

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; $p = 0$;

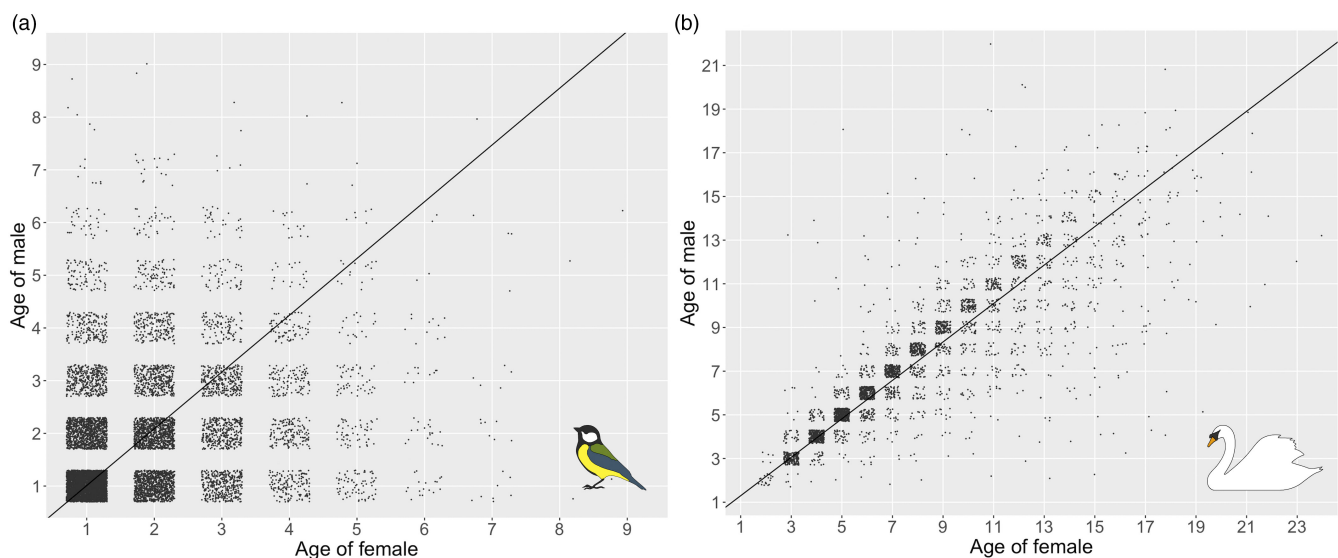


FIGURE 1 Relationship between female and male partner age within mated pairs of (a) great tits 1970–2020 and (b) mute swans 1990–2020. Each point represents a pair with given female and male ages; points are jittered by 0.3 along both axes to avoid over-plotting at the same location. The line is a reduced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

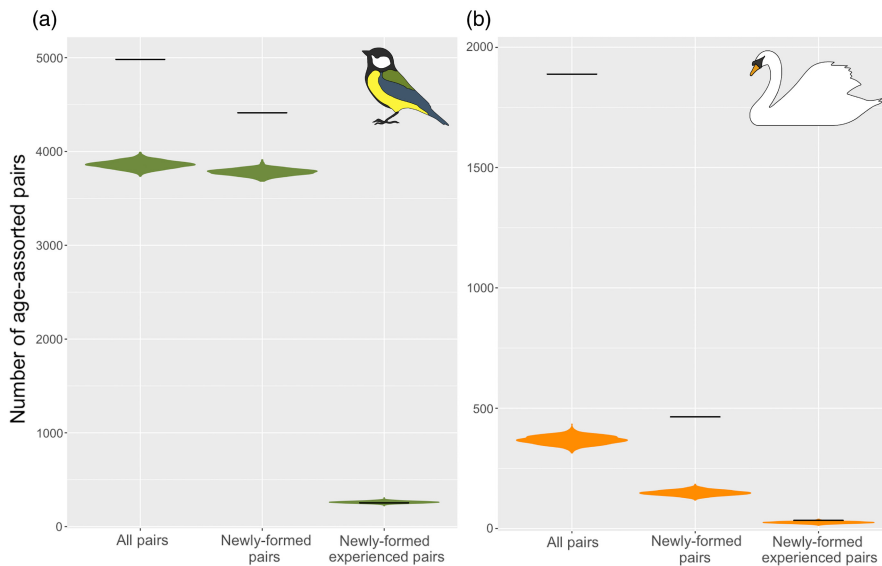


FIGURE 2 The frequency of the number of age-assorted pairs in 1000 permutations where partners are randomly paired with respect to age in (a) all great tit pairs; newly formed great tit pairs; and newly formed experienced great tit pairs; and (b) all mute swan pairs; newly formed mute swan pairs; and 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

