |                  | No neighbours               | 1.308            | [1.089, 1.520]         |
| Local breeding timing mismatch (75m radius level) | Adult            | All adult                   | -0.283           | [-0.576, 0.004]        |
|                                                   |                  | All juvenile                | -0.890           | [-1.171, -0.609]       |
|                                                   |                  | Mixed                       | -0.675           | [-1.013, 0.344]        |
|                                                   |                  | No neighbours               | -0.644           | [-0.875, -0.415]       |
|                                                   | Juvenile         | All adult                   | 1.864            | [1.564, 2.170]         |
|                                                   |                  | All juvenile                | 1.508            | [1.261, 1.774]         |
|                                                   |                  | Mixed                       | 1.593            | [1.277, 1.917]         |
|                                                   |                  | No neighbours               | 1.327            | [1.110, 1.540]         |

Table S3 – Marginal effects from Bayesian regression models modelling breeding timing (either absolute breeding timing; local breeding timing mismatch at the box-level; or local breeding timing mismatch at the 75m radius level) by the proportion of adult neighbours depending on focal female age (either juvenile or adult. We report the posterior median with 95% credible intervals.

| Model                                      | Focal female age | Marginal effect | 95% credible intervals |
|--------------------------------------------|------------------|-----------------|------------------------|
| Absolute breeding timing                   | Adult            | 0.464           | [0.006, 0.919]         |
|                                            | Juvenile         | 0.294           | [-0.163, 0.757]        |
| Local breeding timing mismatch (box-level) | Adult            | 0.428           | [-0.008, 0.877]        |
|                                            | Juvenile         | 0.292           | [-0.155, 0.741]        |
| Local breeding timing mismatch (box-level) | Adult            | 0.521           | [0.052, 0.980]         |
|                                            | Juvenile         | 0.380           | [-0.080, 0.820]        |

### 3 SUPPLEMENTARY FIGURES

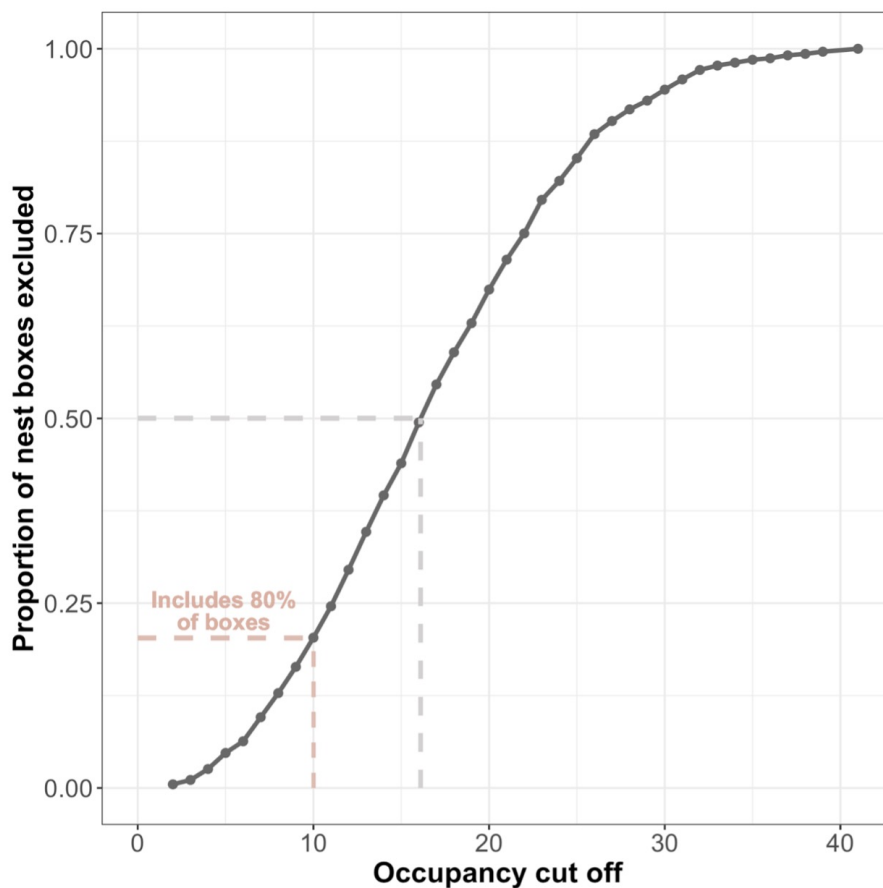


Fig. S1 - The proportion of boxes that would be excluded from our dataset if increasingly stricter occupancy cut off points are used. The grey dashed line indicates an occupancy cut off of 16 times which would exclude 50% of boxes. We decided to use a cut off of 10 times, indicated by the pink line, which leads to the exclusion of 20% of boxes, leaving 80% of the total boxes left to include in the analysis.

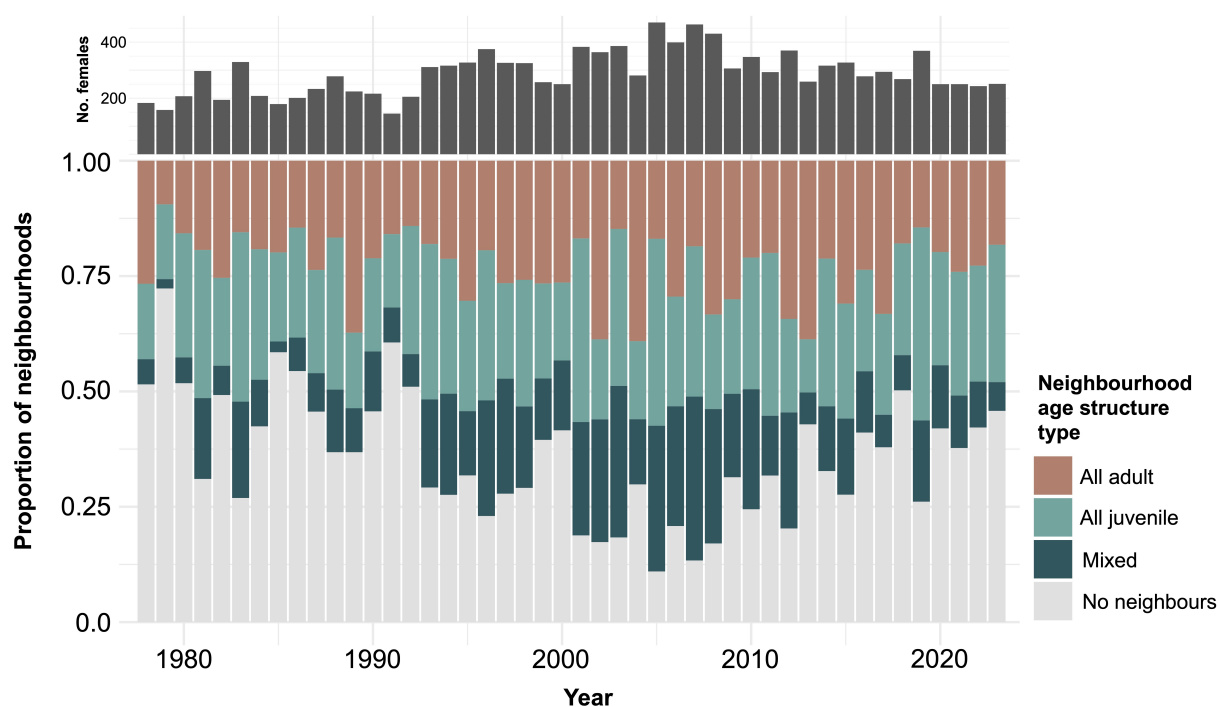


Fig. S2 - The proportion of each annual breeding population consisting of different neighbourhood types and female population size 1978–2023.

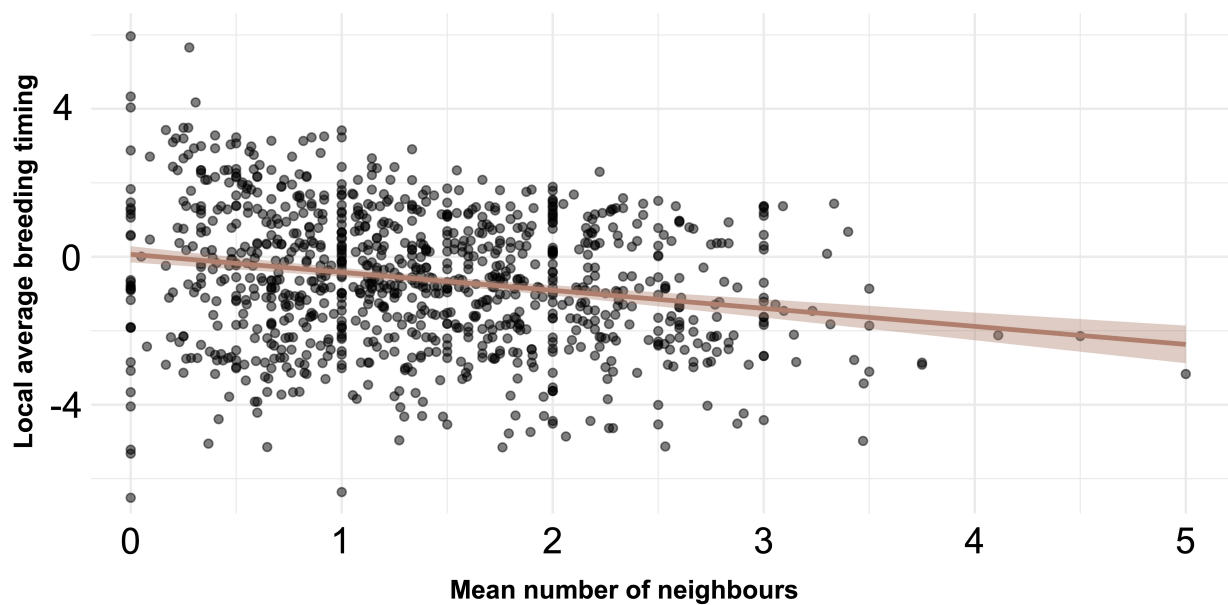


Fig. S3 - Relationship between the mean number of neighbours (individuals found breeding within 75m) and the local average breeding timing for each nest-box. There is a weak negative relationship between these two variables (Spearman's correlation:  $r = -0.119$ ,  $p < 0.01$ ).

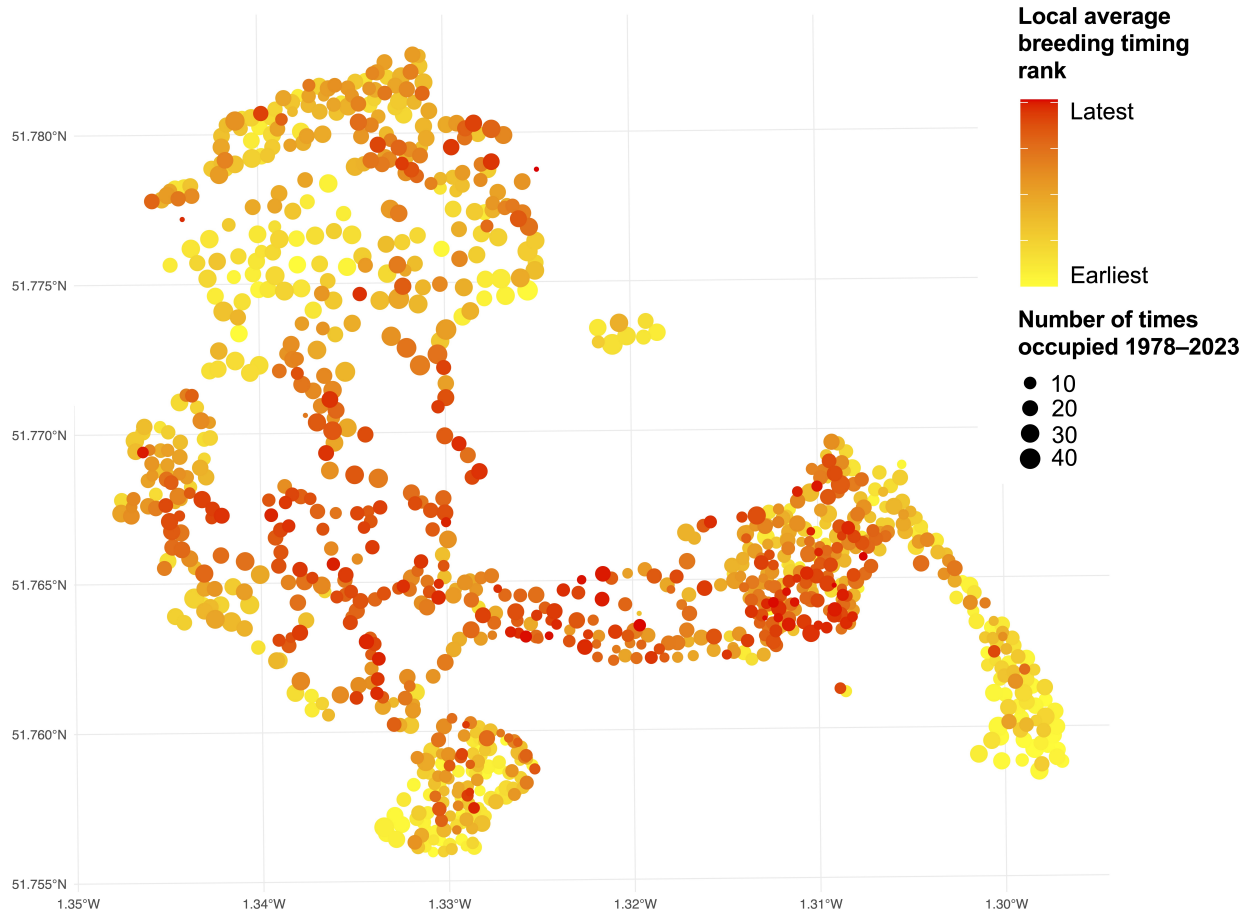


Fig. S4 - Map of nest-boxes across Wytham Woods, with colour on a scale of yellow–red representing the average timing of each nest-box from earliest to latest (i.e. median year-centred lay date of each nest-box), and point size relative to the number of times it has been occupied. As seen, there are regions of the study site where nest-box density relates to the local average timing, due to habitat heterogeneity across the woods. For example, the south-east corner has high box density, but also has early average breeding timing due to lower altitude and being closer to the woodland edge. In contrast, the central south region of the woods has later average timings due to being higher altitude and further from the edge, and this region also has lower than average nest-box density.

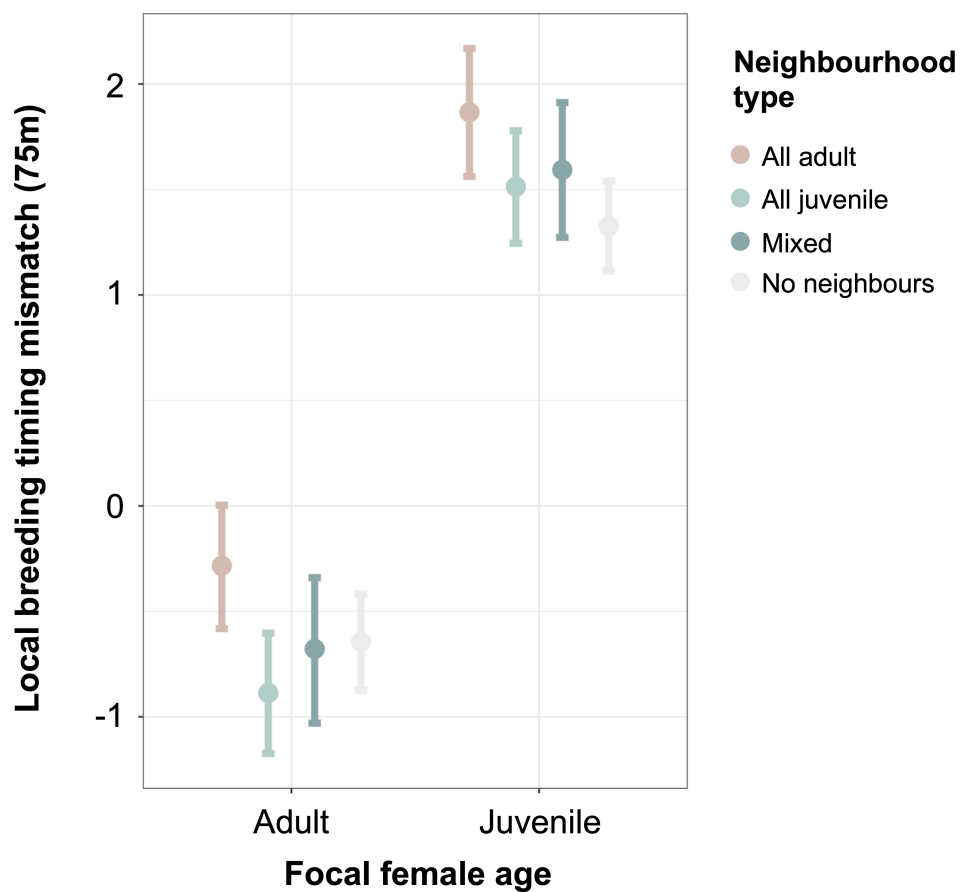


Fig. S5 - Marginal predictions from models using local breeding timing mismatch defined using a 75m radius as opposed to at the box-level. This model shows very similar results to the model that uses box-level mismatch, where adults breed on average 2 days earlier than juveniles. Adults with all adult neighbours slightly later breeding and a reduced mismatch (closer to 0) compared to adults with all juvenile neighbours, with those with a mixed age neighbourhood spanning across these two categories. Juveniles did not show much difference in local breeding timing mismatch depending on the age structure of their neighbourhood.

