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Evolutionary and plastic responses to global warming in jackdaws

Aina Garcia Raventós

Evolutionary and plastic responses to global warming in jackdaws

Tesi doctoral

Aina Garcia Raventós

Direcció i tutela

Dr. Daniel Sol

Dr. Oriol Lapiedra

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El Dr. Daniel Sol Rueda, professor d'investigació del CSIC a l'Institut de Biologia Evolutiva i al Centre de Recerca Ecològica i Aplicacions Forestals, i el Dr. Oriol Lapiedra, investigador al Centre de Recerca Ecològica i Aplicacions Forestals,

Certifiquen que:

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Aina Garcia Raventós

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Chapter 2

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Chapter 3

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Chapter 4

Garcia-Raventós, A., Lapiedra, O., Sol, D. The role of sociality in microevolutionary responses of breeding phenology in a rapidly changing world. *Manuscript in preparation.*

A downloadable copy of the thesis can be found online at
https://www.researchgate.net/profile/Aina-Garcia-Raventos

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Abstract

Global warming disrupts ecosystems and threats species persistence, leading to the extinction of hundreds of bird species. Thus, the potential of populations to adapt to drastically changing environments is a key question in evolutionary ecology. Behavioural decisions, such as when and where to breed, represent rapid responses closely linked to individual fitness. Advancing the timing of breeding to track changes in temperature is a well-known response of animals to global warming. However, it remains generally unclear the extent to which such responses are adaptive and whether they reflect microevolution, plasticity, or both, hindering our ability to predict species persistence. Quantifying the relative contribution of these mechanisms is crucial for understanding the potential of populations to track global warming and hence forecast their future demographic trends.

Life-history strategies of species may shape the contribution of these mechanisms. Species with short generation times facilitate faster evolutionary changes by natural selection. In contrast, drastic environmental changes may challenge adaptation in animals with long generation times that exhibit slow evolutionary responses to selection. Thus, rapid behavioural plastic responses may serve as a key mechanism for slow-lived species to avoid maladaptation.

While there has been extensive research on reproductive timing in small passerines, our understanding of climate change responses remains limited for species with long lifespans and a high propensity for innovation. Here, I address this gap in jackdaws (*Corvus monedula*), a corvid renowned for its exceptional behavioural flexibility to effectively respond to environmental changes. The thesis comprises five chapters. In **Chapter 1**, I introduce the approaches applied to quantify plasticity and microevolution in natural populations, I present the studied species and system, and I give an overview of the approaches and objectives of the thesis. In **Chapter 2**, I present a protocol developed for molecular sexing through individual genotyping. The method is based on the identification of two unique SNP loci located within non-homologous regions of sexual chromosomes. In **Chapter 3**, I use the genetic sex assignments to construct a pedigree for estimating heritability in the timing of breeding, using long-term data from regions in the North and South of the species distribution in Europe. I show that the advancement in egg-laying during warmer years is a highly plastic and adaptive response. However, I detect notable differences in breeding phenology trends between regions, which could reflect variations in the heritability of the life-history trait. In **Chapter 4**, I review the role of the social environment in evolution and to what extent decisions from closely related individuals could impact heritability estimates and plasticity patterns. Finally in **Chapter 5**, I discuss the main findings of the thesis, further recognising the role of

plasticity in hindering or promoting evolution, and interpretating the contrasting evolutionary potential and phenological patterns among populations within species.

Overall, these results demonstrate that although behavioural plasticity may be crucial in effectively tracking global warming and ensuring population persistence, natural selection can still play an important role in reducing maladaptation in the long-term, even in big-brained and long-lived animals.

Resum

L'escalfament global altera els ecosistemes i posa en perill la persistència de les espècies, provocant l'extinció de centenars d'espècies d'ocells. Per tant, el potencial que tenen les poblacions per adaptar-se a ambients que canvien dràsticament és una qüestió clau en ecologia evolutiva. Les decisions comportamentals, com per exemple quan o a on criar, representen respostes ràpides i estretament lligades a la 'fitness' dels individus. L'avançament en l'època de cria per adequar-se als canvis de temperatura és una resposta àmpliament coneguda dels animals a l'escalfament global. No obstant, encara no està del tot clar en quina mesura aquestes respostes són adaptatives ni si reflecteixen microevolució, plasticitat o una combinació de les dues, dificultant la capacitat de predir la persistència de les espècies. Quantificar la contribució relativa d'aquests mecanismes és crucial per comprendre el potencial de les poblacions per adequar-se al canvi climàtic i preveure les tendències demogràfiques en el futur.

Les estratègies vitals de les espècies poden determinar la contribució d'aquests mecanismes. Les espècies amb temps de generació curt faciliten que es produeixin canvis evolutius més ràpids a través de la selecció natural. Per contra, els canvis ambientals dràstics poden dificultar l'adaptació en animals amb temps de generació més llargs que mostren respostes evolutives lentes a la selecció. Per tant, les respostes comportamentals plàstiques i ràpides poden servir com a mecanisme clau per evitar la maladaptació en espècies de vida lenta.

Tot i que l'època de reproducció s'ha investigat àmpliament en petits ocells passeriformes, el coneixement de les respostes al canvi climàtic és limitat per a espècies amb esperances de vida llargues i alta tendència a la innovació. En aquesta tesi, abordo aquest 'gap' amb les gralles (*Corvus monedula*), un còrvid reconegut per la seva excepcional flexibilitat comportamental per respondre de manera efectiva als canvis ambientals. La tesi consta de cinc capítols. Al **Capítol 1**, introdueixo els enfocs aplicats per quantificar la plasticitat i la microevolució en poblacions naturals, presento l'espècie i el sistema d'estudi, i dóno una visió general dels objectius de la tesi. Al **Capítol 2**, presento un protocol desenvolupat per sexar molecularment mitjançant el genotipatge dels individus. El mètode es basa en la identificació de dos SNPs únics en regions no homòlogues dels cromosomes sexuals. Al **Capítol 3**, utilitzo el sexe genèticament assignat per construir un 'pedigree' per estimar l'heretabilitat en l'època de cria, utilitzant dades a llarg termini de regions al Nord i al Sud de la distribució de l'espècie a Europa. Mostro que l'avançament en la data de posta durant anys més càlids és una resposta altament plàstica i adaptativa. No obstant, detecto diferències remarcables en les tendències de la fenologia reproductiva entre les regions, que reflectirien variacions en la heretabilitat del tret. Al **Capítol 4**, repasso el paper de l'ambient social en l'evolució i fins a quin punt les

decisions d'individus estretament relacionats podrien afectar les estimacions de heretabilitat i els patrons de plasticitat. Finalment, al **Capítol 5**, discuteixo els principals resultats de la tesi, aprofundint en el paper de la plasticitat en reduir o promoure l'evolució, interpretant el contrast potencial evolutiu i de patrons fenològics entre poblacions de la mateixa espècie.

En conjunt, aquests resultats demostren que, tot i que la plasticitat en el comportament pot ser crucial per adequar-se de manera efectiva l'escalfament global i garantir la persistència de les poblacions, la selecció natural encara pot jugar un paper important en reduir la maladaptació a llarg termini, fins i tot en animals amb cervell gran i de vida llarga.

Chapter 1

General Introduction

1.1 Global warming is threatening species persistence

The Anthropocene is an era marked by unprecedented global human influence on Earth's functioning, leading to a wide array of new environmental changes and complexities. Among these, a critical and hard-to-address concern is the extreme biodiversity loss caused by the drastic and rapid environmental changes induced by human activities (Bellard et al., 2012; K. J. Gaston et al., 2003; Spooner et al., 2018). Currently, the 28% of all species are facing threats to their survival due to habitat loss, invasive species, over-exploitation and global warming, including 13% of worldwide bird species (Lees et al., 2022). At the same time, growing evidence show that some species are highly successful in coping with drastic environmental changes (Ducatez et al., 2020; Fristoe et al., 2017; Sih et al., 2011). Understanding the varying impact of rapid human-induced environmental changes on species demography is thus critical to predict and mitigate their vulnerability to extinction.

Across generations, natural selection has finely tuned the phenotype of organisms (i.e. their morphology, physiology and behaviour) to successfully reproduce and survive in their environments. When the optimal combination of phenotypic traits of members of a population is critical for existing in a particular environment, any abrupt and rapid changes in the environment can alter the phenotype-environment match and potentially threaten the persistence of the population. The reduction in the average fitness of individuals due to phenotype-environment mismatch is known as maladaptation (Fig. 1.1). Maladaptation can cause negative population growth, ultimately culminating in the extinction of the population.

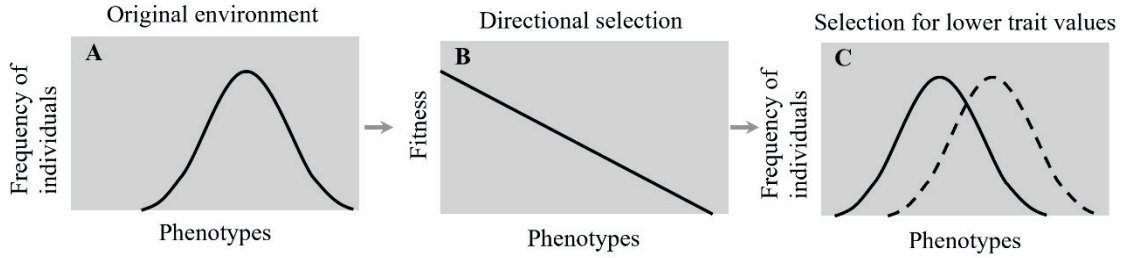

Figure 1.1: Conceptual figure of phenotypic-environment mismatch after an environmental alteration and selection for a new match. (A) Fitness is enhanced when phenotypic traits (e.g. morphology, laying date) match with the optimal conditions from the environment (continuous lines). (B) In cases where directional selection increase fitness for lower trait values (e.g. individuals laying earlier or smaller-sized), (C) the original phenotype (discontinuous lines) is no longer optimal in the novel environment, resulting in a reduced fitness. Organisms may avoid maladaptation by adjusting their phenotype to the new optimal conditions (continuous lines). Adapted from Levin et al. (2009).

Because climatic conditions are a major determinant of a species' ecological niche, climate change is considered one of the components of global change with greater potential to cause maladaptation and local extinction. In birds, the projected extinction of 100-500 bird species for every degree of warming is a growing concern (Sekercioglu et al., 2008). One strategy to avoid maladaptation due to global warming involves dispersing towards northern latitudes or higher elevations to track suitable climates so as to maintain the

phenotype-environment match (W. E. Bradshaw & Holzapfel, 2006; Parmesan & Yohe, 2003). Yet, for some organisms, dispersal may be too costly or obtaining accurate information excessively slow to reconfigure the phenotype-environment match (Edelaar et al., 2017). If organisms vary in the extent to which they can shift their distribution to ultimately enhance fitness in response to increased temperatures, the resulting community structure can drastically disrupt ecosystems (Walther et al., 2002).

1.2 Mechanisms to adjust or adapt the phenotype towards the new environment

An alternative to dispersal and altering the environment to accommodate the phenotype is to modify the phenotype to adjust to the new environment. Selection is a clear mechanism contributing to shifting the phenotype towards a new optimum and locally persist (Fig. 1.1). The observed decline in body size as average temperatures increase reflects an avian morphological adaptation, as smaller-bodied organisms lose heat more efficiently, in line with Bergmann's rule (Youngflesh et al., 2022). However, a stronger selection and a faster rate of change has been reported in phenological traits (Charmantier & Garant, 2005).

One of the multiple consequences of global warming is indeed a mismatch between species phenology and the prevailing climatic conditions. Phenological mismatch can for instance occur when individuals are unable to synchronise their reproduction with the phenology of the resources they rely on (e.g. insects or other arthropods for insectivorous species, or plant productivity in granivorous or frugivorous species) (Gienapp et al., 2014; Harrington et al., 1999; Miller-Rushing et al., 2010; Samplonius et al., 2021; Stenseth & Mysterud, 2002; Visser et al., 2004; Visser & Gienapp, 2019). The advancement of breeding phenology is a well-documented response to global warming, supported by extensive evidence across taxa, particularly in birds (Cohen et al., 2018; Kharouba et al., 2018; Parmesan, 2007; Parmesan & Yohe, 2003; Romano et al., 2023; Root et al., 2003; Thackeray et al., 2016; Visser et al., 2012; Visser & Both, 2005).

Breeding timing is strongly associated with fitness and shifts in response to the unprecedented increase in temperatures has proven to be an adaptive strategy for many species to cope with phenological mismatch (Radchuk et al., 2019). Compared to late breeders, individuals breeding earlier generally match more effectively their reproduction with the period of higher abundance of food resources to feed nestlings (Cohen et al., 2018; Gullett et al., 2013; Kharouba et al., 2018; Vedder, 2012; Visser et al., 2006). Unlike range shifts or changes in morphology or other less labile traits, the adjustment of breeding timing is generally believed to potentially occur rapidly enough to enable the tracking of increasing temperatures. One reason is that behaviour is generally considered to be highly plastic compared to other phenotypic traits (see section 1.3). However, previous work has revealed that variation in breeding timing can have a genetic basis and hence may evolve when breeding earlier or later has fitness consequences, leading to changes in the frequency of genotypes in the population by natural selection (Charmantier & Gienapp, 2014; Nussey et al., 2007; Parmesan, 2006; Sih et al., 2011). While plastic responses are rapid and facilitate population persistence in the short-term,

evolutionary responses tend to occur at slower rates but have the potential to sustain populations in the long-term (W. E. Bradshaw & Holzapfel, 2006; Hoffmann & Sgrò, 2011; Merilä, 2012; Visser, 2008). Thus, the potential of populations to track and adjust to temperature changes depends on the relative importance of both microevolutionary and plastic mechanisms.

1.3 Plastic responses to environmental change

Long-term breeding data from marked individuals studied across environments has shown that the rate of phenotypic change in breeding timing is too rapid to be explained by natural selection alone (Charmantier et al., 2008; Hidalgo Aranzamendi et al., 2019; Romano et al., 2023). Indeed, the advancement in phenology has historically been associated with a mechanism of phenotypic plasticity, with individuals starting earlier in warmer springs and later in less warmer springs (Fig. 1.2B). Because these adjustments go in the direction of improving fitness, such plasticity is considered adaptive and to have potential to evolve (Gienapp et al., 2008; Pigliucci, 2005; Sih et al., 2011).

The pattern of phenotypic expression of a single genotype across a range of environments is known as reaction norm (Fig 1.2C-D). In the reaction norm framework, the decision of when to start breeding is often seen as an automatic response to temperatures. If variation in plasticity among individuals is heritable and leads to differences in fitness, the slope of reaction norms can evolve and accelerate rapid responses to changes in temperature (Brommer et al., 2008; Nussey et al., 2005). Instead, plasticity cannot evolve if reaction norms are similar among individuals (Fig. 1.2C). However, the decision of when to start breeding can also be modified by another form of plasticity, learning (Dukas, 2013; Snell-Rood, 2013; Visser, 2008). By gathering new information over lifetime, learning can increase fitness by allowing individuals to interact with the environment in new ways while avoiding maladaptation. Within populations, individuals might differ in their sensitivity to changes in temperature, with some individuals closely tracking a rapidly changing environment and advancing phenology in a higher rate than others less experienced (Fig. 1.2D). However, this variation is learned, not heritable, and hence it does not generally facilitate the evolution of a new reaction norm (Fig. 1.2E).

Learning can modify decision-making not only based on previous experiences of the individual, but also on information generated by more experienced conspecifics (social learning). This does not only spread more rapidly the benefits of learning, but also reduce the costs of learning in terms of time, energy and risks of exploration(Jaakkonen et al., 2015; Valone & Templeton, 2002). If individuals copy the decisions of more experienced individuals, this should reduce variation among individuals in reaction norms, and again reduce the strength of selection (Fig. 1.2F). The notion that cognition protects individuals against maladaptation through learning is referred to as the cognitive buffer (Sol, 2009; Sol et al., 2016), and its inhibitory effects on adaptive evolution is known as the ‘Bogert’ effect (Bogert, 1949). The ultimate and proximate factors that influence animal decision-making, and the implications of these decisions for population and evolutionary dynamics remain poorly understood.

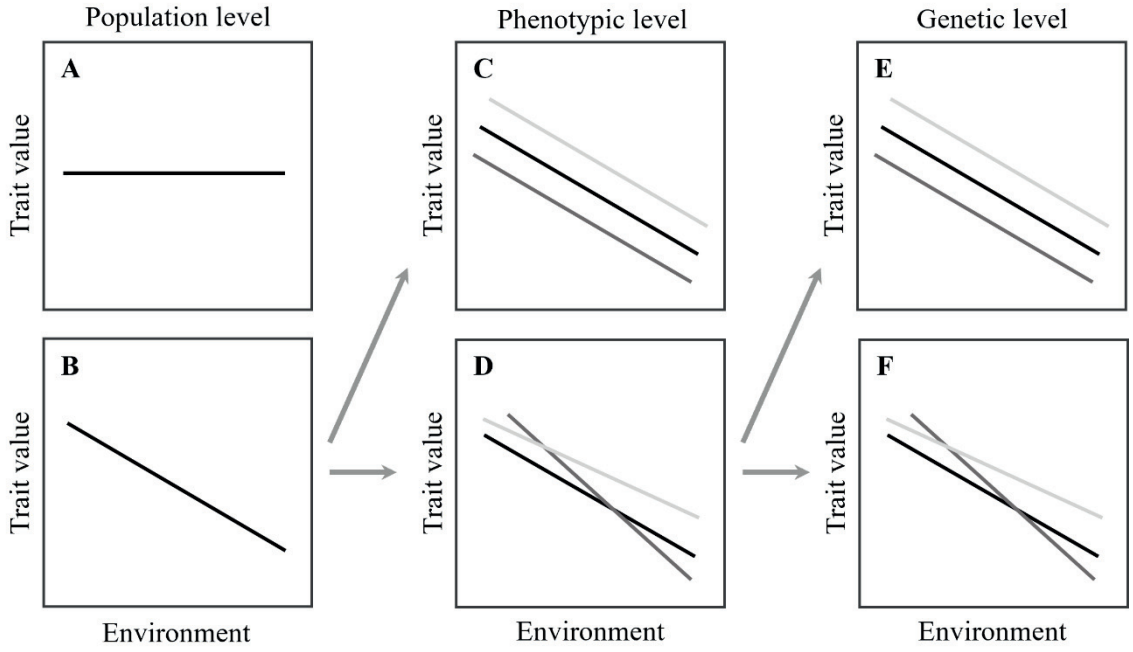

Figure 1.2: Population, phenotype and genetic levels of response. (A) Populations will not respond if traits are not sensitive to an environmental gradient. (B) Populations respond to environmental changes when the mean trait values vary across an environmental gradient during individuals lifetime. (C) At the phenotypic level, individuals may have a similar reaction norm slope (but can differ in their reaction norm estimate), or (D) show among-individual variation in plasticity, termed IxE (individual-environment interaction). At the genetic level, if individuals' reaction norms vary, (E) the variation at the phenotypic level might be due to the interaction with the environment of a non-genetic component (permanent environment), or (F) have a genetic basis due to GxE (genotype-environment interaction). In cases of GxE interactions, the genotype alters its expression as a function of the environment, while when the cause of variation across individuals is explained by non-heritable effects (permanent environment), genotypes do not have the potential to change expression across environments. Adapted from Gienapp & Brommer (2014).

1.4 Microevolutionary responses to environmental change

The persistent increase in temperatures and the consistent selection for earlier timing observed across studies indicates that adaptive plasticity in response to global warming is incomplete (Radchuk et al., 2019). This pattern may indicate potential costs associated with plasticity of early breeding (Sutton & Freeman, 2023), constrains imposed by other life-history traits (Both & Visser, 2005), or physiological factors (Dawson, 2007). In animals that rely in learning to make decisions, the pattern can also reflect the significance of the 'Bogert' effect (Bogert, 1949).

Given that phenotypic plasticity can be either insufficient or no longer adaptive in a changing environment, the microevolutionary potential of the population remains crucial to maintain the match between phenotype and environment in the long-term (Visser, 2008). This process is known as evolutionary rescue and is thought to be crucial to prevent extinction following environmental change (Bell & Gonzalez, 2009). The rate of the microevolutionary response is expected to increase with the strength of directional

selection (covariance between traits and fitness) and the heritability of the trait (how closely offspring traits resemble those of their parents) (Fig. 1.3).

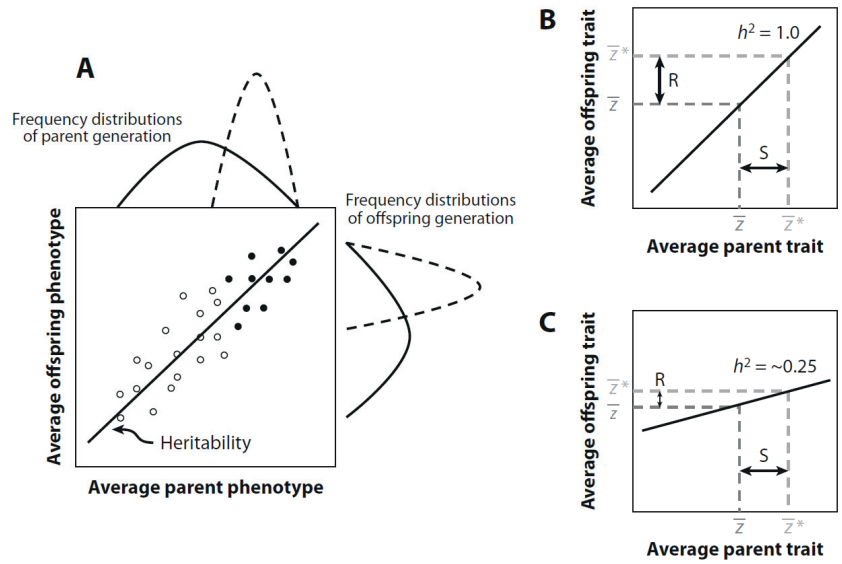

Figure 1.3: Heritability plot and response to selection. (A) The slope of the relationship between the average trait of parents and offspring is the heritability of the trait. On the margins the frequency distributions of each generation are shown (solid curves). In the absence of selection, means of each generation remain unchanged. If truncation selection occurs and only parents with traits above a threshold value reproduce (solid symbols), the distributions change (dashed curves). (B-C) The means of the parent generation and the offspring that would be produced are shown as $\bar{z}$. After truncation selection, the mean of the parent distribution becomes $\bar{z}^*$ and the difference between the parent means is the strength of selection (S). Heritability determines the average traits of the offspring that would be produced after selection, $\bar{z}^*$. The difference between mean of the offspring produced and those that might have been produced is the response to selection, $R = \bar{z}^* - \bar{z}$. The same strength of selection (S) can generate a strong response (B) or a weak response (C) depending on the heritability of a trait. Figure from Brodie (2014).

The heritability of a trait is the proportion of phenotypic variation explained by genetic differences among individuals. The relatedness among individuals can be estimated by means of both social or genetic pedigrees (based on parental assignments from field observations or genetic data, respectively) of free-living populations. Despite the challenges in natural populations, accurate pedigree reconstruction supported by molecular genetic data is increasingly available across a wide range of taxa (Pemberton, 2008). In the field, DNA can be extracted from both invasive (blood, tissue) or non-invasive samples (feathers, hair, saliva, urine, scats, etc.) collected from captured and marked individuals (Carroll et al., 2018). Non-invasive samples, despite having lower-quality DNA, meet more ethical requirements and may be the only alternative for performing genetic analysis on endangered or elusive species that are otherwise challenging to sample (Horváth et al., 2005).

Several approaches can be applied to genotype individuals using a range of markers from microsatellites to single nucleotide polymorphisms (SNPs). SNPs offer increased precision, repeatability and resolution, and lower error rates compared to classic microsatellite markers (Hauser et al., 2011; Weinman et al., 2015). Therefore, SNPs are

becoming a useful marker in ecological and evolutionary studies, successfully applied to low-quality DNA (Helyar et al., 2011; Kraus et al., 2015; Norman & Spong, 2015; Nussberger et al., 2014; von Thaden et al., 2020).

High-throughput SNP genotyping procedure is optimised to handle thousands of samples with efficient lab and analysis workflows (Ekblom et al., 2021; Garvin et al., 2010). In addition to individual identification, population structure inference and sexing, multi-locus SNP panels offer the possibility to infer both population size and relatedness between individuals (Norman & Spong, 2015; Spitzer et al., 2016). However, reconstructing pedigrees presents challenges, such as incomplete sampling, unknown population sizes, overlapping generations with long reproductive lifespans, and a lack of information on individual age or sex. For this reason, complementing genetic data with field data from observations, recaptures or indirect methods (data-loggers, cameras or other advanced devices) is a good practice to collect useful information to determine candidate progenitors in the study area during mating or breeding seasons (Jolles, 2021; Jones & Wang, 2010; Pemberton, 2008).

Pedigree-based methods for estimating quantitative genetic parameters in field studies have proven to be more effective than marker-based estimates (Coltman, 2005). Mixed-effects models known as the 'animal model' decompose phenotypic variance into different genetic and environmental sources (Postma & Charmantier, 2007; Wilson et al., 2010). Both genetic and environmental variances can be further partitioned to include genetic and environmental maternal effects attributable to the mother, as well as cohort, birth year, age, sex, among others (Wilson et al., 2010). In a narrow-sense definition, heritability (h^2) refers to the proportion of the phenotypic variance for some trait that can be attributed to variance of additive genetic effects. Traditionally, the slope of the regression line of offspring phenotype on the average phenotype of the parents is an estimation of heritability (Fig. 1.3). However, animal models are more powerful than traditional analyses such as parent-offspring regression because they use all available pedigree information simultaneously.

Good estimates of the genetic parameters of natural populations, such as heritability, are essential for both understanding how genetic variation is maintained and estimating the evolutionary potential of populations (Visser, 2008). The rate of microevolutionary change in a trait across generations (R) is predicted using both the heritability (h^2) and selection differentials (S) by applying the Breeder's equation, $R=h^2S$ (Lynch & Walsh, 1998). Thus, the stronger the heritability, the more intense the effects of selection in one generation are translated into phenotypic change across generations (Fig. 1.3). A consequence is that the rate of microevolution is expected to be faster in morphometric traits, as the level of heritability is usually higher than in fitness traits (Houle, 1992), while selection pressures may be stronger in life-history traits due to the close association with fitness (Ramakers et al., 2018).

Selection occurs when some values of a trait are associated with higher values of reproductive success. If the covariance is positive, large values of a trait are disproportionately reproduced, whereas smaller values of a trait are overproduced if the

covariance is negative. If the covariance is zero, then all values are equally reproduced on average and no selection occurs (Brodie, 2014). Similarly, a lack of genetic variation in the traits under selection limits the response of populations to environmental change. Because environmental change has the potential to modulate the effect of both selection and genetic variation, it can deeply alter the rate of microevolution among species, populations and individuals.

1.5 The response potential is shaped by species life-history strategies, climate exposure and individuals heterogeneity in phenological sensitivity

Abrupt and rapid changes in the environment may be challenging for adaptation, particularly for animals with long generation times that exhibit slow evolutionary responses to selection (Sol et al., 2020). Consequently, we anticipate that the relative contribution of plasticity versus microevolution will vary according to the life-history strategies of species. Species with short generation times are expected to rapidly adapt to new environments through natural selection if their preferences are genetically determined (Kokko & Sutherland, 2001). In contrast, evolutive responses in slow-lived animals, which prioritise survival over reproduction (Stearns, 1989), may not occur rapidly enough to effectively adapt them to the new context.

Behavioural decisions during laying (e.g. timing and reproductive investment) are an important part of avian life-history strategies, likely imposing constraints and trade-offs with other traits and subsequent behaviours (Daan et al., 1989). As described in previous sections, organisms exhibit a strong relationship between temperature and phenology (Gienapp et al., 2014). The Earth's climate has globally warmed by approximately 0.6 ºC on average over the past 100 years (Walther et al., 2002). However, climate change exposure (ºC/year) varies geographically, with greater rates of climate change at higher latitudes (Parmesan, 2007). At regional scales, the expression of life-history traits and plasticity among populations within species can be affected by the spatial and temporal heterogeneity in environmental conditions (Wright et al., 2019). Thus, populations within species may differ in the rate of change in timing of egg laying, with important implications for understanding the role of behavioural responses and the extent to which local adaptation and phenotypic plasticity govern responses to climate change (Burgess et al., 2018; Cole et al., 2021).

While some populations may successfully track shifting climates, others may exhibit lower rates of change. That is, phenological climate sensitivity (days advanced/ºC) is influenced by locally varying climatic and non-climatic drivers such as population structure, resource availability and the amount of genetic variation in a population for evolutionary adaptation (Thackeray et al., 2016). Indeed, heritability in breeding phenology is not necessarily constant across populations because both the variation in additive and non-additive genetic factors, and the environmental variance, are population-specific (Visser, 2008). For instance, empirical evidence suggests that populations from more variable environments show higher levels of plasticity that might preadapt them to extremes, while heritability is increased in more favourable conditions (Charmantier & Garant,

2005; Chevin & Hoffmann, 2017). However, environmental change can also alter patterns of phenotypic and genetic variation, affecting both selection and heritability, and thus the rate of microevolution of breeding time across populations (Charmantier & Gienapp, 2014; Gienapp et al., 2008; Nussey et al., 2005; Réale et al., 2003). Therefore, the rate of phenological advancement depends on climate exposure and phenological sensitivity, both affected by the biotic and abiotic environment (Bailey et al., 2022).

Individuals are predicted to integrate various sources of information and respond to a combination of multiple environmental variables that best predict variation in the individual-specific phenotypic optimum (Chevin & Lande, 2015). Environmental changes can be gradual, but abrupt changes are also increasingly likely (Ratajczak et al., 2018). When the environment fluctuates on timescales shorter than the generation time, and cues used to choose habitats and resources are no longer reliable (Bonamour et al., 2019), an innate preference for a particular habitat or resource may lead individuals to make suboptimal decisions and fall into ecological traps (Robertson et al., 2013; Schlaepfer et al., 2002). Furthermore, individual-level differences in cue perception can cause reduced or maladaptive plasticity in a population if the response does not shift the trait mean to the optimal from the environment (Gienapp et al., 2014). Thus, cue variability and reliability at different timescales interact to shape plastic responses, altering the adaptive nature of plasticity with potential changes in reaction norms owing to plasticity evolution (Ghalambor et al., 2007). Selection on the heritable component of plastic responses impacts the ability of populations to continue to respond adaptively to environmental variation (Ghalambor et al., 2007; Visser et al., 2004).

Microevolutionary responses are also affected by learning. Learning is expected to be particularly useful in long-lived animals, which show slow evolutionary responses to selection (Maspons et al., 2019; Sol & Maspons, 2016). Individuals with long lifespans are not only more likely of encountering environmental changes throughout their lives but also to utilize acquired behaviours and benefit from an extended learning period (Sayol et al., 2016). Thus, behavioural plastic responses may serve as a key mechanism for slow-lived species to reduce the phenotype–environment mismatch, not also by mitigating new threats but even by exploiting new opportunities presented by the novel environment (Sih et al., 2011; Sol, 2009; Tuomainen & Candolin, 2011). At the same time, a behavioural shift further reduces the strength of natural selection by hiding genetic variation, thereby inhibiting evolutionary change ('Bogert' effect, Bogert, 1949; Huey et al., 2003; Price et al., 2003).

Furthermore, microevolutionary responses are shaped by the social environment. Since most organisms interact with conspecifics, these environmental effects may often include social effects (Moiron et al., 2020). For instance, an individual's decision of when to start breeding may be influenced by the decisions of other individuals (Moore et al., 1997; Schmidt et al., 2010; Teplitsky et al., 2010). Transgenerational plasticity facilitates heritable phenotypic adaptation while reducing genetic loss and allowing for mutations to accumulate (Bonduriansky & Day, 2009; Harmon & Pfennig, 2021). Therefore, our ability to predict the potential of populations is likely to depend on the degree to which

individuals base their decisions on social information, either accelerating or hindering the potential for microevolution.

1.6 Jackdaws (*Corvus monedula*): a big-brained, long-lived, and social bird

Birds play key functional roles within ecosystems and have been highly studied as a model taxon for ecology and evolutionary biology. This is due to the broad understanding of their taxonomic, functional, and phylogenetic diversity, geographic distributions, ecology, and conservation status, which exceeds that of any other group of organisms (Lees et al., 2022). Therefore, the availability of long-term studies on pedigreed and individually marked wild populations makes birds a suitable group for studying the contribution of adaptive plasticity and microevolution. My thesis delves into exploring these mechanisms using jackdaws as a model species.

The Western Jackdaw (*Corvus monedula*) is a small bird species within the corvid family. It inhabits open areas in the Palearctic and it is resident in most of its range, covering a wide distribution across Europe (Madge & de Juana, 2020) (Fig. 1.4A). The black plumage, grey nape and distinctive pale-greyish or silvery white irises are the most notable traits of its phenotype (Fig. 1.4B-D). The species is well-known for its cognitive abilities and its ability to persist in human-altered environments with stable population trends around Europe, listed as least concern by the IUCN. Still, the species is rapidly diminishing in some areas of southern Europe mainly due to anthropogenic alterations of its habitat (Blanco et al., 2022; Blanco & García, 2023).

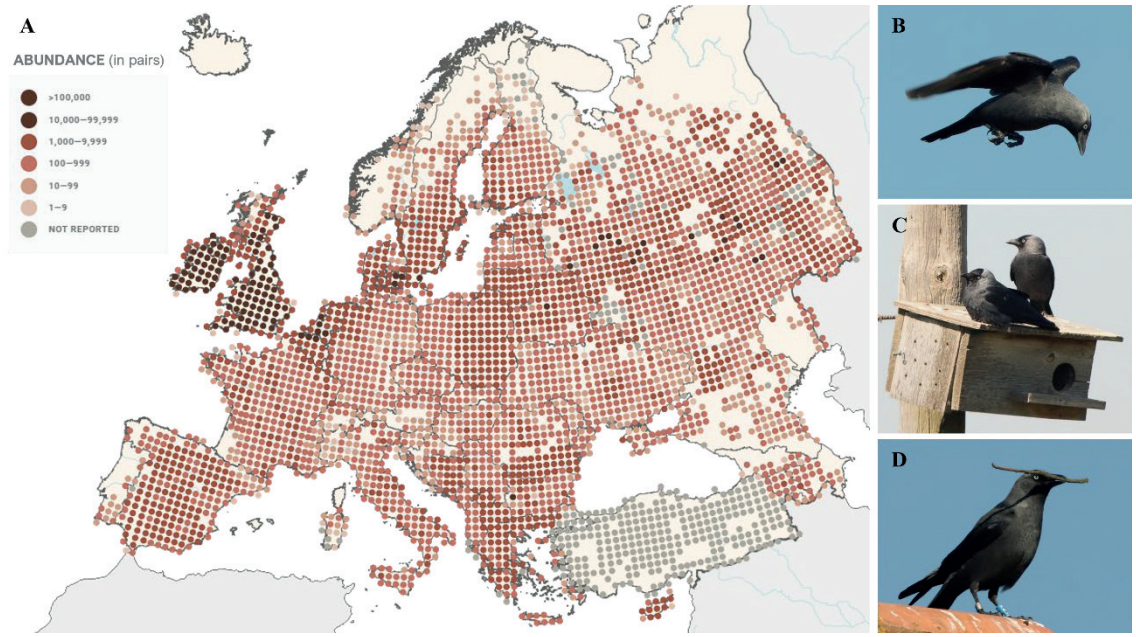

Figure 1.4: Distribution and images of the Eurasian jackdaw (Corvus monedula) across Europe. (A) Abundance map showing numbers of pairs (source: the European Breeding Bird Atlas, EBBA). (B) A wild adult jackdaw taking a flight, (C) a breeding pair above the nest box where they are breeding, (D) a ringed adult jackdaw with a branch in its peak ready to build the nest (source: personal).

Jackdaws are relatively long-lived species, reaching sexual maturity after two years, and with a maximum recorded lifespan of 20.3 years (Tacutu et al., 2018). They establish long-term pair bonds, and are genetically and socially monogamous (Henderson et al., 2000; Röell, 1978), with both sexes participating in nest building and parental care (Hahn et al., 2021; Kings et al., 2023). Similar to many other avian species, adult jackdaws are monomorphic and show little size dimorphism, with some overlap between males and females (Fletcher & Foster, 2010; Henderson, 1991). The head and neck plumage of male birds tends to fade more with age and wear, particularly just before moulting. Notably, juvenile individuals display a brownish colour in their plumage, lack the grey nape, and have light blue-grey eyes. These characteristics are similar between males and females, therefore, the identification of sexes in the field is challenging (Gill et al., 2020).

Jackdaws are highly social birds, breeding semi-colonially in cavity nests. They forage in social groups where individuals vary in social ranks (Verhulst et al., 2014a) and form large flocks, sometimes up to hundreds of roosting birds, coordinated by vocally mediated consensus decisions (Dibnah et al., 2022). Their remarkably intelligence and flexibility to adjust to new contexts have attracted the interest of scientists as a model species for studies on cognition (Arbon et al., 2023; Greggor, Thornton, et al., 2016; Woods et al., 2018). One of the main aims has focused on understanding how the mechanisms of decision-making are shaped by human disturbance and mediated by social learning from conspecifics (Lee et al., 2019).