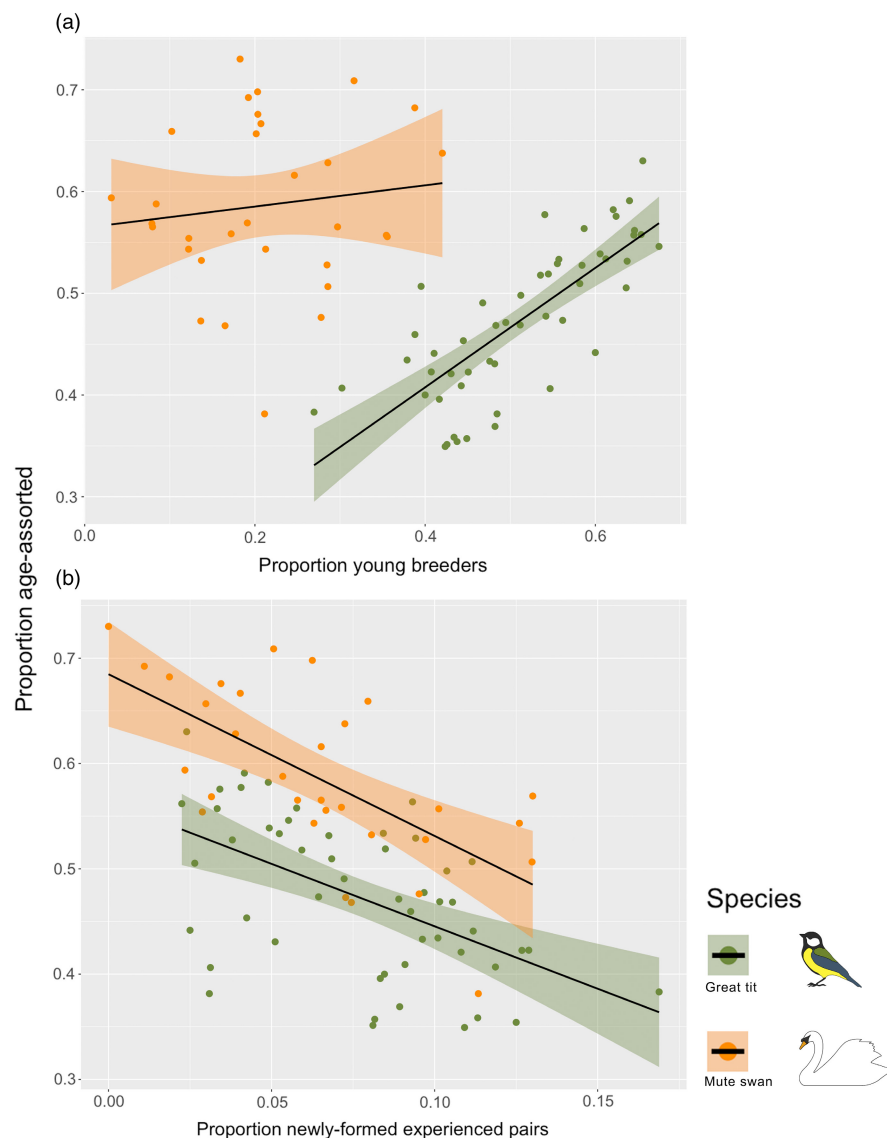
coefficient is within a null distribution of coefficients from 1000 permutations of random pairing (2.5th–97.5th percentiles: -0.176 – 0.441 ; $p = 0.740$; Figure S7). Additionally, there was little evidence for a relationship between proportion of 1–4-year-olds and population age assortment in roundup 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 cyanocephalus* (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 widowing, 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

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