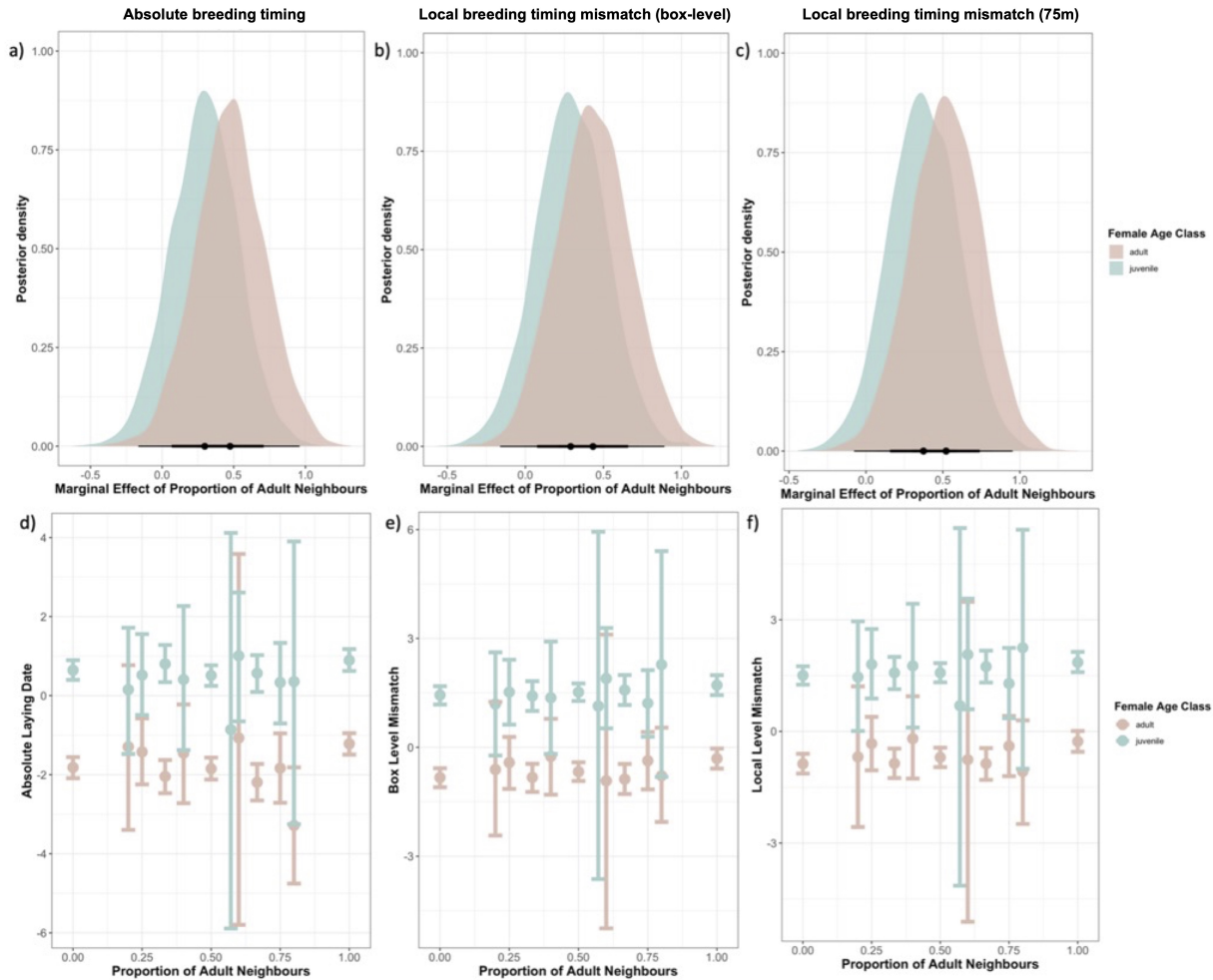


Fig. S6 - The top row of plots shows the marginal effects posterior density of the proportion of adult neighbours on breeding timing as a) absolute breeding timing, b) local breeding timing mismatch calculated at the box-level and c) local breeding timing mismatch calculated at the 75m radius level. The bottom row of plots shows a binned representation of the marginal predictions from the same models as the top row, d) absolute breeding timing, e) local breeding timing mismatch calculated at the box-level and f) local breeding timing mismatch calculated at the 75m radius level.

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# Chapter VI

## Continent-wide drivers of spatial synchrony in age structure across wild great tit populations

*Submitted:*

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# Continent-wide drivers of spatial synchrony in age structure across wild great tit populations

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## ABSTRACT

Spatio-temporal variation in age structure influences population dynamics, yet we have limited understanding of the spatial scale at which its fluctuations are synchronised between populations. Using 32 great tit populations, spanning 3200km and >130,000 birds across 67 years, we quantify spatial synchrony in breeding age structure and its drivers. We show that larger clutch sizes, colder winters and summers, and larger beech crops lead to younger populations. We report distant-dependent spatial synchrony of age structure, which is maintained at approximately 650km. Despite covariation with age structure, reproductive and environmental variables do not influence the scale of synchrony, except for a moderate effect of beech masting. We suggest that local ecological and density-dependent dynamics impact how environmental variation interacts with age structure, influencing estimates of the environment's effect on spatial synchrony. Our analyses demonstrate the operation of synchrony in age structure over large scales, with implications for age-dependent demography in populations.

which affects the number of individuals within different cohorts (Koons et al. 2016; Rollinson et al. 2021). While a considerable amount of research has identified within-population temporal variation in age structure (Coulson et al. 2004, 2005; Gamelon et al. 2016), relatively little is known about the spatial scale at which age structure varies, whether temporal dynamics differ between populations, and what between-population differences in fluctuations in age structure suggest about the drivers of its variation.

Spatial synchrony is the concurrent change in time-varying characteristics of spatially-distinct populations (Bjørnstad et al. 1999a; Liebholt et al. 2004), which operates across many animal populations (Elton 1924; Moran 1953; Wan et al. 2022). Spatial synchrony can be important for population stability (Paradis 1997; Ruxton 1994), but highly synchronous dynamics may impose a risk of species extinction if density crashes occur simultaneously (Heino et al. 1997). Research has identified spatial synchrony in survival (Olmos et al. 2020), body mass (Herfindal et al. 2020), breeding success (Olin et al. 2020; Vriend et al. 2023), phenological timing (Vriend et al. 2023), and population size (Bjørnstad et al. 1999a; Hansen et al. 2020; Koenig 1999), particularly in birds (Mortelliti et al. 2015; Paradis et al. 1999, 2000; Sæther et al. 2007). However, despite the interrelated dynamics between variation in population growth and age structure, there has been little research into spatial synchrony of age structure and the mechanisms that might drive this.

Spatial synchrony arises from three primary mechanisms: dispersal between populations (Kendall et al. 2000; Ripa 2000); interspecific trophic interactions with other organisms that are themselves spatially synchronised (Ims & Andreassen 2000; Jones et al. 2003; Selås 1997); or a common influence on populations from environmental variables that are correlated in space – known as the “Moran effect” (Hudson & Cattadori 1999; Moran 1953; Ranta et al. 1997). Understanding the spatial scale at which population age structure co-fluctuates will provide insight into whether any of these mechanisms drive spatial syn-

## 1 INTRODUCTION

Age-specificity in individual-level traits means that variation in population age structure can feed through to affect various population processes. For example, variation in age structure influences population-level social functioning (Siracusa et al. 2023; Woodman et al. in press), while population growth rate is affected by variation in age structure (Caswell 2000; Sibly & Hone 2002). Further, the influence of age structure on population vital rates is self-reinforcing, in that when demographic rates change, this affects the number of individuals that are recruited and die. Thus, variation in age structure is fundamentally driven by non-stationarity, which arises intrinsically as population demographic rates vary, but also from environmental variability

chrony in age structure. This is particularly important considering climate change is increasingly impacting wild populations through effects on survival (Parmesan 2006) and other population dynamics (Hansen et al. 2020; Ozgul et al. 2010). Thus, gaining insight of spatial synchrony in age structure due to environmental regulation is relevant for understanding the effects of climate change on natural population dynamics, particularly considering that highly synchronous age structure dynamics might induce simultaneous density crashes and prevent the possibility of demographic rescue (Engen et al. 2002; Mills 2012).

In this study, we assess spatial synchrony of variation in age structure across 32 European great tit populations. We first assess whether fluctuations in age structure are explained by reproductive and environmental factors that vary at different spatial scales. Second, we quantify whether temporal fluctuations in age structure depend on distance between populations, and whether such spatial synchrony is explained by variation in reproductive and environmental variables. By assessing the influence of separate explanatory variables, we identify how aspects of reproductive and environmental variability differentially influence variation in age structure, and their role in synchronising population dynamics.

## 2 METHODS

### 2.1 Study system and data collection

The great tit *Parus major* is a passerine bird found in mixed woodlands across much of the Western Palearctic. Their reproductive lifespan ranges from 1–9, averaging 1.8 years, with breeding performance peaking at 2.8 years (Bouwhuis et al. 2009; Woodman et al. 2022). Although there are some continuous changes with age (Bouwhuis et al. 2009), the main age effects on many individual-level traits are captured by two age-classes: first-years (hereafter juveniles) and older (hereafter adults, Gosler 1993; Harvey et al. 1979; Perrins 1979). Great tits are annual breeders with a single breeding season April–June, when they generally undertake one breeding attempt (in some parts of their range second clutches can occur, Verhulst 1998; Visser et al. 2003). Data used here are from 32 populations (Fig. 1), the geographical range of which represents a large part of the species’ breeding range (Sullivan et al. 2009). Generally, data collection at these sites included regular visits to nest-boxes during breeding to track reproductive attempts, individually mark chicks and adults, and record their morphometrics, sex and age. Age is based either on year of hatching for local birds, or plumage characteristics

for immigrants, where juveniles and adults can be discriminated based on retention of juvenile feathers in the wing (Svensson 1992). Metadata for populations can be found through the Studies of Populations of Individual Birds ([www.spibirds.org](http://www.spibirds.org), Culina et al. 2021).

### 2.2 Variation in age structure

We assigned age to all breeding great tits with known identity, across which exact year of hatching (birds caught within their first year) was known for 82.5% of 135,967 captures. Birds first captured with adult plumage were assigned a minimum age of 2 and included in analyses, with subsequent age estimates based on this (15.3% and 20.1% of females and males; given annual mortality rates >50% this assumption is likely to be accurate in most cases – also, in these cases, individuals can still accurately be designated as ‘juvenile’ or ‘adult’). Age was assigned to 62.1% of parents where at least one egg was laid (due to a combination of some studies’ protocols not always including adult identification, nests failing prior to adult capture, and unsuccessful trapping attempts, parental identity was unknown in some cases).

For each annual breeding population, we calculated the proportion of juveniles found breeding (additionally, we calculated: mean population age; proportion of senescent individuals; and change in these structures compared to a running mean as alternative descriptors of age structure, supporting information). We calculated this for every annual population, but only used data from years where the population included at least 20 individuals (mean, IQR: 230, 60–356) and >25% of the population was aged (mean, IQR: 56.0%, 36.1–78.2%). In total, the study period spanned 1956–2022, collectively consisting of 702 study years and 131,150 captures of 77,964 breeding individuals.

### 2.3 Reproductive and environmental variables

We assessed how reproductive and environmental variables that vary at different spatial scales relate to variation in age structure. First, we considered the influence of within-population average clutch size in year  $t - 1$  on population-specific age structure in year  $t$ . We would expect variation in annual mean clutch size to affect the age structure of the following breeding season, where large average clutch sizes would lead to more recruits (Ahola et al. 2009) and therefore a higher proportion of breeding juveniles in the next year, thus we test this prediction here. We calculated population-level average clutch size as the mean number of eggs produced per breeding attempt within a breeding season.



Fig. 1. Map of the 32 great tit study populations across Europe, with point size relative to the number of years in the time series. The box in the top left shows the populations in The United Kingdom, Belgium, and The Netherlands in closer detail. Information for each study population can be found in Table S1.

Second, we considered two climatic variables: temperature and precipitation. We calculated the average mean daily temperature ( $^{\circ}\text{C}$ ) and the average daily precipitation sum (mm) across four periods preceding the focal breeding season for each population: June–August (hereafter summer); September–November (autumn); December–February (winter); and March–May (spring). We also considered the frequency of extreme climatic events (ECEs) by calculating the number of ‘cold ECEs’ June–May; and the number of ‘hot ECEs’ June–May. We define ECEs as events with a  $<5\%$  probability of occurrence across the entire study period (1956–2022) in each population separately (Marrot et al. 2017; Moreno & Møller 2011). Thus, a cold ECE occurred when minimum daily temperature reaches below the 5% threshold June–May; and a hot ECE as when maximum daily temperature reaches above the

95% threshold.

Third, we considered European beech *Fagus sylvatica* masting, an environmental variable which is generally understood to vary at a large spatial scale. Beech masting is the annual production of seeds (Kelly 1994), which constitute part of the winter diet of great tits, thus influencing survival, particularly among juveniles (Källander 1981; Perdeck et al. 2000). The distribution of beech does not extend across the entire range of populations assessed here, and in southern Europe is restricted to higher altitudes (Bolte et al. 2007). However, masting-related demographic fluctuations in tits are synchronised across regions with and without beech. This suggests beech masting may be correlated with fruiting of other tree species important for survival, such that years with a large beech crop are rich in other food resources, promoting survival across different

habitats (Klomp 1980; Perrins 1966). Thus, for each annual population, we obtained a masting value from a long-term continental-scale dataset of beech masting time series up to 2017 (MASTREE+, Hacket-Pain et al. 2022), using the masting value from a data collection site closest to that of each population in the year preceding breeding. The central coordinates for all sites were less than 1500km from the focal breeding population, which is the spatial scale at which masting remains synchronised (Bogdziewicz et al. 2021), and most were much closer (median, IQR: 143.2km, 87.6–297.0km). To assess the influence of masting at a more local scale, we created a subset of populations within the distribution of beech (Fig. S1) and where annual data was collected within 100km of the population (12 populations,  $n = 188$  population-years; further details for reproductive and environmental variables in supporting information).

#### 2.4 Temporal variation in age structure and explanatory variables

First, we investigated the effects of the reproductive and environmental variables on population age structure. For each explanatory variable we constructed a linear mixed-effects model of the form

$$y_{i,j} = \beta_{\text{int}} + u_{\text{int},i} + (\beta_{\text{expl}} + u_{\text{expl},i})Z_{i,j} + \epsilon_{i,j} \quad (\text{Equation 1})$$

where  $y$  is the proportion of juveniles per population  $i$  and year  $j$ ,  $\beta_{\text{int}}$  is an intercept,  $u_{\text{int},i}$  denotes random intercepts for each population assumed to have a normal prior distribution with mean 0 and standard deviation  $\sigma_{u_{\text{int}}}$ ,  $\beta_{\text{expl}}$  is a slope for the explanatory variable,  $u_{\text{expl},i}$  denotes random slopes for the explanatory variable for each population also assumed to have a normal prior distribution,  $Z_{i,j}$  is the explanatory variable for each annual population, and  $\epsilon_{i,j}$  is the residual error, assumed to have a normal prior distribution. This model was run for the 13 explanatory variables separately, as many of the environmental variables are highly correlated, thus leading to multicollinearity issues and making the interpretation of individual effects challenging.

These models were run using *brms* version 2.18.0 (Bürkner 2017). We used default priors and ran four Markov chains for 6000 iterations with a burn-in of 3000, resulting in 12000 posterior samples. Chain convergence was evaluated using the diagnostic  $\hat{R}$  and effective sample size (Vehtari et al. 2021). We also ran the same models using alternative age structure descriptors (supporting information). The explanatory variables and age structure descrip-

tors were z-normalised such that their relative effects could be assessed.

#### 2.5 Spatial synchrony of variation in age structure

Second, we analysed whether age structure fluctuations are spatially synchronous, and whether this is explained by variation in the reproductive and environmental variables. Following Engen et al. (2005), we calculated a spatial autocorrelation function of the form

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

where  $\rho_0$  and  $\rho_{\infty}$  are estimates of the correlation of age structure as distance approaches zero and infinity, respectively;  $e^{d^2/2l^2}$  is a Gaussian positive definite autocorrelation function where  $d$  is distance between populations (in kilometres), and  $l$  is the standard deviation representing a standardised measure of the scale of spatial autocorrelation, i.e. the characteristic spatial scale at which temporal variation of an ecological property remains correlated (Jarillo et al. 2018; Lande et al. 1999). This model assumes that the spatial autocorrelation structure is Gaussian and that the parameters  $\rho_0$ ,  $\rho_{\infty}$  and  $l$  are positive (as described in Engen et al. 2002; Lande et al. 1999). While it is possible that correlation in age structure between any two populations is negative, here we assume that correlation on average cannot be below zero. Modelling negative correlations on average is possible through non-parametric approaches (e.g. Bjørnstad et al. 1999b), but it is well established that using the parametric approach applied here is beneficial when assessing widescale spatial synchrony in ecological variables (Bjørnstad et al. 1999a; Engen et al. 2005; Vriend et al. 2023). The advantage is that the model parameters have a biological interpretation which can be compared when considering synchrony of various demographic traits and, importantly, potential drivers of this synchrony can be quantitatively assessed.

The normalised age structure variables of all populations in each year were assumed to have a multivariate normal distribution where  $\tilde{y}_t \sim \text{MVN}(0, \Sigma_t)$ . The diagonal elements of the variance-covariance matrix were set to 1, and the off-diagonal elements were defined by  $\rho_0$ ,  $\rho_{\infty}$  and  $l$  given distance  $d$  between populations. Data from different populations were collected over a variable number of years, thus time series that overlap for longer were given more weight in the likelihood calculation. Overall log-likelihood was the sum of annual log-likelihoods optimised numerically to provide estimates for  $\rho_0$ ,  $\rho_{\infty}$  and  $l$ . The distributions of these spatial synchrony parameters were obtained

by parametric bootstrapping involving simulation from the multivariate normal distribution, based on the yearly set of populations in the data and the estimated spatial synchrony parameters (Engen et al. 2005; Lillegård et al. 2005). This was undertaken 2000 times, resulting in 2000 bootstrap replicates. The multivariate normal distribution was constructed using *mvtnorm* version 1.1-3 (Genz et al. 2021).