1.7 Objectives and approaches of the thesis

The thesis explores the mechanisms that explain population responses to global warming, with a focus on the relative contribution between phenotypic plasticity and microevolution on the selection for an advancement in breeding phenology within jackdaws. While there is substantial evidence that many birds are advancing their reproduction in response to global warming, it remains uncertain whether the responses reflect plasticity or microevolution. This is notably the case for long-lived, behavioural innovative animals, whose ability to modify decisions by learning may relax the phenotype-environment match and reduce the strength of selection throughout the 'Bogert' effect. The thesis seeks to fill this gap through a comprehensive analysis in the Western Jackdaw (*Corvus monedula*). The Jackdaw is particularly suitable for such study because it combines a long-life with a high ability to learn new behaviours and exchange social information (see section 1.6).

Chapter 3 is the core of the thesis, and it addresses three main objectives: (1) to what extent are individuals adjusting their laying date to changes in temperatures, (2) whether such response is adaptive, and (3) whether the response mechanisms reflect plasticity and/or microevolutionary processes (Fig. 1.5). These aims were investigated by using breeding, life-history and genetic data at the individual-level from two long-term monitoring programs of jackdaw populations, one in northern ranges of the species distribution (Cornwall, UK) and the other southern ranges (Lleida, central Catalonia) (see map in Fig. 3.1).

In **Chapter 2**, I first developed a protocol for molecular sexing by identifying sex-linked single nucleotide polymorphisms in unique regions of the sexual chromosomes and validated with morphological measures of within-pair comparisons (Fig. 1.5). Field work was carried out in Lleida where jackdaws breed in artificial colonies of nest boxes. The study area covers habitats differing in the degree of alteration by agriculture practices in an agroforestry landscape characterized by a marked seasonal and annual fluctuations in food resources between cereal monocultures, agriculture mosaic and natural shrublands/forests. In **Chapter 3**, breeding data from Lleida was complemented with data from the Cornish jackdaw project, assembled during my stage in Alex Thornton's lab at the University of Exeter. By comparing the importance of the mechanisms in both regions we further discussed potential large-scale patterns of plasticity and evolution in life-history trait within species in response to environmental change. Finally, in **Chapter 4** I reviewed the effects of sociality as a key role explaining the potential for microevolution in social species (Fig. 1.5). This last chapter is indented to highlight future lines of research aimed at gaining a deeper understanding of the responses of animals to global change.

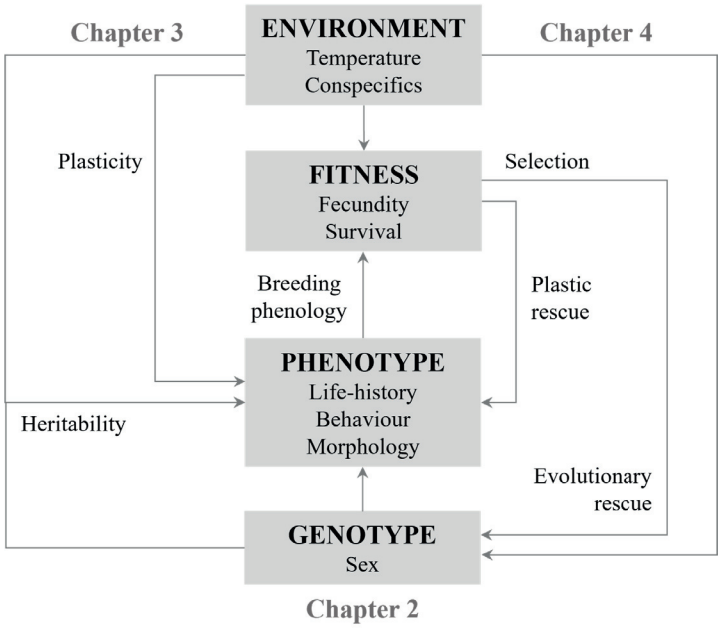

Figure 1.5: Schematic conceptual framework of the thesis. Chapter 2 sets the basis, in which a molecular sexing protocol is developed by means of individual genotyping and validated with morphology. This information will be crucial in chapter 3 to study the mechanisms (plasticity and heritability) on breeding phenology to mitigate the effects of temperature changes in individual fitness. In chapter 4, I review the indirect effects of the social environment to the focal genotype impacting on heritability estimates.

Chapter 2

Identification of sex-linked SNP markers in wild populations of monomorphic birds

Abstract

Single-nucleotide polymorphism (SNP) analysis is a powerful tool for population genetics, pedigree reconstruction and phenotypic trait mapping. However, the untapped potential of SNP markers to discriminate the sex of individuals in species with reduced sexual dimorphism or of individuals during immature stages remains a largely unexplored avenue. Here, we developed a novel protocol for molecular sexing of birds based on the detection of unique Z- and W-linked SNP markers. Our method is based on the identification of two unique loci, one in each sexual chromosome. Individuals are considered males when they show no calls for the W-linked SNP and are heterozygous or homozygous for the Z-linked SNP, while females exhibit both Z- and W-linked SNP calls. We validated the method in the Jackdaw (*Corvus monedula*). The reduced sexual dimorphism in this species makes it difficult to identify the sex of individuals in the wild. We assessed the reliability of the method using 36 individuals of known sex and found that their sex was correctly assigned in 100% of cases. The sex-linked markers also proved to be widely applicable for discriminating males and females from a sample of 927 genotyped individuals at different maturity stages, with an accuracy of 99.5%. Since SNP markers are increasingly used in quantitative genetic analyses of wild populations, the approach we propose has great potential to be integrated into broader genetic research programs without the need for additional sexing techniques.

2.1 Introduction

The growing development of advanced molecular and bioinformatic tools has revolutionised the study of ecology and evolution by allowing the sequencing of hundreds of samples in parallel at a whole-genome scale (Hudson, 2008). Next-generation sequencing (NGS) techniques are sensitive, accurate, and low time-consuming, making them applicable to non-model organisms (Valasek & Repa, 2005). The availability of massive genomic data provides promising potential in the fields of genomics, transcriptomics, and proteomics, as well as wide applications for microsatellites and single-nucleotide polymorphisms (SNP) screening (Mardis, 2008).

SNPs are increasingly being used to study wild populations. They are suitable for population-level genotyping due to their abundance and widespread distribution along the genome, low genotyping error, high-throughput, and low cost per locus (Kaiser et al., 2017). SNP markers are widely used in population genetic analysis, pedigree reconstruction, extra-pair paternity assignments, and phenotypic trait mapping (Garvin et al., 2010), providing crucial information to address important aspects of evolutionary and conservation ecology.

The use of SNP markers also holds great potential for accurately sexing wild animals. The sex of individuals plays a pivotal role in a diverse range of key ecological and evolutionary processes, including habitat use, feeding specializations, parental care, dispersal, and migration (Durell, 2000; Selander, 1966). Thus, devising molecular tools for reliable sex identification has long been on the agenda of wildlife ecologists. However, tools for sexing using SNP markers have only been developed for commercial animals (Andrews et al., 2016), including a range of aquaculture fish and crustacean species for which the factors involved in determining sexes have not yet been identified (Fang et al., 2020; Palaiokostas et al., 2015; Shi et al., 2018; Wang et al., 2019). Despite its significant potential to reduce costs and improve performance, the application of SNPs for sex identification in wild-ranging animals remains largely unexplored. One notable advantage relies in the ability to perform multiple genetic analyses using the same multi-locus panel that includes all SNPs of interest, eliminating the need for additional PCR amplifications and electrophoresis. This approach offers the opportunity for efficient and comprehensive sexing, harnessing the full benefits of SNPs in a cost-effective and time-saving manner.

Here, we describe a novel protocol for molecular sexing of birds based on single nucleotide polymorphisms. Birds are well-known for their extraordinary diversity of sexually dimorphic characters. The elaborate mating performances by colourful males with striking plumage colours, bill sizes and shapes in birds-of-paradise (family Paradisaeidae), or the extreme adaptations in the tail of male peacocks (*Pavo cristatus*), are among the most emblematic displays (Beehler, 1989; Owens & Hartley, 1998). However, the sex of birds cannot always be easily identified by phenotypic traits. In fact, about half of all avian species are sexually monomorphic, with males and females showing very similar appearances (Price & Birch, 1996). These species include geese, cranes, rails, raptors, owls, parrots, doves, auks, shearwaters, and many passerines (Volodin et al., 2015). Even in sexually dimorphic species, males and females rarely show sex-linked morphological

differences shortly after hatching, making it impossible to obtain information on the sex ratio at birth exclusively from phenotypic measurements.

Our method is based on the identification of two unique loci, one in each sexual chromosome. Birds have the ZW sex-determination system, in which males are the homogametic sex (ZZ), while females are heterogametic (ZW) (Bloom, 1974). Similar to the XY system in mammals, Z and W chromosomes share homologous sequences of nucleotides in the pseudoautosomal region (PAR) (Fridolfsson & Ellegren, 1999). In this region, genes are inherited in the same way as any autosomal gene rather than being sex-linked, and both males and females have two copies of this region. Therefore, SNPs found in the PAR region would only distinguish females and males in the rare event that each allele variant is fixed and specific for each sexual chromosome. In those cases, females would be heterozygotes whereas males would be homozygotes. Outside the PAR region, however, discriminating among sexes is expected to be easier because unique Z-linked SNPs would amplify two SNP alleles in heterozygous males and only one in females, while unique W-linked SNPs would amplify only in females. Only hemizygous individuals (individuals in which only one member of a chromosome pair is present) or homozygous males would express one Z allele call but no call for W. ZZ males are then defined by either homozygote or heterozygote genotype calls for the Z-chromosome-linked SNP and the lack of the calling variants in the W-chromosome-linked SNP. Conversely, ZW females would amplify for the W-chromosome-linked SNP but would not show heterozygosity for the Z-chromosome-linked SNP.

To illustrate the method, we use the Western Jackdaw (*Corvus monedula*) as our study system. Jackdaws are small corvids from the Palearctic (Madge & de Juana, 2020), characterised by black plumage, a grey nape, and distinctive pale-blue irises. Sex identification in this species is difficult because sexual dimorphism in plumage is absent and, although adult males tend to be larger than adult females, there is certain overlap between sexes (Fletcher & Foster, 2010; Green & Theobald, 1989; Henderson, 1991). While the power of discriminating between sexes can be greatly reduced by using within-pair comparisons of relative size, the number of accurately sexed samples is restricted to paired individuals (Fletcher & Hamer, 2003). The alternative of sexing individuals based on the traditional PCR amplification of the CHD sexual gene (Griffiths et al., 1998) has proven effective in Jackdaws (e.g. Aastrup & Hegemann, 2021; Arnold & Griffiths, 2003; de Kort et al., 2003; Hahn et al., 2021; Salomons et al., 2006; Woods et al., 2018). However, we show that the use of SNPs can offer a reliable and efficient approach for high-throughput sex identification within broader population genetic studies. Despite the limitation of lacking a W-chromosome reference in the Jackdaw, our protocol made it possible to locate the pseudoautosomal region (PAR) in which both sexual chromosomes share homologous sequences. Locating candidate SNPs outside that region is crucial to detect unique Z- and W-linked markers that can be used to reliably sex individuals. By means of identifying and annotating sexual chromosomes, our approach can easily be extended to other avian species.

2.2 Material and Methods

2.2.1 Sample collection in the field

From 2015 to 2022, we captured both fledgling and adult Jackdaws as part of a long-term study of a population breeding in nest-boxes in the Lleida plain, northeastern Iberian Peninsula (Unzeta, 2020). We banded each individual with a metallic ring, measured the weight and length of the tarsus and third primary wing, and took a sample of feathers from the abdomen for genetic analyses. To help develop the library of SNPs, we also used adults found dead during the visits to the nest-boxes. From dead individuals, we sampled a piece of tissue from the wing shoulder and placed it in Eppendorf tubes. All tissue samples were stored at -20ºC to prevent DNA degradation. Feathers from trapped individuals were first stored in glassine bags at room temperature, and selected samples were later transferred to -20ºC freezers to be preserved until DNA extraction. No storage buffer was used to preserve tissue or feather samples. Permits for animal manipulation and sample collections were provided by the Servei de Fauna i Flora from the Generalitat de Catalunya (SF/430-439/2016, SF/0473-0476/2018, SF/0039/2019, 4/2020/MP, SF/0093/21, SF/0018_2/22).

2.2.2 Sample dissection and DNA extraction in the lab

Feather dissections were performed by taking the cells from the basal tip of the calamus, following Morin et al. (1994). The lysis was performed by adding 400 µl lysis buffer and 40 µl protease K, and incubating samples at 56ºC overnight. DNA was extracted using an automated Chemagic 360 instrument (Perkin Elmer) from a total of 957 samples, which included 905 feathers from fledglings, and 49 feathers and 3 tissue samples from adult individuals. Additionally, a duplicated sample collected from a recaptured individual was included as a genotyping control. The quality and concentration of the extracted DNA were assessed using a NanoDrop spectrophotometer (Thermo Fisher Scientific). Laboratory procedures were performed at the SVGM laboratories (Molecular Genetics Veterinary Service) of the Faculty of Veterinary of the Autonomous University of Barcelona. Some feather samples (N=90), particularly those belonging to adults, had low DNA concentrations (below 50 ng/µL, which is the recommended DNA concentration to ensure proper sample genotyping according to the Thermo Fisher Scientific protocol for QuantStudio™ OpenArray® PCR Plates). For such low-quality samples, liquid was evaporated using a SpeedVac Vacuum Concentrator centrifuge to increase DNA concentrations. This process was carried out at the Centre for Research in Agricultural Genomics (CRAG) facilities. Further details on sample quality, applied thresholds and genotyping success related to DNA concentration are shown in Note A.1 in Appendix A (see also Fig. A.1 and Fig. A.2).

2.2.3 Identification of nine candidate sex-linked SNP loci

The exploration of candidate sex-linked SNP loci was carried out through the compilation of individual sequences using our own data (eight birds from Lleida) and data kindly provided by Weissensteiner et al. (2020) (four whole-genome sequenced birds from Sweden) (see Note A.2 and Table A.1 in Appendix A). To locate the sexual chromosomes

and the PAR region within them, we first assembled the sequences of the four individuals from Sweden. We assumed that the homologous regions between non-autosomal chromosomes should map within the PAR region. Additionally, we annotated and identified the CHD gene (chromo-helicase-DNA-binding), which is traditionally used for sex identification in birds (Griffiths et al., 1998), and it is located within the PAR region. Similar to Palmer et al. (2019), we used the number of reads mapping to this gene to distinguish between males and females. Individuals J01, J02 and J08, with a high number of mapped reads, were classified as males, while individual J03 was classified as a female based on the low number of mapped reads (see Note A.2 in Appendix A). Since reads mapped heterogeneously in multiple regions along the chromosome Z, with variable coverage ranging from 4 to 30 and a median of 12, this approach did not allow us to identify the starting and ending positions of the PAR region accurately. Having the exact positions of the PAR region would help ensure the selection of truly unique SNPs. To address this challenge, we pursued an alternative method by mapping sequences from both chromosomes. We located the chromosome W based on a sequence deposited in NCBI from a female of a closely-related species, the New Caledonia Crow Corvus moneduloides (accession number CM018842.1). Reads that did not map to chromosome Z or any other part of the genome were assumed to be unique to chromosome W.

Once we identified the PAR region and the W-chromosome, we used the sequences from both populations to identify SNPs located in sexual chromosomes, preferably outside the PAR region, to assess their utility for sexing. From the W-chromosome identified using genomic data on the four individuals in Sweden, we selected four SNPs from different regions far from CHD and potentially unique for W. The chosen SNPs were specifically selected from distant positions within the genome to mitigate the potential influence of genetic linkage. From the Z-chromosome, we selected one SNP previously tested in the eight birds of the studied population in Lleida (F9A, see Note A.2 in Appendix A), and four additional SNPs detected in the four birds of Sweden. These four SNPs presumably presented fixed sex-specific allele variants, at least within the four analysed individuals, and were located in regions close to the CHD gene, assumed to be within the PAR region. Although not unique, the interest in including these markers relied on the potential of distinguishing the heterozygote females from the homozygote males (in case genotype variants were fixed in each sexual chromosome). Overall, we used a total of nine SNPs located in sexual chromosomes to evaluate for their usefulness for sexing.

2.2.4 SNP genotyping with OpenArray Real-Time PCR

The OpenArray® technology is an advanced real-time PCR method that enables a broad range of applications, including SNP genotyping and gene expression analysis (Broccanello et al., 2020; Schleinitz et al., 2011). The thermocycler measures FAM and VIC fluorescence signals of the amplified product (SNPs sequences, in our case) that is generated during the reaction. Such fluorescence signals are expressed when the threshold cycle (CT) value is reached, which indicates the number of PCR cycles until the genotype calling groups are specified. The fact that the detection of the DNA amplification occurs while the reaction is proceeding —instead of at the end-point— makes the technology faster, more precise, and accurate than other PCR technologies (Valasek & Repa, 2005).

Excluding 3 blanks and 29 samples without amplified genotype variants of 960 samples, we analysed the genotyping results of 928 samples from 927 individuals.

2.2.5 Validation of the genetic sex assignments

Individuals with the combination of homozygote calls for Z-linked SNP and amplifying for W-linked SNP were assigned as females. Male individuals could show either homozygote or heterozygote calls for the Z-linked SNP. However, since males lack the W-chromosome, they should not show calling variants for the W-linked SNP. To validate the accuracy of the genetic sex assignments of the 927 genotyped individuals, we employed the morphological approach suggested by Fletcher & Hamer (2003). This method is based on the observation that, although in species with sexual size dimorphism there is some overlap in morphology between males and females, within pairs males are consistently larger than females. Thus, morphology within breeding pairs offers a reliable means of distinguishing between sexes (see Fletcher & Hamer, 2003, and references therein). Consequently, we capitalised in the well-documented sexual size dimorphism observed in jackdaws (Henderson, 1991) and used it to identify the sex of individuals within all discernible breeding pairs from the studied population (N=18 pairs). Because jackdaws are socially monogamous species (Hahn et al., 2021), we considered two individuals to form a pair when they were captured in the same nest-box and subsequently observed visiting the nest frequently for incubation and providing food to offspring. Individuals that we could not assign to a pair were excluded. Following Henderson (1991), we assessed body size differences within each pair based on tarsus length in combination with wing length. Wing length was estimated by measuring the length of the third primary feather. In all pairs except one, we consistently observed that the individual with a larger tarsus also had longer wings. Based on this consistent pattern, we confidently assigned this individual as male and their mate as female. The classification based on the previously mentioned criteria was not as straightforward in the only breeding pair in which one member had a larger tarsus but a smaller wing compared to the other. Considering that the wing measurement is less reliable than the tarsus measurement due to changes caused by moulting or abrasion, we presumed the individual with the larger tarsus to be the male. For further evidence supporting the accuracy of using morphology to identify the sex of our breeding jackdaw sample, we refer the reader to Fig. A.7 in Appendix A.

2.3 Results

We found that six out of the nine candidate SNPs included in the OpenArray could not differentiate between sexes among individuals. Four of them (F1C, F2C, F4C and F6C) showed fixed allele expressions without variability between samples. Another SNP (F3C) did not amplify in any sample. The last SNP (F70A) did amplify for the “A” and “G” alleles but not for the heterozygote genotype “A/G”, indicating that the SNP was located within the PAR region on the Z chromosome. SNPs located in the homologous region are useful for sexing only if variants are fixed in each chromosome. Since this assumption was not met, we discarded these six SNPs and focused our attention on the remaining two W-linked SNPs (F5C and F7C) and the Z-linked F9A.

For F9A, 323 samples (34.8%) expressed the allele "A", 360 (38.79%) expressed the allele "G", whereas 236 samples (25.43%) expressed both "A" and "G". Nine samples (0.97%) could not be genotyped because they did not amplify in any of the 928 samples. Scatter plots for allelic discrimination confirmed the existence of three clusters for F9A (Fig. A.3), corresponding to the homozygote genotype for allele 1 ("G/G" with high values of VIC and low values of FAM), the homozygote genotype for allele 2 ("A/A" with high values of FAM and low values of VIC), and the heterozygote genotype ("A/G" with high values of VIC and FAM). Since F9A was found in the Z-chromosome, heterozygote samples could only correspond to ZZ male individuals, while either male or female individuals could express a homozygote genotype.

The results for the F5C and F7C confirmed that they were W-linked and located outside the PAR region (Table 2.1). Fluorescence for F7C and F5C clustered into two groups separating samples that amplified ("A" with high values of FAM and VIC) from those that did not amplify ("NOAMP" with low values of FAM and VIC) (Fig. A.4 and Fig. A.5 respectively). In F7C, 466 samples (50.21%) amplified for the variant "A", and in F5C, 443 samples (47.73%) did so. No other allele variant was expressed in these two SNPs. The fact that only one copy was present indicated hemizygosity; thus, only female individuals carrying the W chromosome amplified for F5C and F7C. Since both W-linked SNPs provided the same information, using only one SNP was sufficient to identify females. Because F7C showed less specificity to amplify other regions of the genome, we considered this SNP to be more reliable for sexing (see Note A.3, Table A.2, Table A.3 and Fig. A.6 in Appendix A for more details regarding this justification).

Table 2.1: Sex-linked SNP markers information (Fw, forward; Rv, reverse; bp, base pairs).

Assay Name	**F9A**	**F7C**	**F5C**
Chromosome	Unique Z-linked, no PAR	Unique W-linked, no PAR	Unique W-linked, no PAR
Location (bp position)	28656895-28657166	1886358-18886578	10603258-10603378
Fw primer name	ANPRYWV_F	ANPRYWW_F	ANMGCR2_F
Rv primer name	ANPRYWV_R	ANPRYWW_R	ANMGCR2_R
Fw primer sequence	GGGTGTAGGTATAGA TTGGCTCTCA	GAAAATAATAACTAT CTGTGTATGGATGGG	ATTAAAAAATAAACC GTTTTCAAGCATTTGCA
Rv primer sequence	CTCAAAGCTCCATGG AACAAACTG	AACTCCATGCTTAAA CCGTCCTT	CACTTTGGAATCCTC TCCATTAGGA
Context sequence	ATTGGCTCTCAATTG ACCTCTAGCT[G/A] GTGGAGATTCTGCAG TTTGTTCCAT	GTAGTTAATGACAAT GCATGGATCT[A/C] TGTGTTGTGTATAAG GACGGTTTAA	AGCATTTGCATATTA TAAATTCGGG[A/G] ATTTTAGTTCTGAAT AAGTGGGTTT

We assigned an individual as female if it amplified for the variant "A" or "G" in the Z-linked SNP F9A and "A" for the W-linked SNP F7C. We assigned an individual as male if it amplified for the variant "A/A", "A/G" or "G/G" in the SNP F9A and did not amplify for the SNP F7C (Fig. 2.1 and Fig. 2.2). Using our method, we identified 456 individuals of the genotyped samples as females and 457 as males, including both adults and fledglings. This represents 99.5% of all genotyped samples successfully sexed. The few cases in which individuals could not be sexed (N=5) showed a heterozygote genotype call for F9A but amplified for F5C (purple triangles in Fig. 2.1, grey areas in group b and c in Fig. 2.2). Accordingly, these individuals (with the sample codes CMF1598, CMF2121, CMF2223, CMF0858, and CMF1808) should have two Z chromosomes and one W chromosome.

To validate the discriminating power of our method, we employed a sample of 18 males and 18 females whose sex was assigned based on differences in body size within reproductive pairs (see section 2.2.5 for details). We found that our SNP approach correctly classified 100% of morphologically assigned females and males (Table A.4 and Fig. A.7).

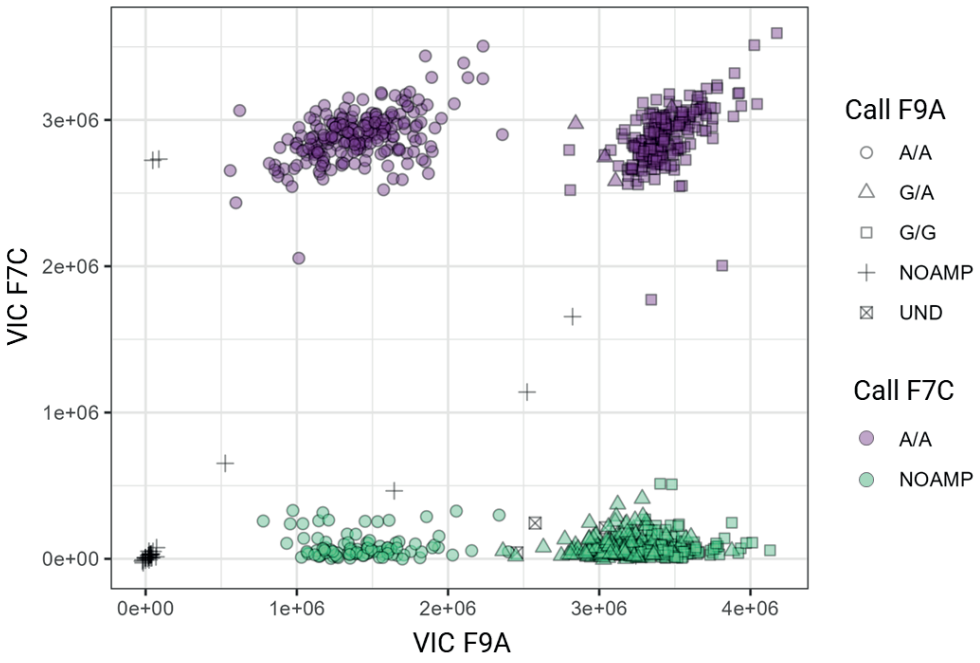

Figure 2.1: Allelic discrimination plot for F9A and F7C SNPs using fluorescence data from allele 1. Each dot represents the genotype of one sample at a specific SNP fluorescence value in VIC Rn units (normalised reporter signal). Genotype calls include F9A homozygotes (A/A and G/G in circles and squares, respectively), F9A heterozygotes (G/A in triangles), samples that did not amplify (NOAMP in crosses for F9A and in green for F7C), or samples with undefined genotypes (UND in crossed squares for F9A and in purple for F7C). Females are depicted in purple (N=456) and males are shown in green (N=457).

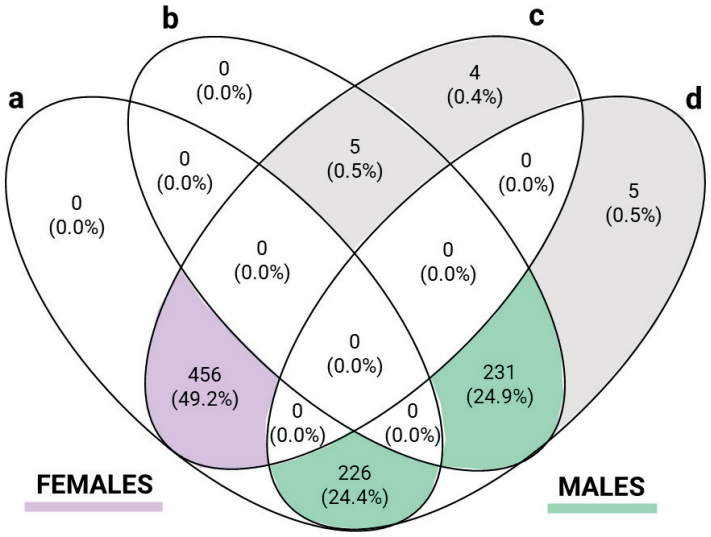

Figure 2.2: Summary of all possible genotype combinations using the Z- and the W-unique loci represented by the overlapping sets of the Venn diagram. The number and percentage of samples matching each condition are indicated within each area. The represented sets include homozygotes for F9A (a), heterozygotes for F9A (b), samples amplified for F7C (c), and samples not amplified for F7C (d). Females are depicted in purple (N=456) and males are shown in green (N=457). Samples that could not be sexed are represented in the grey areas, while conditions not found in any sample are left empty.

2.4 Discussion

We present a general method for sexing wild birds using sex-linked SNP markers based on sequencing unique loci mapping outside the pseudoautosomal region where sexual chromosomes exchange genetic material. Our hypothesis was that heterozygote genotypes for the Z-linked SNP would refer to males, as they are the homogametic sex in birds. Conversely, the detection of W-linked SNP variants would occur only in females. We demonstrate the accuracy and reliability of the method in the monomorphic Western Jackdaw. Below, we provide further insights into the use of our molecular technique to sex wild birds, highlighting its benefits and limitations compared to other available tools for molecular sexing, and discussing the broader implications of the use of sex-linked SNPs in the study of ecology and evolutionary biology.

The high accuracy (100% of individuals correctly sexed) and reliability (over 99% of samples correctly processed) of this newly proposed approach make it an efficient way to sex birds. While there are other powerful approaches for sexing individuals (e.g. Griffiths et al., 1998; Lois-Milevicich et al., 2021), the use of sex-specific SNP markers located in unique fragments of Z- and W-chromosomes, as we propose here, contributes to reliably sex individuals while genotyping samples for other purposes. Although the approach requires reference sequences to identify and annotate sex chromosomes, this information is becoming increasingly available in non-model species through fast and affordable next-generation (NGS) and whole-genome sequencing (WGS). When individuals of both sexes are available, it is preferable to use the sequences from the heterogametic sex as references to facilitate the identification of both sexual chromosomes. However, even in species for

which only one reference sex chromosome is available, as in our case, sex-linked scaffolds can still be identified based on sex differences in genomic coverage (Palmer et al., 2019). In such cases, we recommend blasting the reference sequences with chromosomes from closely-related species to corroborate their location. Since genome assembly and reconstruction are complex processes involving a variety of pipelines to collect and compile a range of read lengths (Andrews et al., 2016), a good practice is to apply high-quality thresholds when filtering by reads mapping. This strategy can also aid in identifying scaffolds with limited sex differences in polymorphism, potentially indicating pseudoautosomal regions. However, determining the boundary between unique and pseudoautosomal regions can be challenging, particularly in certain species where the recombination frequency between sex chromosomes is rare (Palmer et al., 2019).

The proposed technique is expected to be particularly useful in studies aimed at genotyping large numbers of individuals within species and populations. On one hand, our technique can be integrated into multiple genetic analysis based on SNP data without the need of additional PCR amplification and electrophoresis. Together with the use of high-throughput sequencing methods such as the OpenArray® genotyping based on real-time PCR technology (Broccanello et al., 2020), which results in a significant reduction in sequencing time and costs required per sample and locus (Hudson, 2008), the technique represents a cost-effective method for SNP genotyping. It is particularly useful in studies that require genotyping thousands of individuals (Jenkins & Gibson, 2002). The OpenArray platform uses the TaqMan technology to discriminate between allelic clusters, but other SNP genotyping methods such as KASP or rhAmp have proved to be reliable for high-throughput sequencing, with similar concordance in SNP calling, and all three present low genotyping error rates (Broccanello et al., 2018). Moreover, the collection of feathers as a DNA source is considered a non-invasive sampling method that is logistically straightforward and fast to perform in the field, thereby reducing the stress for the animal (Horváth et al., 2005).

In general, feathers provide sufficient quality and quantity of DNA for molecular analyses like ours (Horváth et al., 2005). Indeed, we found that in feathers where the concentration of the extracted DNA was considered low (<50 ng/µL), genotyping was still successful in 86.55% of cases. However, samples that fall below a minimum quality threshold can pose limitations to the genotyping capabilities of OpenArray® technology. Although genotyping proved to be successful in poor-quality samples, 3.03% of the samples (29 of the whole batch of 957) did not amplify for any loci due to low DNA concentrations. From the remaining 928 sequenced samples, the Z-allele could not be identified in 9 of them, leading to a total of 919 genotyped samples. The low mean DNA concentration (47.27 ng/µL) of these samples indicated problems with sample quality rather than sequencing errors. Therefore, increasing the quality threshold should reduce the number of samples that cannot be genotyped.

More challenging to interpret is the observation of five samples (5 of the 919 genotyped samples) that could not be sexed with certainty because they showed two variants in the Z-chromosome and a third in the W-chromosome. A likely explanation is the differential specificity of the F5C and F7C primers for the W-unique loci. Indeed, in 2.4% of the

cases where genotypes were defined, samples showed a mismatch between the genotypic variants amplified with the W-linked F5C and F7C SNPs. The existence of differential specificity of the F5C and F7C primers is further supported by a BLAST analysis, which shows that specificity was higher for F7C. Although we employed F7C in our sexing method, the fact that we still detected samples with two variants in the Z-chromosome may indicate that this may still be insufficient to fully resolve the specificity issue. Alternatively, the observation of ZZW may indicate possible cross-contamination events (mixing samples from male and female individuals) and/or sequencing errors (misassignment of genotype calls). We should also consider the possibility of trisomies which, although rare, have been documented in some bird species like *Gallus domesticus* (Lin et al., 1995), *Charadrius alexandrines* (Küpper et al., 2012), *Ara ararauna* (Tiersch et al., 1991), and *Acrocephalus arundinaceus* (Arlt et al., 2004).

The implementation of OpenArray® genotyping may present difficulties when markers occurring in the population are not known. In our case, the genotyping variants of one locus included in the array were undefined for all of the samples. Because the estimated error rate of automated high-throughput methods for genotyping with SNPs is less than 1 in 2000 genotypes (Ranade et al., 2001), we can safely discard standard sequencing errors as the main source of the observed result. Instead, the allelic variants identified in individuals from the Sweden population for this particular locus might not be present in Lleida's population. Therefore, we suggest using local samples to improve the chances of finding effective candidate SNPs. Furthermore, candidate loci meeting the screening criteria are more challenging to identify from sequencing artifacts in small sample sizes (N=3 males and N=1 females). In practice, multiple individuals of each sex would be required to avoid falsely identifying rare SNP variants as sex-linked contigs (Palmer et al., 2019).

Currently, SNPs are widely used in a variety of research programs, such as human forensics, crop improvement, aquaculture, drug discovery, and wildlife research (Garvin et al., 2010). In ecology and evolution, SNPs are increasingly used for population genetic analysis, pedigree reconstruction, and phenotype mapping (Garvin et al., 2010). Given that males and females often differ in habitat preferences, feeding specializations, parental investment, and dispersion, among many other ecological roles, these studies heavily rely on the accurate identification of the sex of individuals. Thus, we expect that the sex-linked SNPs protocol we present here will be useful to a broad range of fields because it will allow genotyping and sexing a high number of individuals in parallel and independently of their life cycle stage.

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Chapter 3

Phenotypic plasticity and microevolution explain adaptive responses to global warming in a long-lived, behaviourally innovative bird

Abstract

Advancing the timing of breeding to track changes in temperature is a well-known response of animals to global warming. However, it is generally unclear if such changes reflect microevolution, plasticity, or both, which limits our ability to forecast the potential of populations to cope with climate change. Comprehensive studies are particularly rare in highly innovative, big-brained animals. This leaves us with little understanding of whether enhanced decision-making plasticity might override the influence of natural selection —a phenomenon known as 'Bogert' effect. Here, we show that in jackdaws (*Corvus monedula*), a bird renowned for its behavioural innovativeness, individuals start laying eggs earlier during warmer years. This plastic response is adaptive, as early breeders fledge more offspring and in better body condition than late breeders, with no apparent short-term costs for adult survival. Despite differences in climatic regimes between regions in the latitude extremes of the species distribution, selection for earlier breeding phenology across populations was highly consistent over most years, with no variation in plasticity among individuals. However, there was substantial variation in phenology. Northern populations started breeding earlier and advanced 6.9 days over 9 years, reflecting the high heritability of the trait in this region. Here, a projected advancement of up to 0.08 standard deviations per generation shows the role of plasticity is more than 15 times stronger than microevolution. In contrast, heritability in Southern populations was lower and there was no clear temporal trend over years. Our results demonstrate the implications of population-level variability in responses to climate change and suggest that although behavioural plasticity can be crucial for big-brained animals to effectively track global warming, natural selection may still play an important role in reducing maladaptation in the long-term.

3.1 Introduction

The impact of global warming on biodiversity is a growing concern due to its potential to threaten species survival and ecosystem function (Gaston et al., 2003; McKinney, 2014; Spooner et al., 2018; Sunday, 2020; Thomas et al., 2004; Urban, 2015). A significant challenge posed by global warming is that it can disrupt the synchrony of phenological events within communities (Donnelly et al., 2011; Ovaskainen et al., 2013; Parmesan, 2006; Visser et al., 2004). Organisms that cannot adjust their life cycle in response to changes in food availability are at risk of maladaptation due to phenological mismatch and may face population decline or even species extinction (Durant et al., 2003; Gienapp et al., 2014; Harrington et al., 1999; Miller-Rushing et al., 2010; Post et al., 2003; Stenseth & Mysterud, 2002; Visser et al., 2012). As the effects of climate change continue to escalate, there is a growing urgency to understand whether and how organisms will be able to synchronize their life cycles with the rising temperatures (Samplonius et al., 2021).