Finally, we assessed the influence of reproductive and environmental variables in explaining spatial synchrony of age structure. Following previous methods (e.g. Grøtan et al. 2005; Sæther et al. 2007; Vriend et al. 2023), the proportion of juveniles in each annual population was regressed against population-specific explanatory variables in separate linear models. The residuals from these were then normalised and used as the variable of interest in the spatial synchrony model (Equation 2). This allowed us to calculate synchrony in age structure once the effects of the explanatory variables have been accounted for. All analysis was run in R statistical software version 4.2.2 (R Core Team 2021).

### 3 RESULTS

#### 3.1 Temporal variation in age structure and explanatory variables

We found marked temporal variation in age structure, with the annual proportion of juveniles ranging 0–0.89 across the 32 breeding populations over 1956–2022, and a very weak trend toward smaller proportions of juveniles found breeding over time ( $n = 702$  population-years; supporting information; Fig. S3a). We found that increased average annual clutch sizes were associated with a larger proportion of breeding juveniles the following year (posterior mode [95% credible intervals]: 0.437 [0.310, 0.553]).

Variation in age structure related to climatic factors, where breeding populations with a smaller proportion of juveniles followed warmer summers (−0.216 [−0.405, −0.038]) and winters (−0.250 [−0.436, −0.053]), and years with more frequent hot ECEs (−0.101 [−0.186, −0.016]). However, we found no effect of precipitation. Breeding populations had higher proportions of juveniles in years that followed winters with a large beech crop (0.225 [0.130, 0.314]). Moreover, this positive relationship was stronger when only assessing populations within 100km of the beech data collection site (0.365 [0.204, 0.538]; Fig. 2; Table S2).

#### 3.2 Spatial synchrony of variation in age structure

We found moderate spatial synchrony in age structure, with synchrony decreasing as distance between popula-

tions increased ( $\hat{\rho}_{100\text{km}} = 0.340$  [0.260, 0.416];  $\hat{\rho}_{500\text{km}} = 0.253$  [0.163, 0.330];  $\hat{\rho}_{2500\text{km}} = 0.004$  [ $<0.001$ , 0.112]; Fig. 3a; Table 1), and the estimate for the scale of spatial autocorrelation was relatively large ( $\hat{l} = 641\text{km}$  [371km, 1000km]).

Interestingly, neither clutch size nor many of the environmental variables significantly explained spatial synchrony in age structure (Fig. 3b–d; Table S3). There is some evidence that masting may have a synchronising effect on age structure fluctuations when only considering populations within 100km of mast data collection ( $\hat{\rho}_{100\text{km}} = 0.239$  [0.030, 0.419];  $\hat{\rho}_{500\text{km}} = 0.109$  [ $<0.001$ , 0.303]; Fig. 3e). However, these results should be interpreted with caution given that the synchrony estimates are based on a subset of populations across which the maximum distance between populations that overlap their time series (635km) is similar to the estimated spatial scale of synchrony in age structure across all populations.

TABLE 1  
Spatial synchrony of temporal variation in age structure across great tit breeding populations. Estimates are provided for spatial synchrony parameters (calculated in Equation 2); and for synchrony at distances of 100km, 500km, 1000km and 2500km

| Parameter              | Median   | 95% credible intervals |
|------------------------|----------|------------------------|
| $\rho_0$               | 0.344    | [0.264, 0.424]         |
| $\rho_\infty$          | $<0.001$ | [ $<0.001$ , 0.112]    |
| $l$                    | 641km    | [371km, 1000km]        |
| $\rho_{100\text{km}}$  | 0.340    | [0.260, 0.416]         |
| $\rho_{500\text{km}}$  | 0.253    | [0.163, 0.330]         |
| $\rho_{1000\text{km}}$ | 0.115    | [0.035, 0.205]         |
| $\rho_{2500\text{km}}$ | 0.004    | [ $<0.001$ , 0.112]    |

### 4 DISCUSSION

Using 131,150 captures of 77,964 individuals across 32 great tit populations collectively monitored over 702 years, we show that reproductive and environmental variables covary with breeding population age structure, with the strongest relationships between average clutch size from previous breeding, winter temperature, and variation in beech masting. We report moderate distant-dependent synchrony in age structure, with synchrony maintained at approximately 650km. However, despite association between reproductive and environmental factors with populations' age structure, this does not explain overall spatial synchrony (except for some evidence that beech masting partially synchronises fluctuations in age structure).

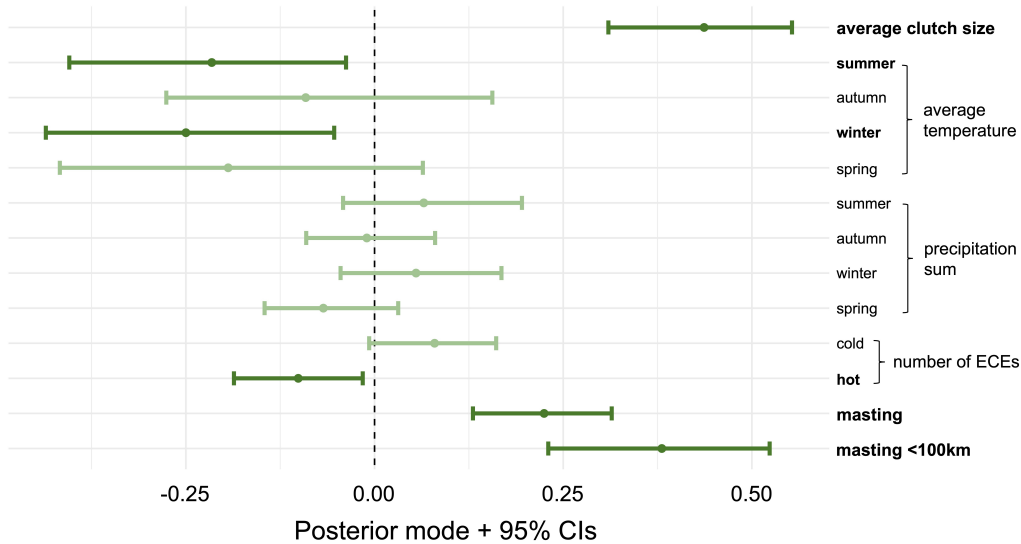


Fig. 2. Posterior modes obtained from linear mixed-effects models which analyse the association between temporal variation in age structure and 13 reproductive and environmental variables across 32 great tit populations. Each point corresponds to a specific predictor variable (on the y-axis), and error bars denote 95% credible intervals. Points and error bars are reduced in saturation when credible intervals overlap zero, and explanatory variable text is bolded when they do not.

#### 4.1 Temporal variation in age structure and explanatory variables

Variation in age structure can have important consequences for demographic and social functioning (Coulson et al. 2005; Gamelon et al. 2019; Siracusa et al. 2023; Woodman et al. in press), yet there has been little research that links its variation across multiple populations directly to reproductive factors and environmental variability. This is because much research has focussed on how variation in population vital rates covary with environmental factors in single populations (Coulson et al. 2000, 2001; Farand et al. 2002), without explicitly linking this to variation in age structure (Hoy et al. 2020). Here, we provide evidence for an effect of reproductive and environmental variability in influencing breeding population age structure.

The strongest predictor of age structure was average clutch size, which predicts younger breeding populations the following year when clutch sizes are larger, suggesting that on average larger clutch sizes lead to more recruits (Ahola et al. 2009). Additionally, greater fecundity in great tits is linked to higher mortality (Payevsky 2006; Sæther 1988), thus there may be a relative increase in the proportion of juveniles the following year if there is high mortality among older individuals due to the cost of producing larger clutches. Directly linking variation in average clutch size and age structure reveals an important aspect of fluctuating population dynamics in great tits. This is because larger clutch sizes are produced when populations are smaller (Kluyver 1951; Lack 1952). Conversely, following

an increase in the proportion of juveniles due to larger clutch sizes (as shown here), density-dependence will be strengthened, not only due to increasing population size, but also because juveniles have the strongest effect on density-dependent regulation, reducing recruitment and survival (Gamelon et al. 2016; Tinbergen et al. 1985) and producing fewer fledglings (Perrins & McCleery 1985).

However, perhaps the most interesting finding regarding the influence of average clutch size on age structure is that it has the greatest relative effect compared to environmental factors. This reveals that reproductive output is more influential for breeding population age structure than age-specific mortality induced by environmental variation between breeding seasons. Of course, variation in clutch size itself is affected by environmental variability, such as temperature and food availability (Both & Visser 2005; Perrins 1965). However, in many species, age structure fluctuates considerably in response to environmental variation linked to mortality, because stressors such as extreme weather have more severe impacts on senescent and juvenile individuals compared to prime-aged individuals (Coulson et al. 2001; Farand et al. 2002; Hoy et al. 2015). Therefore, it is interesting that population-level reproductive output has a greater effect on age structure in this species compared to age-specific mortality events induced by environmental variability.

We report a relationship between age structure and local temperature, but not precipitation. Specifically, warmer summers and winters, and more frequent hot ECEs, are



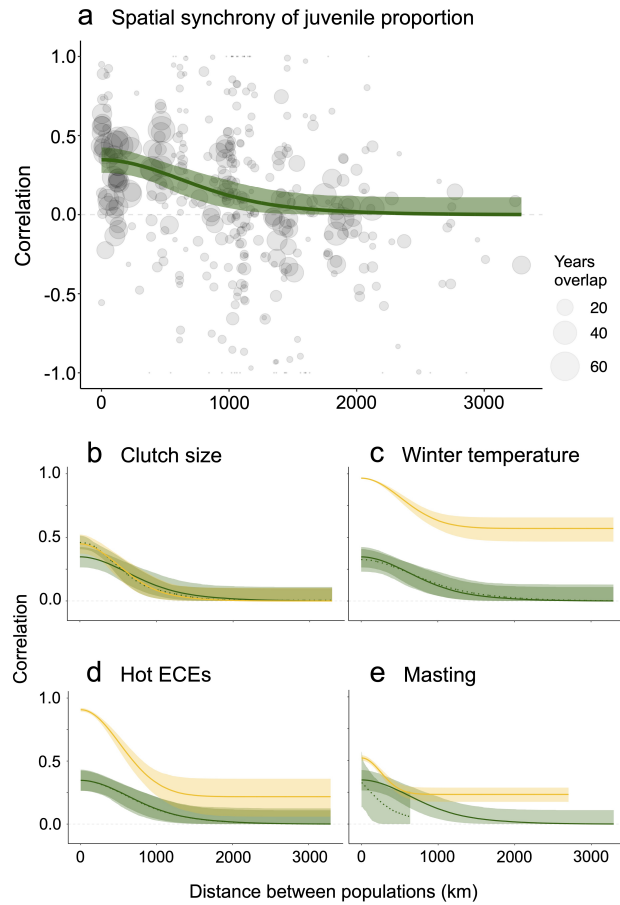


Fig. 3. Spatial synchrony of temporal variation in age structure across great tit breeding populations in relation to distance between populations. In all plots, distance between populations (km) is on the x-axis and correlation between paired sites is on the y-axis. (a) Shows spatial synchrony of temporal fluctuations in the proportion of juveniles, where the green line is the median estimate of spatial synchrony (calculated in Equation 2) based on 2000 bootstrap replicates, with light green shading representing 95% credible intervals, and point size relative to the number of years of overlap between time series of pairwise sites. In (b–e), the dark green solid line is the estimate of spatial synchrony in the proportion of juveniles with 95% credible intervals, the yellow line is the spatial synchrony of the given reproductive or environmental variable, and the green dashed line is the spatial synchrony in the proportion of juveniles once accounting for the given reproductive or environmental variable.

associated with a decrease in the proportion of juveniles. This is contrary to what might be expected where harsher winters would lead to elevated mortality of inexperienced juveniles. However, it has been shown that the reduction of fat following cold temperatures is not age-specific in great tits (Gosler 2002). Thus, mortality driven by colder winters might potentially even bias death in older individuals with lower basal metabolic rates (Broggi et al. 2010) or senescence in other physiological traits (Bouwhuis et al. 2012). A more plausible explanation is that cold temperature-driven mortality is non-age-specific, thus reducing local

population size across all age-cohorts (van Balen 1980; Kluijver 1951; Payevsky 2006). In high-quality great tit habitats (as in many of the populations assessed here), there are often more individuals than available territories where more dominant individuals acquire the breeding sites (Perrins 1979). Great tits resident to a site are more dominant (Krebs 1982; Sandell & Smith 1991), thus upon their death, this likely makes more territories available to subdominant individuals migrating from surrounding lower-quality sites (Verhulst et al. 1997). This might therefore increase the number of immigrants found breeding following high rates of local mortality, for example, due to harsh winters (Grøtan et al. 2009; Tufto et al. 2005). Dispersal between birth and first breeding (natal dispersal) covers greater distances than dispersal between breeding attempts (Greenwood & Harvey 1982). Thus, great tits moving into new environments are often juveniles (Greenwood 1980). This therefore might generate an indirect relationship between colder winters and larger proportions of breeding juveniles the following spring. Further work should test this hypothesis by assessing winter temperature conditions under which immigration increases in great tits and other non-migratory species with sink populations in patchy environments.

We found larger beech mast events are followed by breeding seasons with a larger proportion of juveniles. Beech mast is important for winter survival in great tits, and previous work shows it particularly elevates juvenile survival (Clobert et al. 1988; Källander 1981; Perdeck et al. 2000). However, such studies assess either single populations, or populations close to one another, thus there is limited understanding of how important masting is for great tit demography on a continental-scale (but see Sæther et al. (2007) for its influence on size of populations located several hundred kilometres apart). Moreover, when we restricted analyses to populations that are within 100km of the beech data collection site, we found a greater effect of masting on breeding age structure. This could be due to two reasons: either data collected far from the focal population did not represent actual masting conditions experienced (although there is high spatial synchrony in beech crop cycles, Bogdziewicz et al. 2021); or such populations are in habitats with no or a lower density of beech, thus masting cannot influence demographic fluctuations. Indeed, when assessing population-specific trends, we find marked variation in the effect of masting on age structure (Fig. S71). Further, the strength of this relationship covaries with longitude, which approximates to the European distribution of beech (Fig. S1; S8; S9). Although it has been sug-



gested that masting-related tit population dynamics might be underpinned by synchronous fruiting of multiple tree species that elevate survival across wide-ranging habitats (Klomp 1980; Perrins 1966), our results may indicate that it is specifically beech which links variation in fruiting cycles with juvenile survival.

## 4.2 Spatial synchrony of variation in age structure

We found moderate spatial synchrony in breeding population age structure (Fig. 3a). However, despite covariation between reproductive and environmental factors with age structure (Fig. 2), accounting for such variables does not significantly affect the scale of spatial synchrony, other than evidence that beech masting may contribute to synchronising age structure fluctuations (Fig. 3b–e; Table S3).

For any collection of populations, it is not necessarily expected that the same environmental variables would uniformly influence their age structures between years or synchronise fluctuations over time. An extensive body of demographic theory tells us that density-dependence can lead to complex dynamics, including chaos, in discrete population structures (Caswell 2000; Hastings et al. 1993; Levin 1981). Implicit in our analysis is the assumption that the populations have a fixed-point (stable) equilibrium age structure to which they gravitate, and that all populations are reasonably close to their equilibria. Even if the populations' age structures do have a stable equilibrium, they are likely at different distances from their equilibria at any point in time, and thus going through different phases of transient dynamics (Hastings et al. 2018; Koons et al. 2005). If so, environmental effects may be obscured by the internal demographic processes that might be on divergent or uncorrelated trajectories. While these points serve as caveats concerning the complex dynamics influencing the populations, they also underscore the pronounced impact exerted by the explanatory variables (e.g. beech masting) on age structure, penetrating through the complicating dynamics.

Specifically, when only assessing populations within 100km of beech data collection sites, we find lower estimates of spatial synchrony in age structure once variation in masting has been accounted for. This may indicate that spatial synchrony in beech crop cycles (Bogdziewicz et al. 2021) act to synchronise fluctuations in age structure, but only in populations that breed within the distribution of beech. This is interesting given the effects of climate warming on beech masting, which has increased overall seed production, but reduced between-year variability and reproductive synchrony among individuals (Bogdziewicz

et al. 2020). Thus, we might expect geographically distinct populations which are seed predators of beech, such as great tits, to have reduced synchrony in their age structure dynamics with increasing climate warming. This is particularly pertinent given that masting affects population dynamics across many taxa (Bogdziewicz et al. 2016).

Aside from this, it is striking that there is a lack of an effect from the other environmental variables in synchronising age structure. Spatial synchrony is generated either through dispersal between populations; interspecific trophic interactions with other spatially-synchronised populations; or a common influence from spatially autocorrelated environmental variables (the Moran effect). Dispersal between the assessed populations is unlikely to play a role here, as great tits disperse over smaller spatial scales compared to our estimate of the scale of synchrony in age structure (Greenwood et al. 1979; Tufto et al. 2005). However, dispersal more broadly might synchronise age structure fluctuations if there are simultaneous annual irruptive waves of young immigrants that move into the assessed sites prior to breeding (Nowakowski et al. 2003), especially seeing as annual variation in such waves correlate with years of high recruitment (Grøtan et al. 2009).

Our results may also suggest that the Moran effect does not underpin age structure spatial synchrony, because accounting for climatic variation does not reduce estimates of synchrony. This is pertinent because it suggests that although local environmental variability might induce changes to age structure within populations, broad-scale spatial autocorrelation in climate does not act to synchronise age structure between them. Thus, we would not expect widescale changes induced by climate change to synchronously affect age structure dynamics in this species.

Therefore, other factors may play a role in synchronising fluctuations in age structure. One factor potentially shaping this synchrony is spatial autocorrelation in ecological features that are related to, but not directly captured through the variation in, the environmental variables assessed here. For example, tits are highly susceptible to predation in the first month of fledging (Naef-Daenzer et al. 2001; Perrins & Geer 1980). Thus, if there is spatial synchrony in predator population dynamics, then this might induce synchrony in age structure across great tit populations through its effects on juvenile survival. Additionally, post-fledging food availability is particularly important for survival (Drent 1984; Payevsky 2006), which might also influence the proportion of juveniles found breeding the following season. Diet during this period consists predominantly of caterpillars (Verhulst & Hut 1996), the

availability of which will not only be influenced by local weather, but other factors that affect invertebrate abundance and phenology, such as habitat heterogeneity and density-dependence. Exploring spatial synchrony in age structure while considering multiple trophic levels would be a particularly interesting perspective for future research.