In the last decades, a wealth of evidence has shown that many organisms are changing the timing of their life cycles in response to global warming (Charmantier & Garant, 2005; Crick & Sparks, 1999; McCleery & Perrins, 1998; Visser & Both, 2005; Visser & Gienapp, 2019). Evidence is particularly strong for the timing of reproduction, which has generally advanced in multiple taxa worldwide as average temperature rise (Parmesan, 2006; Parmesan & Yohe, 2003; Root et al., 2003). Phenological advances in response to warming are suggested to be influenced by key selection pressures, including the synchrony with resource availability or accessibility (Kharouba et al., 2018; Thackeray et al., 2016; Visser & Both, 2005) and heat-stress (Bleu et al., 2017; Cohen et al., 2018). However, it is generally unclear if such changes are adaptive (improving the fitness of individuals) and, if so, whether they reflect microevolutionary responses (e.g. a change in the frequency of genotypes in the population due to natural selection on a short timescale) and/or phenotypic plasticity (e.g. a change in the phenotype at the individual-level) (Bell & Gonzalez, 2009; Gienapp et al., 2008; Merilä & Hendry, 2014; Urban et al., 2023).

Quantifying the extent to which populations can adjust to warmer temperatures through plastic and/or evolutionary changes is essential for understanding the potential of populations to track global warming, and hence forecast their future demographic trends. Plastic responses are commonly rapid and can facilitate population persistence in the short-term. However, they may also drive populations to maladaptation if cue reliability decreases in the new environmental conditions, causing phenotypic mismatch with the optimum (Bonamour et al., 2019). Moreover, phenotypic plasticity alone may be insufficient to track environmental changes beyond the range of conditions to which the population has been historically exposed, requiring heritable selection on the reaction norm (Nussey et al., 2005). In contrast, evolutionary responses tend to occur at slower rates but have the potential to sustain populations in the long-term (Bradshaw & Holzapfel, 2006; Hoffmann & Sgrò, 2011; Merilä, 2012; Visser, 2008).

Several factors are expected to determine the relative contributions of plasticity and microevolution. Animal populations from different regions can vary in their sensitivity to

climatic conditions. As a consequence, the relative role of microevolutionary versus plastic adjustments of reproductive timing could vary across populations (Bailey et al., 2022; Cole et al., 2021; Porlier et al., 2012; Thackeray et al., 2016). For instance, a phenological shift may be more expected to occur in regions of faster climate change, especially at northern latitudes, potentially imposing stronger selection on reproductive timing (Parmesan, 2007; Post et al., 2018; Shave et al., 2019; Thackeray et al., 2010). There is also an increased appreciation that the relative importance of microevolutionary and plastic responses should vary according to the life-history of the species. Evolutionary adaptation may be more difficult for long-lived organisms because a long generation time reduces the accumulation of beneficial mutations and slows down changes in allele frequencies (Marshall et al., 2016; Marshall & Connallon, 2023; Morrissey et al., 2012).

An aspect less frequently acknowledged that may also influence the interplay between microevolutionary and plastic responses in animals is cognition. Decision-making processes may be shaped by individuals' cognitive capacity to detect, process, integrate, and discriminate environmental components, thereby facilitating adaptive plastic responses to global warming (Dore et al., 2018). Even if plastic adjustments in laying dates are primarily under genetic control, changes in the timing of breeding may be underpinned by physiological or endocrine plasticity (Dawson, 2007; Verhulst & Nilsson, 2007), but could also be influenced by cognition. Cognition may still remain relevant because of its potential to weaken the strength of selection on heritable variation through the so-called 'Bogert' effect (Bogert, 1949; Huey et al., 2003; Price et al., 2003). This effect occurs when behavioural decisions that buffer individuals against resource variation —such as the innovative adoption of new food resources (Lefebvre et al., 1997)— constrain evolutionary change by hiding heritable variation from selection. While there has been a significant amount of research on reproductive timing in small-sized passerines, our understanding of the responses to climate change remains limited for species in which a long life is combined with substantial innovation propensity, as the case in big-brained animals like corvids and primates (Lefebvre et al., 2004; Sol et al., 2020).

Long-term studies on pedigreed wild populations are essential to detect changes in reproductive timing with temperatures, and to infer the contribution of adaptive plasticity and microevolution (Charmantier & Gienapp, 2014; Postma & Charmantier, 2007). Here, we report such an analysis using 7-9 years of breeding data at the individual-level in jackdaws (*Corvus monedula*), a large-brained bird of the corvid family, from populations located in the South and North latitudes of the species distribution (Fig. 3.1). Specifically, we ask if the breeding phenology of jackdaws tracks changes in temperatures and, if so, whether this is accomplished by adaptive phenotypic plasticity, microevolutionary adjustments or a combination of both. Birds have been an important model system to study these mechanisms because the timing of breeding generally has a direct connection to reproductive fitness (Charmantier et al., 2008; Visser et al., 2004). Being a relatively long-lived bird that exhibits remarkable behavioural flexibility in response to changing conditions (Arbon et al., 2023; Coomes et al., 2019; Greggor, McIvor, et al., 2016; Kings et al., 2023; Lee et al., 2019; Lefebvre, 2021; McIvor et al., 2022; Zandberg et al., 2014), our analyses may shed new light into the question of whether

large-brained, long-lived animals cope with environmental challenges primarily through plastic adjustments rather than microevolutionary changes.

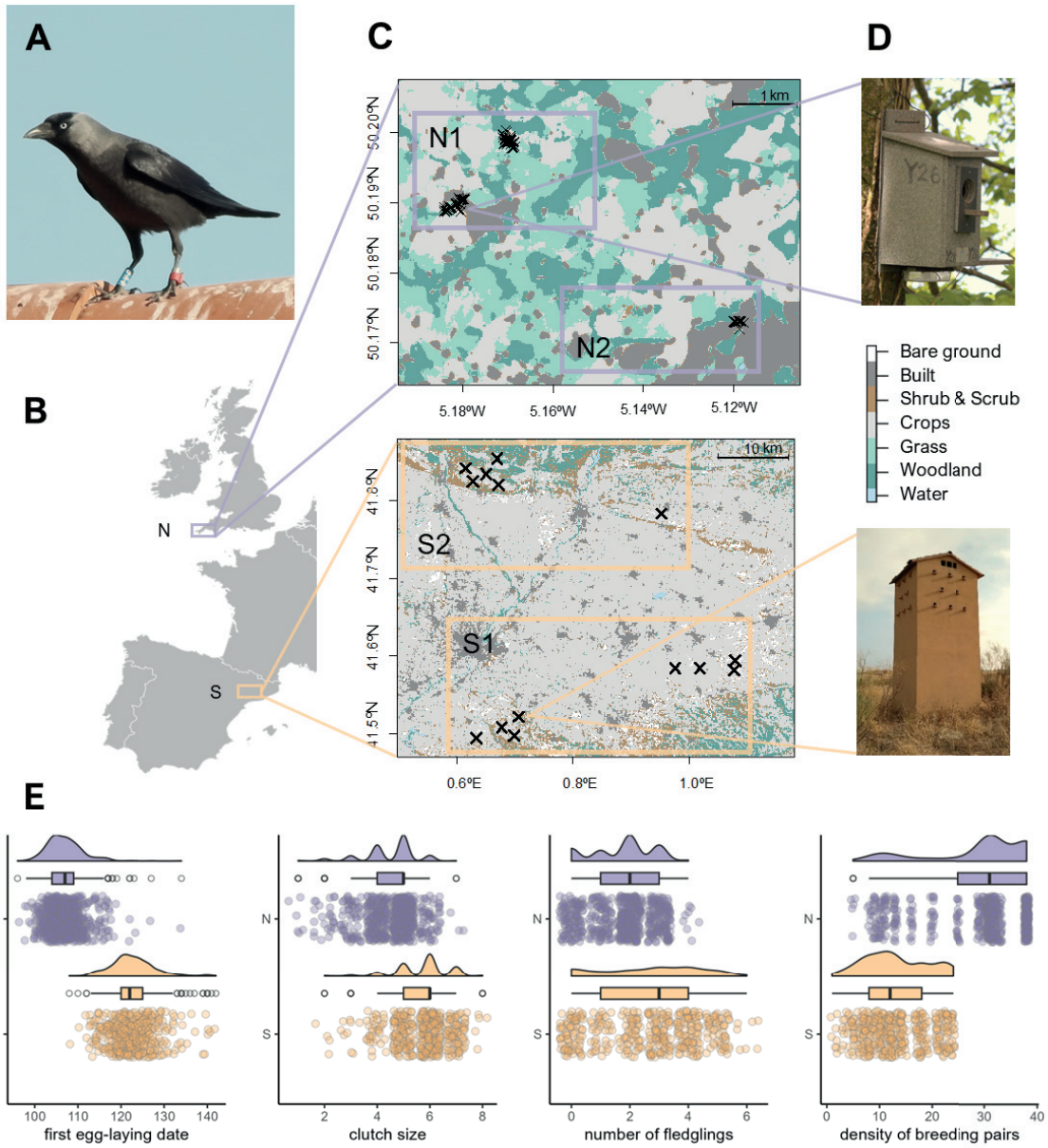

Figure 3.1: Study species and area. (A) Adult jackdaw ringed with a blue alpha-numeric Darvic ring and a red PIT-tag transponder. (B) Location of the populations in Northern (N) and Southern (S) Europe. Within each region, two populations were defined, N1 and N2 in the North (N) and S1 and S2 in the South (S). The location of the nest boxes is indicated by cross symbols on the map with UTM axes. (C) Habitat categories (see legend in the figure) were obtained from the global 10-meter land use land cover mapping developed by Brown et al. (2022). (D) In the North, nest boxes were clustered within three breeding sites with an average of 30 boxes in each, while in the South 14 colonies of 24-37 nest boxes each were established in artificial breeding towers. (E) Boxplots describing differences among northern and southern populations in annual first-egg laying dates, clutch size, number of fledglings and density of breeding pairs (number of pairs in a colony or site per year). Northern populations are represented in violet, while southern populations are represented in orange.

3.2 Material and methods

3.2.1 Nest box monitoring and life-history data

We investigated wild jackdaw populations breeding in nest boxes located in the North (Cornwall, UK) and in the South (Lleida, central Catalonia) of the species distribution (Fig. 3.1). Within each region, we studied two populations (referred as to N1 and N2 in the North, and S1 and S2 in the South). The delimitation of the populations was based on the evidence that jackdaws select breeding sites by proximity and habitat similarity (Unzeta 2020). All populations were located in areas dominated by agricultural landscape, fragmented by sparsely wooded areas with a mix of shrub and scrub vegetation in the South, and dense woodland with grassy patches in the North, except for N2 which was located in a more urbanized area (near the Penryn Campus, University of Exeter).

Nest boxes have been monitored since 2013 in the North and 2016 in the South. Every year, an average of 65 nest boxes were monitored in S1 and 67 in S2 in the South, while 60 were monitored in N1 and 10 in N2 in the North. The structural characteristics and materials were similar among nestboxes within regions to minimise the influence of varying insulation or parasite levels on nestlings' growth (Larson et al., 2018; Scott-Baumann et al., 2022). Adult and fledgling jackdaws were captured by means of ladder traps or by blocking the nest box entrance, and ringed with Darvic/colour rings and PIT tags for individual identification (Kings et al., 2023). During the breeding season, we recorded for each nest the date of the first-laid egg, clutch size and the number of fledglings between 21 and 25 days after hatching. Jackdaws lay one clutch per year, with a median clutch size of 5 eggs in the North, and 6 eggs in the South (see Fig. 3.1E).

We defined laying date as the date the first egg of the clutch was laid. When more than one egg was found during the first visit, we estimated the date assuming that one egg is laid every day. Replacement clutches were very rare during the whole period (only one case in each region) and we did not consider them in the analyses. Reproductive fitness per breeding pair in a given year was measured as the number of fledglings in the nest between 21 and 25 days after hatching. Body condition of fledglings was calculated as the residuals from a linear regression between body mass and tarsus length, both log-transformed. Given the high breeding site fidelity of the species in both regions (Kings, 2018; Unzeta, 2020), we estimated the apparent survival of adults based on the probability of individuals breeding in one year to be resighted the next year breeding in the same site/colony. Resightings and the recovery of dead individuals were established through extensive field observations in breeding and wintering locations within the study area and its periphery. This data was also complemented with pedigree information and PIT-tag records in the nest using data-loggers during the breeding season (Unzeta, 2020).

3.2.2 Non-genetic and genetic pedigree reconstruction

The sex of each individual was identified through molecular sexing of either blood samples (Griffiths et al. 1998) or feather samples (Chapter 2, Garcia-Raventós et al., 2023). The DNA from feather samples was also used to genotype 1,237 individuals based on a panel of 100 single nucleotide polymorphisms (SNPs), using high-throughput sequencing

methods (see Appendix B). SNP data was used for parentage assignment and pedigree reconstruction of southern populations. In the North, where no SNP data were available, we constructed a nongenetic social pedigree based on observations of breeding pairs in the field, assuming the caring parents to be the genetic parents. This is justified because extra-pair paternity is unusual in the species (Gill et al., 2020; Henderson et al., 2000; Hooper, 2021; Liebers & Hans-Ulrich, 1998). We verified the method using data from southern populations, confirming a strong alignment between genetic and field pedigrees. The age of the individuals was determined by their hatching dates or, if unknown, by using a birth year probability distribution inferred after parentage assignment.

3.2.3 Climatological data compilation and time series decomposition

We downloaded daily mean temperature and accumulated precipitation data for the period 2000-2022 within a 5 km^2 area buffer (1.261 km radius) around each nest box (area calculated as the average 95% home range of 10 GPS-tracked individuals during the breeding season; see Unzeta (2020) for details). Daily temperatures were downloaded at 1 km spatial resolution using the Terra Moderate Resolution Imaging Spectroradiometer (MODIS) collection for Land Surface Temperature (MOD11A1) version 6.1, distributed by NASA EOSDIS Land Processes DAAC. Daily temperature records were strongly correlated with mean weekly (Pearson's correlation, $r > 0.96$) and monthly temperatures (>0.92). Therefore, the mean weekly or monthly temperatures were used to handle missing daily values. Precipitation data was downloaded from the European Centre for Medium-Range Weather Forecasts ECMWF (Muñoz-Sabater et al., 2021), using the European Environment Agency ERA5-Land daily aggregated dataset including the sum of total daily precipitation within a spatial resolution of 11,132 meters. For the identification of trends in temperature, we converted the downloaded daily data from 2000 to 2022 into a time series object using the 'xts' function from the *xts* R-package. Then, a seasonal, long-term trend and a random daily variation component were decomposed from the time series using the 'stl' function from the *tsbox* R-package.

3.2.4 Defining breeding periods

We defined three breeding periods: pre-laying, laying, and post-laying. Within each period, we estimated mean daily average temperature and the accumulated precipitation. The laying period was defined from egg laying to egg hatching, trimming the 5% extremes, while the post-laying period was considered from egg hatching to chick fledgling, also trimming the 5% extremes. The pre-laying period, defined as the period that had the most influence on the laying date, was estimated by means of a sliding window analysis, using the *climwin* R-package (Bailey & Van De Pol, 2016). A sliding window analysis identifies a time window for which an environmental variable of interest (daily mean temperature and accumulated precipitation, in our case) best explains variation in a measured biological trait (i.e. laying date). We used an absolute windows approach, assuming that all individuals responded to the same climatic period. We evaluated a time-period of 90 days before the reference date, which was set as the mean annual laying date of all years (April 17^{th} for both northern populations, May 2^{nd} and 4^{th} for S1 and S2, respectively). We used climate windows of at least 7 days long, to increase

biological relevance (see Whitenack et al., 2023 for similar procedures), and assessed the effect of mean temperature and precipitation aggregates for each time window by means of both linear and quadratic models (similar to Hidalgo Aranzamendi et al., 2019). A randomisation approach was employed to account for over-fitting. All windows within 2 ∆AICc of the top climate model were considered equivalent in performance (Whitenack et al., 2023). In these cases, windows with a lower % of models falling within the 90% confidence set were selected as more accurate. The median open and close window for the models falling within the 95% confidence set were selected, thus accounting for model uncertainty and avoiding spurious correlations (Bailey & Van De Pol, 2016).

3.2.5 Modelling temperature effects on laying date and its mediating role in fitness following a Bayesian approach

The sliding window analysis allowed us to identify the period during which climate had the most influence on the laying date, but it did not provide insights into the strength of the relationship between temperature and laying date. To tackle this issue, we employed Bayesian mixed models separately for each population using the *brms* R-package. In these models, laying date was the response variable and the pre-laying temperature was the predictor, considering both linear and quadratic functions. The potential impacts of laying date variation on fitness were also explored using a similar approach. In these models, the fitness measure (response variable), which includes the number of fledglings, body condition of fledglings or adult survival, was modelled as a function of laying date (predictor). A Gaussian distribution was used for the number of fledglings and body condition, while a binary distribution was used for adult survival. To determine the random structure of the models, we explored multiple combinations of year, colony, and nest box and selected the random structure that yielded the lowest AICc.

3.2.6 Plasticity in laying date with response to temperature

We estimated individual plasticity in laying dates as response to changes in temperature using random-coefficients models. This approach allows the estimation of individual "reaction norms" to environmental variables and between-individual variation in plasticity. Models include laying date as response variable and random terms are fitted from simpler to more complex. Most simple models include year as random term to assess differences between years in mean egg-laying date. Additionally, female ID is added as a random term to infer differences between females across years. Lastly, temperature is included as a covariance of female ID to explore whether individual females differ in their response to spring temperature. Only female records with more than one breeding attempt were used to fit these models. The best model was selected based on a likelihood ratio test (LRT), following Nussey et al. (2005) and Charmantier et al. (2008).

3.2.7 Fitness curves to find optimal laying dates

We identified the fitness peak (maximum absolute fitness) within the laying dates distribution per year for each population. Following De Villemereuil et al. (2020), we fitted a generalized additive model (GAM) with integrated smoothness estimation within the function 'gam' from the *mgcv* R-package. We included the number of fledglings per

breeding pair as response variable following a Poisson distribution and laying date as predictor variable. Then, we included the GAM into the function 'fitness.landscape' from the *gsg* R-package (Morrissey & Sakrejda, 2013) to estimate the relationship between population mean fitness and population mean phenotype. We applied parametric bootstrapping (n=50) to obtain a prediction interval for the fitness landscape. Then, we identified the optimal laying date as the laying date leading to the maximum fitness value predicted by the fitness curve.

3.2.8 Selection analyses

We computed standardized selection differentials for each year in each population using the Morrissey & Sakrejda (2013) method. Selection differentials measure the strength of selection on a trait, and are calculated as the covariance of the trait with relative fitness. The relative annual fitness for each breeding pair was the number of fledglings per nest box divided by the population mean in the same year. We calculated linear (S) and quadratic (c) standardized selection differentials for laying date, using the function 'moments.differentials' implemented in *gsg* R-package (Morrissey & Sakrejda, 2014). The standard error and the significance of the selection differentials were estimated after the default 2,000 bootstrap replicates.

3.2.9 Exploring the causality between drivers of phenology and fitness-effects with path analysis

We used path analysis (Li, 1975), as implemented in the *piecewiseSEM* R-package (Lefcheck, 2016), to explore hypothetical causal relationships among climatic and non-climatic factors on phenology and fitness. We first used the approach to ask whether pre-laying temperatures affected reproductive fitness directly or, instead, their effect was indirectly mediated by laying date or the temperatures during the laying and/or post-laying periods. A direct effect on the number of fledglings would suggest that temperatures are not merely acting as a cue but also affecting fitness. Then, we explored the effect of non-climatic factors that could explain laying date variation, such as population density. We expected competition for high-quality breeding sites induced by a high population density could represent a pressure to start laying earlier. Alternatively, a high density of conspecifics may lead to a delay in the initiation of laying if food resources are scarce. We quantified the density of breeding pairs within a colony or site in a given year by counting the number of nest boxes occupied by jackdaws, regardless of reproductive success. We finally used path analysis to explore the direct and indirect effects of time on laying date by including 'year' as a numeric variable. The indirect pathway accounted for effects of time that occur through changes in temperature, while the direct pathway considered other non-climatic factors influencing laying date over time. In the structural equation model, phenological sensitivity was measured as the interaction between temperature and laying date, and climate change exposure was estimated as the interaction between year and temperature (Bailey et al., 2022).

3.2.10 Animal models and heritability on laying date

We were interested in quantifying the genetic component of variation in laying dates among individuals in both regions. For this purpose, we estimated heritability on laying date by means of an animal model approach, as described in Wilson et al. (2010) and Kruuk & Hadfield (2007). Animal models decompose phenotypic variance into genetic and non-genetic (environmental) components to estimate heritability using the relatedness among individuals from pedigrees. We used MCMCglmm (Hadfield et al., 2010) to fit Bayesian mixed-effects models including as a random factor female identity and the pedigree. Because we did not have a priori information about parameter distributions for our models, we conducted sensitivity analysis of the prior posterior distribution. Specifically, this analysis aimed to test whether various priors biased the measure of heritability. We investigated the impact of the inverse-Gamma distribution, commonly used in MCMCglmm that allows for a weakly informative prior on variance components. Additionally, we examined the 'Fisher' prior, which assigns less weight to zero values, along with uninformative priors with parameter extension to improve chain mixing (De Villemereuil, 2012). Lastly, we adjusted the proportion of variance in such standard and expanded priors to assess if reducing residual variance while maintaining the same genetic variance, and vice versa, affected the calculation of heritability (Wilson et al., 2010). Apart from performing sensitivity analysis, we explicitly tested for common environmental effects by fitting the effect of pre-laying temperature (following Husby et al., 2011), as well as spatial and temporal effects on phenology by including population as fixed, and colony or site and year as random factors into the models. Fixed terms were considered statistically significant when 95% CIs did not span 0 and pMCMC values were <0.05. We also explored the potential impacts of ontogeny, cohort, maternal and development effects by including, respectively, age, birth year, mother identity and nest box where the mother was raised as random effects in the model. However, the addition of these random effects was not considered statistically justifiable given the little variance explained by these factors and the similarities in deviance information criterion (DIC) values. We visually inspected trace plots from the resulting Markov chain of all our models to check reliability of the posterior approximation. Specifically, we assessed the level of non-independence between successive samples in the chain, where autocorrelation was less than 0.1 between successive stored iterations. Models were run for 65,000 iterations with a burn-in of 15,000 and a thinning interval of 50, which generated 1,000 samples from each chain. Then, we estimated heritability (h^2) by dividing the posterior distribution of the phenotypic variance explained by additive genetic variance by total variance ($h^2=V_A/V_P$ and $V_P=V_A+V_R$, where V_R is the residual variance).

3.2.11 Observed and predicted microevolutionary change

The observed rate of phenological advancement was quantified by calculating the number of days between the mean egg-laying date at the start and end of the study period, divided by the total standard deviation of the trait (Gingerich, 2009). The resulting value represents the number of days, measured in standard deviations (s.d.) units, by which laying dates advanced for a period of 9 years in the North and 7 years in the South. This observed rate was then compared with the rate predicted by microevolutionary change,

determining the number of times the selection value would need to increase for the predicted rate to match the observed rate. We applied the Breeder's equation (Lynch & Walsh, 1998) to predict rates of evolutionary change using both the heritability and selection estimates ($R=h^2S$).

3.3 Results and Discussion

We found that jackdaw populations exhibited sensitivity to changes in temperature and precipitation (Fig. C.1). We detected temperature windows during the pre-laying period in all four studied populations, indicating that the climatological conditions influenced laying dates (see Note C.1 for further details). Narrower windows in southern populations where phenology is delayed may indicate the need to shorten reproductive activity (Gullett et al., 2013; Halupka & Halupka, 2017). Despite notable differences in phenology between regions (Fig. C.3), jackdaws generally started egg-laying earlier during warmer (Fig. 3.2A-B) and wetter years (Fig. C.1). However, temperature and precipitation operated at different time scales, despite showing certain correlation with each other (Fig. C.2), with temperature being more closely tied to laying date (Table C.1 and Fig. C.3, see also Note C.1 in Appendix C). This finding aligns with long-term studies suggesting that temperature plays a more crucial role than precipitation in determining breeding timing (reviewed in D'Amelio et al., 2022; Englert Duursma et al., 2019; Mares et al., 2017; Marrot et al., 2018; Visser et al., 2009; Visser & Both, 2005).

In birds, the advancement of laying dates in response to rising temperatures often enhances the survival probability of offspring, primarily by improving synchrony between the peak of resource availability and the time of hatching (Bonamour et al., 2019; Crick, 2004; Gaston et al., 2009; McNamara et al., 2011; Parmesan, 2006; Pigliucci, 2005; Rasmussen & Rudolf, 2015; Visser et al., 1998, 2004). To evaluate whether the advancement of breeding phenology observed in jackdaws leads to increased nestling survival, we examined the co-variation between laying dates and reproductive fitness. A negative co-variation would indicate that breeding earlier in warmer years results in improved fitness. Confirming this expectation, we found that early breeders fledged more offspring and in better body condition compared to later breeders, a pattern that was consistent across regions (Fig. C.5A-B).

While early reproduction may be beneficial in terms of reproductive success, it could also reduce the survival of the parents due to the increased reproductive investment required for feeding more fledglings (Maspons et al., 2019; Patrick et al., 2022; Stearns, 1989). However, we found no evidence of reduced survival among individuals that started breeding earlier (Fig. C.5C), indicating that the cost of early reproduction did not negatively affect adult survival within the studied period (less than a decade). Thus, the lack of an observed trade-off between reproduction and survival from our analysis suggested that the response to temperature changes may be adaptive in jackdaws, at least at the short-term.

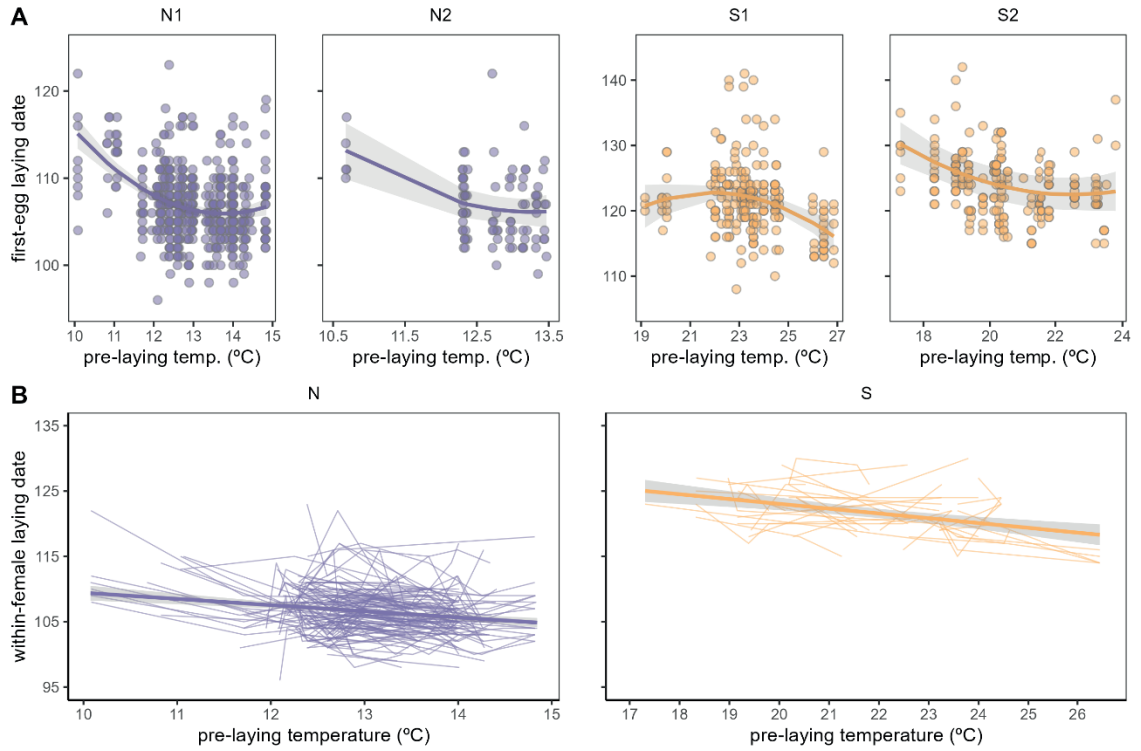

Figure 3.2: Phenological response and plasticity with temperature during the pre-laying period. (A) Date of first egg-laying is advanced in warmer years. Population sensitivity was higher in the North, with N1 advancing at a rate of 0.67 days/ºC, and 1.05 days/ºC in N2, while S1 and S2 exhibit advancements of 0.27 days/ºC and 0.29 days/ºC, respectively. The slope and associated 95% confidence interval for each population are derived from Bayesian mixed-effect models (see Table C.2A). Colony and nest box ID were included as random effects. (B) Individuals adjust laying date according to temperature changes. Each line represents observations from the same individual across multiple breeding events. Females exhibited a similar pattern of plasticity, with no significant rates of change among them (see Table C.3). Laying dates in Julian days. Pre-laying temperature for each year and population was obtained by aggregating daily mean temperatures during the pre-laying period (see Fig. C.3). Values for northern populations in violet, southern populations in orange.

A path analysis provided further insights into the role of temperature in driving breeding timing and reproductive fitness. The best-supported model suggests that temperature was used by individuals as a cue to decide the timing of egg-laying. This is inferred from the observation that the impact of temperature on reproductive fitness was indirectly influenced by the laying date. In contrast, path analysis showed little support for the alternative that temperature had a direct influence on reproductive fitness (Fig. C.6 and Table C.7). Thus, jackdaws tended to start breeding earlier in warmer years, and it was the direct effect of this decision that enhanced their reproductive fitness (as predicted by the 'Bogert' effect).

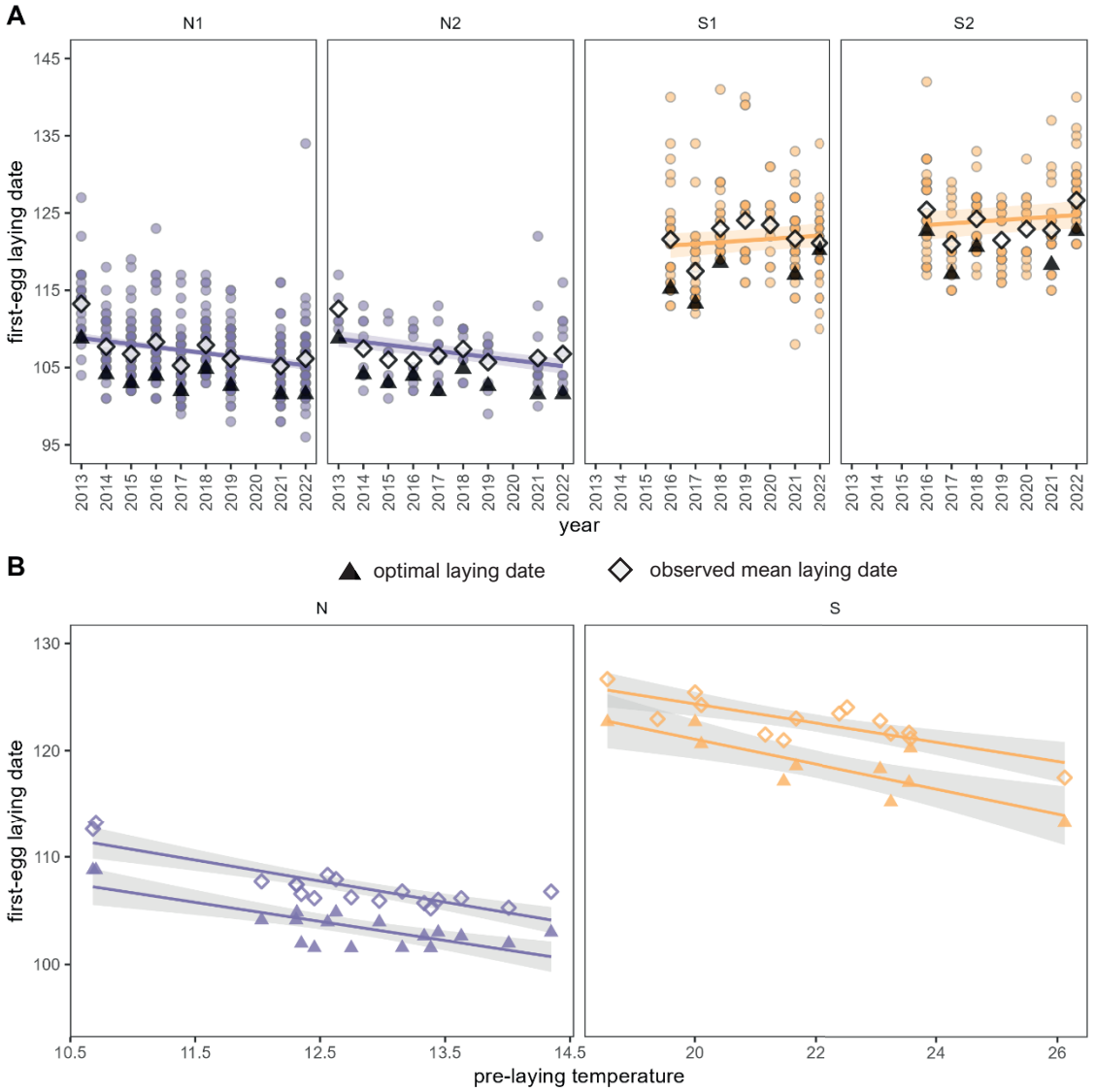

Figure 3.3: Observed mean and optimal population laying dates as a function of (A) time and (B) pre-laying temperatures. Diamonds indicate actual mean laying date while triangles show optimal laying date for each population and year. The optimal is defined as the laying date corresponding to the maximum reproductive fitness (number of fledglings), estimated by means of fitness curves. Note that optimal could not be estimated in 2019 and 2020 in southern populations, due to low sample sizes. Sample size was also low for N2, therefore the showed optimal in northern populations is the result of joining N1 and N2 data. Slope and associated 95% credibility interval for each population are derived from Bayesian mixed-effect models, including colony and nest box ID as random effects (see Table C.2C). Values for northern populations in violet (N=630), southern populations in orange (N=444).

We evaluated whether the observed variation in laying dates reflected adaptive plasticity by analysing laying dates as a response to temperatures, based on females that were observed breeding in multiple years. Our results revealed that individuals exhibited adaptive plasticity in their breeding times, advancing reproduction during warmer years and delaying it during cooler years (Table C.3). There was also significant variation between individuals in breeding time while controlling for age, birth year, maternal and development effects. Instead, the variation in breeding time was partially explained by

the genetic component of the trait, particularly in northern populations, as indicated by the estimated heritability (northern populations: h^2=0.452; southern populations: h^2=0.104; Table C.5-6, Fig. C.7). In contrast, we did not detect significant variation between individuals in plasticity (Table C.3). Indeed, the best-supported reaction norm for both northern and southern populations suggest a common slope for all individuals, indicating that individuals tended to adjust laying dates in response to temperature in a similar way.

Our results agree with previous research that advancing the breeding phenology as response to global warming may be adaptive (Merilä & Hendry, 2014; Romano et al., 2023; Visser et al., 2012). However, some authors have raised doubts that plastic advances may be sufficient to reduce the phenotype-environment mismatch over a long-term warming period (Brommer et al., 2008; Charmantier & Gienapp, 2014; Moiron et al., 2022, 2023; Nussey et al., 2005; Radchuk et al., 2019), particularly in species showing reduced heritable variation for new reaction norms to evolve (Bradshaw, 1991; Charmantier et al., 2008; Marrot et al., 2018; Visser, 2008). To assess this, we compared the annual observed mean laying dates of jackdaws with the optimal laying dates that maximize the number of fledglings, predicted from the fitted fitness curves. We found evidence that populations were not in evolutionary equilibrium (Fig. 3.3A), showing a continuous mismatch where laying occurred later than would be expected to maximise reproductive fitness. Importantly, the distance between actual and optimal laying dates did not shorten with higher temperatures (Fig. 3.3B), despite selection consistently acting in the direction of moving laying dates towards a shifting optimum (Fig. 3.4 and Table C.4).

Although the estimated selection differentials in both northern and southern populations (covariance of trait values and fitness, S≈0.2, Fig. 3.4) indicate weak selection (Kingsolver et al., 2001), the evolutionary response can still be strong when heritability on the selected trait is high (Falconer & Mackay, 1996). Assuming no differences among individuals in other fitness components (Sheldon et al., 2003) or pre-laying body condition (Hennin et al., 2018), the average laying date southern jackdaw populations is expected to decrease up to 0.02 standard deviations (s.d.) each next generation and 0.08 in the North (see Tables C.4 and Table C.6). The strength of selection is comparable with the values found in laying dates from great tits in the UK (Husby et al., 2011), and also in heritability from southern populations (Nussey et al., 2005). However, taking into account the differences in generation time between both species (2 years in great tits and 7.4 years in jackdaws; BirdLife International 2023), the evolutionary potential for jackdaws to advance the timing of breeding to track changes in temperatures is almost four times lower.

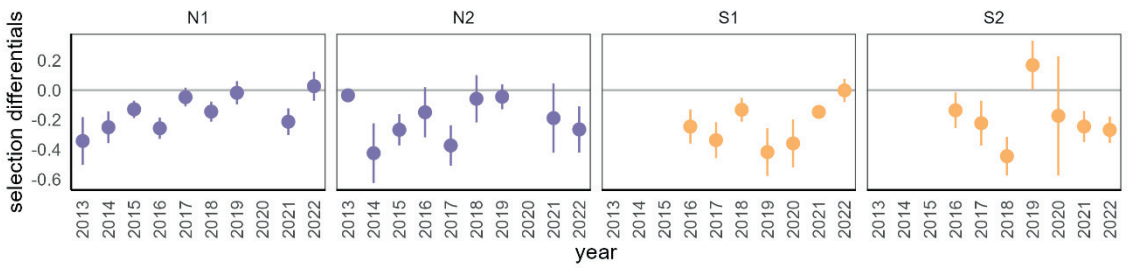

Figure 3.4: Standardized linear selection differential estimates for egg-laying date across years. Average selection differentials during the studied period was $\bar{S}$=-0.18 in the North and $\bar{S}$=-0.21 in the South (details in Table C.4). Interval bars indicate ± 1 standard error. Values for northern populations in violet (N1, N2), southern populations in orange (S1, S2).

While the interplay of plasticity and microevolution holds potential for bringing populations closer to the optimal breeding timing, it is noteworthy that laying dates have advanced over time solely within northern populations (Fig. 3.3A). In the North, the mean egg-laying date in 2013 was 113.15 (in Julian days) and 106.25 in 2022, with a total of 4.17 standard deviations (s.d.). Therefore, the mean egg-laying date has advanced 6.9 days over 9 years in the North (corresponding to the observed change of 1.65 s.d.). This trend coincides with a mean temperature increase in the region of 0.73 ºC since 2010 (Fig. C.8). In great tits, a change of 2 s.d. has only occurred after 47 years (Charmantier et al., 2008), indicating jackdaws breeding in northern latitudes are much more plastic. In contrast, our jackdaw populations in the South did not show a similar advance in breeding time (0.1 days over 6 years, observed s.d.=0.02; Fig. 3.3A), where tendencies in mean temperature increases since 2010 have been lower (0.575 ºC).

The reasons of the differences between populations in egg-laying date advancements are unclear, but they could reflect geographic differences in phenological sensitivity and climate change exposure, mediated by increasing temperatures (Bailey et al., 2022). In the North, populations were both more sensitive and more exposed to climate change than in the South (Fig. C.9 and Table C.7), likely contributing to a strongest phenological advancement (Parmesan, 2007; Post et al., 2018; but see Bailey et al., 2022). However, the differences in laying time advancement may also indicate that factors other than climatic conditions, such as population density or land use change, can also influence breeding timing at the population-level (McLean et al., 2022; Møller et al., 2020). Results from path analysis including population density and annual variation to explore the role of non-climatic effects showed a direct causal effect of both factors on delaying laying date in the Southern populations (Fig. C.9D). No significant effect of these factors on laying date was observed in northern populations, although the number of breeding pairs has increased over years (Fig. C.9A-B; Heywood et al., 2022), contrary to the South where density has declined (Fig. C.9C-D; ICO 2023). Jackdaw populations decline in the South has been related with the scarcity of suitable nesting sites and lower habitat quality (Blanco & García, 2023), which may explain the constrains individuals find to advance laying date over time. Alternatively, the high fluctuations in seasonal temperature across years might hinder such a marked trend (Fig. C.4). Finally, as a generalist, innovative and urban-adapted species, with groups frequently observed on anthropogenic foods, we

also anticipate jackdaws are less reliant on seasonal changes in natural resources, with a weaker dependence on arthropod abundance (Arbon et al., 2023; Meyrier et al., 2017). It may help explain the contrasting patterns in breeding phenology across latitudes when compared to other species (Zhemchuzhnikov et al., 2021), but further work incorporating data from other regions of the species distribution is needed to reach firm conclusions. Clearly, the interplay between climatic and non-climatic factors influences in shaping phenological shifts calls for further scrutiny and consideration in future research.

Our finding that selection towards earlier breeding is adaptive yet imperfect aligns with evidence from other bird and mammal species (Radchuk et al., 2019). In addition, our analyses shed new light into the involved mechanisms. They suggest that the potential for jackdaw populations to cope with increasingly warming temperatures is driven not only by plasticity, as generally reported, but also by microevolutionary changes. Despite the existence of heritable variation and consistent yet weak selection, our results suggest that individuals adjust their breeding time to changing temperatures through phenotypic plasticity. Because mean generation time in jackdaws is 7.4 years, the observed change of 1.65 s.d. in 9 years compared to a predicted change of 0.08 s.d. per generation would require a mean standardized selection differential more than 15 times stronger in northern populations. The opposite scenario is what we detect in southern populations. In this region, the nearly negligible observed change of 0.02 s.d. closely match with the minimal change predicted from similar selection values but with lower trait heritability than in the North. Overall, while a reduced microevolutionary response aligns with the concept of a 'Bogert' effect, our results indicate that even in species with high decision-making plasticity, like corvids, natural selection is not prevented from acting.

Considering the potential influence of cognition on reproductive timing holds relevance, especially in light of the absence of heritable variation in adaptive plasticity —a phenomenon documented not only in jackdaws but also in other species (e.g., Charmantier et al., 2008; Charmantier & Garant, 2005; Ellner et al., 2011; Merilä & Sheldon, 1999). A lack of heritable variation in the reaction norm implies a constrained potential for the evolution of adaptive plasticity. This could pose challenges in adapting populations to future climate scenarios, significantly different from the currently experiencing ones. If environmental information for making adaptive decisions remains reliable, highly behaviourally flexible animals may hold a great potential to mitigate the consequences of climate change through learning, whether from past breeding experiences or through public information shared by more experienced individuals. Alternatively, the impact of bad decisions can be mitigated if learning allows to compensate for the mismatch by shifting to alternative resources (Lefebvre et al., 1997). While recent evidence supports the existence of a link between a species' capacity to learn new behaviours and reduced vulnerability to habitat changes (Ducatez et al., 2020; Garcia-Porta et al., 2022), this avenue warrants further in-depth research.

Acknowledging almost a decade of data at the individual-level, we demonstrate the rapid advancement of breeding phenology is an extremely plastic response under selection. The novelty of estimating evolutionary potential in a highly innovative and long-lived bird yielded insightful results on proving that both mechanisms contribute in adapting

populations to global warming. Yet, it remains unclear whether the observed plasticity is predicted to either promote or hinder microevolution. The remarkable differences among populations in their response rate, the opposing phenology patterns, and the contrasting evolutionary potential, presents a unique opportunity to further explore this question. Studies analysing the diverse responses to climate change within species are crucial in contributing to our understanding of the role of macroecological patterns in influencing populations sensitivity and climate exposure.

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Chapter 4

The role of sociality in microevolutionary responses of breeding phenology in a rapidly changing world

Abstract

The scarcity of evidence for microevolutionary responses to the ongoing climate change raises questions about the conditions under which evolution might be expected, which factors might constrain or promote evolutionary responses, and whether these responses would be sufficient to keep up with rapid climate change. Our understanding of microevolutionary adaptation to climate change is generally challenged by the difficulties in disentangling genetic versus environmental factors to account for phenotypic changes. We review the role of sociality in breeding phenology to contribute to this ongoing debate. The social environment can affect microevolution on breeding timing by inducing indirect genetic effects, facilitating plastic decisions through social learning and altering the strength of selection, among other processes. These processes can theoretically either facilitate or inhibit microevolutionary responses, depending on the social context, the environmental challenges, and the life history of the species. However, current empirical and theoretical evidence is insufficient to generally predict evolutionary responses. We identify future directions to improve our understanding of the implications of social behaviour on evolutionary adaptation to climate change.

4.1 Introduction

The persistence of a population under climate change largely relies on the interplay between phenotypic plasticity and adaptive evolution. Advances in breeding phenology have been found to exhibit adaptive plasticity (Gienapp et al., 2008; Teplitsky & Charmantier, 2019). However, the consistent directional selection for earlier timing suggests these responses are imperfect to sustain populations over long-term warming periods, highlighting the importance of microevolution (Visser, 2008). While numerous field studies have reported evidence for selection towards a moving optimum (Hoffmann & Sgrò, 2011; Radchuk et al., 2019), current support for the existence of evolutionary adaptation to climate change remain scarce (Gienapp et al., 2008; Merilä, 2012).

Studies in heterogeneous environments, where the potential rate of evolution might be constrained by low heritability, commonly attribute changes in phenology to climate, population density or habitat quality (Charmantier & Garant, 2005; Visser et al., 2009). However, considering that the timing of reproduction is often influenced by mating behaviour and interactions between conspecifics, ignoring the social environment is an important neglect (Brandl et al., 2019; Chmura et al., 2020; Cockrem, 1995; Johansson et al., 2014; McDonald et al., 2020). For instance, evolutionary theory postulates that the estimation of the rate and direction of microevolutionary changes for a particular trait depends not only on direct genetic effects (DGEs) but also on indirect genetic effects (IGEs; Bailey et al., 2018; Fisher & McAdam, 2019; McGlothlin et al., 2010; Moiron et al., 2020; Moore et al., 1997). Considerable attention has been focused on the indirect genetic effect of males on the egg-laying timing of the female (Brommer & Rattiste, 2008; Germain et al., 2016; Moiron et al., 2020; Teplitsky et al., 2010). However, while we might anticipate that interactions among individuals within social groups could play a role in evolutionary adaptation, the impact of sociality has rarely been explored, and its consequences remain unknown.

Phenological traits, such as the timing of reproduction, are often influenced by social interactions between conspecifics, making it particularly suitable to study the role of sociality. Heritability in female laying date would not only rely on partner effects but mainly depend on the density of conspecifics (i.e. competition), the genetic relatedness among individuals and the correlation of life-history traits and trade-offs (Araya-Ajoy et al., 2021; Milles et al., 2022; Reed et al., 2015; Wright et al., 2019). This inquiry holds particular significance in species with long generation times, for which genetic responses to selection are typically slow . In these animals, the net benefit of learning from others is also expected to be higher than in fast-lived species (Maspons et al., 2019), bringing into consideration whether the relative importance of plastic and evolutionary responses may be contingent to the sociality and life-history of the species.

In this review, we aim to bridge existing gaps in the understanding of the role of sociality as a driver of microevolutionary responses and plasticity in breeding phenology to adapt to environmental changes. We first summarise the current body of evidence that delineates the potential for microevolution in laying dates as a consequence of climate change. This sets the background to examine the challenges inherent in unravelling the

factors that contribute to the observed limited heritability in these traits. Next, we delve into a critical aspect of the discussion—investigating the role of social interactions as heritable and non-heritable environmental effects influencing breeding phenology and fitness. Finally, we identify the social contexts that warrant further exploration to unravel the role of sociality in shaping the evolutionary potential within species. By presenting this comprehensive theoretical framework, our aim is to make a meaningful contribution to the understanding of how plastic responses to environmental change may either hinder or facilitate microevolution.

4.2 Are evolutionary responses constrained by limited heritability?

The advancement of breeding phenology is one of the best documented responses to the effects of climate change, with overwhelming evidence across taxa, especially birds (Romano et al., 2023). Thus, laying date have been used as a key trait to quantify joint microevolutionary and plastic population responses to mitigate fitness-effects of environmental change (Biquet et al., 2022; Chevin & Lande, 2015; Reed et al., 2013; Visser & Gienapp, 2019). While the advancement in phenology has historically been associated to a mechanism of plasticity (Gienapp et al., 2008; Teplitsky & Charmantier, 2019), we know little about the quantitative genetics of phenological traits.

The evolutionary potential of breeding phenology to adapt to ongoing climate change relies on whether the variation in the timing of reproduction is attributed to heritable genetic differences among individuals within a population (Charmantier & Gienapp, 2014). In natural populations, relatedness among individuals can be estimated from pedigrees, which are implemented in quantitative genetic analyses such as the animal model (Wilson et al., 2010). These models are valuable statistical tools to disentangle the genetic and environmental components within trait variance to assess rates of microevolutionary responses to selection by estimating heritability (Kruuk, 2004). Trait heritability (h^2), the relative importance of additive genetic variance in shaping phenotypic variance, has historically been used together with selection strength (S) as a measure to predict the rate of adaptive evolution across generations (R), as described by the Breeder's equation $R=h^2S$ (Falconer & Mackay, 1996). According to the Breeder's equation, the absence of evolutionary responses may reflect low heritability, weak selection or a combination of both.

Despite longitudinal studies within wild populations show that additive genetic variation persists under strong directional selection (reviewed in Bonnet et al., 2022; Bradshaw & Holzapfel, 2006; Gienapp et al., 2008), the main majority failed to provide evidence for an evolutionary response of laying date to climate changes (Brommer et al., 2005; Charmantier & Sheldon, 2006; Gienapp et al., 2006; Przybylo et al., 2000; Teplitsky et al., 2010). The limited heritability commonly observed has been typically attributed to the low additive genetic variance, high environmental variance, or low cross-environment genetic correlation occurring alternatively or simultaneously (Charmantier & Garant, 2005). However, few published studies revealed laying date is heritable using pedigree data within the animal model approach (Table 4.1). Understanding the factors

contributing to the observed heritability involves recognising the challenges to accurately estimate heritability in the wild (Box 4.1), related to the uncertainties regarding the relative contributions of genetic change and plasticity, and the extent to which phenotypic changes are adaptive (Charmantier & Réale, 2005; Hadfield et al., 2010; Hunter et al., 2022; Merilä & Hendry, 2014; Postma, 2006).

Table 4.1: Summary of studies supporting heritability in breeding phenology. Note that the compiled evidence quantified heritability estimates using the animal model approach.

Species	Location and period	h^2	Reference
Jackdaw (*Corvus monedula*)	Cornwall (2013-2022)	0.491	Garcia-Raventós et al. (*in prep.*)
Jackdaw (*Corvus monedula*)	Lleida (2016-2022)	0.154	Garcia-Raventós et al. (*in prep.*)
Common tern (*Sterna hirundo*)	Banter See (1992-2017)	0.120	Moiron et al. (2020)
Common tern (*Sterna hirundo*)	Banter See (1992-2010)	0.270	Dobson et al. (2017)
Strom petrel (*Hydrobates pelagicus*)	Benidorm Island (1993-2007)	0.187	Kim et al. (2012)
Great tit (*Parus major*)	Hoge Veluwe National Park (1973-2007)	0.069-0.268	Husby et al. (2011)
Common gull (*Larus canus*)	Gotland (1981-2003)	0.145	Brommer & Rattiste (2008)
Great tit (*Parus major*)	Wytham Woods (1960-1998)	0.159	McCleery et al. (2004)
Collared flycatcher (*Ficedula albicolis*)	Gotland (1980-1999)	0.192	Sheldon et al. (2003)

Despite the considerable research on shifts in avian phenology with temperatures and the growing interest in quantifying microevolution in this trait, the number of studies is still very low (Table 4.1). However, the absence of evidence may not imply responses to climate change are not evolutionary but rather a limitation in drawing broad conclusions (Charmantier & Gienapp, 2014). In general, timing of breeding is heritable in some species and under strong negative directional selection in the face of climate change, suggesting potential for adaptive evolution (Charmantier & Gienapp, 2014). Because whether observed changes in phenology are due to plasticity or due to genetic change remains an open question, this review seeks to explore to what extent plastic responses influenced by the social environment may hinder or promote microevolution.

4.3 The effect of sociality in the adaptive evolution of breeding phenology

4.3.1 The social environment

There is ample evidence that animals can base their decisions either on the information they acquired directly from their personal experience or through indirect cues provided by social interactions (Boulinier & Danchin, 1997; Danchin et al., 2004; Doligez et al., 2003). The acquisition of information is crucial to reduce uncertainty and guide decisions to enhance fitness (Dall et al., 2005; Schmidt et al., 2010). The availability of information from conspecifics within social environments allows animals to optimise decisions about predator avoidance, migratory phenology, mate opportunities, habitat choice and

foraging efficiency (Evans et al., 2016; Krause & Ruxton, 2010; Ward & Webster, 2016). Although the exchange of social information may involve several different mechanisms, some relying on advanced cognitive abilities (Heyes, 1994; Laland, 2008), animals from a broad range of species gather and exploit information generated by others (Borg & Channon, 2021; Valone, 2007; Wagner & Danchin, 2003).

Box 4.1. Challenges to study microevolution in wild populations

Obtaining pedigree data is challenging. While individual data is essential to quantify the contributions of plasticity versus microevolution, only a small fraction of studies within the extensive literature utilise this information (Charmantier & Gienapp, 2014). Obtaining data on life-history and pedigrees is especially challenging in species with long generation times. Thus, a bias towards fast-lived and small-sized birds may contribute to the difficulties in understanding how heritable is breeding phenology (Charmantier & Gienapp, 2014).

Detecting microevolutionary responses in wild populations is challenging. These challenges include the difficulties to obtain unbiased estimates of heritability, to detect fluctuations in selection over time and space, to identify selection acting on the non-heritable component of the phenotype, to account for selection on correlated traits, to avoid masking genetic responses with environmental changes, or to obtain enough statistical power to detect patterns when these are weak (extensively reviewed in Hayward et al., 2018; Merilä et al., 2001).

Estimating heritability in wild animals is particularly challenging. For example, the implementation of animal models can be difficult on small datasets, requiring Bayesian approaches that can sometimes be misleading, as the use of weakly informative priors may have large impacts on the posterior distribution (Wilson et al., 2011).

Interpreting heritability is challenging. One reason is that a reduced heritability does not necessarily mean low additive genetic variance in a given trait. Rather, it can also reflect high environmental variance, or low cross-environment genetic correlation occurring alternatively or simultaneously (Hoffmann & Merilä, 1999; Price & Schluter, 1991). For example, some studies on natural populations indicate decreased heritability under stressful environmental conditions (Charmantier & Garant, 2005; Rowiński & Rogell, 2017). Other studies showed heritability in breeding phenology to increase with rising spring temperature, potentially speeding up the rate of microevolution to adapt to environmental changes (Husby et al., 2011). Constrained evolution can result from genetic trade-offs or genetic correlations between avian life-history traits, including laying date, clutch size, the onset of incubation or the migration timing (Both & Visser, 2005; Pulido, 2007; Sheldon et al., 2003; Teplitsky & Charmantier, 2019). For instance, stabilizing selection in clutch size could constrain a phenological response in some species (Teplitsky & Charmantier, 2019) whereas the low heritability in laying date in long-distance migrant birds is due to its correlation with migration arrival (Both & Visser, 2001; Moiron et al., 2020). The difficulties of disentangling environmental from genetic components often results in attributing the observed changes in breeding phenology to plasticity (Postma, 2006; Postma & Charmantier, 2007).

The exchange of social information is pivotal as it allows interacting individuals within a social group to acquire relevant information without the risks or costs associated with individual learning. However, the reliability on social information can be influenced by both environmental predictability and individual characteristics (leadership, social status

and rank, genetic relatedness, sex, personality, condition, etc). For instance, social information may be outdated when the environment is highly variable, or less valuable when the environment is very stable. As social groups are heterogenous, some individuals may also be more sensitive to environmental changes than others and, therefore more informed about their environment (Giraldeau et al., 2002; Jolles et al., 2020). At the same time, variation in social behaviour suggests some individuals might rely more in social information than others (Hofmann et al., 2014; Martin et al., 2023; Valone & Templeton, 2002). Depending on how variable is the environment, acquiring public information from a more experienced or less matching individual would have contrasting fitness and evolutionary consequences.

In breeding decisions, the use of social information is widely recognised in several bird species (Evans et al., 2016). An avenue of evidence also suggest social information is used to synchronize breeding time within conspecifics (Brandl et al., 2019; Cockrem, 1995; Evans et al., 2009; Germain et al., 2016; Helm et al., 2006; Innes & Johnston, 1996; Meijer & Langer, 1995; Moore et al., 2005), although the indirect effect of the mating partner has received much greater attention.

4.3.2 Why the social environment could affect heritable phenotypic variation?

Behaviour allows animals to quickly respond to environmental stimuli. Consequently, all aspects of the environment can have marked impacts on the behavioural phenotype of an individual with social interactions playing a crucial role in shaping the way behaviours are expressed and evolve (Bailey et al., 2018). In many species, the establishment of social bonds are tightly linked to reproductive success and represent a key process for the development of kin associations and subsequent evolution of cooperative breeding in birds (Brandl et al., 2019; Grabowska-Zhang et al., 2012). Significant heritable variation has been found in cooperative breeding behaviours suggesting social behaviour has an important evolutionary impact (Capilla-Lasheras et al., 2023; Charmantier et al., 2007).

Variation in social behaviour can be explained by genetic relatedness, but in other cases, social behaviour can be transmitted by nongenetic inheritance. Social cues perceived during development or other elements transmitted from parent to offspring contribute to parent-offspring resemblance, but the involved phenotypic effects do not depend on, or are not the consequence of, changes in gene expression (Edelaar et al., 2021). When information is transmitted across generations, we would expect transgenerational plasticity to evolve (Leimar & McNamara, 2015). Over broader timescales, the transmission of behavioural traditions via social learning could even lead to cultural inheritance (Creanza et al., 2017). The impact of culture on evolution has been extensively studied in human psychology (Uchiyama et al., 2022), and this research has inspired evolutionary biology in nonhuman animals (reviewed in Whiten, 2019).

Social behaviour can induce variation on several traits and individual differences in social plasticity can further modify the rate and direction of adaptive social evolution (Martin et al., 2023). Thus, the heritable variation in a trait is likely to depend not only on DGEs (direct genetic effects), but also on indirect genetic effects (IGEs), where the genotype of

a focal individual is influenced by the genotype of an interacting individual (Griffing, 1967; Moore et al., 1997). Given phenotypes are the expression of genotypes, we expect individuals conforming a social environment (e.g. parents, competitors, mating partners) to mutually affect their phenotypic traits. The presence of IGEs in combination with DGEs can accelerate, retard, remove or reverse evolutionary change (Fisher & McAdam, 2019; Moore et al., 1997).

Heritability estimates for fitness-related traits are expected to be inflated if individuals that share genes are also likely to share similar environments (Gervais et al., 2022). The relative role of genes and the environment are confounded when the environment is social because genetic differences among interacting individuals contribute to differences in the social environment, creating a heritable environmental effect (Bailey et al., 2018). Thus, indirect genetic effects are becoming increasingly well appreciated in evolutionary ecology, particularly in the adaptation of behavioural phenotypes, as behaviour is inherently responsive to social context. While the important contribution of IGEs to social evolution has been shown (Bailey et al., 2018; McGlothlin et al., 2010), their role in driving evolutionary changes across various species and social contexts remains relatively unexplored.

4.3.3 What are the consequences of IGEs for microevolutionary changes in breeding phenology?

Evidence of microevolution in breeding phenology induced by the social environment comes mainly from empirical studies supporting the role of the mate inducing IGEs, together with assortative mating and other common environmental effects. The interplay between mates has an impact if females alter their breeding date with respect to their partner. For instance, studies in monogamous species showed the effect of male genotype can impact on the condition of females before breeding, likely to determine egg-laying timing (Brommer & Rattiste, 2008; Germain et al., 2016; Murray et al., 2023; Teplitsky et al., 2010). Some studies demonstrated that considering heritable variation for laying date expressed in both members of a breeding pair resulted in a total heritable variance that was 50% larger than what traditional models estimated (Evans et al., 2020). Others revealed very low levels of both direct and indirect and indirect additive genetic variation in breeding timing (Liedvogel et al., 2012).

The resemblance in laying date between individuals may not only be due to shared genes between breeding pairs but also to common environmental effects or ontogeny. In the migratory Common tern (*Sterna hirundo*), females that arrive early from the wintering grounds breed with males that also arrive early (Moiron et al., 2020). Assortative mating creates a covariance between phenotypes and genotypes whereby any effects of the conspecific phenotype on female fitness will be correlated with laying date and can contribute to the net selection affecting evolutionary dynamics. Experiments in semi-natural conditions showed an impact of environmental and social influences on breeding timing (Caro et al., 2007). When the environment for the offspring provided by early laying pairs differs from that by late pairs and the laying dates of these offspring when

they reproduce themselves is affected by this environment, this may lead to inflated heritability estimates (Gienapp et al., 2013; Postma & Charmantier, 2007).

In the case of breeding phenology in resident and colonial species, if the interaction between closely related conspecifics highly influences their synchronization in laying and reproductive fitness, we should expect an evolutionary response. The study from Garcia-Raventós et al. (*in preparation*) (Chapter 3) provides rare evidence of finding high heritability estimates in breeding phenology in a social breeding and big-brained bird (Box 4.2). Although they did not explicitly test for IGEs, assortative mating or common environmental effects, the significant evolutionary potential in this long-lived species suggests an influence of the social environment shaping breeding phenology.

Box 4.2. Case study: Empirical evidence of highly heritable breeding phenology quantified in a wild population of a behaviourally innovative and long-lived corvid in its northern range.

A. Jackdaws are highly social species, known for acquiring information from social cues to consume novel foods, prospecting behaviour at conspecific nests, and solving complex tasks (Arbon et al., 2023; Greggor, Thornton, et al., 2016; Mioduszewska et al., 2020; Röell, 1978; Schuett et al., 2012).

B. Heritability values of ~0.5 suggest microevolution in response to climate-mediated selection for an early breeding is potentially an important mechanism mitigating negative consequences of climate change.

C. However, the strength of selection should be 15 times higher than measured to explain the observed temporal trend in advancing laying dates over years, suggesting an important role of phenotypic plasticity in this species.

D. The lack of heritable variation in the slope of reaction norms suggests no opportunities for plasticity to evolve, or that other forms of plasticity have already been removed from the population.

E. Differences in climate (seasonal fluctuations, time windows), habitat quality, connectivity between breeding sites or genetic variation may explain the contrasting trends compared with southern populations where heritability in breeding timing shoed lower estimates (Table 4.1).

F. Being a highly social species, it is expected that indirect genetic effects resulting from interactions with conspecifics could also influence microevolutionary responses by altering the amount of heritable variation and the adaptive landscape.

4.3.4 Impacts of sociality on the evolutionary potential

We expect the evolutionary potential to adapt to temperature changes to differ among species with varying generation times, with plasticity in breeding timing more crucial in slow life-histories owing to their lower evolutionary potential (Marshall et al., 2016;

Vedder et al., 2023). Yet, the evidence compiled herein (Table 4.1) does not indicate a clear pattern where species at the slow-extreme of the fast-slow continuum consistently exhibit lower values of heritability in this specific life-history trait. Instead, we highlight that microevolution can be an important mechanism even in highly plastic and slow-lived species when plasticity is heritable (Chevin & Lande, 2010; Nussey et al., 2007). Phenotypic plasticity is expected to interplay with microevolution if variation in laying date in response to selection is adaptive and also genetic, being early and late breeders genetically diverse (Catullo et al., 2019; Chevin & Hoffmann, 2017; Dochtermann et al., 2019). In this case, we should predict an evolutionary response acting upon this individual variation in response to environmental change (Ghalambor et al., 2007; Moiron et al., 2022; Pigliucci, 2005; Reid & Acker, 2022; Scheiner, 1993). For plasticity to evolve, individuals within populations must show heritable variation in the slope of their reaction norms, with some individuals responding more plastically than others in advancing breeding timing with increasing temperatures (Nussey et al., 2005; Reid et al., 2020; Visser, 2008). Hence, it is crucial to acknowledge that evolutionary responses at the population-level may be shaped by heritable plasticity.

Different rates of responses to climate change are expected within-populations, as individuals vary in perception and sensitivity to multiple cues and respond in different ways to changes in their environments (Abbey-Lee & Dingemanse, 2019; Bonamour et al., 2019; Kim et al., 2012; Porlier et al., 2012). Among-individual variation in breeding phenology has been usually explained by intrinsic differences associated with adult quality, body condition, age, sex, genotype, diet, dispersal, among others. However, variation in plasticity is not always observed. In some populations of great tits, patterns of plasticity appeared to be equal among individuals (Charmantier et al., 2008; Ramakers et al., 2019) whereas considerable individual variation in the slope of the laying-date temperature reaction norm was found in other populations of the same species (Nussey et al., 2005). Interestingly, the social context is also considered an environmental cue that individuals use to adjust their decisions for increased fitness (Dingemanse & Araya-Ajoy, 2015; Dore et al., 2018). Variations in sociality could amplify diverse patterns in plasticity among individuals, yet this variability might be homogenised if individuals within social groups respond collectively. Therefore, we expect social interactions involving multiple individuals and in rapidly variable contexts to influence plastic responses, ultimately affecting the evolution of plasticity.

Decisions from conspecifics within a social group on when to start laying may influence the individual's phenotype and fitness. As a result, behavioural decisions that determine the social environment that an individual is exposed to will shape the evolution of phenotypic traits and influence the direction and strength of natural selection (Edelaar & Bolnick, 2019; Porter & Akcali, 2020). When environments change, altering the expression of phenotypic variation within populations may expose or mask traits from selection, thereby influencing the ability of populations to respond to ongoing change (Kopp & Matuszewski, 2014). Social learning in breeding phenology can improve the match between an individual's phenotype and local conditions if they share similar individual optimal. However, IGEs can hinder population adaptation if they shift laying

date to the opposite direction of the individual optimal. It is thus of key importance to understand the evolutionary dynamics of the traits causing the IGEs, otherwise their consequences for adaptive tracking of the optimum laying date cannot be predicted (Murray et al., 2023). We recommend future studies aiming to explore responses on breeding phenology in similar contexts to consider the effect of indirect social environments when interpreting results or drawing conclusions.

Certain contexts might enhance the relative importance of social effects on microevolution, either constraining or promoting the potential to evolve. The role of social behaviour is relevant in studies with long-lived, big-brained species that use experience (both personal and social) to make decisions (Doligez et al., 2003), and hence show high behavioural flexibility to modify these decisions (Sol et al., 2016). We expect cognition to help animals with long generation times cope with environmental challenges primarily through plastic adjustments rather than microevolutionary changes. However, as previously discussed, indirect effects have the potential to shape evolution in behavioural traits. Indirect genetic effects from conspecifics can play an important role in speeding up microevolution if individuals that share genes are also likely to share similar environments. If the social environment is shared by remotely related individuals, homogenising the response can constrain evolution (Gervais et al., 2022). Therefore, density-dependence effects would interact with trait heritability and strength of selection, either delaying population decline and bringing time for evolutionary rescue, or limiting evolutionary responses by inbreeding depression and Allee effects (Boulding & Hay, 2001; Reed et al., 2015; Svensson & Connallon, 2019; Willi et al., 2006). New emerging approaches are being proposed to quantify the effect of social environments on breeding decisions from multiple perspectives (Evans et al., 2020; Fisher, 2023; Martin et al., 2023; Radersma, 2021).

Social environments can affect microevolutionary responses in yet another way, that is, reducing the strength of selection. If sociality offers fitness benefits (Krause & Ruxton, 2010; Ward & Webster, 2016), the network of interactions should buffer individuals against environmental changes, altering how selective pressures impact populations (Bailey et al., 2018). Such a buffer effect can potentially reduce the strength of selection on heritable phenotypic variation–a phenomenon known as the Bogert effect (Bogert, 1949; Huey et al., 2003; Price et al., 2003). In terms of breeding timing, this may mean that in highly social species the fitness differences of breeding sooner or later may be less significant that in non-social species. However, this is not necessarily true if delaying reproduction implies exposing juveniles to higher mortality, for example when predation pressure increases along the breeding season. Alternatively, the association between laying date and reproductive success may be caused by female's nutritional condition rather than indirectly though food availability for offspring (Price et al., 1988). This may happen if the individuals that are more social attain best condition, enabling them to start breeding earlier and to have greater breeding success.

4.4 Final insights and concluding remarks

Laying date depends on both genetic and non-genetic effects (Bonduriansky & Day, 2009), yet these two sources of variation do not respond at the same rate or in the same direction to a given selection pressure (Helanterä & Uller, 2020; Townley & Ezard, 2013). The complex interplay between genetic and non-genetic influences is expected to be largely affected by the social environment. A consequence of sociality is to modify the amount of heritable variation for selection through indirect genetic effects. The complexity of predicting population responses to climate change is further heightened by the role of social learning in affecting selection on laying date. Finally, the social environment can also affect microevolutionary responses by providing direct benefits that reduce the strength of selection. The social environment can facilitate microevolution, but it may not effectively advance breeding phenology unless climate-driven selective pressures directly impact physiological components intrinsically controlling laying date (Caro et al., 2013). Expanding the theoretical framework we present here to other behavioural traits or social contexts, and in species with diverse life-history strategies should greatly help improve our understanding of the eco-evolutionary implications of social interactions.

The lack of studies testing for microevolutionary changes may be explained by the challenges in obtaining long-term individual-based data (Charmantier & Gienapp, 2014). Birds have contributed immensely to our knowledge on how animals are impacted by climate change due to extensive scientific and public interest in ornithology, nest box monitoring, and ringing programs. Long-term studies that collect genetic data from individually marked birds provide a valuable resource for quantitative genetic analysis (Postma & Charmantier, 2007). Therefore, promoting collaboration under a code of ethics concerning data usage among groups involved in studies generating long-term data is crucial (Mills et al., 2015). Integrating large-scale databases with spatial and temporal variation could reveal patterns of natural selection on reproductive timing across populations. Platforms such as SPI-Birds offer unique opportunities to connect long-term data on avian phenology from multiple populations and species across Europe and other regions (Culina et al., 2021). Hence, collaborative studies involving experts in the analyses of microevolution, plasticity, and selection could initiate a cascade of novel perspectives and enhance our understanding of the role of sociality in the microevolutionary responses of breeding phenology in a rapidly changing world.

Chapter 5

General Discussion and Conclusions

5.1 Is plasticity hindering or promoting evolution?

This thesis focuses on exploring the role of plasticity in either hindering or promoting evolution. Our findings reveal that changes in breeding phenology are a plastic response under selection. However, the rate of response over time and the evolutionary potential can considerably vary among populations within a species. Although the answer remains unclear, my research has yielded insightful results suggesting that both plasticity and microevolutionary mechanisms contribute to the adaptive responses in breeding phenology to global warming, even in a species known for its flexibility in effectively responding to environmental changes.

Data from over nearly a decade of monitoring multiple breeding events in marked jackdaws in northern UK populations has revealed that the relative contribution of plasticity in altering breeding phenology was greater than that the predicted rate of microevolution. The observed trend of advancing laying dates over time is too fast to be solely explained by heritability and selection. Hence, we attribute the rapid advancement in the timing of reproduction to individual plasticity. In Chapter 3, we show an observed change in laying date of 1.65 s.d. over 9 years of nest box monitoring that sharply contrasts with the predicted 0.08 s.d. per generation time (7.4 years). A number of studies across a wide range of species have also shown the role of plasticity to be more important than microevolution in advancing breeding timing (reviewed in Gienapp et al., 2008). For instance, great tits in the UK have advanced laying dates 14 days in 47 years (Charmantier et al., 2008). However, jackdaws reveal a more dramatic shift: in only 9 years, they have advanced laying dates on average 6.9 days. If selection towards early breeding is constant and jackdaw populations maintain their phenological advancement rate, we predict that in 47 years these populations could be laying eggs over a month earlier. However, despite plasticity is clearly the main mechanism explaining the observed change in laying dates, we question whether this accelerated rate will be maintained over the next four decades.

One of the main contributions of this thesis is to provide evidence of evolutionary potential in plastic populations. Both plasticity and evolutionary mechanisms play crucial roles in mitigating phenological mismatches, despite being expected to occur at different timescales (Visser, 2008). In future climate change scenarios, the role of microevolution could gain importance if plasticity alone is not sufficient for adults to adjust their phenology with the increasing temperatures (Radchuk et al., 2019). Although jackdaws are sensitive to the defined pre-laying temperatures, with early pairs showing higher fitness, other intrinsic factors such as physiology or hormonal regulation, or even less labile traits like morphology are expected to constrain an indefinite advancement in phenology (Verhulst & Nilsson, 2007). For instance, day length acts as a cue for gonadal development, suggesting that photoperiod may impose a definitive limitation beyond which laying date might remain unresponsive to other environmental stimuli (Dawson, 2007). Additionally, temperatures from a shifting pre-laying period are expected to vary, particularly if the projected shift extends beyond one month (e.g. temperatures in March versus April). Therefore, the sensitivity to the detected pre-laying periods might be altered, or even induce an opposite response, potentially reducing fitness for early

breeders and leading to stabilizing selection (Gienapp et al., 2014). Finally, we explored fitness consequences in the short-term (encompassing a period no longer than 10 years). Given a maximum lifespan of 20 years for this species (BirdLife International 2023), evaluating potential long-term costs for survival or reproduction requires continued data collection in the future.