Further, ecological features might not just act to synchronise population age structure through effects on age-specific survival, but also through their effects on reproduction. For example, great tit reproductive rates vary along an urban–natural gradient (Bukor et al. 2022; Charmantier et al. 2017), and reproductive responses to weather depend on whether breeding takes place in urban or natural habitats (Saulnier et al. 2023). Thus, if populations that are closer together experience more similar habitat types, this might induce spatial synchrony in their population dynamics.

Finally, we should expect that fluctuations in age structure are not fully explained by variation in environmental variables because of population-specific density-dependent dynamics. Local density-dependence can affect reproductive responses to environmental stochasticity (Møller et al. 2020), and differences in these dynamics between populations reduces spatial synchrony between them (Hugueny 2006; Walter et al. 2017). Thus, the spatial scale at which density-dependence remains similar between populations should influence the interaction between age structure and environmental variability, and the resultant spatial synchrony of fluctuations in age structure.

## 5 CONCLUSIONS

Using multiple overlapping time series from 32 wild great tit populations, our study quantifies associations between reproductive and environmental variables with age structure in spatially distinct breeding populations. Our findings emphasise the complex interaction between demographic processes and environmental variability, and we suggest that local ecological features and density-dependence will affect the dynamics of spatial synchrony between populations. Specifically, we report spatial synchrony of fluctuations in age structure at approximately 650km, but apart from some evidence of a synchronising effect of beech masting, we find that accounting for variation in reproductive and environmental factors does not reduce the scale of spatial synchrony. Further research should focus on how additional ecological features and population-specific density-dependent dynamics may contribute to the observed scale of spatial synchrony in age structure fluctuations that we find here.

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# Continent-wide drivers of spatial synchrony in age structure across wild great tit populations - SUPPORTING INFORMATION

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## 1 SUPPORTING METHODS

### 1.1 Variation in age structure

In addition to analysis on the proportion of breeding juveniles, we also calculated breeding population age structure through five alternative methods.

First, we calculated the mean breeding population age. As stated in the main text, exact year of hatching is known for all locally-hatched individuals that are ringed at the nest. Although annual immigration rates can be high in the assessed populations (mean, interquartile range: 69.7%, 57.2–88.3%), in many cases adults are first caught as juveniles (mean, IQR: 57.9%, 44.1–81.4%), and thus can be aged accurately. Therefore, exact age was known for 82.5% of 135,967 captures. For the remaining 17.5% of captured individuals (i.e. birds first caught with adult plumage), a minimum age of 2 was assigned, and subsequent age estimates were based on this (15.3% and 20.1% of females and males). This uncertainty does not affect accuracy of calculating our main age structure descriptor, because individuals can still be designated as ‘juvenile’ or ‘adult’ with certainty. For the calculation of mean breeding population age, this assumption may affect accuracy of the age structure descriptor. However, given annual mortality rates >50% (Bouwhuis et al. 2009; Clobert et al. 1988), the assumption is likely to be accurate in the majority of cases. Given that individuals first encountered as adults in the first year of data collection in each population are all assigned an age of 2, the first three years of data collection were removed from each population in the analysis of mean breeding population age such that more accurate individual age estimates were used (n = 637, whereas n = 702 in the main analyses).

Second, we calculated the proportion of senescent individuals in the breeding population. We assume that senescence begins in great tits at 2.8 years (Bouwhuis et al. 2009); therefore, due to annual breeding, senescent individuals are defined as those of 3-years or older. Individuals assigned a minimum age of 2 in the first year of data collection which survive to the next year are accurately assigned as ‘senescent individual’ (because they must be 3-years or older). Thus, only the first year of data collection was removed from each population (n = 688).

Finally, we calculated  $\delta_t$ , the temporal deviations in the described structures (proportion of juveniles, mean breeding population age, and proportion of senescent individuals) compared to population-specific moving averages with a window size of 3 years. Specifically,  $\delta_t = i_t - \frac{\sum_{t=3}^{t-1} i_t}{3}$ , where  $i_t$  is any of the above structural measures in year  $t$ . This metric addresses how the explanatory variables might induce momentary change in structure, beyond how those variables correlate with static measures of yearly structure. In order to compare the static age structure measure to a three-year average, data were restricted to populations with at least four years of continuous data. All age structure descriptors were highly correlated (Fig. S2).

In addition to testing for associations between reproductive and environmental variables and variation in age structure, as in the main text, we also explored overall time trends in variation in population age structure. We did this by using the same linear mixed-effects model of the form

$$y_{i,j} = \beta_{\text{int}} + u_{\text{int},i} + (\beta_{\text{year}} + u_{\text{year},i})Z_{i,j} + \epsilon_{i,j}$$

where  $y$  is the age structure descriptor per population  $i$  and year  $j$ ,  $\beta_{\text{int}}$  is an intercept,  $u_{\text{int},i}$  denotes random intercepts for each population assumed to have a normal prior distribution with mean 0 and standard deviation  $\sigma_{u_{\text{int}}}$ ,  $\beta_{\text{year}}$  is a slope for the linear time trend,  $u_{\text{year},i}$  denotes random slopes for the linear time trends of each population also assumed to have a normal prior distribution,  $Z_{i,j}$  is the time indicator per annual population, and  $\epsilon_{i,j}$  is the residual error, assumed to have a normal prior distribution.

## 1.2 Reproductive and environmental variables

In the main text, we consider the role of reproductive and environmental variables that vary at different spatial scales on temporal variation in, and spatial synchrony of, population age structure. First, we considered the influence of average clutch size in year  $t - 1$  on age structure in year  $t$ . An individual's clutch size may vary in response to several demographic and environmental factors, such as local population size, predation risk, weather conditions, chick-rearing resource availability and parental quality (Boyce & Perrins 1987; Julliard et al. 1997; Møller et al. 2020; Perrins 1965; Pettifor et al. 2001). We would expect the variation in the within-year mean clutch size to affect the age structure of the following annual breeding population, where higher average clutch sizes would lead to greater numbers of recruits (Ahola et al. 2009) and therefore a higher proportion of breeding juveniles, thus we test this prediction here. Although the number of fledglings may provide a more accurate proxy for recruitment, data on fledgling number were less complete compared to clutch size across the populations, and the number of eggs laid strongly relates to the number of recruits at the pair-level (Perrins 1965; Perrins & Moss 1975).

We also consider the influence of climatic variables on breeding population age structure: temperature and precipitation, which have both been linked to great tit survival and reproduction (van Balen 1980; Bejer & Rudemo 1985; Bordjan & Tome 2014; Greño et al. 2007; Perrins 1965). We extracted daily temperature and precipitation records from a corresponding  $0.1^\circ \times 0.1^\circ$  grid cell in the E-OBS dataset version 27.0e for each population (Cornes et al. 2018). From these, we assessed the impact of weather on age structure by considering weather averages across given time periods (as outlined in the main text). We also considered the influence of the frequency of extreme climatic events (ECEs). Here, we define ECEs as an event with a 5% or less probability of occurrence across the entire study period (1956–2022) in each population separately (Bailey & van de Pol 2016; Marrot et al. 2017; Moreno & Møller 2011), which has been linked to great tit survival and reproduction (Regan & Sheldon 2023). Thus, a 'cold ECE' is defined as when the minimum daily temperature reaches below the 5% threshold June–May; and a 'hot ECE' as when maximum daily temperature reaches above the 95% threshold June–May.

We also considered an environmental variable which varies at a larger spatial scale by using masting data from European beech *Fagus sylvatica*. This variable represents the annual production of beech seeds (Kelly 1994; Silver-



town 1980), where maximum production correlates negatively with summer temperatures two years previously, but positively with summer temperatures the year before (Vacchiano et al. 2017). Beech masting maintains significant synchrony at spatial scales up to 1500km (Bogdziewicz et al. 2021), and its variation has been linked to spatial synchrony of population size in tits (Sæther et al. 2007). We obtained data from a long-term continental-scale dataset of masting time series of beech up to 2017 (MASTREE+, Hacket-Pain et al., 2022). For each year of data collection for each breeding population, we extracted a masting value from the year prior to breeding from the site closest to that of the population. Beech masting was measured on an ordinal scale 1–5 where 1 represents lowest reproductive output (Hacket-Pain et al. 2022). The central coordinates for masting sites were all less than 1500km from the focal breeding population, which is the spatial scale at which beech masting remains synchronised (Bogdziewicz et al. 2021), and most were much closer (median, IQR: 143.2km, 87.6–297.0km). However, as set out in the main text, to assess the influence of beech masting measured at a more local spatial scale, we created a subset of the data including only annual populations where beech mast data was collected 100km or closer to the breeding site (13 populations,  $n = 223$ ).

Finally, in addition to analysis outlined in the main text, we considered an environmental variable that varies at a continental scale by assessing the influence of the North Atlantic Oscillation (NAO) index. The NAO index is based on the difference in sea-level pressure between the subtropical high-pressure centre near the Azores and the subpolar low-pressure centre south and east of Greenland, the variation of which is linked to annual fluctuations in temperature and precipitation (Hurrell 1995; Lamb & Pepler 1987; Wanner et al. 2001). Generally, positive NAO values during the winter correspond to wetter, warmer weather and earlier springs in northern Europe and drier, warmer weather and advanced springs in southern Europe (Gordo & Sanz 2010; Post & Stenseth 1999). We extracted an annual winter NAO value from The Climate Data Guide (Hurrell & Phillips 2003; Schneider et al. 2013).

## 2 SUPPORTING RESULTS

### 2.1 Temporal variation in age structure and explanatory variables

We found very weak but significant temporal trends in breeding population age structure. Specifically, we find that over time there was a slight decrease in the proportion of breeding juveniles (posterior mode [95% credible intervals]: -0.007 [-0.011, -0.002]) and a slight increase in the breeding population mean age (0.005 [ $<0.001$ , 0.010]). We found no significant time trend in the proportion of breeding senescent individuals (0.002 [-0.002, 0.007]); or on temporal deviations in the described structures (proportion of juveniles, mean breeding population age, and proportion of senescent individuals) compared to population-specific moving averages ( $>-0.001$  [-0.003, 0.002];  $<0.001$  [-0.002, 0.003];  $<0.001$  [-0.001, 0.003], respectively).

We found similar associations between the reproductive and environmental variables with age structure whether defining age structure as the proportion of breeding juveniles (as in the main text; Fig. 2), the mean breeding population age (Fig. S4; Table S2), the proportion of senescent individuals (Fig. S5; Table S2), or changes in these structures compared to a population-specific moving average (Fig. S6; Table S2). In addition to the environmental variables assessed in the main text, we found that, slightly older breeding populations followed winters with higher NAO values (proportion of juveniles posterior mode [95% credible intervals]: -0.115 [-0.189, -0.028]). This may be interpreted similarly to our results found regarding increased winter temperatures, in that when winter NAO values are higher this is associated with warmer winters (see main text discussion).

### 3 SUPPLEMENTARY TABLES

Table S1 – The 32 great tit populations used in this study, with information provided for: the location; the population identifier code (used in Fig. 1 in the main text, in Fig. S1 & S7, and in analysis); initials of data provider(s); latitude (Lat) and longitude (Lon), in decimal degrees; the time series of data used in this study (with total number of years in parentheses); the average within-year population size over the study period (estimated as the number of observed individuals + the number of inferred breeders, where it is assumed there are two individuals per breeding attempt); and the average within-year percentage of aged individuals (calculated as the number of aged individuals divided by the estimated breeding population size, which includes non-captured individuals). Metadata for each population can be found through the Studies of Populations of Individuals Birds (SPI-Birds; [www.spibirds.org](http://www.spibirds.org), Culina et al. 2021).

| Location                         | Population code | Data provider(s) | Lat     | Lon     | Time series (total years)                                  | Mean pop. size | Mean % aged |
|----------------------------------|-----------------|------------------|---------|---------|------------------------------------------------------------|----------------|-------------|
| Ammersee-Starnbergersee, Germany | AMM             | ND               | 47.5800 | 11.1400 | 2011-2019 (9)                                              | 597            | 73.8        |
| Bagley Wood, United Kingdom      | BAG             | SRE              | 51.7000 | -1.2500 | 2005-2014 (10)                                             | 255            | 83.7        |
| Balatonfüred, Hungary            | BAL             | ALi, GS          | 46.5700 | 17.5300 | 2014-2019 (6)                                              | 47             | 69.5        |
| Boshoeek, Belgium                | BOS             | FA, EM           | 51.0800 | 4.3200  | 1994-2018 (25)                                             | 465            | 74.2        |
| Buunderkamp, Netherlands         | BUU             | MEV              | 52.0100 | 5.4500  | 1984-1992, 1995-2005, 2007-2014 (28)                       | 204            | 58.6        |
| Can Catà, Spain                  | CAC             | JCS              | 41.4600 | 2.1400  | 2003-2004, 2011, 2013, 2015-2016 (6)                       | 253            | 28.9        |
| East Dartmoor, United Kingdom    | EDM             | MDB              | 50.5900 | -3.7200 | 2014-2015, 2018 (3)                                        | 69             | 30.8        |
| Gotland, Sweden                  | GOT             | LC, BD           | 57.1000 | 18.2000 | 2005-2016, 2021-2022 (14)                                  | 889            | 58.7        |
| Gulya-Domb, Hungary              | GUL             | ALi, GS          | 47.0500 | 17.5300 | 2019-2022 (4)                                              | 61             | 54.5        |
| Harjavalta, Finland              | HAR             | TE               | 61.2000 | 22.1000 | 1991-1994 (4)                                              | 343            | 33.9        |
| Hoge Veluwe, Netherlands         | HOG             | MEV              | 52.0200 | 5.5100  | 1956-2018 (63)                                             | 337            | 76.0        |
| Kilingi-Nõme, Estonia            | KIL             | ALe              | 58.1500 | 24.9600 | 1972-1992, 1996-2001 (27)                                  | 545            | 65.4        |
| Liesbos, Netherlands             | LIE             | MEV              | 51.3500 | 4.4200  | 1956-1967, 1971-1974, 1976-2003, 2005-2011, 2014-2018 (56) | 116            | 63.8        |

| Location                 | Population code | Data provider(s) | Lat     | Lon           | Time series (total years)                                          | Mean pop. size | Mean % aged |
|--------------------------|-----------------|------------------|---------|---------------|--------------------------------------------------------------------|----------------|-------------|
| Mayachino, Russia        | MAY             | AA               | 60.4600 | 32.4900       | 1983, 1985, 1990, 2001, 2007-2008, 2013-2016, 2018, 2020-2021 (13) | 29             | 70.4        |
| Montpellier City, France | MON             | SPC, AC, AG, ML  | 43.5900 | 3.8600        | 2013-2018 (6)                                                      | 275            | 50.8        |
| Mont Ventoux, France     | MTV             | SPC, AC, AG, ML  | 44.1000 | 5.1600        | 1987-1991, 1993 (6)                                                | 48             | 49.7        |
| Muro, France             | MUR             | SPC, AC, AG, ML  | 42.3600 | 8.5800        | 2000-2005, 2008, 2012 (8)                                          | 42             | 68.6        |
| Oosterhout, Netherlands  | OOS             | MEV              | 51.5200 | 5.5000        | 1958, 1964-2018 (56)                                               | 100            | 76.1        |
| Oulu, Finland            | OUL             | MO, SR, EV       | 65.0500 | 25.5300       | 1970, 1972-1989, 1995, 1999-2021 (43)                              | 266            | 51.7        |
| Peerdsbos, Belgium       | PEE             | FA, EM           | 51.1600 | 4.2900        | 1983-2007, 2009-2012, 2014-2018 (36)                               | 230            | 62.6        |
| Rouvière, France         | ROU             | SPC, AC, AG, ML  | 43.4000 | 3.4000        | 1992-2006, 2008-2010, 2012-2018 (25)                               | 65             | 56.7        |
| Sagunto, Spain           | SAG             | EA, EB           | 39.4200 | -0.1500       | 1993-2022 (30)                                                     | 184            | 86.0        |
| Szentgál, Hungary        | SZE             | ALi, GS          | 47.0600 | 17.4100       | 2013-2021 (9)                                                      | 100            | 61.4        |
| Veszprém, Hungary        | VES             | ALi, GS          | 47.0500 | 17.5400       | 2013-2022 (10)                                                     | 104            | 69.9        |
| Vilma-pusztá, Hungary    | VIL ALi, GS     | 47.0500          | 17.5200 | 2014-2022 (9) | 42                                                                 | 71.8           |             |
| Vlieland, Netherlands    | VLI             | MEV              | 53.1700 | 5.0300        | 1956-2018 (63)                                                     | 349            | 79.2        |
| Warnsborn, Netherlands   | WAR             | KVO              | 52.0000 | 5.5200        | 1983, 1987-2018 (33)                                               | 91             | 71.9        |
| Westerheide, Netherlands | WES             | KVO              | 52.0100 | 5.5000        | 1992-2018 (27)                                                     | 359            | 67.1        |
| Warsaw Kampinos, Poland  | WRSKPN          | MS               | 52.2123 | 20.4714       | 2018-2022 (6)                                                      | 39             | 62.1        |
| Warsaw Palmiry, Poland   | WRSPAL          | MS               | 52.2211 | 20.4649       | 2018-2021 (4)                                                      | 31             | 63.3        |

| Location                        | Population code | Data provider(s)   | Lat     | Lon     | Time series (total years) | Mean pop. size | Mean % aged |
|---------------------------------|-----------------|--------------------|---------|---------|---------------------------|----------------|-------------|
| Warsaw Pole Mokotowskie, Poland | WRSPOL          | MS                 | 52.1247 | 21.0698 | 2017-2022 (6)             | 53             | 69.6        |
| Wytham Woods, United Kingdom    | WYT             | EFC, JAF, BCS, JPW | 51.7700 | -1.3400 | 1966-2022 (57)            | 602            | 68.0        |