Even in the absence of fitness differences, evidence suggests potential limitations towards early breeding but not on late laying dates among genotypes selected for early and late laying (Lindner et al., 2023). This recent study exemplifies that while early breeding is generally expected to be more favourable, the intrinsic quality of individuals may impose variations in the optimal breeding times among individuals (Verhulst & Nilsson, 2007). Therefore, selection might not uniformly affect individuals within a population, with some more favoured to start laying earlier and others later (Blums et al., 2005). The main factor contributing to phenotypic variation among individuals, body condition, has not been examined here due to a lack of reliable data—adults were only weighed after they already started breeding. Further discussion on this subject is presented in sections 5.3 and 5.4.

Variation in laying dates is expected to be influenced by individual differences in age (Verhulst et al., 2014). We tested these effects in our animal models, which revealed the role of age in explaining the variation in laying date was not statistically significant. We note that while a lack of precise data on the known age of the individuals (only in cases when offspring born in our nestboxes return to breed or when inferred from parentage assignments) could contribute to this outcome, we do not observe differing patterns in plasticity among individuals. If jackdaws rely on information from experience to make decisions, we expect that learning will modify the slopes of reaction norms, particularly if some individuals effectively track environmental changes at a faster rate than others. One plausible explanation for the consistent patterns in plasticity among individuals is that reaction norms have been selected over time, resulting in a fixed slope within the population (Charmantier et al., 2008). Essentially, individuals with lower levels of plasticity might have had fewer opportunities to breed and contribute to population recruitment. Another argument accounting for the uniform plasticity among individuals breeding in the monitored nest boxes is regarding the characteristics of the study systems. If these monitored nest boxes offer high-quality breeding conditions compared to natural cavities, replacing other adult individuals from lower social ranks trying to breed in such nest boxes could homogenize differences in age, breeding experience, and even fitness among individuals (Verhulst et al., 2014b; Verhulst & Salomons, 2004).

5.2 Contrasting evolutionary potential within species

Our findings from Chapter 3 regarding heritability in laying dates contradicted our expectations. Considering the behavioural flexibility and remarkable innovation capacity in this species, we initially expected plasticity to be the main mechanism facilitating an adjustment to environmental changes. More unexpected was the contrasting estimates in heritability, probably due to the contrasting trends observed in the advancement of laying dates between regions.

While the estimated heritability is reliable (h^2=0.104 [0,0.2] in the South, and h^2=0.452 [0.24,0.58] in the North), improving the precision of these estimates (by narrowing the 95% confidence intervals) would benefit by gathering more data on both laying date variations and parental assignments. For instance, expanding data collection across subsequent breeding seasons and genotyping more samples could increase accuracy. However, sensitivity analyses showed that heritability estimates remained within the defined confidence intervals, indicating that variation in prior specification was not impacting the estimates. The differences observed between regions are not attributable to either the varying number of observations or the distinct methods used to reconstruct pedigrees. Firstly, comparison between field and lab pedigree in the South led to a high match on parental assignments due to the monogamous behaviour and the rare extra-copulation events in the species (see Appendix B). Secondly, while a larger number of observations might be critical if models failed to converge, this is not the case in our datasets (see Appendix C).

If evolution is ultimately the only mechanism explaining population persistence, we anticipate that the impact of global warming on demographic declines will be more pronounced in southern populations, owing to their lower evolutionary potential. Extending these approaches to other species is crucial to understand the broader implications in other species as well. We expect to find varying evolutionary potential among species, likely associated with their distinct life-history, as supported by the literature review in Chapter 4. Interestingly, within-species differences in heritability estimates have been underrepresented in the literature, likely due to a lack of studies exploring microevolution among populations of the same species. An exception was showed in the common tern (Moiron et al., 2023), where varying heritability estimates were found within the same population but across different periods, implying the influence of the environment on shaping microevolution. Our findings align with these findings, suggesting lower heritability estimates probably related to the higher spatial and temporal environmental variability in southern populations.

Further research should investigate whether the impact of indirect genetic effects is shaped by differences in natal recruitment between regions or other complex combination of selective pressures including non-climatic factors. Our focus centred on the capacity of learning and prospecting behaviour of jackdaws and its correlation with reproductive success (Schuett et al., 2012). We argue that indirect genetic effects hold particular relevance in social scenarios where individuals are closely related and that they can vary according to population size. The mixture of cues, combining both climatic and non-climatic factors, to which animals respond likely extends beyond laying dates and may encompass a broad range of behavioural traits. Despite the importance of cognition in shaping these decisions and facilitating adaptation to changes (Ducatez et al., 2020), studying its effects at the individual level presents significant challenges.

Based on our findings, we show that southern populations exhibit reduced evolutionary potential, and the observed trend is matching the predicted microevolutionary changes, which appear to be notably lower in the South (R=0.02) compared with the North (R=0.08). Despite this limited potential for microevolution, we have identified individual

plasticity in adjusting laying dates with temperature. The lack of advancement in laying dates within southern populations despite rising temperatures in the region raises intriguing questions regarding either masked or constrained plasticity. Regional differences in climate exposure, environmental fluctuations, or habitat characteristics affects populations differently (Jantzen & Visser, 2023). Although populations show the capacity for plastic responses, it may not be sufficient considering current selection pressures and the high rates of change in projected temperatures. Moreover, the flexibility in relying less on the phenology of natural resources and instead foraging in artificial sites or alternative habitats could potentially mask plasticity in breeding timing. Conversely, plasticity in breeding earlier might not be masked but constrained by body condition or lower habitat quality. This notion is reinforced by the general principle that population density tends to be higher at the center of a species range, gradually declining towards the periphery, leading to greater maladaptation in low-density areas (Brown, 1984). If selection pressures are not strong enough to significantly impact fitness, late breeders might continue producing fledglings, thereby maintaining variation in laying dates. Alternatively, we might have failed in detecting potential trade-offs associated with earlier reproduction for long-term adult survival or even for post-fledgling offspring survival.

To further confirm the outlined predictions, we recommend continuous recording of breeding data for prolonged periods of time with the opportunity to repeat analysis in the future and help detecting long-term costs in fitness, intensified selective pressures due to rising temperatures, or complemented with analysis on diet or foraging sites. Exploring the relative contributions of microevolution versus plasticity and disentangle the effects of environment and genetics in explaining the variation in a trait could be achieved through common-garden or cross-fostering experiments (Lamers et al., 2023). While acknowledging the logistical and ethical challenges of these practices, transferring eggs or individuals among populations with diverse phenologies presents an avenue for quantifying whether translocated individuals adjust breeding timing to their new social context (indicating high plasticity) or breed in periods more similar to the original population (indicating high heritability).

5.3 Contrasting macroecological patterns in phenology

Patterns in phenology differ between regions, not only on the response rates in the advancement of breeding timing but also on the starting of the breeding season. All studied populations showed sensitivity to the same cue (mean daily temperatures during specific sliding windows). However, despite a clear causal interaction between temperature and laying date, individuals across regions may rely on distinct additional cues to schedule phenology (Caro et al., 2013). Alternatively, the same temperature cue may indicate an optimal breeding time unique to each location. Such latitude-specific sensitivity to environmental conditions could result in spatial variation or local adaptation, assuming minimal connection by gene flow between regions (Gienapp et al., 2010; Schoech & Hahn, 2007).

Latitudinal trends in the duration of sliding windows over which mean temperature best predicts spatiotemporal variation in first egg dates, as observed in the studied jackdaws,

have been observed to vary both among and within species (Phillimore et al., 2016). While breeding phenology typically follows a geographical trend with later timing at higher latitudes (Baker., 1939), jackdaws show an opposite pattern, with lower latitudes starting breeding later and displaying narrower sliding windows. This variation cannot be attributed to multiple breeding, as jackdaws are single-brooded and second clutches are very rare (personal data). Other life-history traits in jackdaws such as clutch size also show opposite patterns across latitude from the general trend observed in the majority of bird species (Soler & Soler, 1992), with jackdaws laying larger clutches in the South but larger eggs in the North, following a quality-quantity trade-off (Soler and Soler 1992). Whether intraspecific variation in clutch size is a response to global warming or the relative contributions of plasticity and heritability remains unexplored in our study. However, evidence from other species suggests that individuals at higher latitudes or elevations often exhibit slower life-histories (Boyle et al., 2016; Tieleman, 2009). However, the trend is generally related to shorter and later breeding seasons, also linked with body size variation across latitude following the Bergmann's rule, with implications for responses to global warming (Ashton, 2002; Teplitsky et al., 2008).

The contrasting macroecological patterns in life-history traits observed in our study populations remain unclear. Being a more generalist and flexible species that relies less on natural food resources might be an explanation. However, we need to acknowledge that comparing two regions from extreme locations within the species distribution might not be representative of the environmental factors typically differing between South and North. This thesis serves as a starting point to identify variation in cue sensitivity that may underpin the observed contrasting patterns. One promising avenue that this work presents is the opportunity to develop further research including multiple populations across the latitudinal pattern. Local datasets are essential in unravelling broader macroecological patterns. However, we recognise the challenges related to both sampling effort and funding to collect data from almost a decade through nest box monitoring, ringing, and resighting in natural populations. Hence, the value of data accessibility and sharing is growing with the creation of repositories and data bases such as SPI-Birds Platform (Culina et al., 2021), AVONET (Tobias et al., 2022), GBIF (Telenius, 2011), or COMADRE (Salguero-Gómez et al., 2016), among others. Linking breeding data with genetic data is valuable for constructing pedigrees and estimating heritabilities. The increasing accessibility and affordability of genotyping methods for obtaining high-quality data to sex individuals and construct pedigrees from non-invasive sampling underscore the benefits highlighted in Chapter 2.

5.4 The role of advancing hatching time to adjust to global warming

Reproductive investment varies among individuals within species. These differences are expected to be shaped by the ability to allocate resources used for reproduction (Pettifor et al., 2001; van Noordwijk & de Jong, 1986). Reproduction is costly, particularly for females. In birds, the development of eggs prior to laying, the time spent on incubation, and parental care to rear the brood until fledging require high levels of energy (Orrell &

Kunz, 2016). In some species, females can lose up to 13% in body mass during the breeding season (Freed, 1981). In an attempt to minimise the costs and maximize the benefits, individuals breeding in seasonal environments are expected to adjust their breeding decisions to their internal and external conditions (Hennin et al., 2018). As we have seen in Chapter 3, individuals advancing laying dates in warmer years improve their fecundity fitness by rearing a higher number of fledglings with more chances to survive. However, in climate change scenarios, advancing laying dates would be particularly challenging for individuals in low body conditions (Dunn & Møller, 2019).

Body condition is expected to be a major constrain for reproductive success (Houston et al., 1983). Females showing better body condition at the time of laying are expected to lay larger clutches and early in the season (Pettifor et al., 2001). Delaying breeding to improve parental body condition comes at the cost of facing a decline in the probability of offspring survival due to a decrease in the availability of resources as the season progresses (Hennin et al., 2018; Lepage et al., 2000). Therefore, decisions like where and when to breed, or how much parental investment is provided are major sources of variation in individuals fitness. For instance, a high parental effort can improve fecundity but reduce survival by increasing the future mortality of adults (Santos & Nakagawa, 2012). Larger broods allow to fledge more chicks but also increase offspring competition reducing their quality and probability of recruitment (quantity-quality trade-off). The onset of incubation is also a key decision within parental care. If incubation starts before the clutch laying is complete, it results in hatching asynchrony. In larger clutches, the asynchrony in the time of hatching between the first and the last-hatched chicks is enhanced. Hatching asynchrony leads to differences in age and size between chicks within a nest and disadvantages the last-hatched survival, therefore reducing the overall reproductive success of the parents (Slagsvold et al., 1995).

Hatching asynchrony is a widely observed pattern among altricial birds. Multiple hypotheses have been suggested to explain the adaptive benefits of the hatching asynchrony strategy, being the brood reduction hypothesis the most accepted (Amundsen & Slagsvold, 1998; Lack, 1947; Ricklefs, 1965). According to Lack (1947), the last-hatched chick which received less parental investment only survives when the abundance of resources enables to rear all chicks. Thus, the brood is reduced in years when food resources are insufficient to avoid the loss of the full brood (Royle & Hamer, 1998). This strategy has been suggested to be beneficial in unpredictable environments when food supply for nestlings varies widely and cannot be predicted before the time of egg-laying (Mock & Forbes, 1994; Parejo et al., 2015). Alternatively, other hypotheses consider variation in hatching asynchrony as a result of other constraints acting on other traits such as an early onset of incubation. In any case, the role of hatching asynchrony remains controversial because the size hierarchy among nestlings has been considered beneficial, partially beneficial or detrimental depending on the environmental context.

Jackdaws follow a hatching asynchrony strategy and show high variability in reproductive investment among pairs (Arnold & Griffiths, 2003; Heeb, 1994; Slagsvold et al., 1984; Soler, 1988). Unpublished data from our research group not included here suggest that last-hatched nestlings in early broods grow faster and the mortality associated to

hatching asynchrony is lower. The survival and body condition of the chicks is not affected by brood size, supporting the fact of spreading out hatching times and the peak food demands of offspring ('peak-load reduction hypothesis', Mock & Schwagmeyer, 1990) to explain the benefits of hatching asynchrony. Contrary to the brood reduction hypothesis, the peak load reduction hypothesis is beneficial when parents are limited by the amount of time per day during which they can forage, regardless of the food supply. Conversely, in late broods, nestling mortality is concentrated during the first week after hatching because survival is compromised by the number of chicks reared. Together with the trade-off between quality and quantity, it supports the 'brood reduction hypothesis', which postulates that the loss of last-hatched chicks is an adaptive mechanism to adjust the number of offspring to the level of available resources each year.

In a context of global warming, whether individuals vary their onset of incubation apart from laying date to adjust the time of hatching presents an intriguing question worthy of further research. As discussed above, laying date is not the sole determinant of hatching date. Birds can reduce the interval between laying and hatching by laying smaller clutches, shortening the gap between the last egg and the onset of incubation, or even reducing the duration of the incubation period (Kluen et al., 2011; Visser et al., 1998). The period between the first egg and hatching is of about 20 days in jackdaws, but shortening this interval could represent an adaptive response in warmer springs. This decrease may involve a reduction of the gap between clutch completion and incubation, independently of changes in mean clutch size (Vedder, 2012). In scenarios where temperature cues during the pre-laying period are less predictable, birds may adjust the onset of incubation in an attempt to advance their hatching date (Both & Visser, 2005). If constraints during egg-laying intensify, birds might trade-off the costs of producing eggs early against initiating incubation before clutch completion, leading to the asynchronous hatching of the chicks as possible outcome.

5.5 Conclusions

1. The molecular protocol, developed based on the sequencing of sex-linked SNPs, enables the simultaneous genotyping and sex identification of a large number of individuals independently of their life cycle stage, with an accuracy of 99.5%. This method relies on the sampling of non-invasive feather samples and the identification of SNPs in unique regions of the two sexual chromosomes, making it applicable across a broad range of fields and species.

2. Accurate sex identification, combined with flexible approaches that customise confidence thresholds and error rates, along with assigning non-genotyped parents to sibling clusters, facilitates the reconstruction of multigenerational pedigrees within natural populations. This methodology proves particularly valuable in situations where the number of SNP loci is limited, individual ages are unknown, or the proportion of non-genotyped individuals within the population is high. Complementing the genetic pedigree with field observations further enhances the quantity and reliability of assignments.

3. Long-term monitoring of marked individuals and pedigree data is essential for investigating plasticity and quantifying microevolution mechanisms in natural populations. Despite adjusting breeding phenology is a highly plastic response to global warming in the long-lived and behaviourally innovative studied species, the evolutionary potential is expected to help populations persist at the long-term. However, a lack of heritable variation in the reaction norm implies a constrained potential for the evolution of adaptive plasticity, which could pose challenges in adapting populations to future climate change scenarios.

4. The potential of populations to respond to environmental changes varies among populations with differing climate exposure, despite similar cues and selection strength affecting breeding phenology. Jackdaw populations are tracking temperature changes and mitigating reproductive fitness-effects of temperature by breeding earlier in warmer years. However, while this response to global warming is adaptive and under selection with no apparent short-term costs for adult survival, only populations from northern latitudes are showing a shift towards advancing breeding phenology following an increase in temperatures over time. Other non-climatic factors such as population density are influencing the rate of this response, yet their effect remains unclear.

5. Whether plasticity is hindering or promoting evolution is complex because indirect genetic effects from social behaviour and spatial or temporal fluctuations may influence heritability estimates. Genetic and environmental components may be confounded when social cues influence the phenotype of closely related individuals, thereby promoting evolutionary changes. At the same time, copying decisions from other individuals may modify the slope of reaction norms affecting plastic responses. Further investigation testing the role of these factors in multiple populations, encompassing other behavioural traits or social contexts, may shed new light on explaining the evolutionary and plastic responses to global warming in jackdaws.

Appendix A

Supplementary material from Chapter 2

A.1 Notes A

Note A.1 DNA quality thresholds

The quality of DNA concentration used as threshold to decide whether to include or exclude a certain sample was set to 15 ng/µL. This decision was based on checking the proportion of genotyped loci related to DNA concentration in a test batch of 48 samples (the number of subarrays that fit in one OpenArray PCR plate). Among the samples that were concentrated using a centrifuge, a 41.74% reached values above the determined threshold and could be recovered. From the first group of selected samples for the study (N total=1097, N fledglings=924 and N adults=173), only 28.82% of the samples extracted from adult feathers showed DNA concentration values high enough to be included in the genotyping array. In contrast, 97.94% of the samples extracted from fledgling feathers showed high values of DNA concentration. Ultimately, a total of 957 good-quality samples were included for genotyping.

After genotyping, 29 samples (corresponding to 23 fledglings and 6 adults) out of the initially selected 957 did not amplify, and therefore, the individual genotypes could not be identified. This represents a success rate of 96.97%. The two sample replicates from the same individual (captured as fledgling and later as an adult) showed the same genotype calls for all SNPs, despite a 6.56% and 53.28% of SNPs not amplifying, respectively. The proportion of amplified and defined SNPs per sample was explained by the DNA concentration of the samples, as expected (Fig. A.1). The proportion of genotyped loci increased to 0.9 above 50 ng/µL. No trend was identified in adults, likely due to the low number of samples included compared to fledglings. The year when the sampling was performed had no effect on sample quality (Fig. A.2). This suggests that the storage of the samples was not compromised over time, even though some samples were stored at room temperature for at least 5 years.

Note A.2 Exploration of candidate sex-linked SNP loci

Due to the limited availability of SNP information for the Jackdaw (e.g. Knief et al., 2019; Kryukov, 2019; Vijay et al., 2016; Weissensteiner et al., 2020), we conducted an extensive literature search to identify potential SNPs. We focused on primers tested in species from all avian orders, but particularly in jackdaws or closely-related species. We found only one fragment with potential SNPs located in the Z-chromosome. This SNP (namely ACO1, Kimball et al., 2009) was further tested using local samples from eight individuals captured in different locations across our study area (between 2 and 40.22 km apart). We aimed to maximise the diversity of genetic variations among individuals and include representatives from both sexes. The PCR replication for this marker was successful, and we were able to sequence and identify the alleles at the specific locus (hereafter F9A). The genetic analyses using traditional PCR methods were conducted in collaboration with the Vetgenomics laboratories, a spin-off company from UAB (Universitat Autònoma de Barcelona).

Because reliable sex assignment required a higher number of SNP coverage for testing, including SNPs located in the W-chromosome, we used additional data from another wild

population of the same species to build a more complete SNP library. Raw short-read sequencing from four individuals (J01, J02, J03, and J08) originally from Rimbo, Sweden, was obtained from Weissensteiner et al. (2020) using paired-end libraries sequenced on an Illumina HiSeq2000 machine. Genome assembly was performed using a published long-read-based reference of the Western Jackdaw (with a length of 1,035.86 Mb) downloaded from NCBI repository under the GenBank assembly accession GCA_013407035.1 (Weissensteiner et al., 2020). Read mapping was performed using BWA (v.0.7.12), followed by variant calling through samtools (v.1.11), and SNP selection was carried out with the program bcftools (v.1.11). More than 6,000 high-quality SNPs were found across the whole genome using reads quality score=60 and depth=100 filters, with 3,949 located in the Z-chromosome (see Table A.1). From the overall panel of sex-linked SNPs, we selected both loci outside the homologous region, which is not shared between the paired chromosomes, or loci with presumably fixed sex-specific allele variants. Following these criteria, eight SNPs were found as potentially unique and fixed for each sexual chromosome (four found in the Z-chromosome and four more in the W-chromosome, respectively) and were therefore useful for sexing. Together with the SNP selected from the literature and successfully identified in our population, we analysed a total of nine sex-linked SNPs. Since the design of the genotyping array was part of a bigger project with the aim to reconstruct the pedigree of the studied population, we also selected autosomal SNPs apart from the nine sex-linked SNP markers. The OA PCR plates were designed to screen a set of 122 both autosomal and sex-linked SNPs using the online Custom Taqman® Assay Design Tool (Thermo Fisher). From the 6,000 SNPs panel previously detected (Table A.1), the criteria to select the remaining 113 to include into the assay were: 1) a SNP for each fragment where we found variation in our population independently of their position in the genome, 2) SNPs in putative regions of interest, and 3) SNPs in neutral regions and as distanced as possible.

Note A.3 Variation in the affinity between W-linked SNPs

Both F7C and F5C were found to be W-linked and unique (not located in the PAR region). However, genotyping results did not match for all samples. A mismatch in 25 samples (2.69%) suggested a differing affinity between both primer pairs (Table A.3). In 96% of these mismatch cases (N=24), F7C amplified while F5C did not, and only in the remaining 4% (N=1) did we find the opposite situation. This suggested a higher affinity of F7C to bind to the W-chromosome. To test the affinity of both primer pairs in other regions across the species genome, we used the alignment algorithm BLASTN (v.2.2.31+) implemented in NCBI (Zhang et al., 2000). Despite similar primer lengths, the Expect E-values (number of expected hits of similar quality that could be found just by chance) were considerably higher for both F7C pairs compared to F5C (Table A.3). This result indicated that F7C primers had less specificity in binding to other chromosomes excluding W. The lower scores for F7C (median 28.8) compared to F5C (median 32.5) also supported that primer binding was less strong for the former. Therefore, F7C was apparently a more reliable SNP to identify females due to lower specificity for other chromosomes. We also explored the potential effect of the frequency of errors in the remaining SNPs (including autosomal) and sample concentration as complementary

factors explaining the non-amplification of these W-linked SNPs (Fig. A.6). In samples with lower DNA concentration and lower proportion of genotyped loci, the W-chromosome was amplified only when using F7C, suggesting a higher specificity.

A.2 Figures A

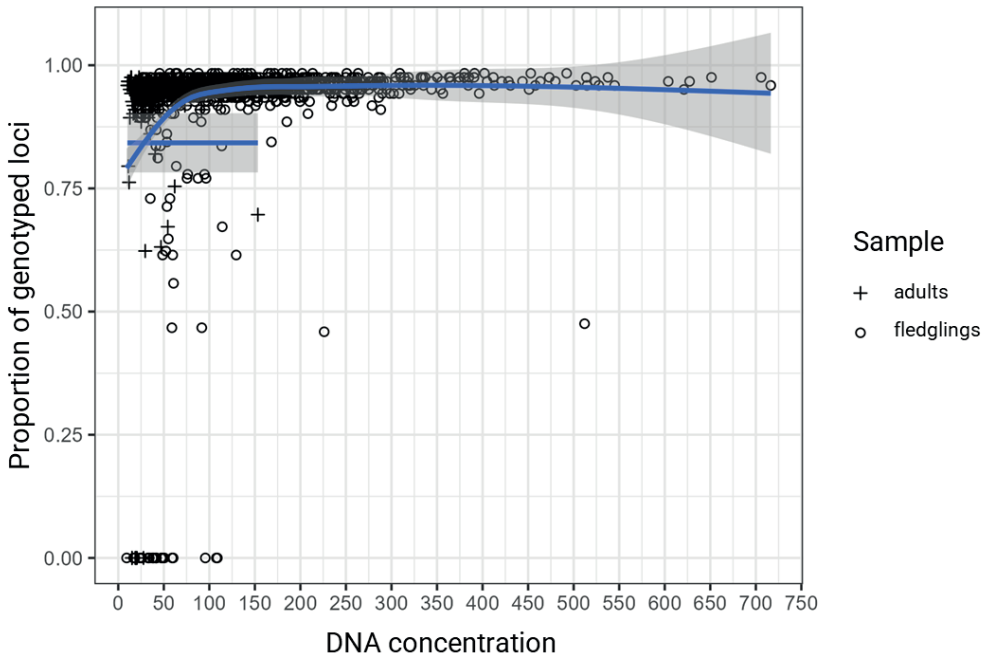

Figure A.1: Proportion of genotyped SNP loci and DNA concentration for both adult (represented by cross shape) and fledgling samples (depicted as open circles). The blue line represents the predicted values obtained from a Generalized Additive Model (GAM).

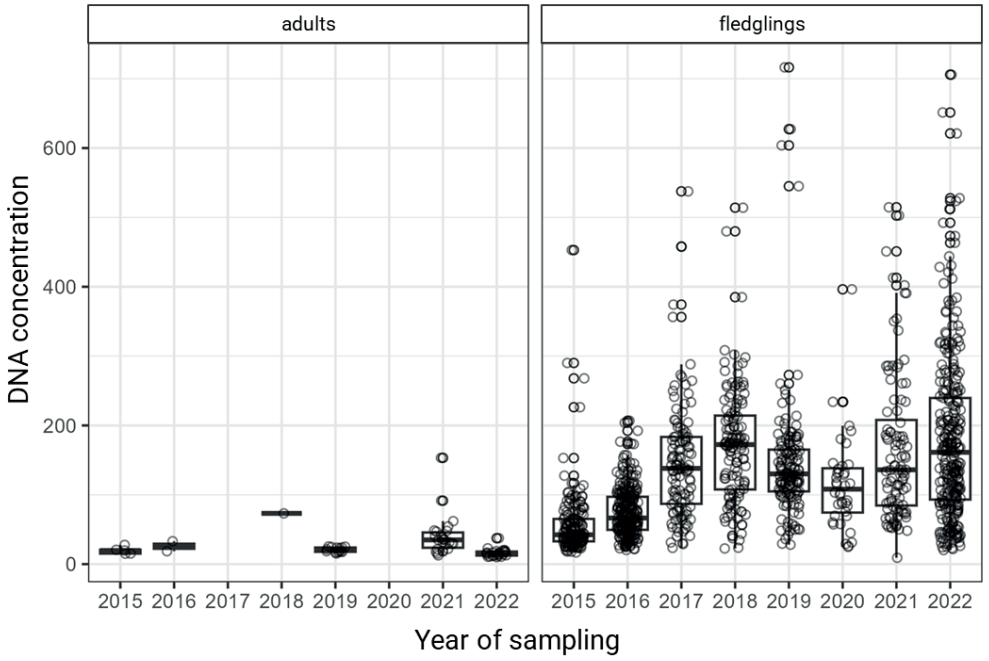

Figure A.2: Boxplot illustrating the concentration of samples according to the year of sampling for both adult individuals and fledglings.

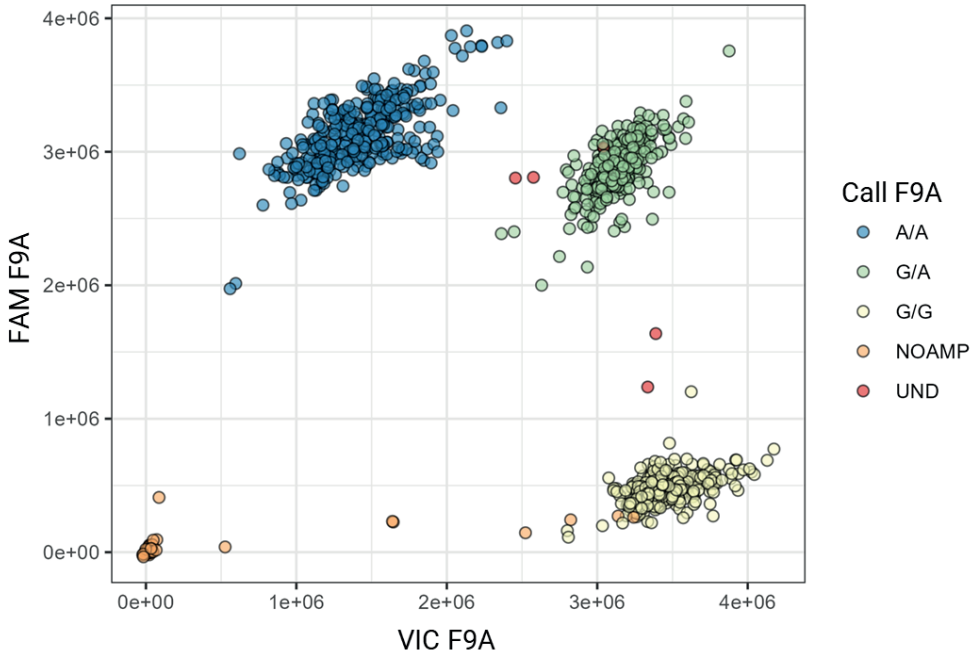

Figure A.3: Allelic discrimination scatter-plot of fluorescence data for F9A SNP genotype calling. The x-axis represents the intensity values of allele 1 in VIC Rn units (normalized reporter signal), while the y-axis represents the intensity values of allele 2 in FAM Rn units. Each dot on the plot represents the genotype calling of a specific sample. Blue dots indicate homozygote samples for allele 1 (A/A), yellow dots represent homozygote samples for allele 2 (G/G), green dots represent heterozygote samples (G/A), orange dots represent non-amplifying samples (NOAMP), and red dots indicate undefined genotypes (UND).

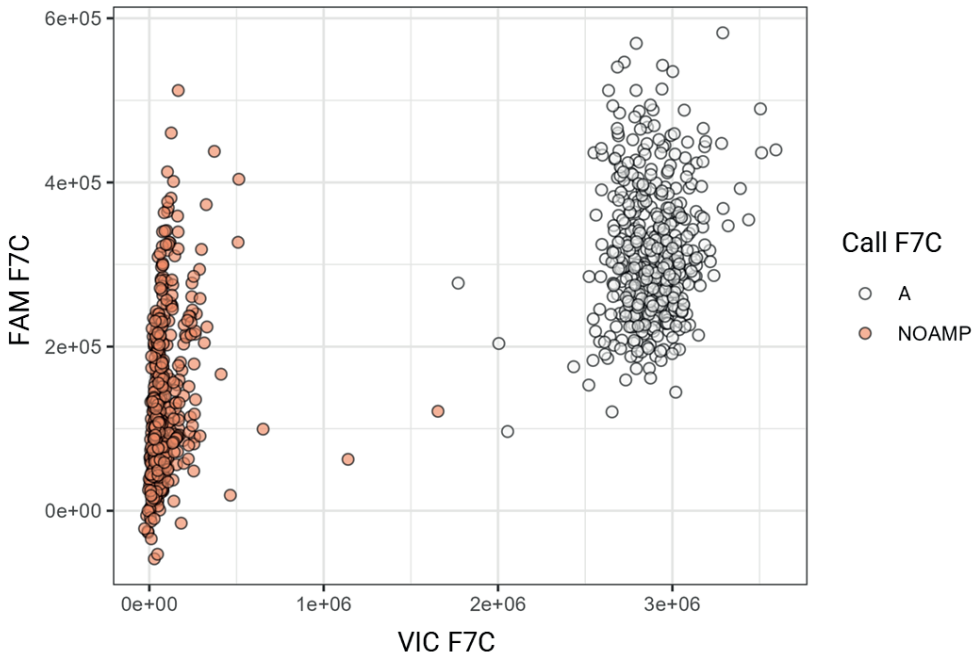

Figure A.4: Allelic discrimination scatter-plot of fluorescence data for F7C SNP genotype calling. The x-axis represents the intensity values of allele 1 in VIC Rn units (normalized reporter signal), while the y-axis represents the intensity values of allele 2 in FAM Rn units. Each dot on the plot represents the genotype calling of a specific sample. White dots indicate samples amplifying for F7C (A) and orange dots represent non-amplifying samples (NOAMP).

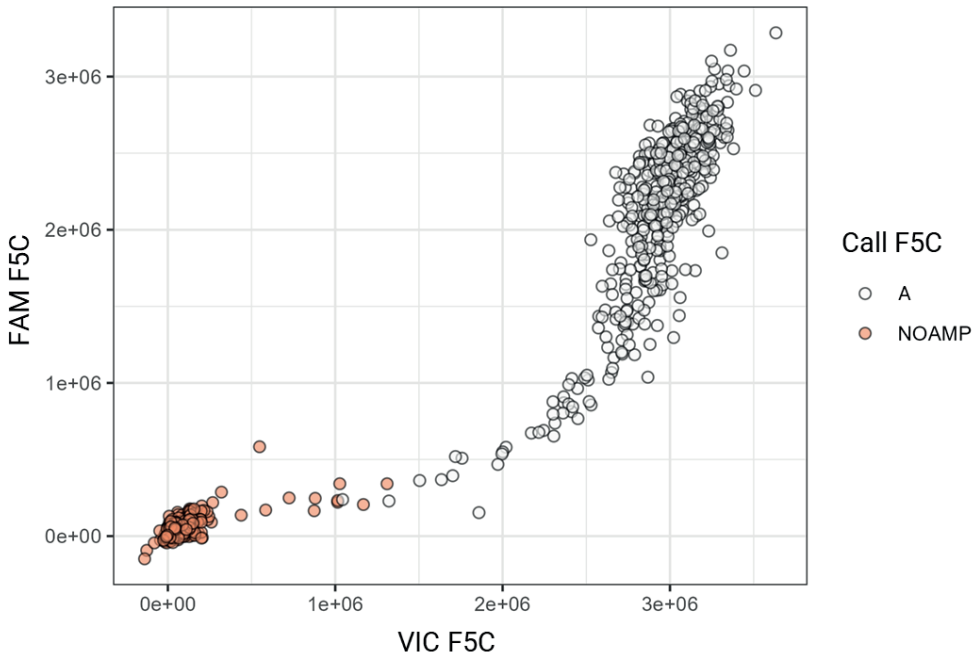

Figure A.5: Allelic discrimination scatter-plot of fluorescence data for F5C SNP genotype calling. The x-axis represents the intensity values of allele 1 in VIC Rn units (normalized reporter signal), while the y-axis represents the intensity values of allele 2 in FAM Rn units. Each dot represents the genotype calling of a specific sample. White dots indicate samples amplifying for F5C (A) and orange dots represent non-amplifying samples (NOAMP).

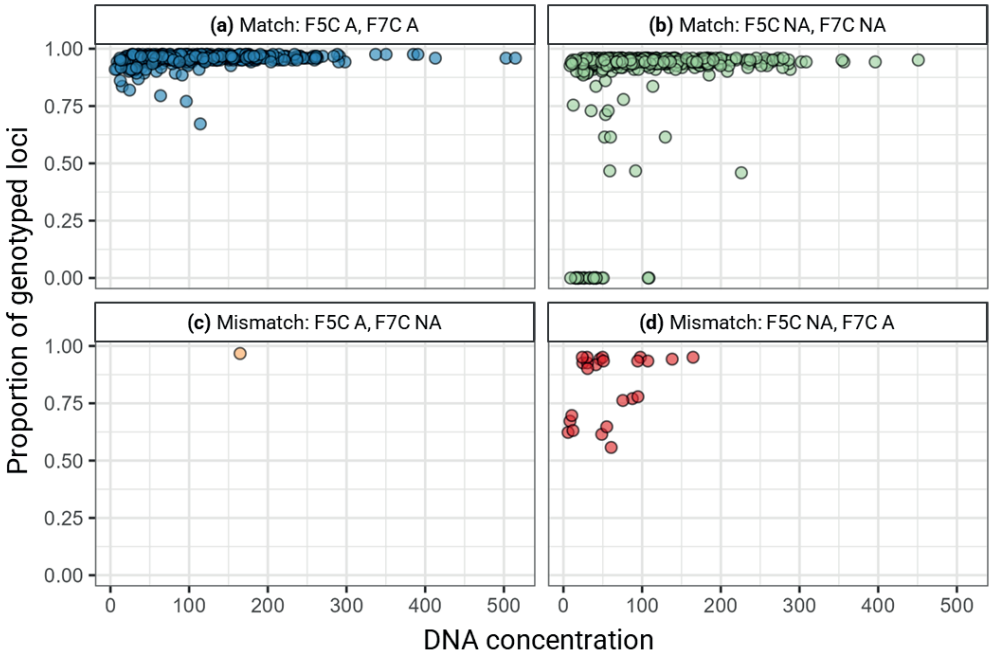

Figure A.6: Proportion of genotyped SNP loci according to DNA concentration per sample for the F5C and F7C genotypes: (a) Match between F5C and F7C with both showing amplification (A) represented in blue; (b) match between F5C and F7C with both not showing amplification (NA) shown in green; (c) mismatch with F5C showing amplification (A) and F7C not showing amplification (NA) indicated in orange; and (d) mismatch with F5C not showing amplification (NA) and F7C showing amplification (A) represented in red.

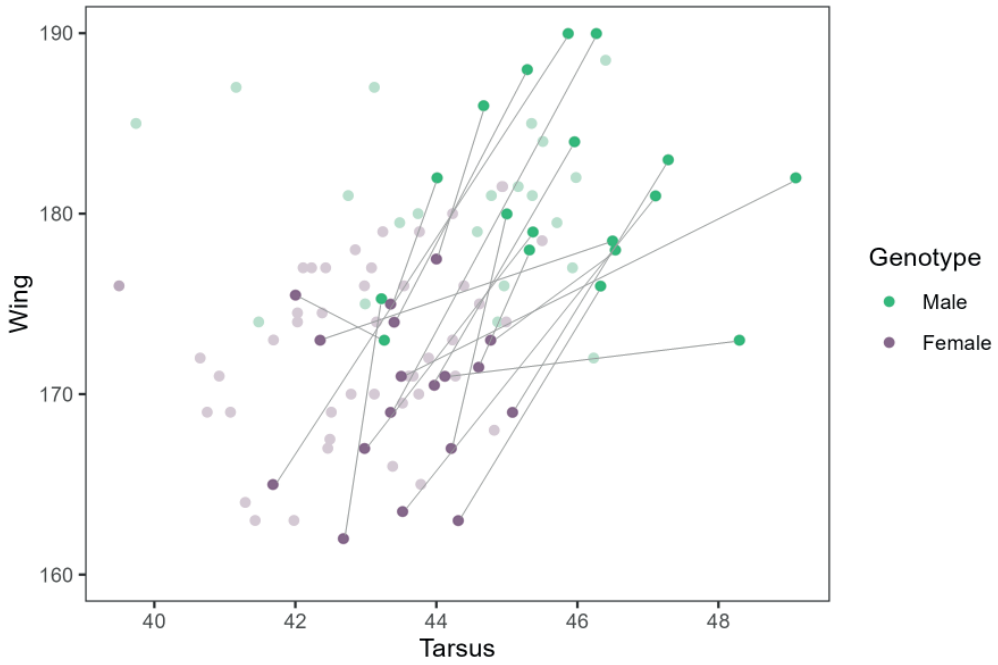

Figure A.7: Morphological characterization of the 36 individuals from breeding pairs used for sex validation (represented by solid dots) overlapping the morphological measures of 65 other adult individuals (represented by transparent dots). It is noteworthy that the majority of individuals within pairs could be clearly categorised into two distinct groups based on tarsus and wing length (in mm), which corresponded to their assigned sexes based on genotype. However, there were two individuals (G7351 and L001618) that possessed male genotypes but exhibited tarsus and wings resembling those of females (see Table A.4). Upon further examination within pairs (represented by solid lines), it was revealed that one of these individuals with a male genotype (G7351) displayed a larger tarsus and wing compared to its partner, indicating that morphologically it should also be assigned as male. The other individual (L001618) had a larger tarsus but a shorter wing. Considering that the wing measurement is less reliable than the tarsus measurement, the individual with the larger tarsus was presumed to be the male.

A.3 Tables A

Table A.1: Number of SNPs resulting from the mapping between the reference genome and four individuals from Sweden, according to different filters for read cleaning and assemblage. The SNPs are classified as biallelic or triallelic, and they are either mapping to the sexual chromosome Z or an autosome. A single variant from any combination between the reference and the four individuals is considered a SNP.

Filters options	SNPs total	SNPs chrZ	3 variants	3 variants chrZ
Original	7297633	586370	26965	2556
Reads quality=60 and depth=20	5756854	403246	15202	956
Reads quality=60 and depth=50	1761566	70865	4498	199
Reads quality=60 and depth=100	6266	3949	51	25

Table A.2: Summary table of genotype combinations in Z- and W-chromosomes for the 928 tested samples. Sex assignment matches in 96.23% samples, W-chromosome SNPs show a mismatch in 2.38%, there are uncertain assignments in 0.86%, and 0.21% are attributed to sequencing errors.

F9A (Z-chr)	F7C (W-chr)	F5C (W-chr)	N	Percentage	Sex assignment
A/G	NOAMP	NOAMP	231	24.89 %	males
G/G	A/A	A/A	223	24.03 %	females
A/A	A/A	A/A	214	23.06 %	females
G/G	NOAMP	NOAMP	126	13.58 %	males
A/A	NOAMP	NOAMP	99	10.67 %	males
G/G	A/A	NOAMP	11	1.19 %	females (mismatch)
A/A	A/A	NOAMP	9	0.97 %	females (mismatch)
NOAMP	NOAMP	NOAMP	5	0.54 %	NA (uncertain)
A/G	A/A	NOAMP	3	0.32 %	NA (mismatch)
NOAMP	A/A	A/A	3	0.32 %	NA (uncertain)
A/G	A/A	A/A	2	0.21 %	NA (error)
A/A	NOAMP	A/A	1	0.11 %	males (mismatch)
NOAMP	A/A	NOAMP	1	0.11 %	NA (mismatch)

Table A.3: Nucleotide BLAST results of W-chromosome primer forward (Fw) and reverse (Rv) pairs for F5C and F7C specificity across species genome using Zhang et al. (2004) algorithm. Length is given in number of nucleotides. Only the best match for each chromosome and its accession number in NCBI are provided. Matches are ranked according to their score from highest to lowest. The alignment score is calculated from the sum of the rewards for matched nucleotides and penalties for mismatches and gaps. E value represents the number of expected hits of similar quality that could be found just by chance. Identities represent the percentage of matching nucleotides for a set of aligned segments. Gaps indicate the number of nucleotides and the percentage according to primer length not found within the primer sequence.

Primer	Length	Chr	Accession	Score	E value	Identities	Gaps
F5C	32	2	CM023913.1	34.4	0.42	18/18 (100%)	0/18 (0%)
Fw		Z	CM023938.1	32.5	1.5	19/20 (95%)	0/20 (0%)
		9	CM023920.1	32.5	1.5	19/20 (95%)	0/20 (0%)
		4	CM023915.1	32.5	1.5	25/27 (89%)	1/27 (4%)
		3	CM023914.1	32.5	1.5	17/17 (100%)	0/17 (0%)
F5C	25	5	CM023916.1	32.5	0.5	20/21 (95%)	1/21 (5%)
Rv		9	CM023920.1	30.7	1.8	16/16 (100%)	0/16 (0%)
		8	CM023919.1	30.7	1.8	16/16 (100%)	0/16 (0%)
		2	CM023913.1	30.7	1.8	16/16 (100%)	0/16 (0%)
		1	CM023912.1	30.7	1.8	16/16 (100%)	0/16 (0%)
F7C	30	4	CM023915.1	36.2	0.091	21/22 (95%)	0/22 (0%)
Fw		1	CM023912.1	34.4	0.33	18/18 (100%)	0/18 (0%)
		3	CM023914.1	32.5	1.2	17/17 (100%)	0/17 (0%)
		7	CM023918.1	30.7	4.2	16/16 (100%)	0/16 (0%)
		5	CM023916.1	30.7	4.2	16/16 (100%)	0/16 (0%)
F7C	23	5	CM023916.1	30.7	1.8	16/16 (100%)	0/16 (0%)
Rv		Z	CM023938.1	28.8	6.5	15/15 (100%)	0/15 (0%)
		4	CM023915.1	28.8	6.5	15/15 (100%)	0/15 (0%)
		1	CM023912.1	28.8	6.5	15/15 (100%)	0/15 (0%)
		1A	CM023939.1	28.8	6.5	15/15 (100%)	0/15 (0%)

Table A.4: Morphological measures of the 36 individuals from breeding pairs used for sex validation. Each pair is assigned a unique code (ID pair) indicating the colony, nest box, and year of capture. The individuals within the pairs are identified by an alpha-numeric code (ID individual), corresponding to the code on their metallic ring. Tarsus and wing length measurements using the third primary wing are recorded in millimetres (mm). To aid in visualizing the size differences, a colour scale is used, with purple representing the lowest values (tarsus=41.68 and wing=162.00), white for medium values (tarsus=44.70 and wing=175.40), and green for the highest values (tarsus=49.10 and wing=190.00). Morphology is utilised to classify each individual within a pair as either the smaller (small-sized) or larger (large-sized) individual. The genetic sex assignment of each individual is indicated in the final column.

ID pair	ID individual	Tarsus	Wing	Morphology	Genotype
BI_34_2015	G7400	42.68	162.00	Small-sized	Female
BI_34_2015	G7351	43.22	175.30	Large-sized	Male
FU_4_2016	RX02783	44.21	167.00	Small-sized	Female
FU_4_2016	RX02779	45.00	180.00	Large-sized	Male
IV_11_2018	G31438	43.40	174.00	Small-sized	Female
IV_11_2018	G31347	45.29	188.00	Large-sized	Male
IV_17_2015	G7092	42.35	173.00	Small-sized	Female
IV_17_2015	G7093	46.50	178.50	Large-sized	Male
IV_17_2021	RX07822	43.35	175.00	Small-sized	Female
IV_17_2021	L001205	44.01	182.00	Large-sized	Male
IV_21_2016	GX31841	44.12	171.00	Small-sized	Female
IV_21_2016	42A	48.30	173.00	Large-sized	Male
IV_21_2018	5120453	44.77	173.00	Small-sized	Female
IV_21_2018	G31293	46.54	178.00	Large-sized	Male
OB_23_2015	G7356	45.08	169.00	Small-sized	Female
OB_23_2015	G7037	47.29	183.00	Large-sized	Male
PA_31_2021	L001073	43.50	171.00	Small-sized	Female
PA_31_2021	L001072	49.10	182.00	Large-sized	Male
PR_25_2019	RX05804	44.00	177.50	Small-sized	Female
PR_25_2019	RX05802	44.67	186.00	Large-sized	Male
PR_36_2020	G7468	44.31	163.00	Small-sized	Female
PR_36_2020	G7204	46.33	176.00	Large-sized	Male
RG_16_2022	L001656	41.68	165.00	Small-sized	Female
RG_16_2022	G7251	45.87	190.00	Large-sized	Male
RG_18_2021	L001257	43.35	169.00	Small-sized	Female
RG_18_2021	G31400	46.27	190.00	Large-sized	Male
RG_24_2015	G7100	44.60	171.50	Small-sized	Female
RG_24_2015	G7099	45.32	178.00	Large-sized	Male
STB_35_2015	G7088	43.52	163.50	Small-sized	Female
STB_35_2015	G7086	47.11	181.00	Large-sized	Male
TF_24_2021	L001206	42.98	167.00	Small-sized	Female
TF_24_2021	L001329	45.37	179.00	Large-sized	Male
TR_7_2022	L001300	42.00	175.50	Small-sized	Female
TR_7_2022	L001618	43.26	173.00	Large-sized	Male
VP_29_2021	RX05136	43.97	170.50	Small-sized	Female
VP_29_2021	L001011	45.96	184.00	Large-sized	Male

Appendix B

Methods for reconstruction of multi-generational pedigrees from SNP data using the 'sequoia' R-package

B.1 Notes B

Note B.1 Sample material selection for genotyping

The criteria employed for selecting samples to construct a pedigree involved the inclusion of individuals potentially related to one another based on field data. Samples from adults were primarily selected as reproductive individuals highly contribute to population recruitment. In cases where at least one progenitor was known, two chicks per nest were selected. We also aimed to improve covering individuals relatedness including samples across the entire study system including samples from individuals breeding in distant colonies or other solitary nest boxes. DNA was extracted from a total of 1293 feather and tissue samples following the protocol outlined in section 2.2.2.

Note B.2 Exploration and identification of candidate SNP loci

Due to limited research on the molecular basis of the Eurasian jackdaw, there is a dearth of valuable information regarding genome sequencing and SNP data in this species. To address this gap, we compiled a list of 70 candidate fragments covering multiple genetic regions with potential SNPs found in Corvus monedula or closely related species, based on an extensive literature search. From the initial list, we tested 20 primers using local samples from 13 unique individuals captured in distant breeding areas to maximize the chances to find genetic variations among them. PCR replication was successful in 11 of the selected fragments, revealing 15 SNPs in nine of them. Recognizing the need for greater genetic variation, we designed 20 new primers de novo, utilizing reference sequences from isolated genomic scaffolds available in the NCBI database, which resulted from shotgun sequencing in a closely related species (*Corvus cornix cornix*). Using these 20 new sets of primers, we successfully amplified 17 fragments and detected 29 SNPs in 12 different fragments. All genetic analyses described above were conducted in collaboration with Vetgenomics Laboratories, a spin off company from UAB. In total, we identified 44 SNP loci occurring in at least 13 individuals within our study population. From these, we selected only one SNP per fragment to avoid linked recombination, giving priority to SNPs that displayed heterozygous alleles.

However, to achieve a comprehensive pedigree reconstruction and obtain robust statistical support for parentage analyses, a higher number of SNPs is required. To address this, additional data from a separate natural population of jackdaws was incorporated to create a more complete SNP library. Raw short-read sequencing data for four individuals originally from Rimbo, Sweden, were obtained from Weissensteiner et al. (2020), which were generated using paired-end libraries sequenced on an Illumina HiSeq2000 machine. Genome assembly was conducted using a published long-read-based reference of the Eurasian jackdaw (with a length of 1,035.86 Mb) downloaded from NCBI repository under the GenBank assembly accession GCA_013407035.1. Read mapping was performed using BWA (v.0.7.12), followed by variant calling through samtools (v.1.11). SNP selection was carried out using the program bcftools (v.1.11), resulting in the identification of more than 6,000 SNPs after applying the highest quality reads and depth filters (see Table A.1).

Functional annotation was performed to predict the location (chromosome) and position (putative or neutral genes) of SNPs across the genome. The AmiGO database, which provides online access to ontology and annotation data, was consulted to identify genes linked to behaviour using "behaviour" and "Gallus" as keywords for the search. Out of the initially selected 70 genes, we included SNPs located within the coding region of 6 genes that were successfully identified in the population. additionally, we aimed to incorporate SNPs located on the sexual chromosomes for sex identification, selecting 2 unique Z- and W-linked markers outside the pseudoautosomal region (PAR) for reliable sexing (Chapter 2, Garcia-Raventós et al., 2023). Finally, within the autosomal chromosomes, we chose 4 SNPs on the larger chromosomes, 3 on the medium-sized ones, and 2 on the small ones, strategically spaced and distributed along each chromosome.

Samples were genotyped using OpenArray real-time PCR plates specifically designed to screen a set of 122 SNPs. From the initial panel of 6,000 SNPs, the criteria for selecting the 122 for inclusion in the OpenArray were as follows: 1) a SNP from each fragment showing variation in our population, regardless of their genomic position, 2) SNPs located in coding regions of interest, 3) SNPs for sex identification located in sexual chromosomes, and 4) SNPs in neutral regions, distributed as widely as possible across the genome.

Note B.3 SNP and sample filtering

Filtering non-amplified, undefined or SNPs with fixed variants, resulted in a reduction in the number of SNPs from 122 to 107. Following the guidelines outlined by Huisman (2017), we further excluded SNPs with high error rates, low minor allele frequency (MAF), and low missingness (proportion of missing calls) before initiating pedigree reconstruction (Fig. B.1). Out of the total of 1293 sequenced samples, we removed 33 samples that were either not amplified or undefined, 2 duplicated individuals, and 21 samples with fewer than 80% of SNPs successfully scored.

Note B.4 Customization of age prior and mating system

Using a matrix of 100 SNPs and 1237 samples, we implemented customized age priors to enhance the accuracy of parent-offspring pair assignments. Setting a customized age difference between a pair of individuals based on our understanding of the species' ecology, serves two crucial proposes. Firstly, it aids in eliminating certain relationship possibilities from consideration; for instance, parent and offspring cannot share the same birth year. Secondly, it assists in distinguishing between various types of second-degree relatives, given that the age disparity between siblings is typically much smaller compared to that between grandparents and grand-offspring. As jackdaws do not reach maturity until their second year, we harnessed individual birth year data and sex information to calculate the probability of assigning parentage to individuals with a minimum age difference of 2 years (Fig. B.2).

Specifying a mating system can be particularly valuable when working with small SNP panels, as it aids distinguishing between full siblings and half-siblings during the parentage assignment process. Given that jackdaws are highly monogamous species forming long-term pair bonds, we conducted tests to assess the impact of incorporating

a monogamous mating assumption on pedigree reconstruction. Specifically, we examined how this assumption influenced two key factors: the number of SNPs at which pairs display opposing homozygotes and the log10-likelihood ratio (LLR) between parent-offspring relationships versus unrelated, without conditioning on any previously assigned parents. Results improved when considering a monogamous mating during pedigree reconstruction, with a reduction in Mendelian errors and an increase in parental LLR distributions (Fig. B.3).

Note B.5 Field and lab pedigree comparison for parentage assignment

A non-genetic pedigree was constructed based on field data on individual observations, captures and datalogger records spanning several breeding seasons. Since jackdaws are socially monogamous species (Hahn et al., 2021), nestlings in a nest were considered the offspring of the two adult individuals captured in the same nest box and subsequently observed or recorded visiting the nest frequently for incubation and food provisioning. Assignments for which parentage was uncertain were excluded from our analysis. The match of assigned parents between field and lab pedigrees was compared (Fig. B.4).

Note B.6 Simulations to determine assignment and error thresholds

We conducted simulations to explore the impact of a range of assignment and error thresholds on the proportion of relationship matches, misassignments, non-assignments or confidence probabilities. Our objective was to identify the set of threshold combinations that yielded the highest proportion of matches and confidence probabilities while minimising the occurrence of non-assignments and misassignments. We accomplished this by comparing the results obtained from simulated pedigrees against the field pedigree, which served as our reference dataset (Fig. B.5). Given no differences were observed between Tfilter thresholds, we applied the default value (Tfilter=-2) on the following simulations (Fig. B.5A). Misassignments were minimised when Tassign≥0.5 (Fig. B.5B). However, we observed a higher occurrence of non-assignments when the values for 'Tassign' and 'Err' were high (Fig. B5.C). The highest confidence probabilities were observed when Tassign=0.5 (Fig. B.5D). Finally, the number of cases with the highest confidence was observed when applying an error of Err=1e-04 (Fig. B.5E).

Note B.7 Pedigree reconstruction

We reconstructed a pedigree while considering a monogamous mating system, involving the incorporation of customized age priors and the application of previously determined parameters (Err=1e-04, Tassign=0.5, Tfilter=-2). For the purpose of comparison, we reconstructed a second pedigree under the assumption of a polygamous mating system, omitting complex relationships such as inbred or unusual relationships. Despite jackdaws forming long-term pair bonds and exhibiting genetic monogamy (Gill et al., 2020), it is worth noting that they may replace an original partner from year to year in the event of loss. Subsequently, we merged both pedigrees and assigned parents to each individual based on the pedigree with the higher log-likelihood ratio (LLR). Assignments with LLRdam, LLRsire or LLRpair values of ≤0 were removed. Our approach for constructing a high-likelihood pedigree from SNP data, implemented using the 'sequoia' R-package

(Huisman, 2017), is especially valuable when the true parent is not genotyped. In such cases, genotyped half- and full-siblings for which the parent is not genotyped are clustered into sibships and a "dummy parent" is assigned to each sibship. These dummy individuals are denoted by a 4-digit number, with prefixes 'F' for females and 'M' for males. Then, dummy parents were matched to non-genotyped parents within the field pedigree and replaced accordingly. We used the GetMaybeRel function to identify additional relatives, either first or second-degree. Additionally, the CalcOHLLR function was employed to calculate the parental log-likelihood ratios and to acquire missing life-history data such as birth year or individual sex. The final pedigree comprised four generations from 558 founders with 1230 dams and 1202 sires assigned to 1626 individuals. This accounted for 74.78% of all individuals with at least one parent assigned, with 36.93% of them represented by dummy parents (Fig. B.6).

B.2 Figures B

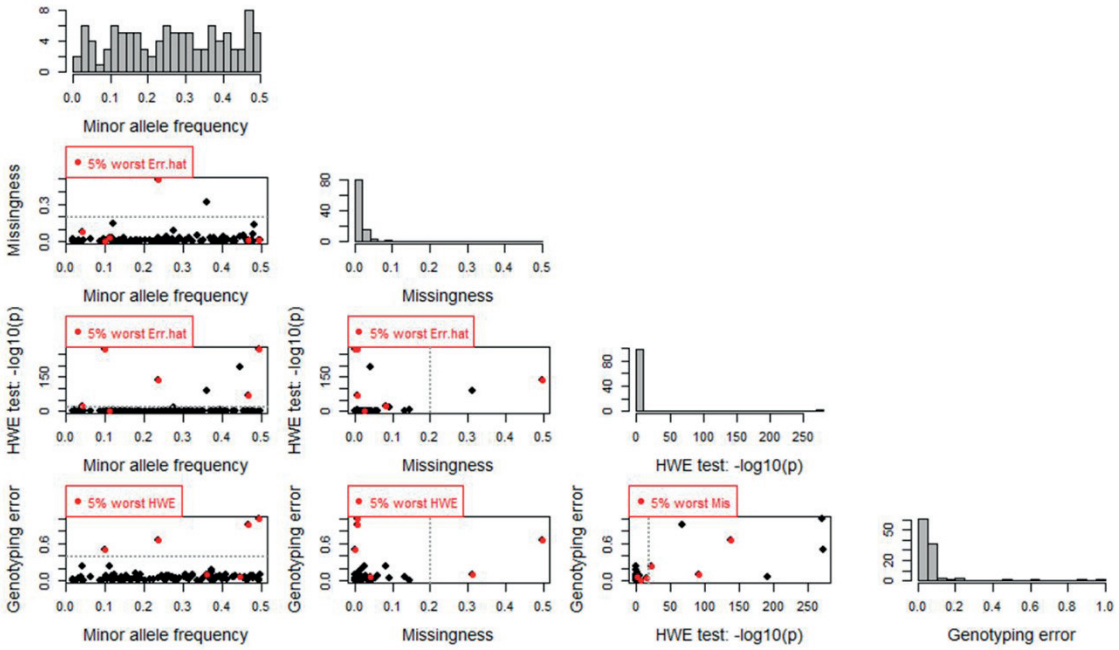

Figure B.1: Summary statistics and SNP filtering criteria using the 'SnpStats' function within the 'sequoia' R-package. SNPs were filtered based on the specified thresholds: missingness < 0.2, Hardy-Weinberg Equilibrium (HWE) < 20, and genotyping error < 0.4, depicted by discontinuous grey lines. SNPs not meeting these specific thresholds were excluded from further analysis, ensuring data quality and reliability.

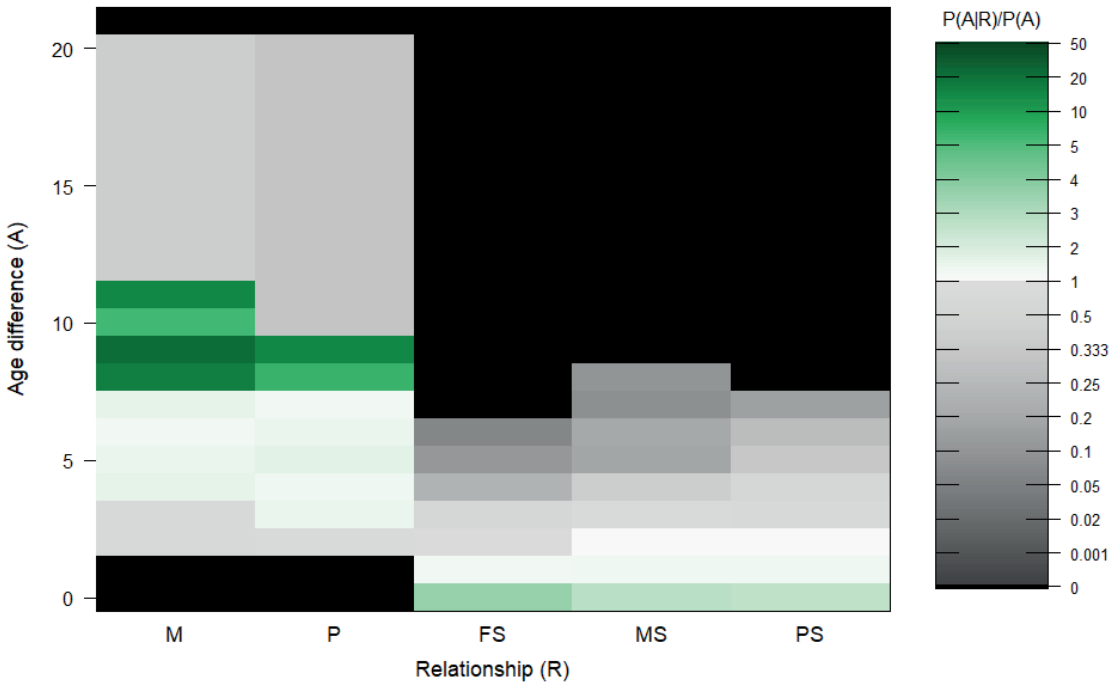

Figure B.2: Heatmap showing the conditional probability of specific family relationships (R) as a function of the age difference (A), represented as P(A|R)/P(A). Parent-offspring and sibling pairs include five categories of pairwise relatives: mother-offspring (M), father-offspring (P), full siblings (FS), maternal siblings (MS), and paternal siblings (PS). Plot visualization was provided by the '*PlotAgePrior*' function within the 'sequoia' R-package. Black areas indicate impossible combinations, while colour gradient ranging from grey to green indicate the probability distribution from lower to higher values.

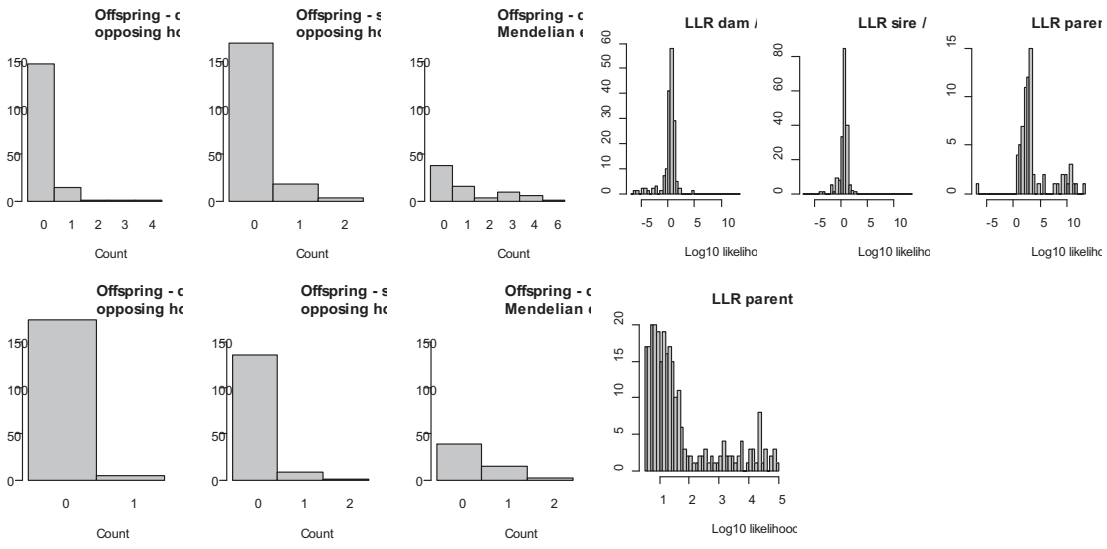

Figure B.3: Frequency of opposing homozygotes (left) and parental LLR (right) on parentage assignment using customized age priors considering a simple mating system (top) or monogamous (bottom). Less opposing homozygotes and higher LLR parent pair when parentship was restricted to monogamous mates. Plot was generated using the '*SummarySeq*' function within the 'sequoia' R-package.

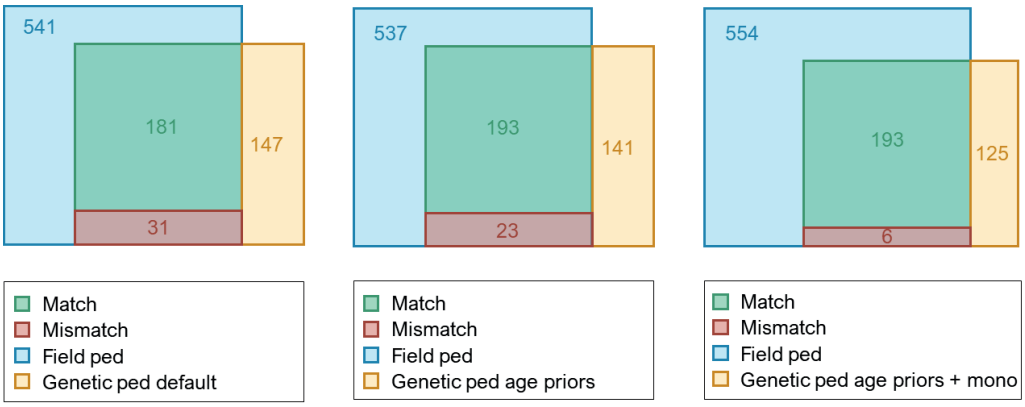

Figure B.4: Venn diagrams comparing the match of assigned parents between field and genetic pedigrees, generated using the '*PedCompare'* function within the 'sequoia' R-package. In green, the number of cases where assigned parents matched between the field and the genetic pedigrees, in red the number of mismatches, in blue the number of cases where a parent was exclusively assigned to a focal individual in the field pedigree, and in yellow the number of cases where a parent was solely assigned to a focal individual in the genetic pedigree. (A) The number of mismatches was higher when the age of maturity was not considered whereas (B) the number of matches increased and mismatches decreased when age priors were customized. (C) The number of mismatches decreased even further when only monogamous assignments were considered.

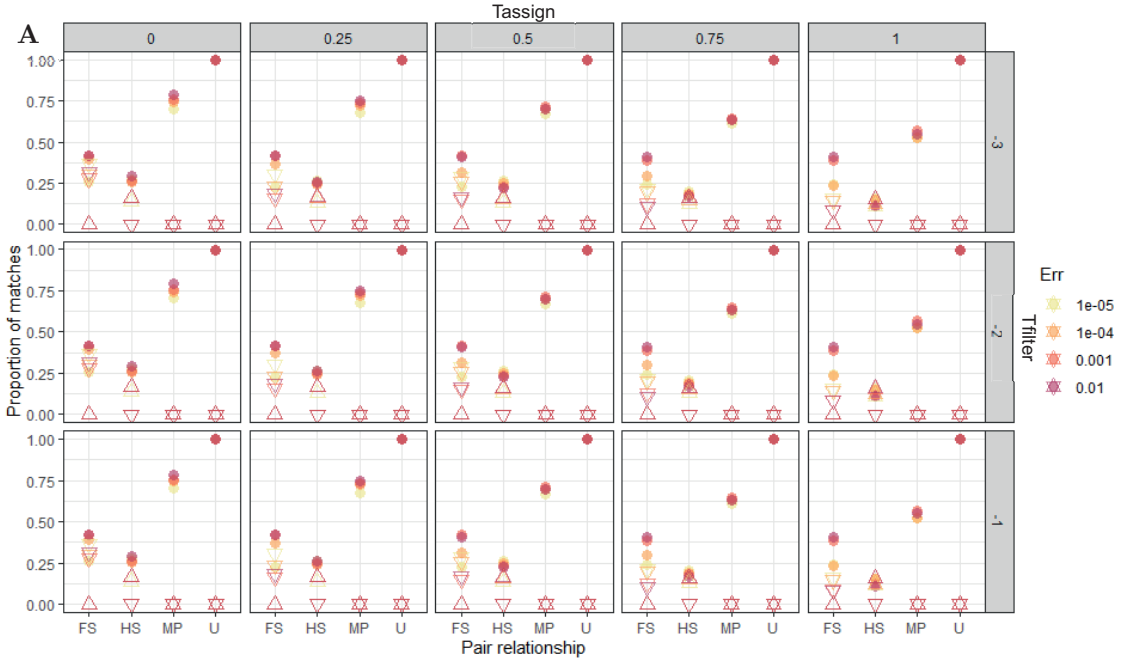

Figure B.5: Summary of the results obtained from simulations conducted with the '*sequoia'* function in sequoia R-package to determine assignment and error thresholds. (A) Proportion of relationship matches between the simulated and the field pedigree according to a combination of Tfilter (LLR threshold between a proposed relationship versus unrelated), Tassign (threshold used for acceptance of a proposed relationship, relative to next most likely relationship), and Err (genotyping error rate) values generated by the '*ComparePairs'* function. Triangles indicate the number of pairs with 'higher' relationship in the simulated pedigree as in field pedigree (e.g. FS instead of HS or HS instead of FS; ranking is the order given below), while inverse triangles indicate 'lower' rank relationships (e.g. HS instead of FS). When Tassign≤0.5, the proportion of MP (parent) matches exceeded 0.7.

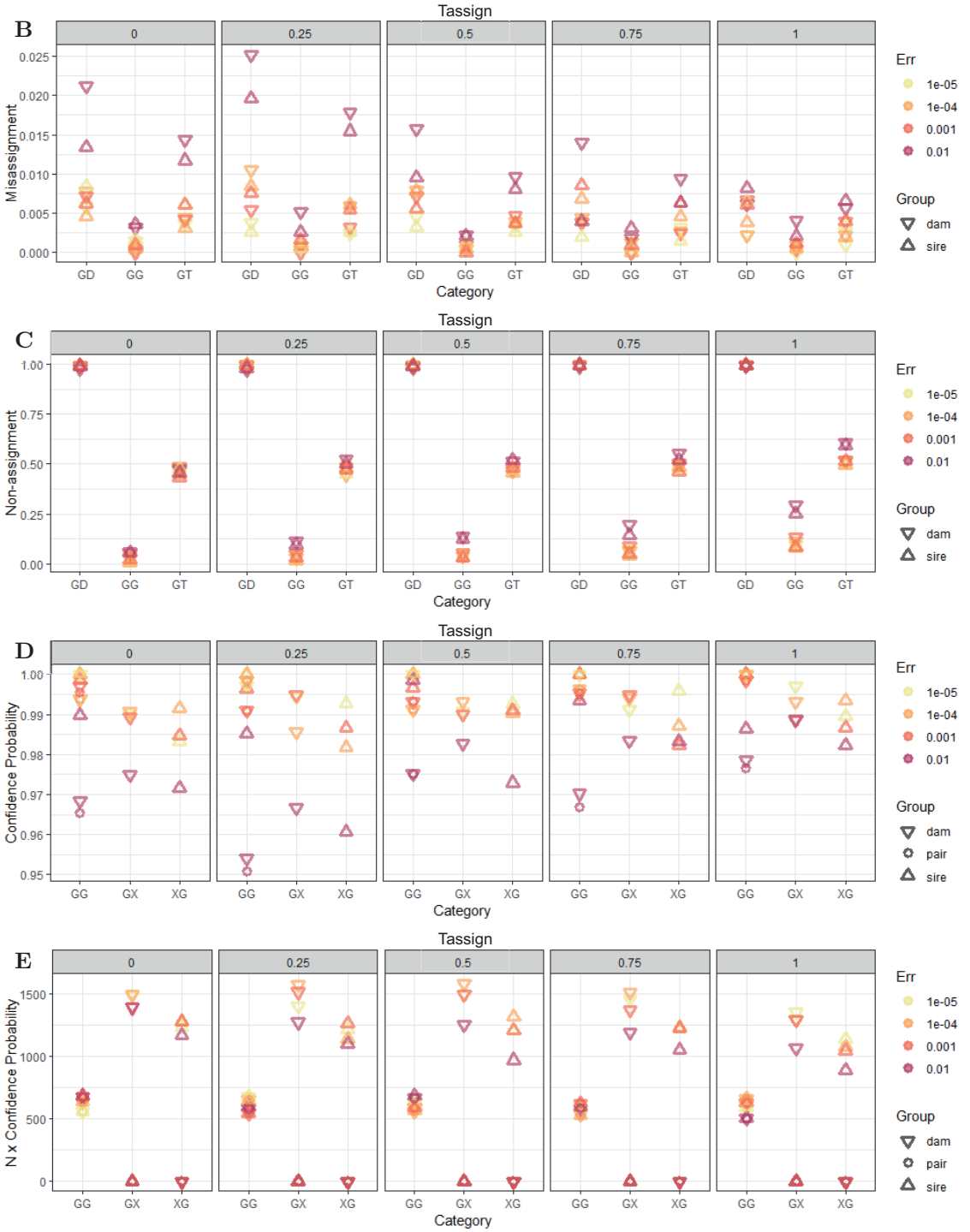

Figure B.5: *Continued from previous page.* (B) Number of misassignments (sum of false positives and mismatches) calculated separately for dams, sires or pair and categorised based on whether both the focal individual and the parent were genotyped (GG), the focal individual was genotyped and assigned to a dummy (non-genotyped) parent (GD), or considering the total (GT). False positives indicated potential misassignments, while mismatches occurred when different parents were assigned to the same individual. (C) Non-assignments (false negatives). (D) Confidence probability across GG (genotyped sire and genotyped dam), GX (genotyped sire and no dam) and XG (no sire and genotyped dam) categories for each group (dam, sire, pair). (E) Number of cases (N) per confidence probabilities. The '*EstConf*' function was used to calculate parameters showed in B-E, including a fixed number of SNPs=100 and a proportion of non-genotyped parents=0.46, given that the field pedigree included 141 progenitors, of which 76 were genotyped (54%).