Table S2 - Associations between temporal variation in age structure and 14 reproductive and environmental variables across 32 great tit populations. Results are obtained from linear mixed-effects models of the form

$$y_{i,j} = \beta_{\text{int}} + u_{\text{int},i} + (\beta_{\text{expl}} + u_{\text{expl},i})Z_{i,j} + \epsilon_{i,j}$$

where  $y$  is the proportion of juveniles per population  $i$  and year  $j$ ,  $\beta_{\text{int}}$  is an intercept,  $u_{\text{int},i}$  denotes random intercepts for each population assumed to have a normal prior distribution with mean 0 and standard deviation  $\sigma_{u_{\text{int}}}$ ,  $\beta_{\text{expl}}$  is a slope for the explanatory variable,  $u_{\text{expl},i}$  denotes random slopes for the explanatory variable for each population also assumed to have a normal prior distribution,  $Z_{i,j}$  is the explanatory variable for each annual population, and  $\epsilon_{i,j}$  is the residual error, assumed to have a normal prior distribution. The posterior mode denotes the estimated effect size of the explanatory variable on the age structure descriptor ( $\beta_{\text{expl}}$ ), drawn from 12000 posterior samples, with 95% credible intervals.

| Age structure descriptor      | Variable             | Posterior mode | 95% credible intervals |
|-------------------------------|----------------------|----------------|------------------------|
| Proportion breeding juveniles | Clutch size          | 0.437          | [0.310, 0.553]         |
|                               | Summer temperature   | -0.216         | [-0.405, -0.038]       |
|                               | Autumn temperature   | -0.091         | [-0.276, 0.156]        |
|                               | Winter temperature   | -0.250         | [-0.436, -0.053]       |
|                               | Spring temperature   | -0.194         | [-0.417, 0.064]        |
|                               | Summer precipitation | 0.065          | [-0.042, 0.195]        |
|                               | Autumn precipitation | -0.010         | [-0.091, 0.080]        |
|                               | Winter precipitation | 0.055          | [-0.045, 0.168]        |
|                               | Spring precipitation | -0.068         | [-0.146, 0.031]        |
|                               | Cold ECEs            | 0.080          | [-0.007, 0.161]        |
|                               | Hot ECEs             | -0.101         | [-0.186, -0.016]       |
|                               | Masting              | 0.225          | [0.130, 0.314]         |
|                               | Masting <100km       | 0.365          | [0.204, 0.538]         |
|                               | NAO                  | -0.115         | [-0.189, -0.028]       |
| Mean breeding population age  | Clutch size          | -0.450         | [-0.584, -0.323]       |
|                               | Summer temperature   | 0.275          | [0.068, 0.493]         |
|                               | Autumn temperature   | 0.216          | [-0.002, 0.418]        |
|                               | Winter temperature   | 0.180          | [-0.109, 0.414]        |
|                               | Spring temperature   | 0.227          | [-0.063, 0.500]        |
|                               | Summer precipitation | -0.078         | [-0.214, 0.041]        |
|                               | Autumn precipitation | 0.002          | [-0.085, 0.086]        |
|                               | Winter precipitation | -0.009         | [-0.108, 0.093]        |
|                               | Spring precipitation | 0.040          | [-0.047, 0.131]        |
|                               | Cold ECEs            | -0.060         | [-0.161, 0.051]        |
|                               | Hot ECEs             | 0.137          | [0.052, 0.230]         |

| Age structure descriptor                                     | Variable             | Posterior mode | 95% credible intervals |
|--------------------------------------------------------------|----------------------|----------------|------------------------|
| Proportion breeding senescent individuals                    | Masting              | -0.173         | [-0.250, -0.094]       |
|                                                              | Masting <100km       | -0.248         | [-0.519, -0.071]       |
|                                                              | NAO                  | 0.094          | [0.009, 0.169]         |
|                                                              | Clutch size          | -0.390         | [-0.496, -0.289]       |
|                                                              | Summer temperature   | 0.173          | [-0.001, 0.350]        |
|                                                              | Autumn temperature   | 0.205          | [-0.011, 0.407]        |
|                                                              | Winter temperature   | 0.126          | [-0.146, 0.343]        |
|                                                              | Spring temperature   | 0.180          | [-0.082, 0.425]        |
|                                                              | Summer precipitation | -0.026         | [-0.140, 0.088]        |
|                                                              | Autumn precipitation | -0.005         | [-0.086, 0.076]        |
|                                                              | Winter precipitation | -0.022         | [-0.121, 0.080]        |
|                                                              | Spring precipitation | 0.031          | [-0.070, 0.122]        |
|                                                              | Cold ECEs            | -0.032         | [-0.133, 0.077]        |
|                                                              | Hot ECEs             | 0.098          | [0.005, 0.193]         |
| Proportion breeding juveniles temporal deviation             | Masting              | -0.081         | [-0.159, 0.002]        |
|                                                              | Masting <100km       | -0.117         | [-0.278, 0.046]        |
|                                                              | NAO                  | 0.071          | [-0.009, 0.151]        |
|                                                              | Clutch size          | 0.190          | [0.086, 0.287]         |
|                                                              | Summer temperature   | -0.023         | [-0.139, 0.079]        |
|                                                              | Autumn temperature   | -0.009         | [-0.150, 0.109]        |
|                                                              | Winter temperature   | -0.091         | [-0.300, 0.020]        |
|                                                              | Spring temperature   | -0.035         | [-0.150, 0.073]        |
|                                                              | Summer precipitation | 0.061          | [-0.034, 0.191]        |
|                                                              | Autumn precipitation | -0.018         | [-0.107, 0.078]        |
|                                                              | Winter precipitation | 0.014          | [-0.075, 0.119]        |
|                                                              | Spring precipitation | -0.046         | [-0.137, 0.050]        |
|                                                              | Cold ECEs            | 0.056          | [-0.063, 0.150]        |
|                                                              | Hot ECEs             | -0.058         | [-0.156, 0.031]        |
| Mean breeding population age temporal deviation              | Masting              | 0.284          | [0.162, 0.385]         |
|                                                              | Masting <100km       | 0.480          | [0.289, 0.766]         |
|                                                              | NAO                  | -0.153         | [-0.252, -0.058]       |
|                                                              | Clutch size          | -0.215         | [-0.342, -0.101]       |
|                                                              | Summer temperature   | -0.002         | [-0.147, 0.235]        |
|                                                              | Autumn temperature   | 0.017          | [-0.107, 0.223]        |
|                                                              | Winter temperature   | 0.114          | [-0.017, 0.507]        |
|                                                              | Spring temperature   | 0.027          | [-0.098, 0.193]        |
|                                                              | Summer precipitation | -0.060         | [-0.195, 0.049]        |
|                                                              | Autumn precipitation | 0.007          | [-0.085, 0.116]        |
|                                                              | Winter precipitation | 0.028          | [-0.097, 0.141]        |
|                                                              | Spring precipitation | 0.074          | [-0.018, 0.182]        |
|                                                              | Cold ECEs            | -0.037         | [-0.169, 0.133]        |
|                                                              | Hot ECEs             | 0.064          | [-0.046, 0.194]        |
| Proportion breeding senescent individuals temporal deviation | Masting              | -0.250         | [-0.362, -0.139]       |
|                                                              | Masting <100km       | -0.365         | [-0.590, -0.149]       |
|                                                              | NAO                  | 0.109          | [0.008, 0.234]         |
|                                                              | Clutch size          | -0.183         | [-0.358, -0.078]       |
|                                                              | Summer temperature   | 0.091          | [-0.035, 0.288]        |

| Age structure descriptor | Variable             | Posterior mode | 95% credible intervals |
|--------------------------|----------------------|----------------|------------------------|
|                          | Autumn temperature   | 0.036          | [-0.078, 0.276]        |
|                          | Winter temperature   | 0.060          | [-0.064, 0.251]        |
|                          | Spring temperature   | 0.060          | [-0.042, 0.231]        |
|                          | Summer precipitation | -0.061         | [-0.184, 0.035]        |
|                          | Autumn precipitation | 0.014          | [-0.078, 0.109]        |
|                          | Winter precipitation | -0.055         | [-0.196, 0.058]        |
|                          | Spring precipitation | 0.037          | [-0.061, 0.131]        |
|                          | Cold ECEs            | -0.005         | [-0.170, 0.231]        |
|                          | Hot ECEs             | 0.096          | [-0.002, 0.202]        |
|                          | Masting              | -0.096         | [-0.201, 0.016]        |
|                          | Masting <100km       | -0.203         | [-0.46, 0.000]         |
|                          | NAO                  | 0.125          | [-0.027, 0.244]        |

Table S3 – Spatial synchrony of temporal variation in the proportion of juveniles in great tit breeding populations after accounting for variation in reproductive and environmental variables. Estimates are provided for spatial synchrony parameters (calculated in Equation 2 in the main text); and for synchrony at distances of 100km, 500km, 1000km and 2500km.

| Variable accounted for | Parameter              | Median | 95% credible intervals |
|------------------------|------------------------|--------|------------------------|
| Clutch size            | $\rho_0$               | 0.302  | [0.215, 0.392]         |
|                        | $\rho_\infty$          | <0.001 | [<0.001, 0.111]        |
|                        | $l$                    | 564km  | [267km, 964km]         |
|                        | $\rho_{100\text{km}}$  | 0.297  | [0.212, 0.383]         |
|                        | $\rho_{500\text{km}}$  | 0.201  | [0.092, 0.282]         |
|                        | $\rho_{1000\text{km}}$ | 0.075  | [0.009, 0.175]         |
|                        | $\rho_{2500\text{km}}$ | 0.002  | [<0.001, 0.112]        |
| Summer temperature     | $\rho_0$               | 0.348  | [0.262, 0.433]         |
|                        | $\rho_\infty$          | <0.001 | [<0.001, 0.127]        |
|                        | $l$                    | 618km  | [314km, 1018km]        |
|                        | $\rho_{100\text{km}}$  | 0.343  | [0.258, 0.425]         |
|                        | $\rho_{500\text{km}}$  | 0.250  | [0.147, 0.330]         |
|                        | $\rho_{1000\text{km}}$ | 0.110  | [0.025, 0.215]         |
|                        | $\rho_{2500\text{km}}$ | 0.004  | [<0.001, 0.127]        |
| Autumn temperature     | $\rho_0$               | 0.339  | [0.251, 0.431]         |
|                        | $\rho_\infty$          | <0.001 | [<0.001, 0.119]        |
|                        | $l$                    | 646km  | [334km, 1046km]        |
|                        | $\rho_{100\text{km}}$  | 0.335  | [0.248, 0.423]         |
|                        | $\rho_{500\text{km}}$  | 0.251  | [0.153, 0.332]         |
|                        | $\rho_{1000\text{km}}$ | 0.118  | [0.032, 0.220]         |
|                        | $\rho_{2500\text{km}}$ | 0.006  | [<0.001, 0.119]        |
| Winter temperature     | $\rho_0$               | 0.326  | [0.231, 0.410]         |
|                        | $\rho_\infty$          | <0.001 | [<0.001, 0.128]        |
|                        | $l$                    | 709    | [332km, 1199km]        |
|                        | $\rho_{100\text{km}}$  | 0.322  | [0.229, 0.402]         |
|                        | $\rho_{500\text{km}}$  | 0.251  | [0.149, 0.324]         |
|                        | $\rho_{1000\text{km}}$ | 0.133  | [0.040, 0.231]         |
|                        | $\rho_{2500\text{km}}$ | 0.010  | [<0.001, 0.130]        |

| Variable accounted for | Parameter              | Median | 95% credible intervals |
|------------------------|------------------------|--------|------------------------|
| Spring temperature     | $\rho_0$               | 0.344  | [0.262, 0.430]         |
|                        | $\rho_\infty$          | <0.001 | [<0.001, 0.146]        |
|                        | $l$                    | 693km  | [357km, 1107km]        |
|                        | $\rho_{100\text{km}}$  | 0.340  | [0.259, 0.424]         |
|                        | $\rho_{500\text{km}}$  | 0.265  | [0.168, 0.343]         |
|                        | $\rho_{1000\text{km}}$ | 0.139  | [0.043, 0.233]         |
|                        | $\rho_{2500\text{km}}$ | 0.010  | [<0.001, 0.147]        |
| Summer precipitation   | $\rho_0$               | 0.335  | [0.248, 0.421]         |
|                        | $\rho_\infty$          | <0.001 | [<0.001, 0.126]        |
|                        | $l$                    | 672km  | [339km, 1118km]        |
|                        | $\rho_{100\text{km}}$  | 0.332  | [0.246, 0.414]         |
|                        | $\rho_{500\text{km}}$  | 0.254  | [0.156, 0.332]         |
|                        | $\rho_{1000\text{km}}$ | 0.127  | [0.033, 0.230]         |
|                        | $\rho_{2500\text{km}}$ | 0.007  | [<0.001, 0.127]        |
| Autumn precipitation   | $\rho_0$               | 0.323  | [0.241, 0.412]         |
|                        | $\rho_\infty$          | <0.001 | [<0.001, 0.119]        |
|                        | $l$                    | 612km  | [310km, 1014km]        |
|                        | $\rho_{100\text{km}}$  | 0.319  | [0.239, 0.403]         |
|                        | $\rho_{500\text{km}}$  | 0.233  | [0.129, 0.314]         |
|                        | $\rho_{1000\text{km}}$ | 0.107  | [0.022, 0.204]         |
|                        | $\rho_{2500\text{km}}$ | 0.004  | [<0.001, 0.119]        |
| Winter precipitation   | $\rho_0$               | 0.347  | [0.258, 0.433]         |
|                        | $\rho_\infty$          | <0.001 | [<0.001, 0.110]        |
|                        | $l$                    | 604km  | [330km, 997km]         |
|                        | $\rho_{100\text{km}}$  | 0.341  | [0.255, 0.426]         |
|                        | $\rho_{500\text{km}}$  | 0.247  | [0.247, 0.328]         |
|                        | $\rho_{1000\text{km}}$ | 0.104  | [0.104, 0.211]         |
|                        | $\rho_{2500\text{km}}$ | 0.003  | [0.003, 0.111]         |
| Spring precipitation   | $\rho_0$               | 0.348  | [0.259, 0.432]         |
|                        | $\rho_\infty$          | <0.001 | [<0.001, 0.133]        |
|                        | $l$                    | 662km  | [338km, 1101km]        |
|                        | $\rho_{100\text{km}}$  | 0.343  | [0.257, 0.426]         |
|                        | $\rho_{500\text{km}}$  | 0.260  | [0.159, 0.335]         |
|                        | $\rho_{1000\text{km}}$ | 0.127  | [0.035, 0.228]         |
|                        | $\rho_{2500\text{km}}$ | 0.006  | [<0.001, 0.133]        |
| Cold ECEs              | $\rho_0$               | 0.327  | [0.242, 0.415]         |
|                        | $\rho_\infty$          | <0.001 | [<0.001, 0.118]        |
|                        | $l$                    | 675km  | [325km, 1148km]        |
|                        | $\rho_{100\text{km}}$  | 0.323  | [0.239, 0.410]         |
|                        | $\rho_{500\text{km}}$  | 0.247  | [0.146, 0.328]         |
|                        | $\rho_{1000\text{km}}$ | 0.122  | [0.033, 0.220]         |
|                        | $\rho_{2500\text{km}}$ | 0.007  | [<0.001, 0.120]        |
| Hot ECEs               | $\rho_0$               | 0.347  | [0.264, 0.432]         |
|                        | $\rho_\infty$          | <0.001 | [<0.001, 0.125]        |
|                        | $l$                    | 632km  | [343km, 1001km]        |
|                        | $\rho_{100\text{km}}$  | 0.342  | [0.260, 0.425]         |
|                        | $\rho_{500\text{km}}$  | 0.254  | [0.153, 0.334]         |

| Variable accounted for | Parameter              | Median | 95% credible intervals |
|------------------------|------------------------|--------|------------------------|
| Masting                | $\rho_{1000\text{km}}$ | 0.117  | [0.028, 0.215]         |
|                        | $\rho_{2500\text{km}}$ | 0.005  | [<0.001, 0.125]        |
|                        | $\rho_0$               | 0.272  | [0.185, 0.362]         |
|                        | $\rho_\infty$          | <0.001 | [<0.001, 0.134]        |
|                        | $l$                    | 793km  | [324km, 1440km]        |
| Masting < 100km        | $\rho_{100\text{km}}$  | 0.269  | [0.183, 0.357]         |
|                        | $\rho_{500\text{km}}$  | 0.221  | [0.132, 0.295]         |
|                        | $\rho_{1000\text{km}}$ | 0.136  | [0.037, 0.220]         |
|                        | $\rho_{2500\text{km}}$ | 0.019  | [<0.001, 0.137]        |
|                        | $\rho_0$               | 0.301  | [0.104, 0.573]         |
| NAO                    | $\rho_\infty$          | <0.001 | [<0.001, 0.261]        |
|                        | $l$                    | 255km  | [19km, 437924km]       |
|                        | $\rho_{100\text{km}}$  | 0.239  | [0.030, 0.419]         |
|                        | $\rho_{500\text{km}}$  | 0.109  | [<0.001, 0.303]        |
|                        | $\rho_{1000\text{km}}$ | NA     | NA                     |
|                        | $\rho_{2500\text{km}}$ | NA     | NA                     |
|                        | $\rho_0$               | 0.315  | [0.228, 0.402]         |
|                        | $\rho_\infty$          | <0.001 | [<0.001, 0.119]        |
|                        | $l$                    | 697km  | [329km, 1220km]        |
|                        | $\rho_{100\text{km}}$  | 0.311  | [0.226, 0.394]         |
|                        | $\rho_{500\text{km}}$  | 0.240  | [0.140, 0.319]         |
|                        | $\rho_{1000\text{km}}$ | 0.127  | [0.032, 0.227]         |
|                        | $\rho_{2500\text{km}}$ | 0.009  | [<0.001, 0.120]        |