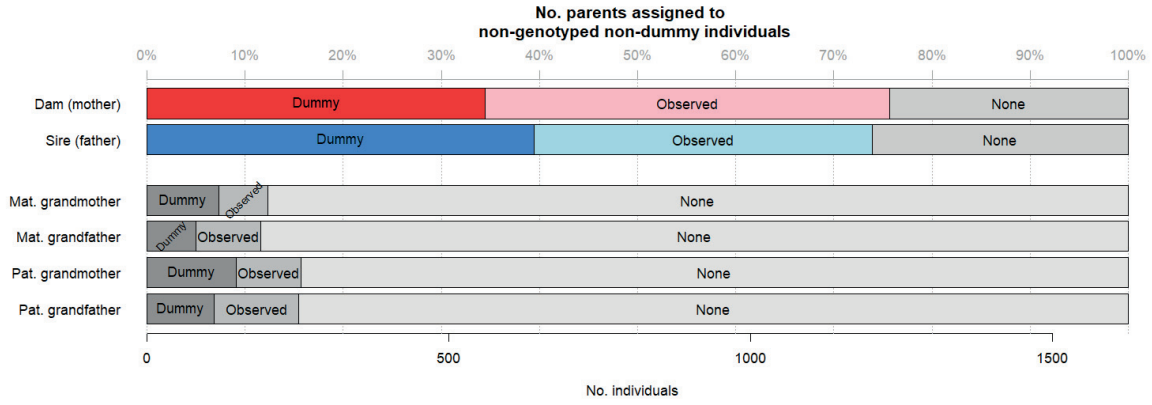

Figure B.6: Number of assigned parents and grandparents split by dummy and observed occurring in the pedigree. Results from '*SummarySeq*' plot function in sequoia R-package.

Appendix C

Supplementary material from Chapter 3

C.1 Notes C

Note C.1 Sliding window analysis

Within populations, quadratic functions provided a better fit to the climatological data, with precipitation windows being highly supported (Table C.1). However, differences in the average delay (the difference between the window midpoint and the mean laying date; Bailey et al., 2022) between climatic cues was noteworthy. Despite highly correlated variables at daily basis (Fig. C.2), temperature and precipitation windows operated at different time scales. Temperature cues were closely tied to the laying date, with 21-30 midpoints (Table C.1 and Fig. C.3). Conversely, precipitation had a longer-term influence, with 45-52 midpoints (Table C.1 and Fig. C.3). These findings align with long-term studies suggesting that temperature plays a key role in determining breeding timing (reviewed in Visser & Both, 2005). While rainfall is expected to precede an increase in food availability, seasonal temperature changes are more predictable, making it a more reliable environmental cue (D'Amelio et al., 2022; Mares et al., 2017).

We detected temperature windows during the pre-laying period in all four studied populations. however, in N2, the p-values were close to 0.5, suggesting weaker support for the detection of climatic windows compared to the other populations. We account for the lower sample size in N2 likely explaining these results (an average of 10 nest boxes were available in N2 in contrast to around 60 in S1, S2 and N1; see Fig. 3.1). Nevertheless, pre-laying window highly overlapped between N1 and N2. In the South, temperature-driven pre-laying periods were a week shorter, while precipitation-driven periods were 12 days longer in the North (Fig. C.3). The period during which temperature and precipitation most strongly affected phenology also varied in midpoint among regions, likely reflecting the pronounced climatic contrasts between the two studied regions (Fig. C.4). Notably, a temperature midpoint 8-14 days later in the South where mean temperatures were higher and exhibited more variation, suggest more time constraints and limited opportunities to initiate breeding in this region. The difference in window durations among populations is consistent with results from other studies showing shorter windows for populations with delayed thermal sensitivity (Bonamour et al., 2019; Phillimore et al., 2016).

Although our study assumed that individuals within a population would respond to the same climatic period, it is worth noting that individual-level variation may exist due to differences in body condition. Low-quality individuals are expected to delay the onset of breeding to gain in greater condition (Hennin et al., 2018) despite responding to the same climatic cue. A potential direct effect of pre-laying female body condition on laying date remains to be explored.

C.2 Figures C

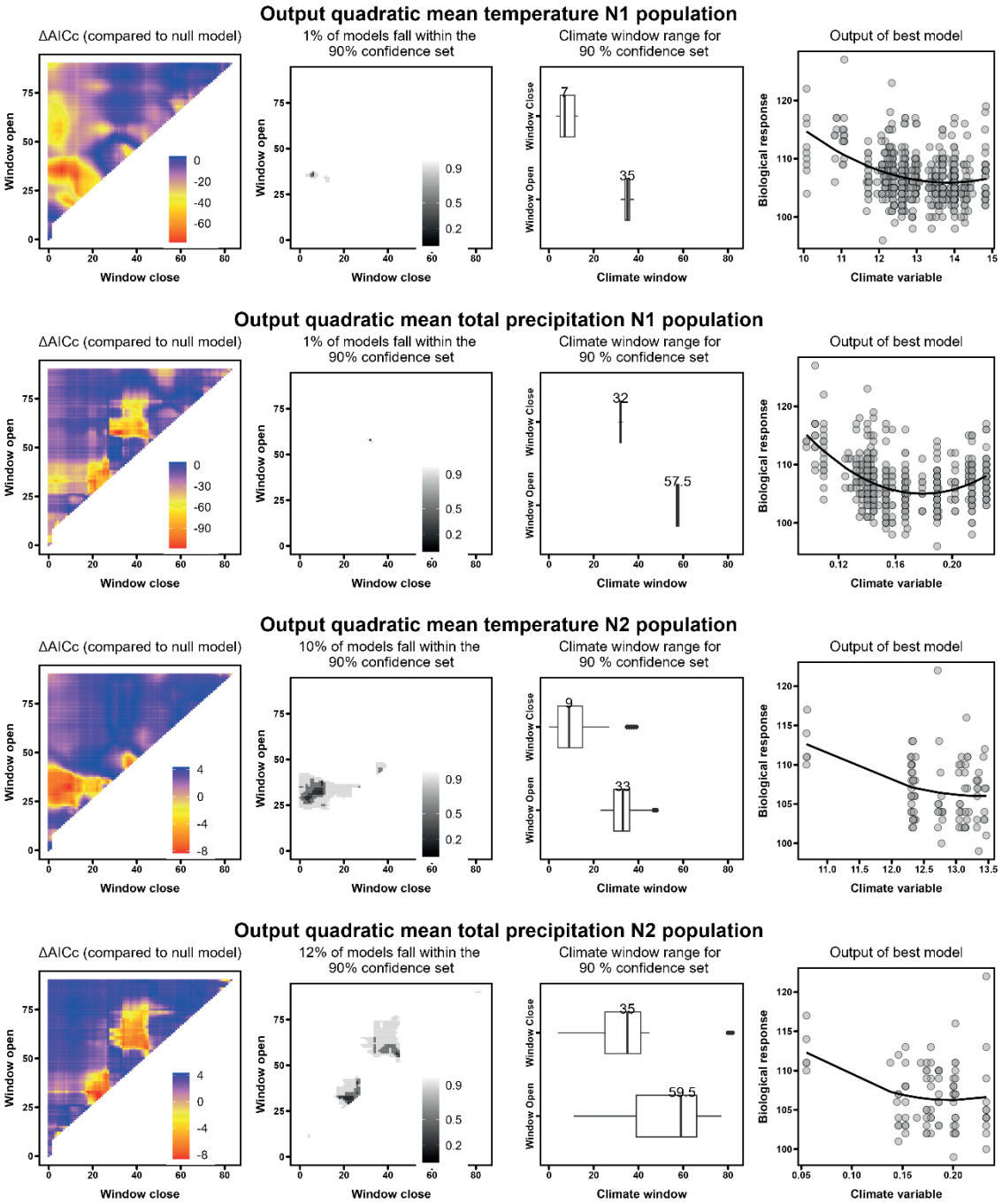

Figure C.1: Climwin model diagnostics showing the most supported temperature and precipitation windows selected to explain annual variation in laying dates of northern jackdaw populations. From left to right (1-4): (1) A heatmap of ΔAICc for the best environmental variable (mean temperature and total precipitation) compared to the null model across all possible windows. The area in red show the optimal windows. (2) The model weights with the 90% confidence set, of which only those within 2 AIC of the best model were used to calculate the best average timing window. (3) Median values of the 90% confidence set. (4) Fit of the predictions from the most supported model. "Window open" and "window close" refer to the number of days before the reference day taken as the mean of the population egg laying date in Julian days (107).

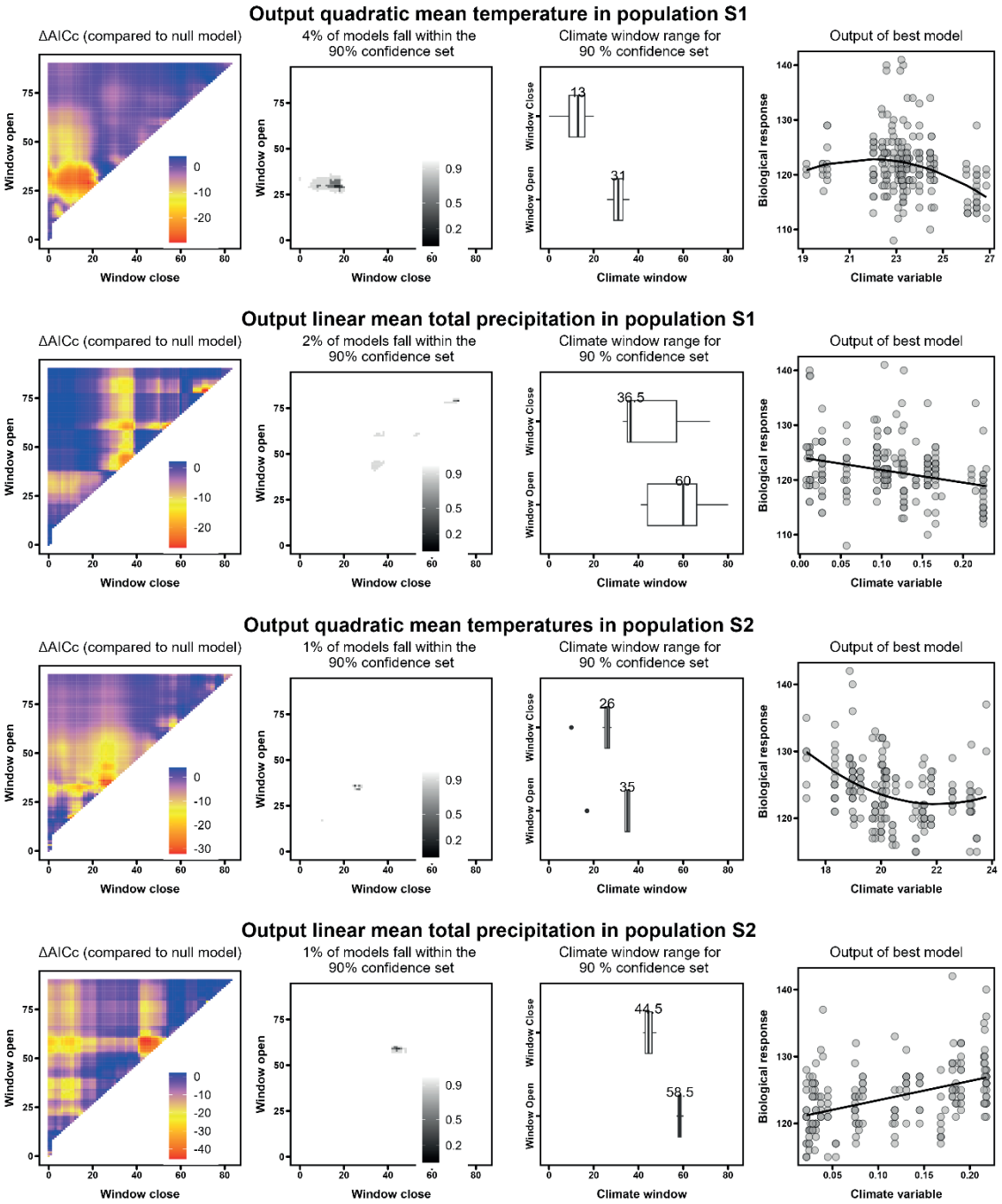

Figure C.1: *Continued from previous page.* Climwin model diagnostics showing the best temperature and precipitation windows selected to explain annual variation in laying dates of southern jackdaw populations. The number of days before the reference day taken as the mean of the population egg laying date in Julian days is 122 and 124 for S1 and S2 respectively.

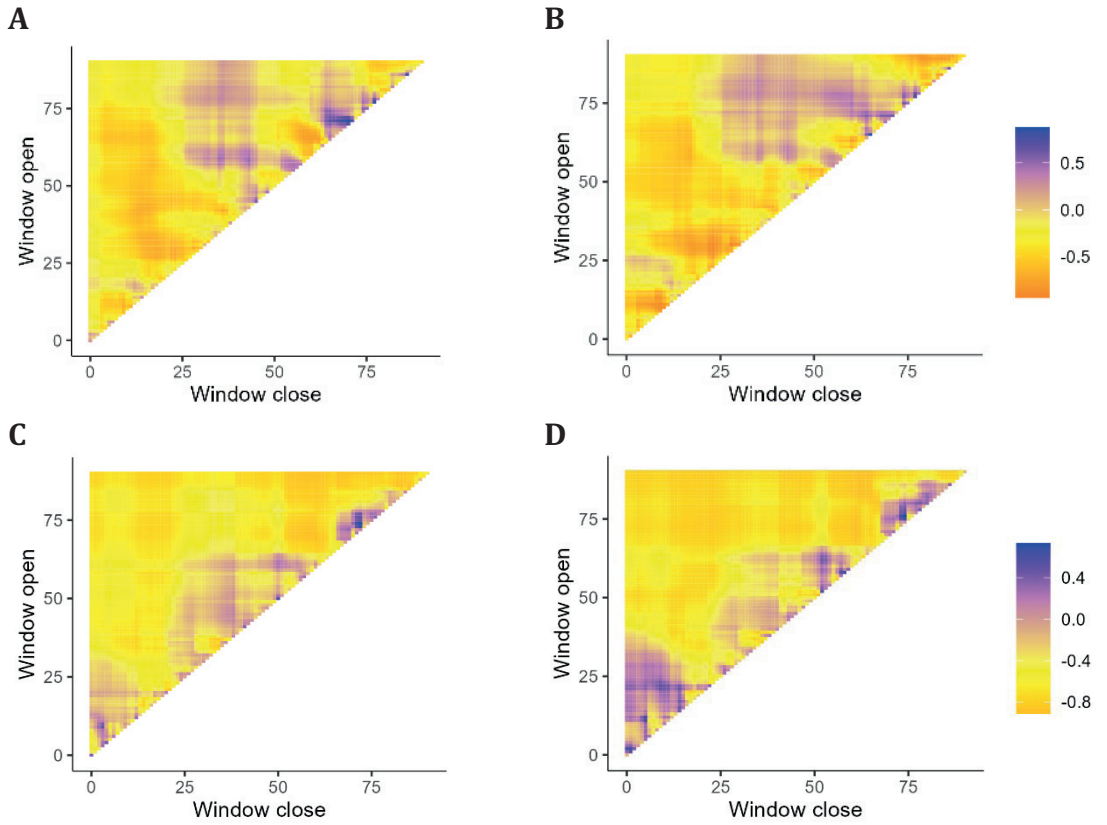

Figure C.2: Correlation between mean daily temperature and mean daily precipitation time windows for each population. during the pre-laying temperature window, precipitation was correlated (A) -0.51 in N1, (B) -0.57 in N2, (C) -0.58 in S1, (D) and -0.35 in S2. See population-specific pre-laying temperature windows in Fig. C.3.

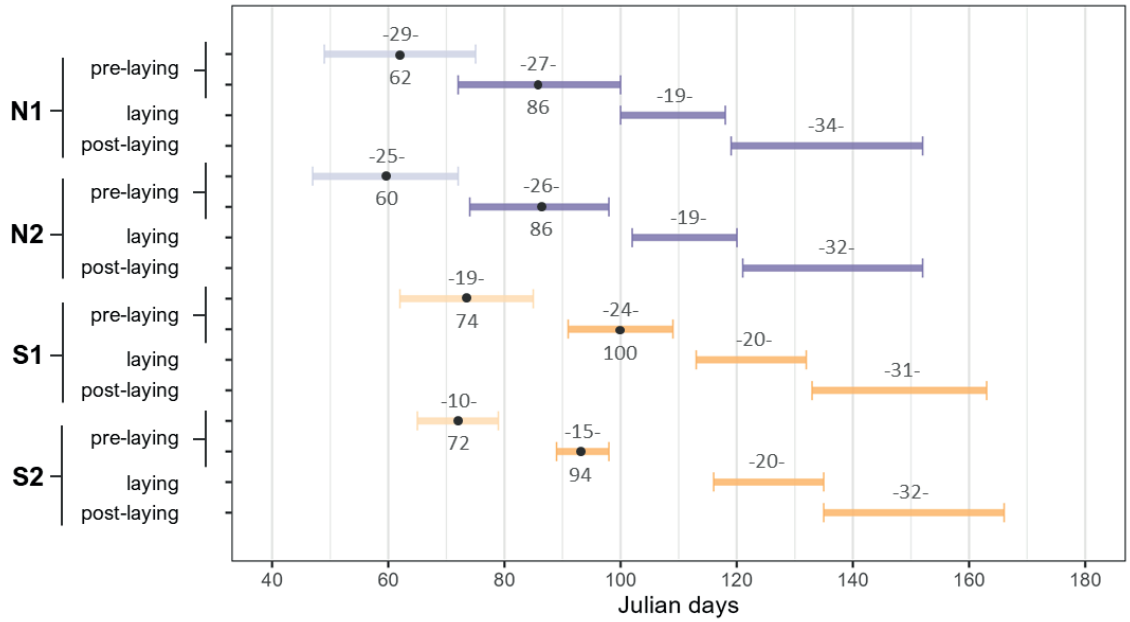

Figure C.3: Phenology of the three breeding periods specific for each population: the pre-laying period, defined by the best-fit climate window predicting the start of egg-laying using daily mean temperature (dark tone) or total precipitation (light tone); the laying period, from egg laying to egg hatching, trimming the 5% extremes; and the post-laying period, from egg hatching to chick fledgling, also trimming the 5% extremes. Temperature aggregations within these windows were used for further analysis. Populations are ordered by latitude. The duration of each period in number of days is displayed at the top of the bars between dashes, while pre-laying midpoints are indicated at the bottom of the bar. Reference mean laying dates were established on April 17 (107 jd) in N1 and N2, and May 2 (122 jd) and 4 (124 jd) in S1 and S2 respectively.

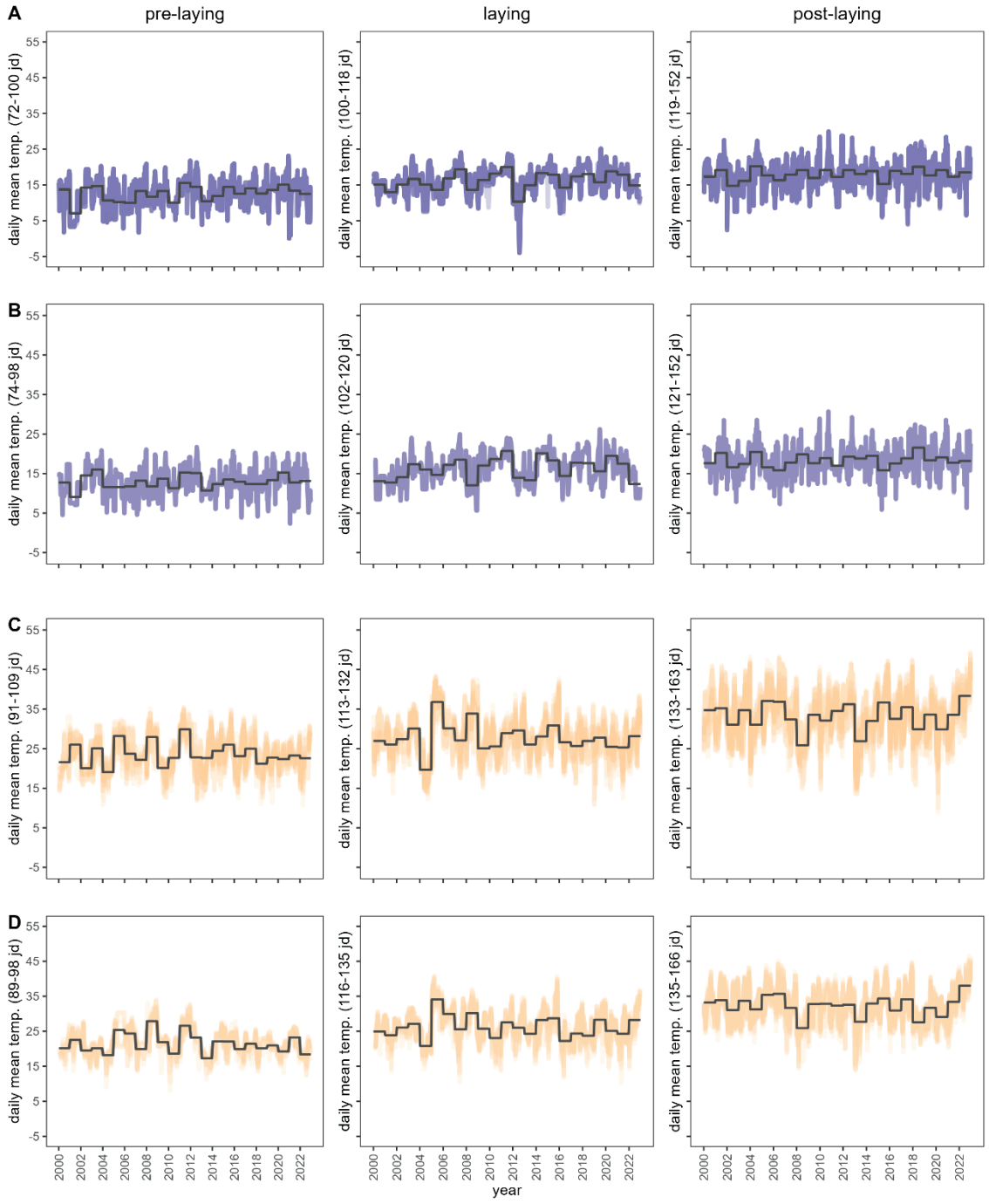

Figure C.4: Daily climatic trends since 2000 in northern (violet) and southern (orange) populations for the pre-laying, laying and post-laying periods (from left to right). Daily mean temperatures (°C) are grouped according to the specific breeding period (in Julian days) in each population: A) N1, B) N2, C) S1 and D) S2.

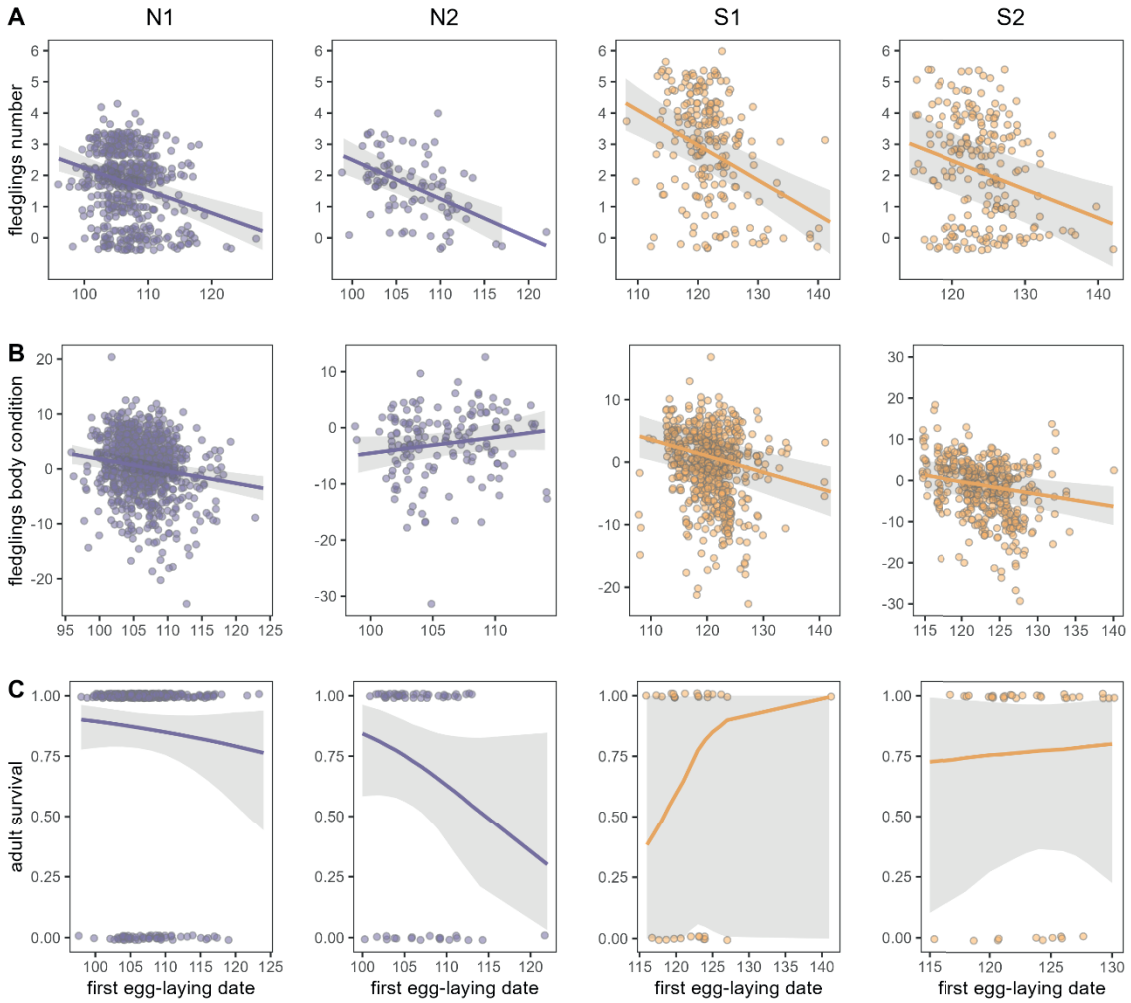

Figure C.5: Effects of first egg-laying date on reproductive success and adult survival. (A) Early breeding pairs rear a higher number of fledglings. (B) Fledglings from early breeding pairs have a better body condition. Y-axis scaled to 100 times for visual comprehension. (C) Adult survival is not affected by the laying date. Year and nest box ID were included as random factors in northern populations. In southern populations, colony ID was additionally included as random factor. Slope and associated 95% confidence interval for each population is included (see Table C.2B). Values for northern populations in violet, southern in orange. Points in A and C were jittered to avoid overplotting observations.

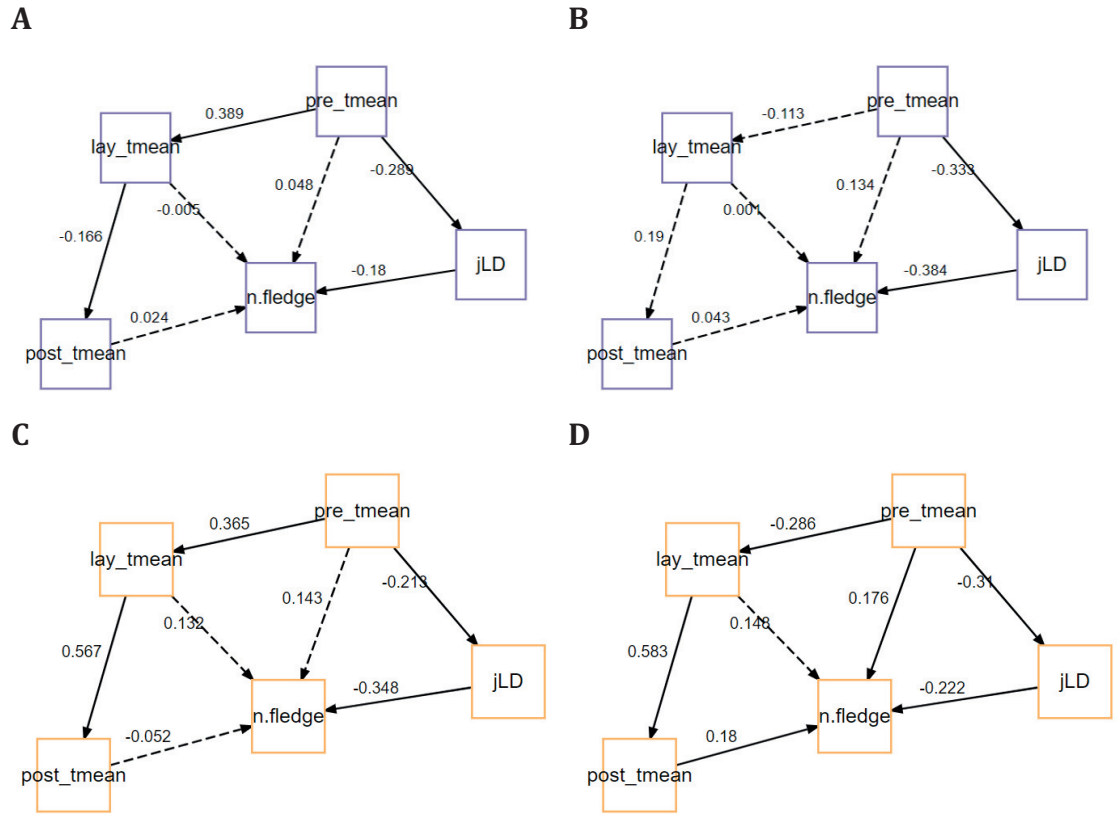

Figure C.6: Path diagram of the structural equation models used to account for the potential effect of temperatures on the variation in the number of fledglings that are not directly caused by the first-egg laying date. The causality between pre-laying and laying temperatures, and between laying and post-laying temperatures is used to assess the degree of predictability. Northern populations in violet nodes, (A) N1 (N=540) and (B) N2 (N=90), and southern populations in orange, (C) S1 (N=224) and (D) S2 (N=206). Values indicate standardized coefficients in each path showing the causality of laying date in Julian days (jLD), pre-laying (pre_tmean), laying (lay_tmean) and post-laying temperatures (post_tmean) on the number of fledglings (n.fledge). Arrows indicate directional relationships between observed variables with solid and dashed lines indicating significant and non-significant correlations, respectively (see summary output in Table C.7). Not including year, colony or site ID as random factors resulted in lower model AIC.

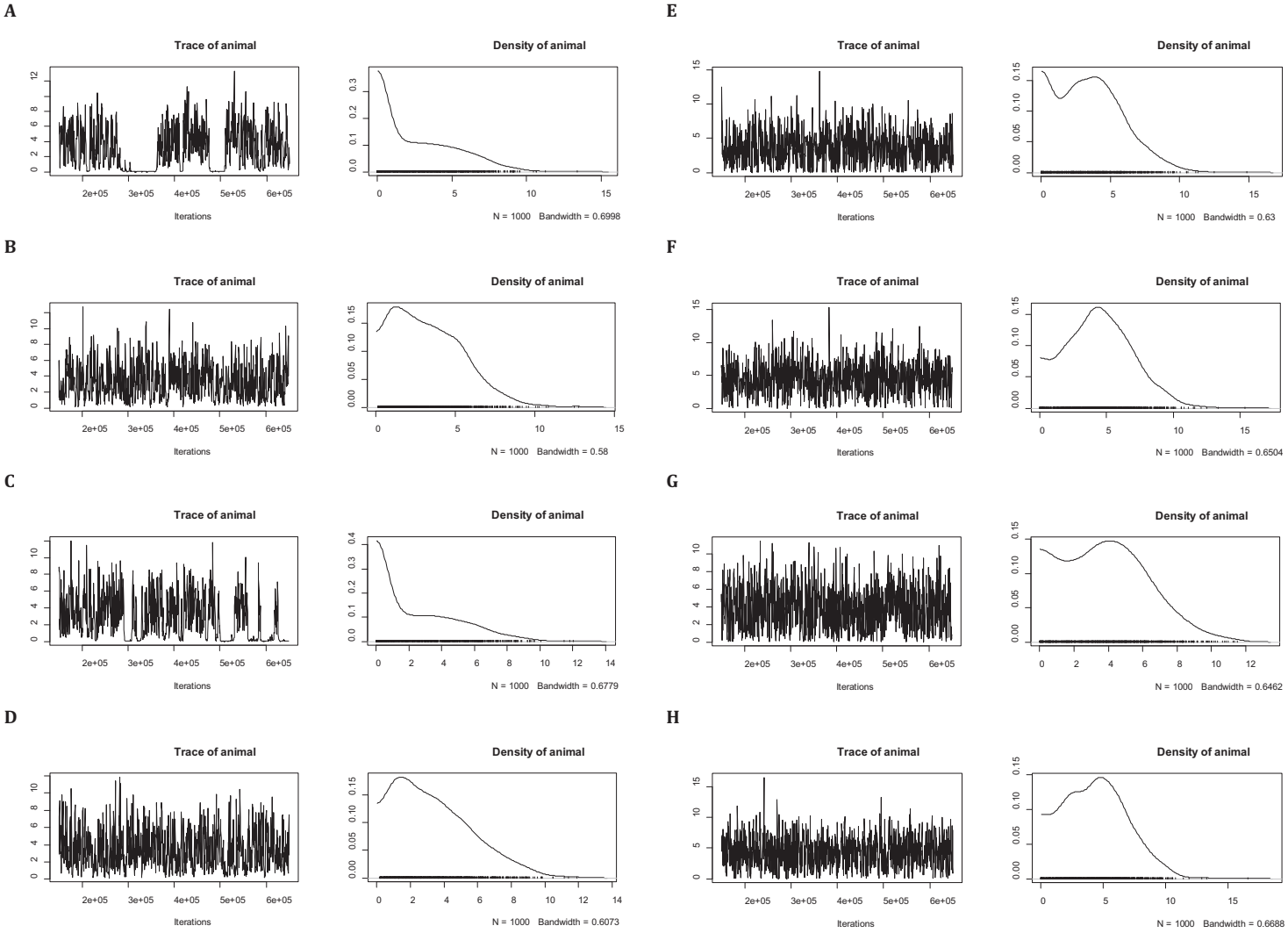

Figure C.7A: Trace and density plots from sensitivity analysis using southern populations. Used priors (A-H) defined in Table C.5.

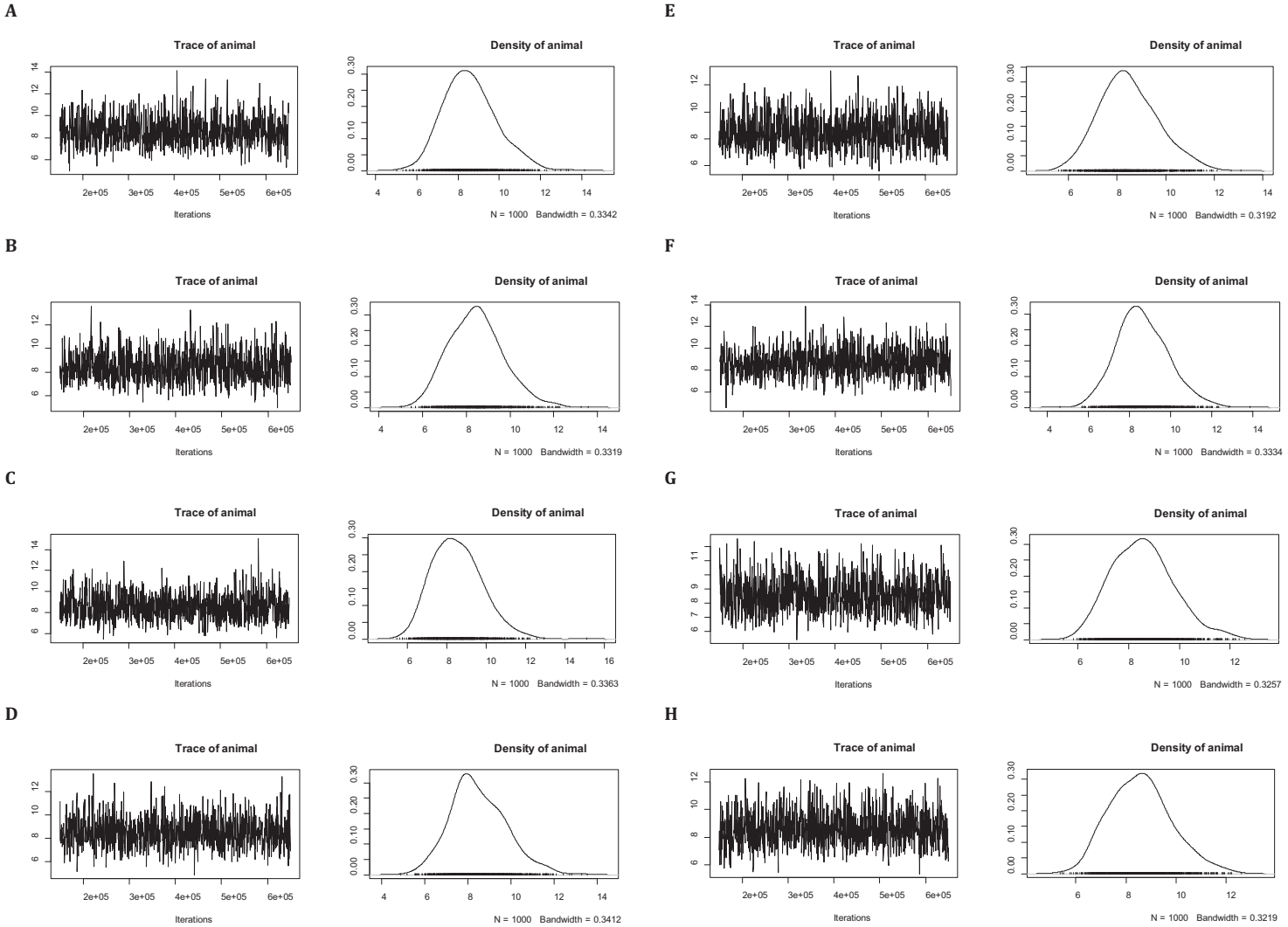

Figure C.7B: Trace and density plots from sensitivity analysis using northern populations. Used priors (A-H) defined in Table C.5.

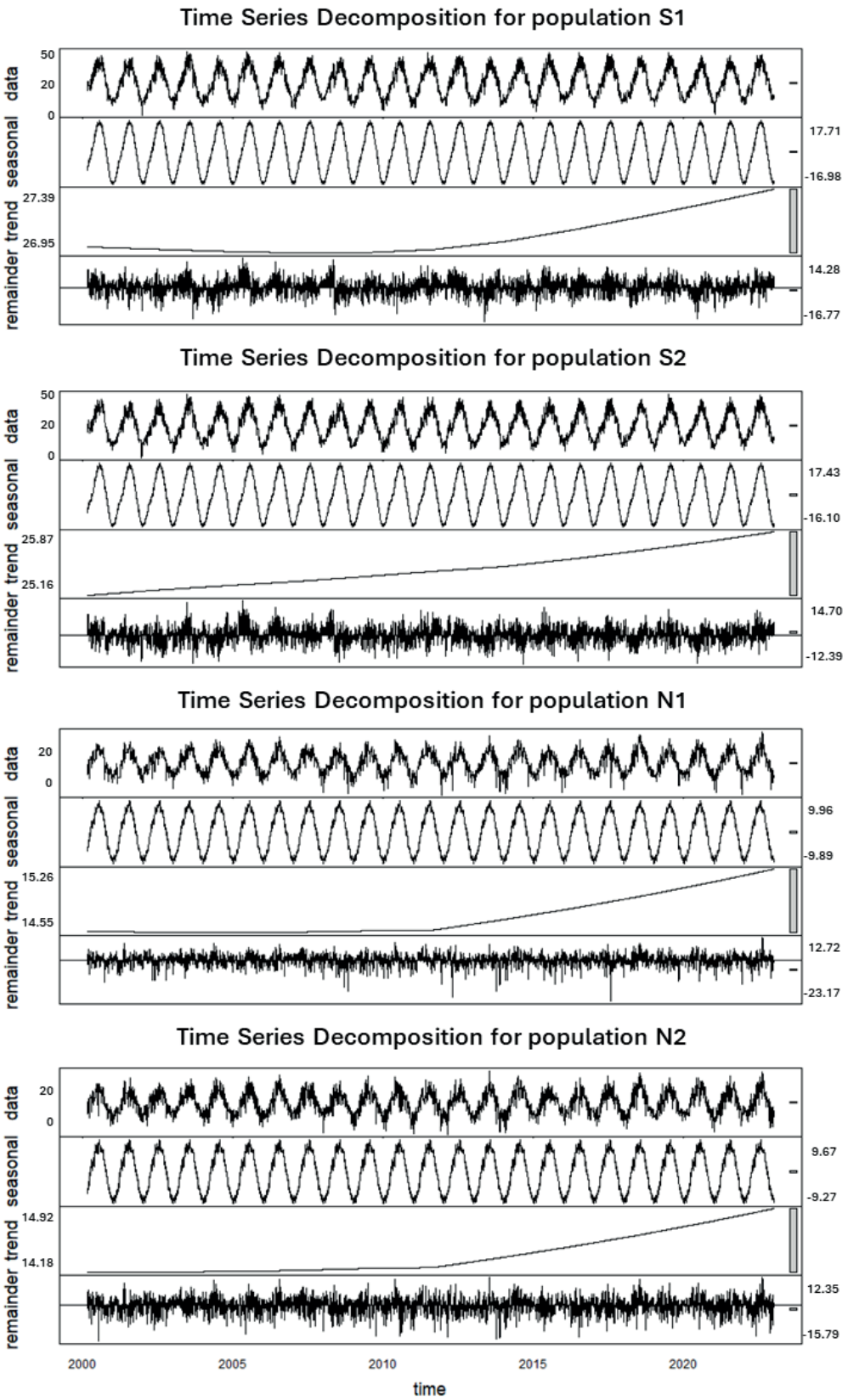

Figure C.8: Time series decomposition of daily mean temperature from 2000 to 2022 in each population. The trend has been 0.44ºC, 0.71ºC, 0.71ºC and 0.74ºC for S1, S2, N1 and N2 respectively. Mean from southern populations is 0.575ºC and 0.725ºC in the North.

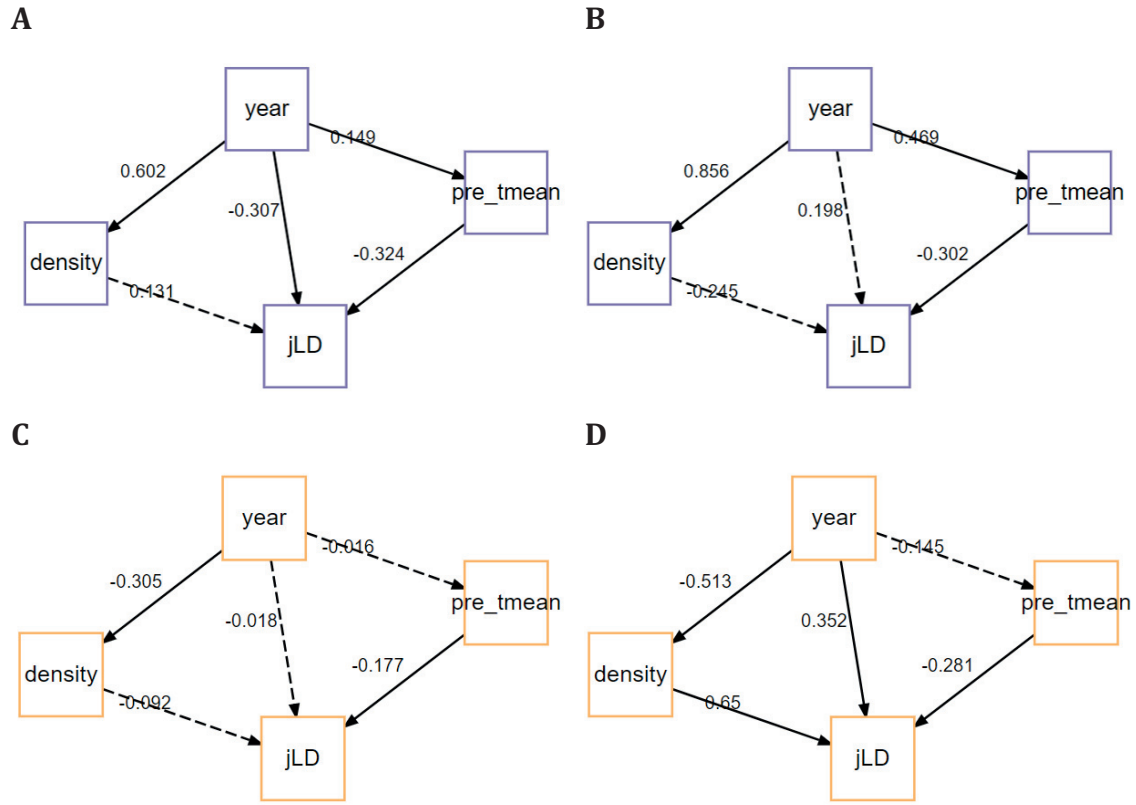

Figure C.9: Path analysis to investigate the effect of other non-climatic factors to laying date. Northern populations in violet nodes, (A) N1 (N=540) and (B) N2 (N=90), and southern populations in orange, (C) S1 (N=224) and (D) S2 (N=206). Values indicate standardized coefficients in each path showing the causality of laying date in Julian days (jLD), pre-laying (pre_tmean), density as the number of breeding pairs in a colony/site. Arrows indicate directional relationships between observed variables with solid and dashed lines indicating significant and non-significant correlations, respectively (see summary output in Table C.7). We partitioned the effect of time (year) on laying date into a direct and indirect pathway. The indirect pathway accounted for effects of time that occur via changes in temperature, such as climate change. The relationship between year and temperature in the structural equation model was used as the measure of climate change exposure (ºC/year). The relationship between temperature and laying date in the structural equation model was used as the measure of phenological sensitivity (days/ºC). The direct pathway accounted for any changes in laying date over time that occurred through effects other than temperature change. This is particularly relevant in populations N1 and S2, where among-year variations unrelated to temperature have a significant impact on breeding timing. The declining density of breeding pairs in the South may be attributed to a decreasing number of available artificial nest boxes over time.

C.3 Tables C

Table C.1: Sensitivity to climatic cues to start laying. Results of sliding window analysis using mean daily temperature and total daily precipitation as climatic cues and laying date as biological variable in each population (Pop.). We tested linear and quadratic functions (Fun.) to model the relationship between the mean aggregated climatic cue and the biological response. Each model is compared to the AICc value of a null model (a model containing no climate predictor), therefore, delta AICc indicates how well the absolute best window (w. open and close abs.) is adjusted. P_C: likelihood that an observed delta AICc value would occur by chance. The confidence set (90% CI), quantifies the extent to which there are several models with very similar explanatory power, and thus provides a confidence interval on window limits. Median windows resulting from the top 90% confidence set (w. open and close 90% CI). Top climatic models selected for each variable indicated in bold. All windows within 2 ΔAICc of the top climate model were considered equivalent in performance. Nest box and colony were included as spatial replicates. Year was not included as a categorical random factor to account for differences between seasons because ΔAICc increased in all models (results not shown).

Pop.	Clim.	Stat.	Fun.	ΔAICc	W. Open abs.	W. Close abs.	P_C	90% CI	W. Open 90% CI	W. Close 90% CI
N1	Tmean	Mean	Lin	-68.52	34	13	0.012	1	34	13
			Quad	**-77.79**	36	6	**0.015**	**1**	**35**	**7**
	Rain	Mean	Lin	-101.98	33	21	0.012	0	33	21
			Quad	**-118.34**	58	32	**0.010**	**1**	**58**	**32**
N2	Tmean	Mean	Lin	-8.98	32	8	0.525	61	63	14
			Quad	**-8.30**	32	9	**0.053**	**10**	**33**	**9**
	Rain	Mean	Lin	-9.13	33	26	0.430	67	60	23
			Quad	**-8.64**	32	22	**0.046**	**12**	**60**	**35**
S1	Tmean	Mean	Lin	-19.38	29	18	0.014	4	29	13
			Quad	**-29.76**	29	18	**0.026**	**4**	**31**	**13**
	Rain	Mean	**Lin**	**-26.84**	79	72	**0.011**	**2**	**60**	**37**
			Quad	-27.35	60	52	0.025	6	69	9
S2	Tmean	Mean	Lin	-23.48	36	24	0.019	7	44	26
			Quad	**-32.12**	36	25	**0.011**	**1**	**35**	**26**
	Rain	Mean	**Lin**	**-45.50**	59	45	**0.013**	**1**	**59**	**45**
			Quad	-45.52	56	41	0.013	2	58	44

Table C.2: Results from Bayesian mixed-models analysing the effect of pre-laying temperatures on laying date (A), its mediating role in reproduction and survival (B), and its temporal trend (C) for each population separately. We fitted gaussian functions when laying date, fledglings or body condition were included as response variables, and Bernoulli functions for survival. All models in A produced a better-fitting output when including nest box ID as a random factor, but not when including year ID. Therefore, the effect of among-year variation in laying date was further explored in a path analysis (see results in Fig. C.9). Colony ID was included only in southern populations.

(A) Effect of pre-laying temperatures on laying date

Population	**N1** (N=539, nest box levels=73)				**N2** (N=90, nest box levels=15)				**S1** (N=236, colony levels=8, nest box levels=119)				**S2** (N=208, colony levels=6, nest box levels=82)			
Effects	**Est.**	**Est. error**	**l-95% CI**	**u-95% CI**	**Est.**	**Est. error**	**l-95% CI**	**u-95% CI**	**Est.**	**Est. error**	**l-95% CI**	**u-95% CI**	**Est.**	**Est. error**	**l-95% CI**	**u-95% CI**
Temperature	-18.53	2.80	-23.91	-12.93	-27.80	12.87	-52.98	-2.32	11.86	3.77	4.43	18.94	-12.88	4.18	-21.29	-4.78
Temperature^2	0.67	0.11	0.46	0.88	1.05	0.53	-0.00	2.08	-0.27	0.08	-0.42	-0.11	0.29	0.10	0.09	0.49
Colony ID	-	-	-	-	-	-	-	-	0.80	0.62	0.03	2.32	2.5	1.09	1.09	5.25
Nest box ID	1.83	0.23	1.41	2.30	2.32	0.62	1.33	3.74	1.72	0.70	0.21	2.92	0.67	0.46	0.03	1.72
Sigma	3.30	0.11	3.09	3.52	3.22	0.26	2.77	3.78	4.54	0.29	3.99	5.11	3.93	0.22	3.53	4.37

(B1) Effect of laying date on the number of fledglings

Population	**N1** (N=539, nest box levels=73, year levels=9)				**N2** (N=90, nest box levels=15, year levels=9)				**S1** (N=236, colony levels=8, nest box levels=119, year levels=7)				**S2** (N=208, colony levels=6, nest box levels=82, year levels=7)			
Effects	**Est.**	**Est. error**	**l-95% CI**	**u-95% CI**	**Est.**	**Est. error**	**l-95% CI**	**u-95% CI**	**Est.**	**Est. error**	**l-95% CI**	**u-95% CI**	**Est.**	**Est. error**	**l-95% CI**	**u-95% CI**
Laying date	-0.07	0.01	-0.10	-0.05	-0.13	0.02	-0.17	-0.09	-0.11	0.02	-0.15	-0.07	-0.09	0.03	-0.14	-0.04
Year ID	0.40	0.14	0.21	0.75	0.39	0.16	0.16	0.79	0.42	0.25	0.06	1.02	0.28	0.22	0.01	0.82
Colony ID	-	-	-	-	-	-	-	-	0.58	0.26	0.24	1.22	0.99	0.51	0.35	2.26
Nest box ID	0.23	0.08	0.05	0.36	0.58	0.15	0.35	0.93	0.53	0.20	0.09	0.90	0.48	0.20	0.06	0.85
Sigma	0.99	0.03	0.92	1.05	0.66	0.06	0.56	0.78	1.38	0.09	1.21	1.56	1.44	0.09	1.28	1.63

(B2) Effect of laying date on the body condition of fledglings

Population	**N1** (N=968, nest box levels=73, year levels=9)				**N2** (N=155, nest box levels=15, year levels=9)				**S1** (N=664, colony levels=8, nest box levels=93, year levels=6)				**S2** (N=441, colony levels=6, nest box levels=69, year levels=6)			
Effects	**Est.**	**Est. error**	**l-95% CI**	**u-95% CI**	**Est.**	**Est. error**	**l-95% CI**	**u-95% CI**	**Est.**	**Est. error**	**l-95% CI**	**u-95% CI**	**Est.**	**Est. error**	**l-95% CI**	**u-95% CI**
Laying date	-0.22	0.05	-0.32	-0.12	0.29	0.18	-0.06	0.66	-0.26	0.06	-0.37	-0.15	-0.30	0.10	-0.50	-0.10
Year ID	1.73	0.58	0.92	3.14	1.69	1.00	0.16	4.03	3.50	1.20	1.91	6.49	3.28	1.26	1.68	6.42
Colony ID	-	-	-	-	-	-	-	-	2.07	0.87	0.88	4.19	2.26	1.37	0.23	5.75
Nest box ID	1.91	0.23	1.48	2.41	2.24	0.92	0.54	4.25	2.69	0.33	2.10	3.38	2.05	0.52	1.02	3.09
Sigma	4.49	0.10	4.28	4.69	5.72	0.35	5.07	6.45	4.08	0.12	3.85	4.33	5.77	0.21	5.38	6.20

Table C.2: *Continued from previous page.*

(B3) Effect of laying date on adult survival

Population	**N1**(N=363, nest box levels=72, year levels=7)				**N2** (N=61, nest box levels=14, year levels=7)				**S1** (N=30, colony levels=8, nest box levels=28, year levels=6)				**S2** (N=38, colony levels=4, nest box levels=25, year levels=6)			
Effects	**Est.**	**Est. error**	**l-95% CI**	**u-95% CI**	**Est.**	**Est. error**	**l-95% CI**	**u-95% CI**	**Est.**	**Est. error**	**l-95% CI**	**u-95% CI**	**Est.**	**Est. error**	**l-95% CI**	**u-95% CI**
Laying date	-0.04	0.04	-0.12	0.04	-0.12	0.08	-0.28	0.04	0.45	1.03	-0.91	3.19	0.03	0.16	-0.31	0.32
Year ID	0.47	0.33	0.04	1.24	0.44	0.40	0.02	1.47	1.69	1.66	0.06	6.03	0.68	0.62	0.02	2.26
Colony ID	-	-	-	-	-	-	-	-	2.24	2.13	0.09	7.73	1.04	0.96	0.04	3.43
Nest box ID	0.74	0.35	0.07	1.43	0.57	0.44	0.02	1.65	12.32	15.70	1.75	46.27	1.34	1.18	0.05	4.22

(C) Temporal trend on laying date

Population	**N1** (N=540, nest box levels=73)				**N2** (N=90, nest box levels=15)				**S1** (N=236, nest box levels=119, colony levels=8)				**S2** (N=208, nest box levels=82, colony levels=6)			
Effects	**Est.**	**Est. error**	**l-95% CI**	**u-95% CI**	**Est.**	**Est. error**	**l-95% CI**	**u-95% CI**	**Est.**	**Est. error**	**l-95% CI**	**u-95% CI**	**Est.**	**Est. error**	**l-95% CI**	**u-95% CI**
Year	-0.42	0.06	-0.53	-0.30	-0.25	0.14	-0.52	0.02	0.23	0.17	-0.09	0.57	0.17	0.16	-0.14	0.49
Colony ID	-	-	-	-	-	-	-	-	1.45	0.82	0.15	3.40	2.20	1.01	0.91	4.78
Nest box ID	1.80	0.24	1.34	2.29	2.24	0.65	1.18	3.74	1.96	0.74	0.29	3.22	0.55	0.40	0.02	1.45
Sigma	3.63	0.12	3.41	3.87	3.55	0.30	3.01	4.20	4.71	0.31	4.15	5.36	4.32	0.22	3.90	4.77

Table C.3: Likelihood ratio test of linear mixed-effects models of plasticity in egg-laying date with response to pre-laying temperature for (A) 139 females that bred in two or more years, observed on a total of 535 occasions between 2013 and 2022 in the North, and (B) 40 females that bred in two or more years, observed on a total of 95 occasions between 2016 and 2022 in the South. All three models control for pre-laying temperature (T) as fixed effect. Model comparison is hierarchical, from the simplest to the most complex, and contains the log-likelihood (LogLik), the difference in degrees of freedom (∆Df), likelihood ratio Chi-squared statistic (LikRatio) and corresponding p-value.

Model fit		**(A) Northern populations**				**(B) Southern populations**			
id	**Formula**	**LogLik**	**∆Df**	**LikRatio**	**p-value**	**LogLik**	**∆Df**	**LikRatio**	**p-value**
1	LD ~ T	-1476.5				-266.48			
2	LD ~ T + (1|year)	-1472.9	1	7.1602	0.0074**	-265.84	1	1.2715	0.2595
3	LD ~ T + (1|year) + (1|ID)	-1386.9	1	171.9799	<0.001***	-263.01	1	5.6763	0.0172 *
4	LD ~ T + (1|year) + (T|ID)	-1386.3	2	1.2753	0.5285	-263.10	2	0.1879	0.9103

*P < 0.05, **P < 0.01, ***P < 0.001

Table C.4: Selection estimates on laying dates across years. Directional (S) and quadratic (c) selection differentials for phenology from 9 years (2013-2019 and 2021-2022) in the two populations of North Europe, and 7 years (2016-2022) in the two populations of South Europe. Abbreviations: NA = non-available due to a limited number of observations.

		Northern populations		**Southern populations**	
Parameter	**Year**	**N1**	**N2**	**S1**	**S2**
$S \pm SE$	2013	-0.342 ± 0.161	-0.035 ± NA	NA	NA
	2014	-0.25 ± 0.107*	-0.425 ± 0.201*	NA	NA
	2015	-0.129 ± 0.059*	-0.267 ± 0.106	NA	NA
	2016	-0.257 ± 0.071***	-0.149 ± 0.169	-0.245 ± 0.115*	-0.136 ± 0.121
	2017	-0.047 ± 0.063	-0.373 ± 0.136**	-0.337 ± 0.121**	-0.223±0.152
	2018	-0.144 ± 0.068*	-0.058 ± 0.159	-0.132 ± 0.08*	-0.445±0.13**
	2019	-0.018 ± 0.078	-0.044 ± 0.084	-0.417 ± 0.16*	0.169±0.164
	2020	NA	NA	-0.359 ± 0.162*	-0.173±0.402
	2021	-0.213 ± 0.089*	-0.188 ± 0.233	-0.147 ± 0.043**	-0.245±0.104**
	2022	0.027 ± 0.098	-0.265 ± 0.155	-0.002 ± 0.078	-0.268±0.088**
$c \pm SE$	2013	-0.282 ± 0.275	-0.565 ± NA	NA	NA
	2014	-0.297 ± 0.155	0.205 ± 0.477	NA	NA
	2015	-0.096 ± 0.112	-0.166 ± 0.15	NA	NA
	2016	-0.332 ± 0.128*	-0.027 ± 0.182	-0.399 ± 0.16*	-0.373±0.168*
	2017	-0.13 ± 0.132	-0.027 ± 0.227	-0.533 ± 0.195	0.114±0.221
	2018	-0.128 ± 0.13	0.128 ± 0.214	-0.035 ± 0.118	-0.003±0.192
	2019	-0.112 ± 0.092	0.082 ± 0.098	-0.577 ± 0.189	-0.029±0.147
	2020	NA	NA	-0.274 ± 0.179	0.99±NA
	2021	-0.117 ± 0.176	-0.627 ± 0.362	-0.051 ± 0.068	-0.412±0.163*
	2022	0.495 ± 0.296	-0.345 ± 0.18	-0.383 ± 0.102***	-0.348±0.116*

*P < 0.05, **P < 0.01, ***P < 0.001

Table C.5: Results from sensitivity analysis by using different priors and testing the sensitivity of the posterior distribution to the priors, using southern (A) and northern (B) datasets. Priors listed below the table and selected prior in bold. Trace and density plots were visually examined (see Fig. C.7A-B). Animal autocorrelation for Markov chains and effective sample sizes were also checked. h^2=narrow-sense heritability (V_G/V_R). HPD=highest posterior density intervals. All models were run for 650,000 iterations with a burn-in of 150,000 and a thinning interval of 500, thus the minimum effective sample size per model was 1,000.

(A) South

***Priors**	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**
Heritability (h^2)	0.0005623359	0.03776832	0.001368888	0.1159853	0.002249069	0.2320436	0.2176245	0.214989
HPD lower	3.401086e-05	0.006598992	2.450e-05	0.0111923	1.223e-05	0.0002031168	7.900658e-07	1.285081e-05
HPD upper	0.3783053	0.373805	0.3716008	0.3887663	0.3887681	0.4275013	0.3883129	0.431837
Autocorr. Lag 0	1.0000000	1.0000000	1.0000000	1.0000000	1.0000000	1.0000000	1.0000000	1.0000000
Autocorr. Lag 500	0.6257025	0.38259273	0.61738751	0.361994508	0.05305724	-0.002377711	0.051920031	0.00392152
Autocorr. Lag 2500	0.3858776	0.01524391	0.38297940	0.002491305	0.07167732	0.015962301	-0.002214531	-0.03353526
Autocorr. Lag 5000	0.2947639	0.01650832	0.28792073	0.023812284	-0.06691737	0.055046933	-0.005943943	0.01196869
Autocorr. Lag 25000	0.1313914	-0.04340379	0.06392902	0.030624956	-0.03711542	0.025992125	-0.039701291	-0.01926651
Effective size	26.23606	402.9376	75.30603	424.7922	809.5306	1000	900.3830	1000

(B) North

***Priors**	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**
Heritability (h^2)	0.5663335	0.5852304	0.5729459	0.5621032	0.5784029	0.5600932	0.5904044	0.5633124
HPD lower	0.4796558	0.4701846	0.4881023	0.4653713	0.482678	0.4837178	0.4823868	0.4830576
HPD upper	0.6473788	0.6406901	0.6510072	0.637978	0.6485753	0.6535516	0.6456545	0.6471712
Autocorr. Lag 0	1.0000000	1.0000000	1.0000000	1.0000000	1.0000000	1.0000000	1.0000000	1.0000000
Autocorr. Lag 500	-0.007623832	-0.026462457	-0.03038528	0.001809919	0.027812393	-0.01332700	0.041723832	-0.0002232615
Autocorr. Lag 2500	-0.030222241	-0.036805034	0.04229879	-0.059998010	0.016876020	0.03577841	0.009703293	-0.0069071424
Autocorr. Lag 5000	0.007413474	-0.054879077	-0.06518295	-0.014781721	0.028751624	-0.03754454	0.019366373	-0.0103477584
Autocorr. Lag 25000	-0.009915145	0.001989487	-0.03023492	-0.064737358	0.006767141	-0.01661318	-0.061648939	-0.0201418037
Effective size	1000	1000	1000	1679.829	1000	1294.222	1014.141	1000

*Priors:

A) prior_std1 <- list(R = list(V = 1, nu = 0.002), G = list(G1 = list(V = 1, nu = 0.002)))

B) prior_std2 <- list(R = list(V = 1, nu = 1), G = list(G1 = list(V = 1, nu = 1)))

C) prior_std3 <- list(R = list(V = 0.05, nu = 0.002), G = list(G1 = list(V = 1, nu = 0.002)))

D) prior_std4 <- list(R = list(V = 0.05, nu = 1), G = list(G1 = list(V = 1, nu = 1)))

E) prior_exp1 <- list(R = list(V = 1, nu = 0.002), G = list(G1 = list(V = 1, nu = 0.002, alpha.mu = 0, alpha.V = 1000)))

F) prior_exp2 <- list(R = list(V = 1, nu = 1), G = list(G1 = list(V = 1, nu = 1, alpha.mu = 0, alpha.V = 1000)))

G) prior_exp3 <- list(R = list(V = 1, nu = 0.002), G = list(G1 = list(V = 0.05, nu = 0.002, alpha.mu = 0, alpha.V = 1000)))

H) prior_exp4 <- list(R = list(V = 1, nu = 1), G = list(G1 = list(V = 0.05, nu = 1, alpha.mu = 0, alpha.V = 1000)))

Table C.6: Animal models to estimate heritability in laying date for the northern and southern jackdaw populations. All models include laying date as response variable, and the pedigree and female ID as random effects. Models were run for 650,000 iterations with a burn-in of 150,000 and a thinning interval of 500, thus the minimum effective sample size per model was 1,000. We used parameter-expanded priors for the random effects variance (G) and standard for residual variance (R). The Confidence Intervals (CI 95%) or the variance are given when models include a fixed or a random factor as additional terms in the formula (underlined), respectively. Highest posterior density (HPD) intervals for heritability (h^2). Deviance information criterion (DIC). Selected model highlighted in bold. Models from northern populations (N.1-N.9) include 580 observations from 191 unique females. Models from southern populations (S.1-S.9) include 218 observations from 163 unique females.

Model id	Fixed terms	Random terms	*Priors	CI 95% or variance	h^2	HPD interval	DIC
N.1	Null	Null	1	-	0.570	[0.47, 0.64]	2874.214
N.2	Temp	Null	1	[-1.33, -0.85]	0.604	[0.52, 0.68]	2781.703
N.3	Temp + Pop	Null	1	[-1.53, 1.04]	0.615	[0.52, 0.67]	2782.209
N.4	Temp	Site	2	-0.136	0.605	[0.14, 0.68]	2779.396
N.5	**Temp**	**Year**	**2**	**2.991**	**0.452**	**[0.24, 0.58]**	**2721.946**
N.6	Temp	Year + Age	3	0.001	0.457	[0.23, 0.57]	2724.177
N.7	Temp	Year + BirthYear	3	0.079	0.415	[0.23, 0.57]	2721.929
N.8	Temp	Year + MotherID	3	0.016	0.376	[0.24, 0.58]	2722.129
N.9	Temp	Year + NestboxID	3	0.037	0.434	[0.24, 0.56]	2722.282
S.1	Null	Null	1	-	0.186	[1.74e-06, 0.42]	1247.122
S.2	Temp	Null	1	[-1.00, -0.47]	0.215	[1.98e-06, 0.41]	1221.798
S.3	Temp + Pop	Null	1	[-1.62, 1.79]	0.277	[1.56e-07, 0.40]	1223.591
S.4	Temp	Colony	2	1.731	0.001	[3.92e-08, 0.29]	1200.975
S.5	**Temp**	**Colony + Year**	**3**	**2.097**	**0.104**	**[2.14e-07, 0.30]**	**1175.970**
S.6	Temp	Colony + Year + Age	4	0.017	0.129	[1.94e-04, 0.31]	1173.838
S.7	Temp	Colony + Year + BirthYear	4	0.010	0.114	[8.02e-06, 0.29]	1176.650
S.8	Temp	Colony + Year + MotherID	4	0.030	0.117	[3.68e-05, 0.29]	1177.120
S.9	Temp	Colony + Year + NestboxID	4	0.053	0.159	[7.62e-06, 0.30]	1176.758

*Priors:

```
Prior1 <- list(R = list(V = 1, nu = 1),
               G = list(G1 = list(V = 1, nu = 1, alpha.mu = 0, alpha.V = 1000)));
Prior2 <- list(R = list(V = 1, nu = 1),
               G = list(G1 = list(V = 1, nu = 1, alpha.mu = 0, alpha.V = 1000),
                        G2 = list(V = 1, nu = 1, alpha.mu = 0, alpha.V = 1000)));
Prior3 <- list(R = list(V = 1, nu = 1),
               G = list(G1 = list(V = 1, nu = 1, alpha.mu = 0, alpha.V = 1000),
                        G2 = list(V = 1, nu = 1, alpha.mu = 0, alpha.V = 1000),
                        G3 = list(V = 1, nu = 1, alpha.mu = 0, alpha.V = 1000)));
Prior4 <- list(R = list(V = 1, nu = 1),
               G = list(G1 = list(V = 1, nu = 1, alpha.mu = 0, alpha.V = 1000),
                        G2 = list(V = 1, nu = 1, alpha.mu = 0, alpha.V = 1000),
                        G3 = list(V = 1, nu = 1, alpha.mu = 0, alpha.V = 1000),
                        G4 = list(V = 1, nu = 1, alpha.mu = 0, alpha.V = 1000)))
```

Table C.7: Coefficient results from structural equation modelling path analyses (A) to explore post-laying temperature effects on the number of fledglings and (B) to explore the effect of non-climatic factors on laying date variation. See path diagrams representing the structural equation models in Fig. C.6 and Fig. C.9. Response and predictor variables were coded as n.fledge (number of fledlgings in a nest), jLD (laying date in Julian days), pre_tmean, lay_tmean and post_tmean (daily mean temperature aggregations during the pre-laying, laying and post-laying period, respectively), year (categorical in A and numeric in B), and density (number of breeding pairs in a given year and site or colony).

Pop	Response	Predictor	Estimate	Std. Error	DF	Crit. Value	P-value	Std. Est.	
(A) N1	n.fledge	jLD	-0.0466	0.0115	535	-4.0427	0.0001	-0.1795	***
	n.fledge	pre_tmean	0.0525	0.0608	535	0.8639	0.3881	0.0480	
	n.fledge	lay_tmean	-0.0033	0.0304	535	-0.1083	0.9138	-0.0050	
	n.fledge	post_tmean	0.0200	0.0414	535	0.4827	0.6295	0.0243	
	jLD	pre_tmean	-1.2194	0.1739	538	-7.0127	0.0000	-0.2894	***
	post_tmean	lay_tmean	-0.1330	0.0341	538	-3.8999	0.0001	-0.1658	***
	lay_tmean	pre_tmean	0.6449	0.0658	538	9.7972	0.0000	0.3891	***
N2	n.fledge	jLD	-0.0905	0.0245	85	-3.6974	0.0004	-0.3845	***
	n.fledge	pre_tmean	0.2020	0.1806	85	1.1180	0.2667	0.1340	
	n.fledge	lay_tmean	0.0005	0.0400	85	0.0136	0.9892	0.0014	
	n.fledge	post_tmean	0.0292	0.0786	85	0.3721	0.7107	0.0429	
	jLD	pre_tmean	-2.1286	0.6434	88	-3.3081	0.0014	-0.3326	**
	post_tmean	lay_tmean	0.1114	0.0615	88	1.8123	0.0734	0.1897	
	lay_tmean	pre_tmean	-0.4238	0.3981	88	-1.0645	0.2900	-0.1128	
S1	n.fledge	jLD	-0.1146	0.0209	219	-5.4972	0.0000	-0.3481	***
	n.fledge	pre_tmean	0.1629	0.0889	219	1.8332	0.0681	0.1428	
	n.fledge	lay_tmean	0.1404	0.0795	219	1.7652	0.0789	0.1320	
	n.fledge	post_tmean	-0.0256	0.0435	219	-0.5878	0.5573	-0.0518	
	jLD	pre_tmean	-0.7380	0.2271	222	-3.2502	0.0013	-0.2131	**
	post_tmean	lay_tmean	1.2218	0.1192	222	10.2533	0.0000	0.5669	***
	lay_tmean	pre_tmean	0.3917	0.0670	222	5.8475	0.0000	0.3653	***
S2	n.fledge	jLD	-0.0800	0.0249	201	-3.2073	0.0016	-0.2222	**
	n.fledge	pre_tmean	0.1900	0.0774	201	2.4537	0.0150	0.1755	*
	n.fledge	lay_tmean	0.1014	0.0571	201	1.7766	0.0771	0.1476	
	n.fledge	post_tmean	0.0863	0.0389	201	2.2178	0.0277	0.1795	*
	jLD	pre_tmean	-0.9317	0.2002	204	-4.6528	0.0000	-0.3097	***
	post_tmean	lay_tmean	0.8324	0.0813	204	10.2350	0.0000	0.5825	***
	lay_tmean	pre_tmean	-0.4515	0.1058	204	-4.2674	0.0000	-0.2863	***
(B) N1	density	year	1.3580	0.0777	538	17.4679	0.0000	0.6016	***
	pre_tmean	year	0.0544	0.0155	538	3.5018	0.0005	0.1493	***
	jLD	pre_tmean	-1.3662	0.2280	536	-5.9931	0.0000	-0.3242	***
	jLD	year	-0.4717	0.0819	536	-5.7593	0.0000	-0.3074	***
	jLD	density	0.0891	0.0455	536	1.9583	0.0507	0.1311	
N2	density	year	0.6299	0.0406	88	15.5246	0.0000	0.8559	***
	pre_tmean	year	0.1053	0.0211	88	4.9866	0.0000	0.4694	***
	jLD	pre_tmean	-1.9296	0.7501	86	-2.5724	0.0118	-0.3015	*
	jLD	year	0.2837	0.2809	86	1.0099	0.3154	0.1976	
	jLD	density	-0.4786	0.3904	86	-1.2260	0.2235	-0.2453	
S1	density	year	-0.8882	0.1863	222	-4.7686	0.0000	-0.3048	***
	pre_tmean	year	-0.0110	0.0452	222	-0.2435	0.8078	-0.0163	
	jLD	pre_tmean	-0.6120	0.2499	220	-2.4490	0.0151	-0.1767	*
	jLD	year	-0.0426	0.1620	220	-0.2627	0.7930	-0.0182	
	jLD	density	-0.0734	0.0607	220	-1.2095	0.2278	-0.0916	
S2	density	year	-1.3351	0.0738	199.2331	-18.0856	0.0000	-0.5126	***
	pre_tmean	year	-0.1039	0.0539	91.5307	-1.9270	0.0571	-0.1451	
	jLD	pre_tmean	-0.8463	0.1872	198.8963	-4.5209	0.0000	-0.2813	***
	jLD	year	0.7579	0.2271	104.6828	3.3378	0.0012	0.3521	**
	jLD	density	0.5374	0.1296	70.1465	4.1469	0.0001	0.6502	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05

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