#### 4 SUPPLEMENTARY FIGURES

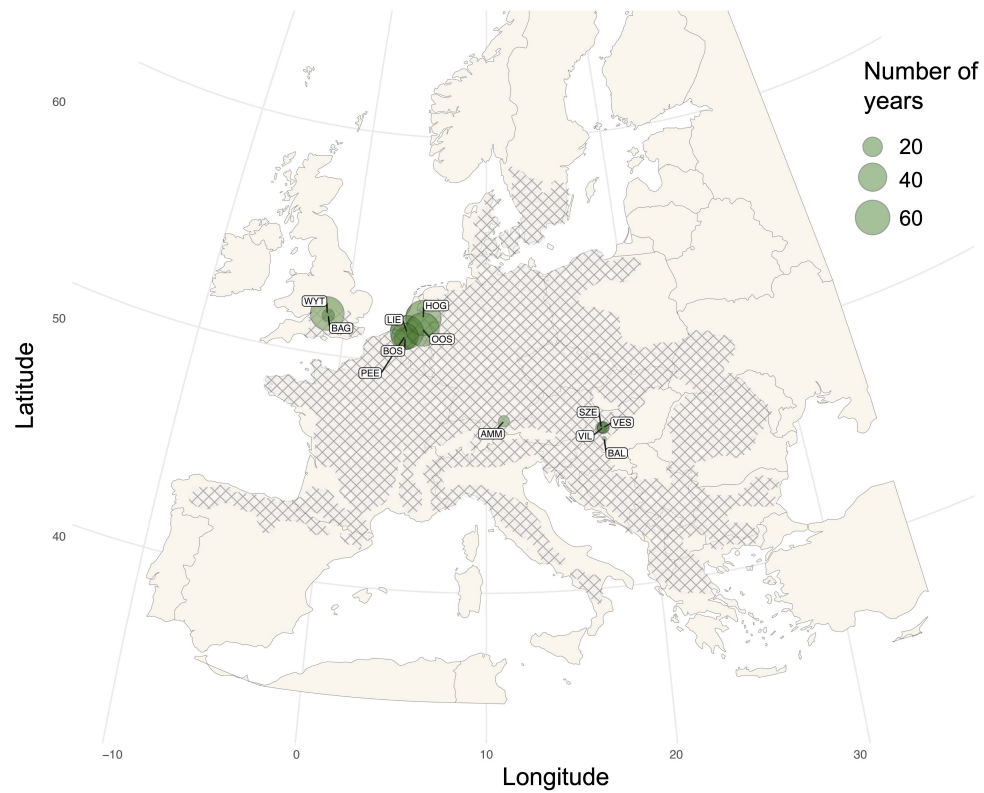


Fig. S1 – Map of the 12 great tit study populations across Europe included in our sub-analysis assessing the influence of masting at a more local spatial scale. The annual populations include those that are within the continuous distribution range of beech (shown approximately in cross-hatching on the map, adapted from Bolte et al. 2007) and where the beech data was collected within 100km of the populations. Dark green points represent the great tit populations, with point size relative to the number of years in the time series.

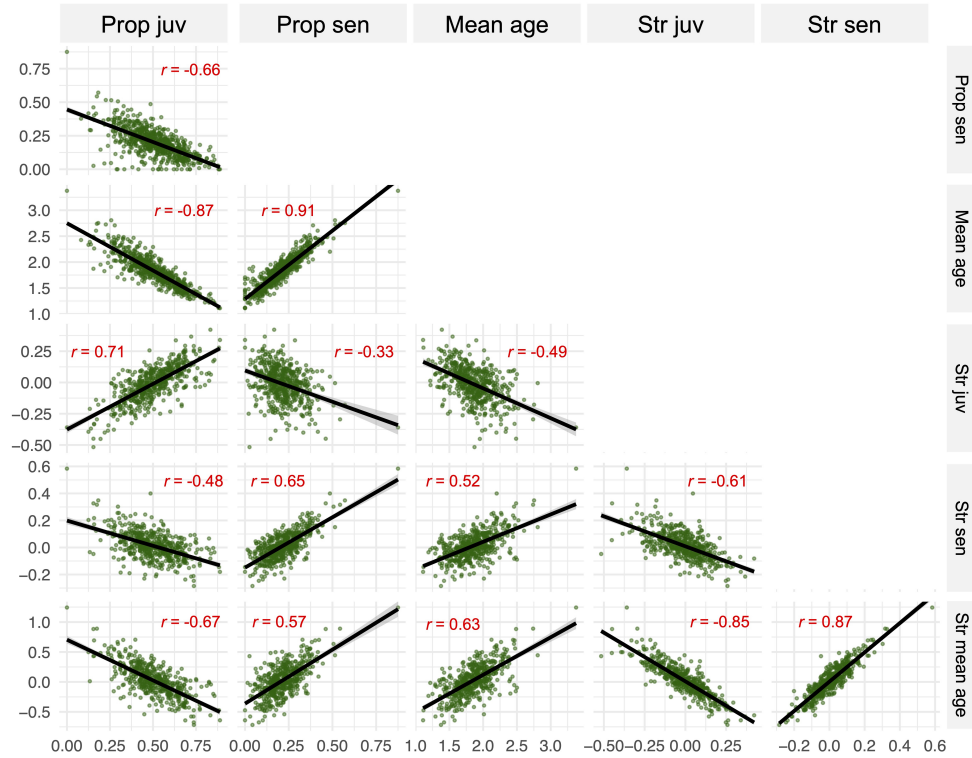


Fig. S2 – Correlations between the different age structure descriptors (proportion of breeding juveniles, proportion of senescent individuals, mean breeding population age, and the temporal deviations in these three measures compared to population-specific moving averages) used in this study. In all plots, the black line is a linear regression which models the relationship between the two age structure measures, and the shading around this shows the 95% confidence intervals. The relationship is significant where  $p < 0.05$  in all cases, and the  $r$  value obtained from a Spearman's rank correlation labelled in red on all plots.

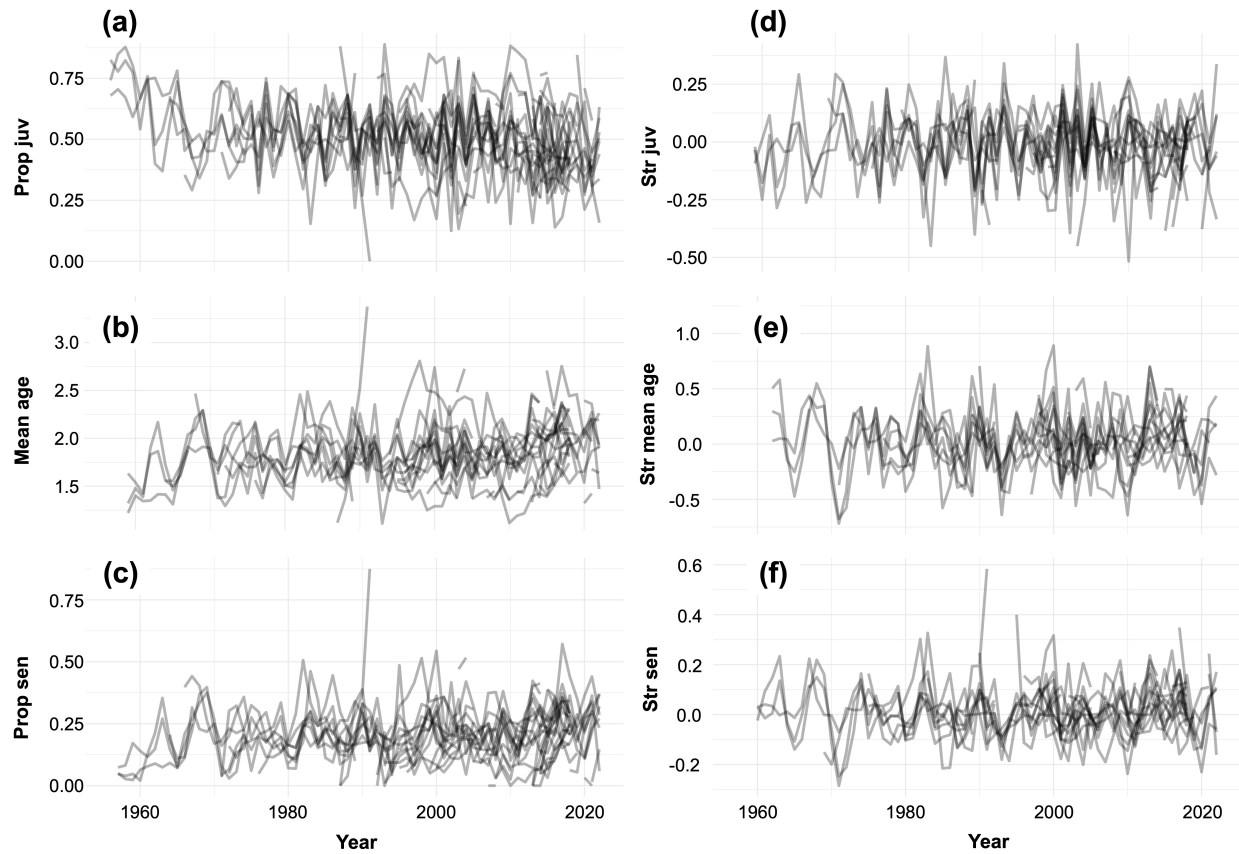


Fig. S3 – Temporal variation in breeding population age structure across European great tit populations. In all plots and analysis, annual populations were only included if the population included at least 20 individuals (mean, IQR: 230, 60–356) and at least 25% of the population was aged (mean, IQR: 56.0%, 36.1–78.2%). Each line corresponds to a continuous time series from a single population (i.e. broken lines represent time series where some annual breeding populations consisted of either less than 20 individuals or less than 25% aged individuals). (a) Shows the proportion of breeding juveniles (32 populations,  $n = 702$ ); (b) mean breeding population age (32 populations,  $n = 637$ ); (c) proportion of breeding senescent individuals (32 populations,  $n = 688$ ); (d) change in the proportion of juveniles compared to a 3-year running mean (30 populations,  $n = 549$ ); (e) change in the mean breeding population age compared to a 3-year running mean (25 populations,  $n = 493$ ); and (f) change in the proportion of senescent individuals compared to a running mean (27 populations,  $n = 536$ ).

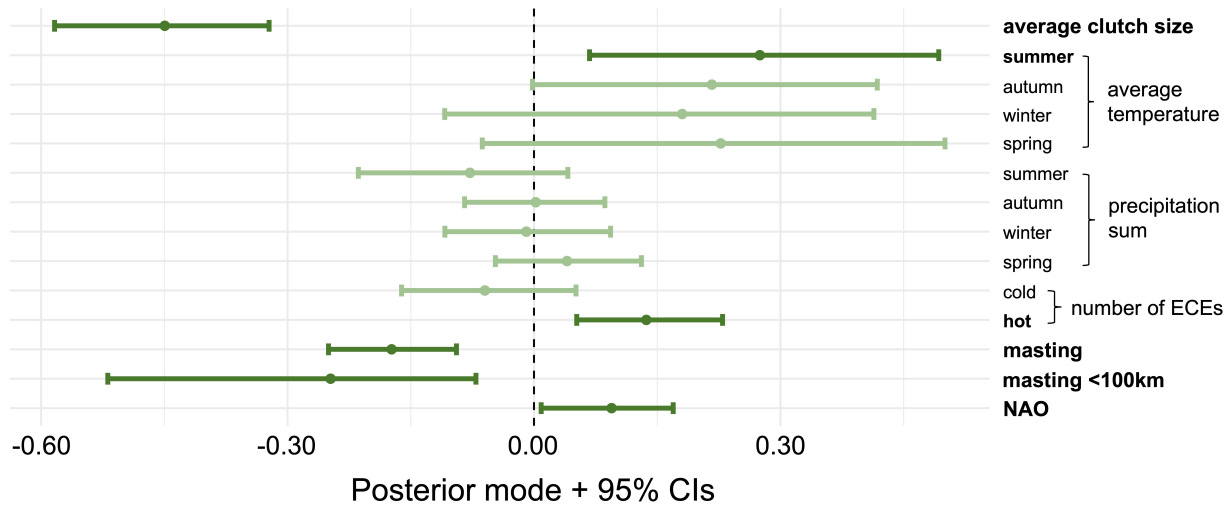


Fig. S4 – Posterior modes obtained from linear mixed-effects models which analyse the association between temporal variation in mean breeding population age and 14 reproductive and environmental variables across 32 great tit populations. Each point corresponds to a specific predictor variable (on the y-axis), and error bars denote 95% credible intervals. Points and error bars are reduced in saturation when credible intervals overlap zero, and explanatory variable text is bolded when they do not.

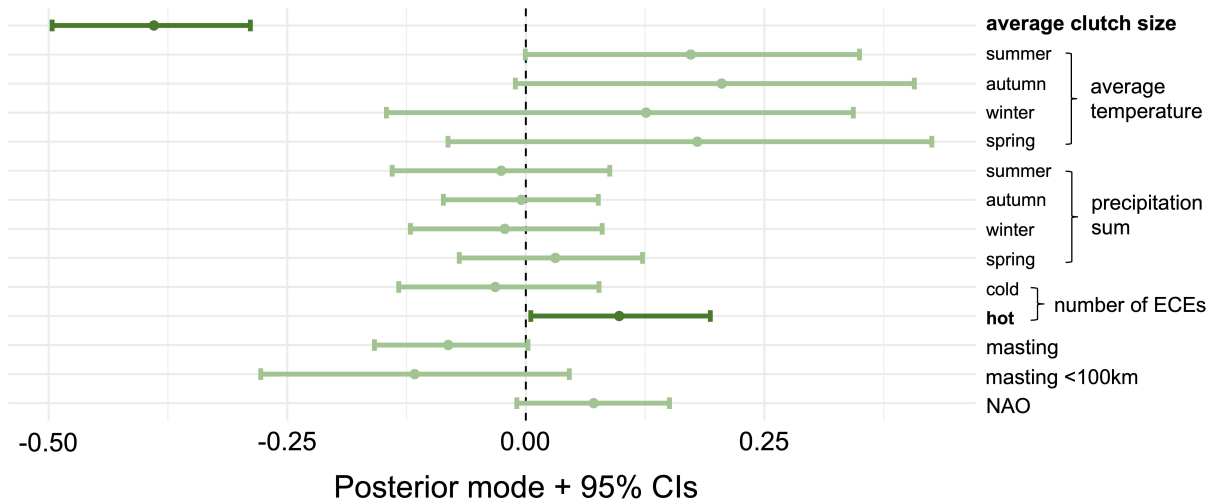


Fig. S5 – Posterior modes obtained from linear mixed-effects models which analyse the association between temporal variation in the proportion of breeding senescent individuals and 14 reproductive and environmental variables across 32 great tit populations. Each point corresponds to a specific predictor variable (on the y-axis), and error bars denote 95% credible intervals. Points and error bars are reduced in saturation when credible intervals overlap zero, and explanatory variable text is bolded when they do not.

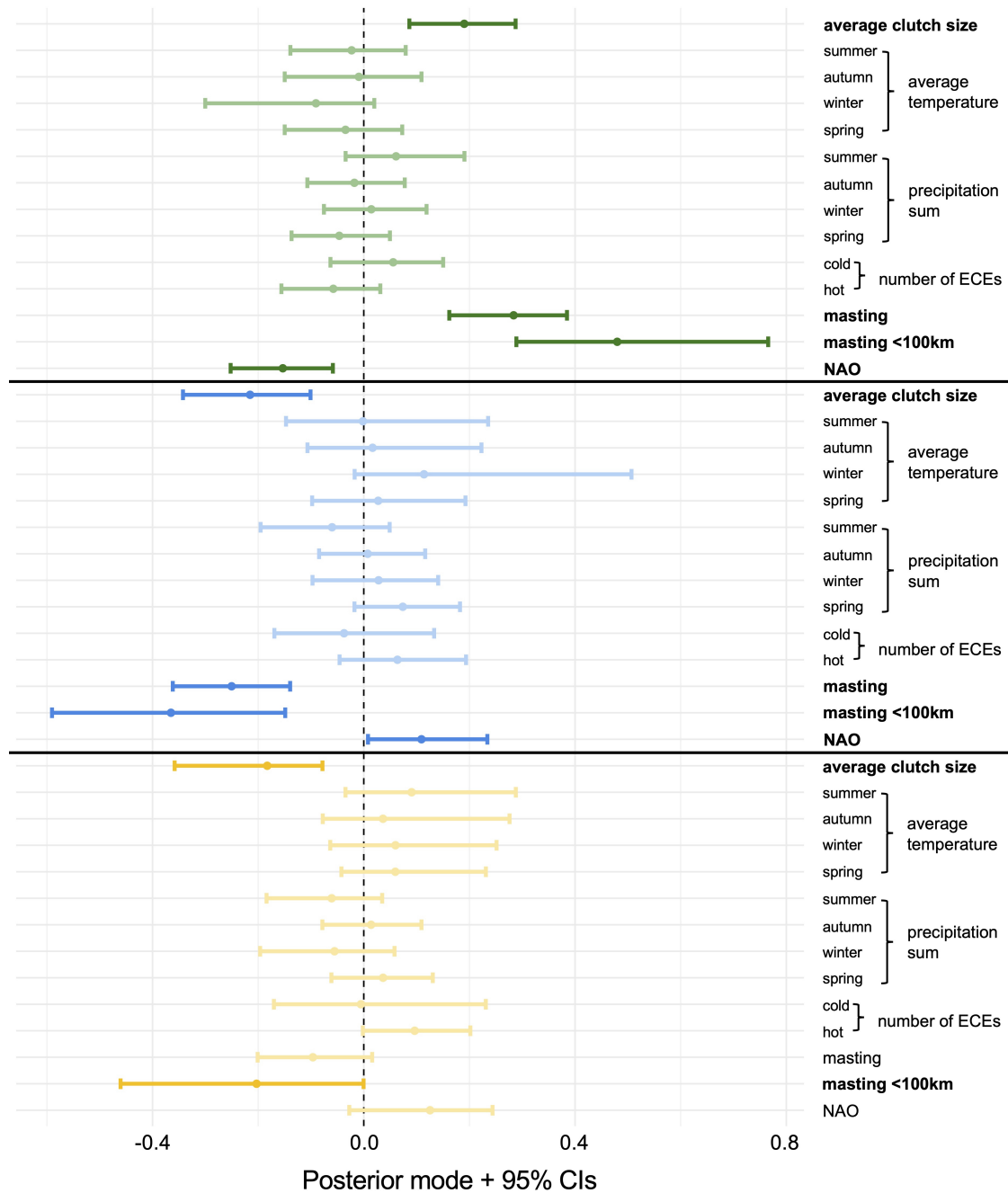


Fig. S6 – Posterior modes obtained from linear mixed-effects models which analyse the association between temporal variation in breeding population age structure (defined as the difference between the within-year static age structure measure and that of a running average calculate as the mean in the three years previous) and 14 reproductive and environmental variables across 32 great tit populations. Each point corresponds to a specific predictor variable (on the y-axis), and error bars denote 95% credible intervals. Points and error bars are reduced in saturation when credible intervals overlap zero, and explanatory variable text is bolded when they do not. Green points are from analysis assessing the proportion of breeding juveniles, blue for the breeding population mean age, and yellow for the proportion of senescent individuals.

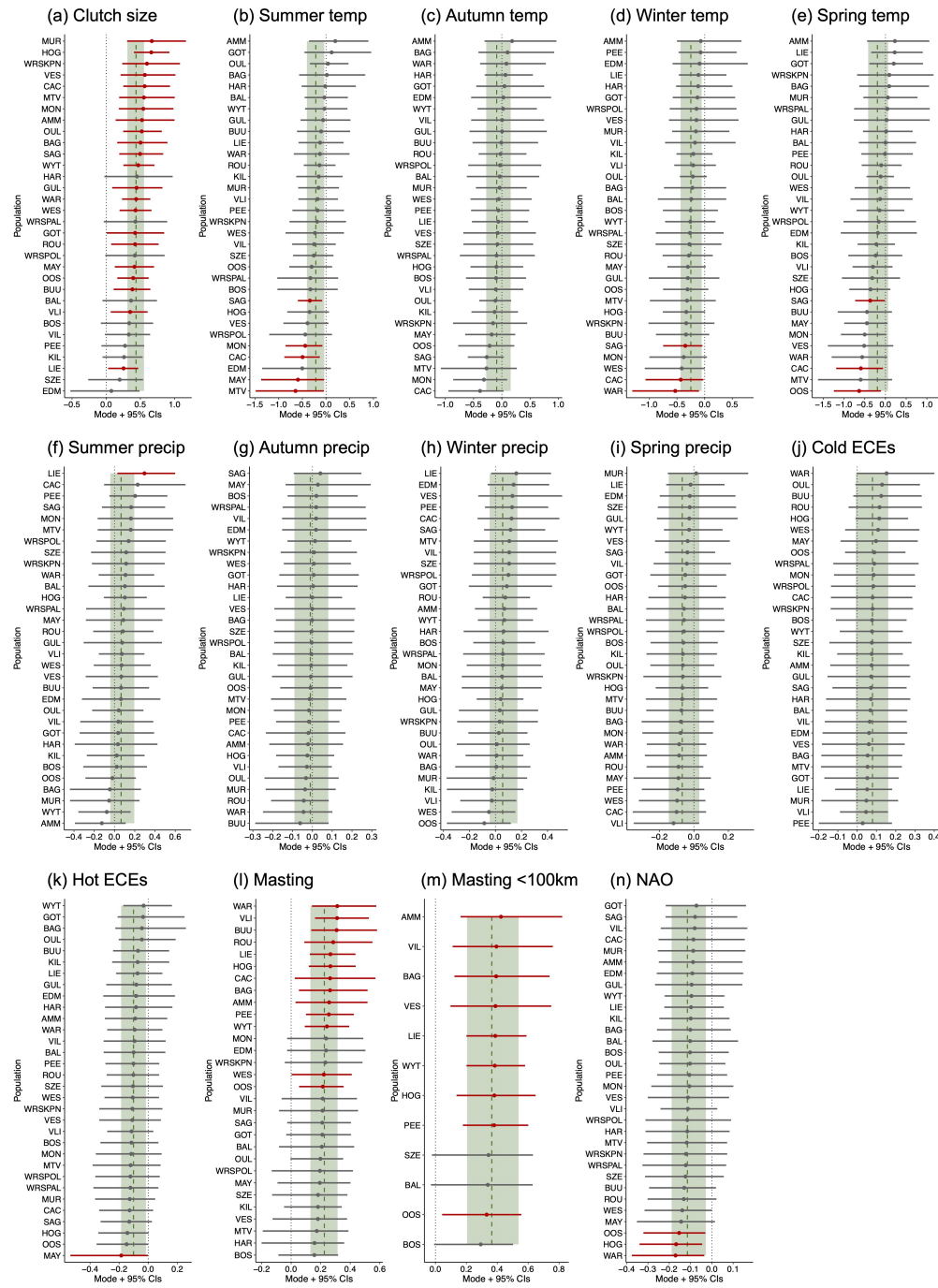


Fig. S7 – Population-specific posterior means obtained from linear mixed-effects models which analyse the association between temporal variation in the proportion of breeding juveniles and 14 reproductive and environmental variables (a–n). Each point corresponds to a specific population (on the y-axis), and error bars denote 95% credible intervals. Red points and error bars denote significant effects where credible intervals do not overlap zero (black dashed line). Dotted green line and shading are the overall posterior mode and 95% credible intervals across all populations (as shown in the main text Fig. 2).

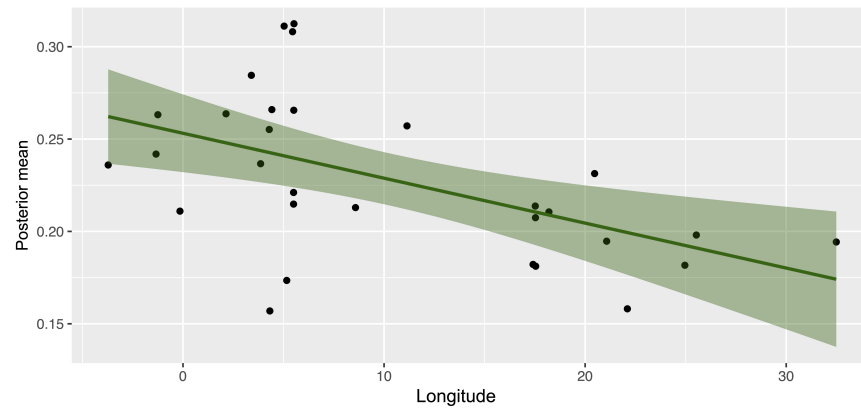


Fig. S8 – Relationship between beech mast value and the proportion of breeding juvenile great tits (posterior means from linear mixed-effect model) along the longitude of a population. The line is a linear regression which models the relationship between these two variables, and the shading around this shows the 95% confidence intervals. The relationship is significant and negative (Spearman's correlation:  $r = -0.517$ ,  $p = 0.003$ ).

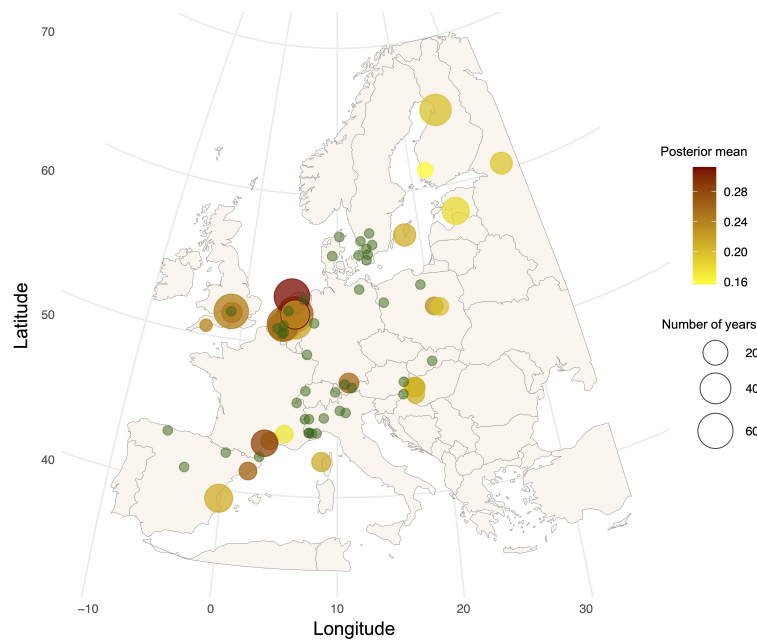


Fig. S9 – Map of the 32 great tit study populations across Europe, with point size relative to the number of years in the time series and colour on a scale of yellow to dark red to indicate the strength of association between the proportion of breeding juveniles and beech mast value (the magnitude of the posterior mean obtained from a linear mixed-effects model). The small green points refer to the locations at which mast data was collected and used in this analysis.

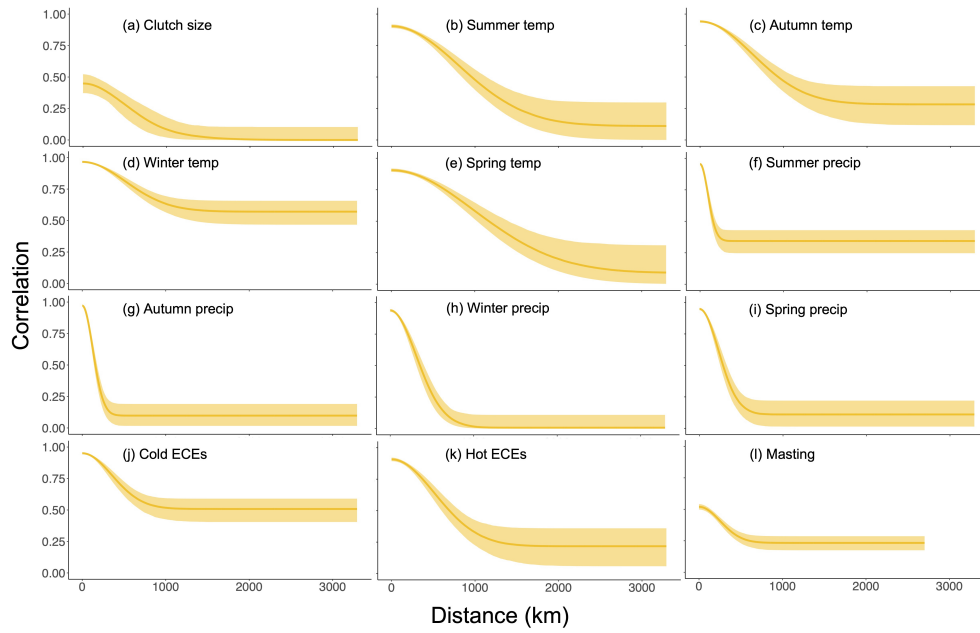


Fig. S10 – Spatial synchrony of the reproductive and environmental variables in relation to distance between sites of data collection (i.e. the site of the 32 great tit populations for all variables except beech mast data). In all plots, distance between sites (km) is on the x-axis and correlation between paired sites is on the y-axis. The yellow line is the median estimate of spatial synchrony (calculated in Equation 2 in the main text) based on 2000 bootstrap replicates, with light yellow shading representing 95% credible intervals.

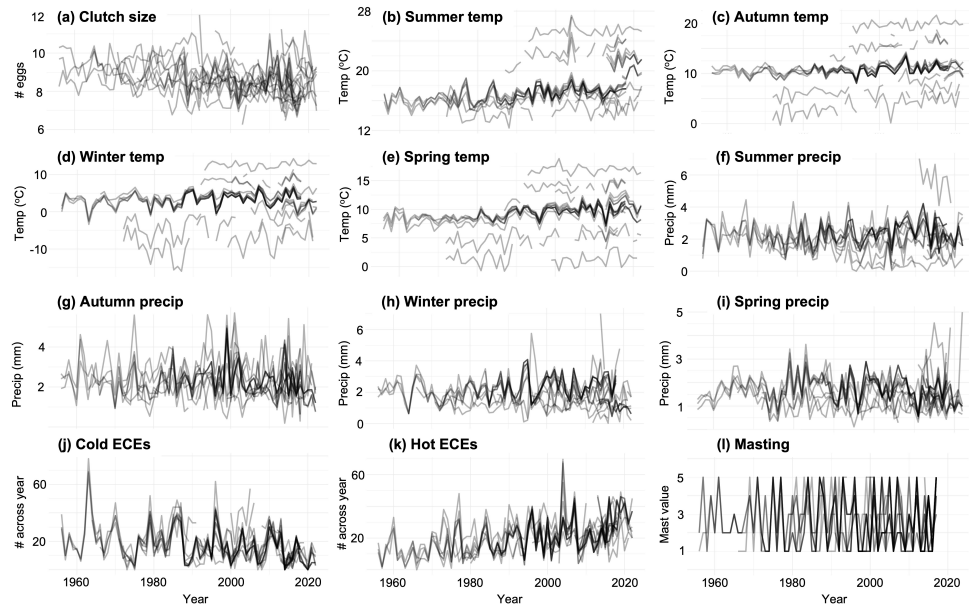


Fig. S11 – Local temporal variation in the assessed reproductive and environmental variables for each population of great tits assessed in this study. Each line corresponds to a continuous time series for a single population.



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# **Chapter VII**

## **General discussion**

# General discussion

## Thesis aims

The interplay between age-based changes throughout lifespan and variation in population processes is central for our understanding of the ecology and evolution of wild populations. It has now been over 65 years since the ecologist LaMont Cole stated that challenges involving age structure are “[...] *among the most critical and complex issues that demographers must address*” (Cole 1957). Indeed, since this time, there have been great advances in linking demographic dynamics with variation in age structure in natural populations (Jorgenson et al. 1997; Caswell 2000; Coulson et al. 2000, 2001, 2005; Preston et al. 2001; Ezard et al. 2006; Pelletier et al. 2012; Gamelon et al. 2016, 2019; Koons et al. 2016; Hoy et al. 2020; Salguero-Gómez and Gamelon 2021). However, previous research on this topic has predominantly deepened our understanding of specifically how demographic variation relates to age structure at the population-level. Thus, there is still much to be explored regarding the causes and consequences of variation in age structure with respect to the broader socio-ecology of populations at different spatio-temporal scales. Consequently, concerns involving age structure are now among the most intricate problems that ecologists must address.

The scientific aspiration to explore hypotheses under these research themes is facilitated by the growing number and increasing data richness of long-term study populations in the wild (Clutton-Brock and Sheldon 2010; Sheldon et al. 2022). Employing statistical analyses to link fundamental individual-based traits (such as age) with spatio-temporal variation in population processes requires complete and long-term sampling of natural populations. Thus, my ambitions for this thesis were to use long-term individual-based data from wild animal populations to extend our understanding of age structure, assessing not only how it links to demographic variation, but also the causes and consequences of its variation across time and space on the broader socio-ecology of wild populations.

## **The causes and consequences of spatio-temporal variation in age structure in natural populations: key findings and future directions**

How should we expect variation in population age structure to affect wild populations? Setting out specific predictions for future work to test is important in any field of biology, particularly for newly-arising areas of research. In **Chapter 2**, I delved into the world of research on social ageing, writing a comprehensive review on how we should expect variation in age structure to affect population sociality given our current understanding of individual-based changes in social behaviour with age, and how this might interact with ecology more broadly. Specifically, I set out predictions of how spatio-temporal variation in age structure has the profound potential to affect social structure, the patterning of breeding behaviour, and rates of cooperation versus competition within and between wild populations. I end this chapter by synthesising the current state of the topic and the most timely areas for further research. Particularly, I highlight that there is an increasing potential for future work to use empirical data from natural populations in combination with social network approaches to uncover pathways linking individual social ageing, population age structure and societal functioning.

However, to gain a more complete understanding of the interplay between age structure, sociality, and ecology, it is necessary to undertake empirical investigation using natural systems. In **Chapters 3–6** of this thesis, I have used long-term data from natural populations of great tit (a model species which shows age-specificity in a number of traits, e.g. Greenwood et al. 1979; Perrins and McCleery 1985; Sandell and Smith 1991; Bouwhuis et al. 2009; Broggi et al. 2010) to quantify and assess the causes and consequences of variation in age structure. I used a variety of approaches to address questions regarding variation in age structure at multiple different social, spatial and temporal scales (including at the pair, neighbourhood, within-population and between-population level).

In **Chapter 3**, building from predictions set out in **Chapter 2**, I assessed how age structure interacts with breeding behaviour by evaluating the drivers of age-assortative pairing behaviour in species with contrasting life-history strategies. This work highlighted two key findings regarding age structure and breeding behaviour at two different socio-spatial scales: 1) at the pair-level, the structuring of age is tightly linked to the life-history strategy of a species; 2) at the population-level,

in species at the fast end of the fast–slow continuum of life-history, temporal fluctuations in age structure can have profound impacts on population-level age-related breeding behaviour. In the case of great tits, we found that high mortality rates and the resulting population age structures can generate age-assortative pairing through purely passive means, as younger individuals may dominate the age distribution, a pattern which was not observed in longer-lived mute swans. Considering this, there is a greater contribution of pair fidelity in generating age-assortative mating across swan pairs, as partners who pair together at the same age live longer and therefore remain age-assorted for longer.

This chapter, based on empirical investigation, provides proof-of-concept that the consequences of variation in age structure can be highly variable in different species. Namely, although two species show superficially similar patterns of behaviour regarding age-assortative mating, we show that the drivers of the process are distinct and can be resolved given the species' different age structures. We suggest in this chapter that the reason we find evidence of active age-assortative pairing in mute swans, but not great tits, might be linked to greater age-dependent variation in fitness in swans (Charmantier et al. 2006; McCleery et al. 2008). This is a non-trivial finding, as it suggests that a widespread breeding behaviour seen in many taxa (Reid 1988; Jiang et al. 2013; Wang et al. 2019) might in some cases be under selection to evolve, while in other lineages it arises as a consequence of species-specific life-history and demographic structures. Thus, extensions of future research that could stem from this work includes critically assessing age-related behaviour that occurs across species (such as those highlighted in **Chapter 2**) and evaluating how the drivers of population-level patterning of such behaviours is affected by between-species differences in age structure.

While **Chapter 3** provides insights regarding how variation in age structure at the population-level relates to age-structuring within pairs, it is also important to consider how age is structured across larger socio-spatial scales to understand how age structure interacts with social and ecological processes. In **Chapter 4**, again using the great tit population as an ideal model system for these questions, we provide evidence for weak positive structuring of age across breeding territories in some years, but a general pattern where age is distributed randomly in space within any single breeding season. This is consistent with a process of a passive socio-spatial structuring of age in most years, similar to the passive assortment of age found within pairs in **Chapter 3**. However,

the mechanisms that we would expect to drive active age assortment across territories compared to within pairs are different. Specifically, we might expect older individuals to retain familiar neighbours as this is adaptive across taxa (Liebgold and Cabe 2008; Grabowska-Zhang et al. 2012b, 2012a; Siracusa et al. 2021; Gokcekus et al. 2023), thus potentially leading to clusters of territories occupied by older birds. Moreover, older individuals might use their greater site familiarity and social dominance (Sandell and Smith 1991; Piper 1997, 2011; Poston 1997; Sol et al. 2000) to outcompete younger individuals for the territories of highest quality, which show spatial autocorrelation across many habitats (including Wytham), thus we would expect this to lead to active age assortment across territories.

The fact that these mechanisms do not produce a strong signal of age-structuring across breeding territories is interesting in that it tells us that the age-effects on reproduction at the individual- or pair-level are not structured across space. Specifically, prime-aged individuals tend to be more reproductively successful than young or senescent individuals across taxa (Sæther 1990; Forslund and Pärt 1995; Loison et al. 1999; Bouwhuis et al. 2012; Nussey et al. 2013; Lemaître et al. 2015), thus if age is structured across space, we would expect this to contribute to spatially-variable demography. However, given our findings that age is rarely significantly assorted in space, and age-structured regions show almost no repeatability over time, this suggests that habitat heterogeneity may be more important for generating repeatable spatially-variable demography in short-lived territorial species.

In **Chapter 4**, we suggest that the overall weak spatial age structure might be mediated by high mortality rates in short-lived species, where even though it is adaptive for adults to retain familiar neighbours, a high proportion will die between years leading to high rates of territory turnover and re-occupation of neighbouring territories by individuals breeding for the first time. This is a hypothesis that suggests why there is weak overall spatial age structure at a reasonably proximate scale, but future work could take our findings further to ask whether it is actually adaptive for territories to be assorted by age within years. Given we know that retaining familiar neighbours is adaptive at the dyadic-level, this should lead to the expectation that positive age-structuring among older individuals leads to greater reproductive output, therefore providing a mechanism for selection to promote positive age-assortment in territorial populations. However, if this behaviour

were to arise evolutionarily, it would force younger individuals in populations to occupy territories close to one another, which might mask the positive effects of age-structuring if this is non-adaptive for younger individuals. While there is no current research to suggest that juvenile–juvenile age-structuring across territories has a negative effect on reproduction compared to juveniles breeding close to older individuals, a long-term study such as that at Wytham provides a suitable system to address such questions, both due to the individual-level detail and long-term nature of the dataset.

In **Chapter 5**, the link between local breeding age structure with age-specific reproductive behaviour was explored by evaluating whether age-specific breeding timing co-varies with the age structure of territorial neighbours, using the great tit population as an ideal model system. We assessed this from two perspectives: the effect of local age structure on 1) absolute breeding timing; and 2) breeding timing mismatch to a local environment. We found that older individuals bred earlier even when accounting for fine-scale local phenological differences, providing evidence of advanced breeding with age potentially linked to experience-based improvement of breeding performance. Interestingly, we found that the age structure of breeding neighbourhoods had no effect on reproductive timing in young individuals, but older individuals breed relatively later when their neighbours are also old. This indicates that younger individuals do not use social cues to time breeding, potentially due to limited phenotypic plasticity and an inability to adjust timing due to the associated energetic costs. I also suggest that differences in breeding timing among older individuals depending on local age structure could be underpinned by both adaptive or nonadaptive mechanisms, either where older individuals actively delay their breeding to gain mutual benefits of synchronised breeding among familiar neighbours, or breeding is delayed due to increased competition in their social environment. Linking back to my findings in **Chapter 4**, this provides yet more reason to warrant future research that assesses the adaptive value of age-structuring across territorial populations, particularly seeing as local age structure has separate consequences on breeding depending on the age of focal individuals.

While **Chapters 3–5** uncover new findings regarding the causes and consequences of variation in age structure within populations, it is important to consider how these insights are likely to affect natural population functioning at wider spatio-temporal scales. Specifically, if we find these patterns within populations, at what scale should we expect them to act between populations? In **Chapter 6**, I used



a collective 702 years of annual variation in breeding age structure to quantify whether fluctuations are explained by environmental variability and if they are spatially synchronous across 32 great tit populations spanning >3200km. I found that temporal variation in age structure is associated with reproductive and environmental variability across populations, and that age structure fluctuations remain synchronous at spatial scales of up to 650km. However, I found that the scale of spatial synchrony was not significantly explained by spatial autocorrelation in the environment, except for some evidence that beech crop cycles may act to synchronise fluctuations in age structure.

**Chapter 6** offers broad insights for fields at the interface of animal ecology and demography, providing evidence of widescale synchronicity in age-structured population dynamics. While the finding of this broad-scale synchrony is compelling evidence that great tit population dynamics are likely simultaneously influenced by phenomena acting at large spatial scales, it is interesting that the environmental variables assessed do not explain synchrony. This might suggest that widescale climate change is unlikely to generate simultaneous density crashes across great tit populations, seeing as we find no effect of local temperature variation in synchronising age structure between populations. Considering there is increasing evidence that climate change influences population dynamics (Ozgul et al. 2010; Hansen et al. 2020), and that highly synchronous age structure dynamics can induce simultaneous density crashes across populations (Engen et al. 2002; Mills 2012), the findings presented here are a valuable contribution as to how we might expect climate change to influence population dynamics in great tits and similar species. As discussed in this chapter, I suggest that variation in ecological features not assessed within this study may explain the synchrony of age structure dynamics across populations, such as synchronous fluctuations in predator or prey populations, or spatial autocorrelation in habitat type.

In the broader context of my doctoral research on advancing understanding regarding variation in age structure, **Chapter 6** provides convincing evidence that its temporal variation co-fluctuates between populations at great spatial scales. This prompts the question of what are the lower spatial limits of such synchrony? This relates to work undertaken in **Chapter 4**, where we assess spatial age structure at the within-population level. Since we found almost no temporal repeatability of spatial age structure at various within-population spatial scales, this might suggest that fluctuations in age structure are temporally synchronised even within-populations, where when the age structure

of the entire population fluctuates over time, it does so also at finer spatial scales. However, initial analysis of this shows, perhaps surprisingly, that the estimates of spatial synchrony in age structure at the within-population level are lower than that between populations found in **Chapter 6** (Figure 1).

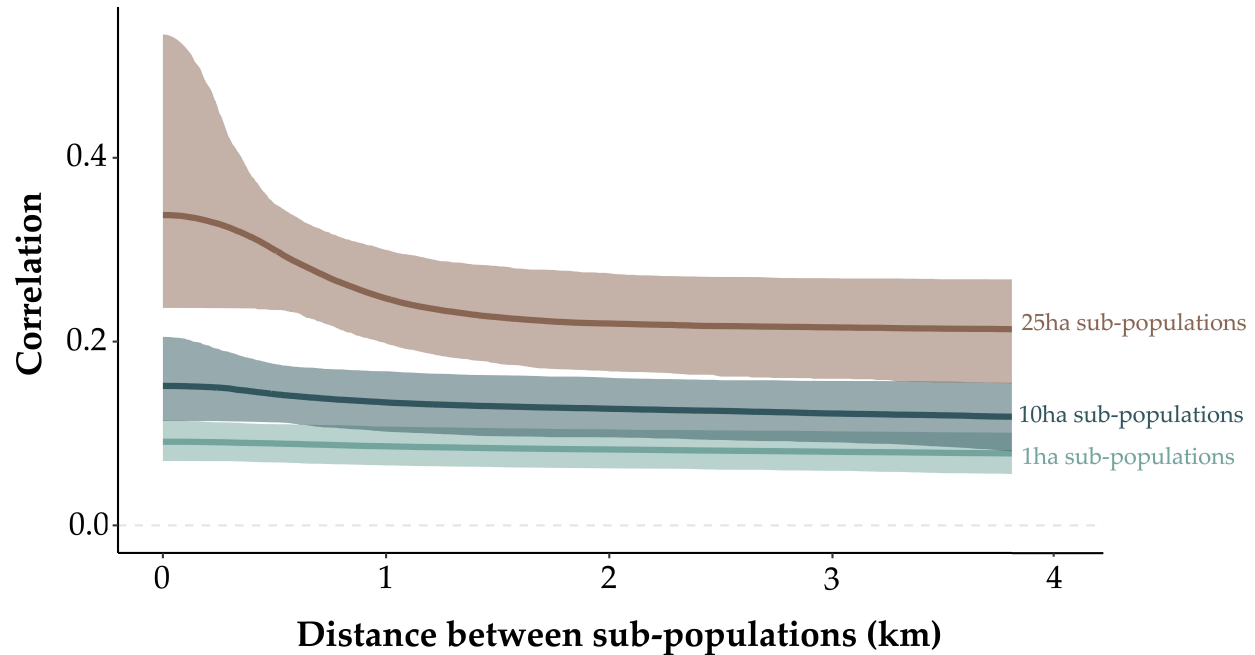


Figure 1 – Spatial synchrony of temporal variation in age structure across subpopulations in the Wytham great tit breeding population 1965–2023 in relation to distance between subpopulations. In all plots, distance between subpopulations (km) is on the x-axis and correlation between paired sub-populations is on the y-axis. The lines are the median estimates of spatial synchrony in the proportion of juveniles in each subpopulation (calculated as in **Chapter 6**) based on 500 bootstrap replicates, with light shading representing 95% credible intervals. The light blue line indicates the synchrony across subpopulations that are defined by 1ha quadrats (nest-box mean number and range in each quadrat = 3, 1–13); the dark blue line for subpopulations defined by 10ha subpopulations (nest-box mean number and range = 11, 1–54); and the brown line for subpopulations defined by 25ha subpopulations (nest-box mean number and range = 33, 1–126). The estimate of spatial synchrony at 3km ( $\hat{\rho}_{3\text{km}}$  [95% credible intervals]) across the subpopulations defined by 1ha,

10ha and 25ha quadrats is 0.080 [0.063, 0.096]; 0.122 [0.093, 0.155]; and 0.215 [0.164, 0.268]. Thus, subpopulations that are larger and have central coordinates at greater distances from each other have higher estimates of spatial synchrony within the population.

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This likely highlights the difference between the underlying mechanisms that induce fluctuations in age structure at these two spatial scales. Across territories within a population, although temporal changes in local age structure will be affected by recruitment and mortality between year  $t - 1$  and year  $t$ , it will also be influenced by individual stochasticity in dispersal and breeding decisions between annual breeding seasons linked to mate and territory choice. For example, unsuccessful breeding attempts are associated with divorce and repairing with a new individual the following season (Culina et al. 2015). Unsuccessful breeding attempts in great tit populations can be spatially-structured, for example if they are induced by predation events linked to fine-scale predator abundance such as weasels *Mustela nivalis*, which can lead to high brood mortality in specific regions (Perrins 1965; Dunn 1977; Figure 2). Thus, this might induce spatially-structured divorce rates (or widowing if one adult is also predated) within breeding populations, which can be associated with greater breeding dispersal from previously unsuccessful territories (Harvey et al. 1979). Additionally, as shown in **Chapter 3**, divorce and widowing rates can mediate age-assortative mating, where greater proportions of newly-formed experienced pairs are associated with greater rates of age-disassortative mating. Thus, spatially-structured divorce or widowing rates will induce differential changes in age structure between years across space, potentially decreasing the spatial synchrony of temporal variation in age structure within populations.

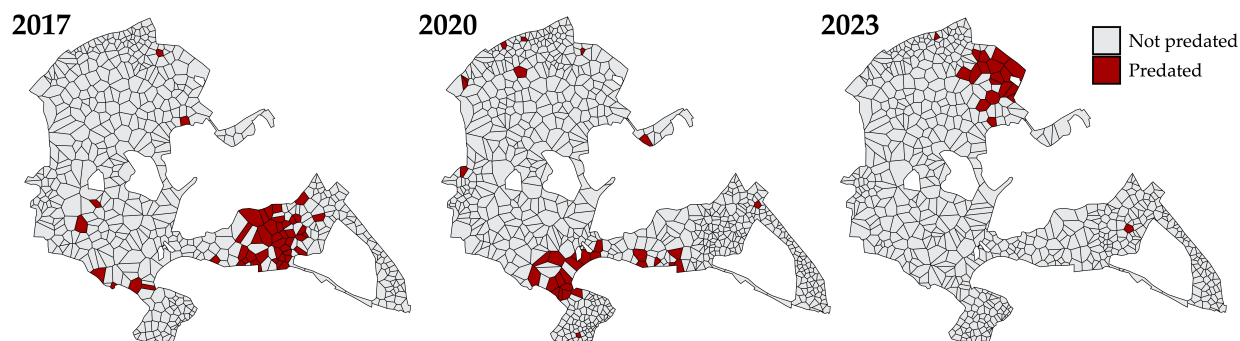


Figure 2 – Predation of *Paridae* broods in territories across Wytham Woods during the 2017, 2020 and 2023 breeding seasons. As can be seen, weasel predation events are highly spatially-structured, which might induce greater breeding dispersal away from the unsuccessful territories for future breeding attempts.

While research carried out in this thesis provides new insights regarding how variation in age structure interacts with the sociality, demography, ecology and evolution of natural populations, it also provides a base from which future research could assess how wild population dynamics interact with contemporary issues in biology. For example, in **Chapter 2**, we highlight that anthropogenic-driven changes in the environment might induce changes in age structure and the emergent social structure and functioning of wild populations (Langvatn and Loison 1999; Robb et al. 2008; Hsieh et al. 2010; Hixon et al. 2014; Festa-Bianchet 2017; Valle et al. 2018; Griffiths et al. 2024). However, the broader findings presented in this thesis also highlight the profound potential for such human-driven changes to natural population age structure to affect various other aspects of population ecology and evolution.

At a proximate scale, human-induced changes to natural habitats might influence the dynamics of spatio-temporal variation in age structure. For example, some research has shown that anthropogenic impacts can alter age structure in wild bird populations depending on age-specific tolerance to noise pollution (Habib et al. 2007; McClure et al. 2017), whereas age-specific harvesting can greatly affect variation in age structure, as discussed in **Chapter 2**. Additionally, increased urbanisation and anthropogenic changes in land use have led to habitat fragmentation across many environments, the negative effects of which on biodiversity and population dynamics are well es-

established (Fahrig 2003; Fuller 2012). However, there is also great potential for anthropogenic-driven change in habitats to influence wild population demography by altering age structure. For example, in **Chapter 4** we find that older individuals breed in territories that are on average at higher densities. Thus, adults might be more tolerant of breeding at higher densities in habitats within patchy environments following habitat fragmentation compared to juveniles, leading to spatially-structured demography. Further, the effects of this on breeding dynamics in natural populations might be affected by our finding in **Chapter 5** that reproductive timing among older individuals is influenced by local age structure, where older local age structures delay breeding.

On an evolutionary scale, anthropogenic change might also have great consequences for natural populations' age structure. For example, in **Chapter 6** we show that while continental-scale spatial autocorrelation in temperature does not synchronise temporal fluctuations in age structure across populations, increased local temperatures are associated with older age structures within populations. With warming temperatures linked to climate change over the entire breeding range of great tits, this might then lead to gradual but persistent shifts in the age structure of great tit breeding populations. Indeed, in **Chapter 6**, we report a weak but significant reduction in the proportion of juveniles found in breeding populations over time. This is a non-trivial finding considering that changes to populations' age structures over evolutionary timescales are associated with alterations to life-history strategies (Schaffer 1974; Stearns 1976, 2000), even promoting species divergence when life-histories become distinct between populations (Johnson et al. 2011; Puritz et al. 2012; Visser et al. 2016). Therefore, the associations between age structure and environmental variability found in this thesis are noteworthy for future research that endeavours to make predictions on how climate change might impact natural population demography and evolution.

## Conclusions

Research into how age structure relates to natural population demography has made great strides over the last few decades. However, an ever-increasing wealth of research evidencing age-based changes in individual traits in wild animals provides ample evidence that we might expect the broader socio-ecology of wild populations to be related to variation in age structure. While this topic is relatively unexplored compared to research linking age structure with strictly demographic

processes, the ongoing investigation of related research themes and the growing number of analyses using data from long-term population studies in the wild demonstrate notable progress.

The research conducted in this thesis has contributed to our advancement of understanding regarding the causes and consequences of spatio-temporal variation in age structure in natural populations. I have shown that age structure has the capacity to induce changes in population social structure and functioning, and demonstrate that its variation differentially mediates population-level breeding behaviour depending on life-history strategy. I show that age structure is temporally variably structured across space within populations, and contributes little to spatially-variable demography compared to structure in habitat features, but that over such spatial scales its variation can have fine-scale consequences on behaviours related to reproductive success. Finally, I provide evidence that temporal fluctuations in age structure are spatially synchronous at a continental-scale across breeding populations. The findings presented from this research, in addition to the methods and frameworks that I have developed, provide a foundation for future work to further our understanding of the causes and consequences of spatio-temporal variation in age structure in natural populations.

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