The role of temperature in timing of reproduction and reproductive success of gray jays, *Perisoreus canadensis*

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Abstract

Although early reproduction within a breeding season often leads to higher reproductive success in seasonal environments, it is still not well understood how reproductive success can be influenced by climate both indirectly through the timing of breeding or by directly altering parental behaviour. In this thesis, I investigate the role of ambient temperature in reproductive success through its effects on the timing of reproduction and brooding in a population of gray jays, *Perisoreus canadensis*. In chapter 2, I test whether (i) female gray jays adjust laying date in response to temperature, (ii) individual or environmental characteristics constrain this plasticity, and (iii) laying date influences reproductive success. Females laid earlier in warmer years than in colder years; females partnered with older males laid earlier than females partnered with younger males at colder temperatures, but not at warmer temperatures. Early layers were more likely to rear at least one nestling and have a dominant juvenile survive the summer. These findings suggest that male experience could advance female laying date at cold temperatures and subsequently increase the probability of a positive nesting outcome. Though cold temperatures appear to limit timing of reproduction in gray jays, previous work in this system suggests that cold temperatures could better preserve perishable winter food stores. Thus, in chapter 3, I test whether temperatures during early offspring development interact with timing of reproduction to influence reproductive performance. Colder ambient temperatures during incubation were associated with larger brood sizes than warmer temperatures among late breeders, but temperature did not influence brood size among early layers, indicating that costs of late breeding may be amplified by temperatures that are unfavourable for food storage. This thesis contributes to our understanding of the environmental factors that determine reproductive performance, both through effects on timing of reproduction and after eggs are laid.

Résumé

La reproduction hâtive conduit souvent à un succès reproducteur élevé dans les environnements saisonniers. Par contre, nous ne comprenons pas encore bien comment le climat influence le succès reproducteur, soit indirectement via son effet sur le moment de la reproduction, ou directement en modifiant les comportements parentaux. Dans cette thèse, j'étudie l'influence de la température ambiante sur le succès reproducteur à travers ses effets sur le moment de la ponte et de couvaison chez une population de mésangeais du Canada, *Perisoreus canadensis*. Dans le chapitre 2, j'examine (i) si les mésangeais femelles ajustent leur date de ponte en fonction de la température, (ii) si les caractéristiques individuelles ou environnementales limitent cette plasticité, et (iii) si la date de ponte influence le succès de la reproduction. Les femelles mésangeais ont pondu plus tôt lors des années plus chaudes. Aussi, les femelles appariées avec un mâle plus âgé ont pondu plus tôt que les femelles appariées avec un jeune mâle lors de températures froides, mais pas lors de températures plus chaudes. Celles qui ont pondu plus tôt étaient plus susceptibles d'élever au moins un oisillon et d'avoir un juvénile dominant survivant à la fin de l'été. Ces résultats suggèrent que l'expérience des mâles pourrait avancer la date de ponte des femelles lors de températures froides et pourrait augmenter la probabilité du succès de nidification. Bien que les températures froides semblent limiter l'initiation de la reproduction chez les mésangeais, des travaux antérieurs suggèrent que les températures froides pourraient aussi mieux préserver les réserves hivernales d'aliments périssables. Ainsi, dans le chapitre 3, je tente de déterminer si l'interaction de la température au cours du développement de la progéniture avec le moment de la ponte affecte le succès reproducteur. Les températures ambiantes froides durant l'incubation étaient associées à des couvées plus grandes que lors de températures élevées chez les femelles qui se reproduisaient tard en saison, alors que la température n’influençait pas la taille des couvées hâtives, indiquant que les coûts de la reproduction tardive peuvent être amplifiés par des températures qui ne sont pas favorables à la conservation des réserves d’aliments périssables. Cette thèse contribue à notre compréhension des facteurs environnementaux qui déterminent la capacité reproductive, à travers leurs effets sur le moment de la reproduction, ainsi que leurs effets sur les étapes de développement subséquentes à la ponte.

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Statement of Contributions

Chapters 2 and 3 were prepared as manuscripts to facilitate submission for publication. Chapter 2 was published in the November 2016 issue of *Animal Behaviour*. Chapter 3 has been submitted for publication in *Ecology and Evolution*. Some material is repeated across chapters because each was intended to be read independently. Though I wrote this thesis myself, I used the first-person plural narrative throughout the manuscripts because both are co-authored by Dan Strickland, Julie Morand-Ferron, and Ryan Norris.

Both original research chapters utilized data from a long-term study led by Dan Strickland and Ryan Norris, with the assistance of many volunteers and several graduate students. Alex Sutton performed the reduced major axis regression transformation of temperature data, which was also used in both chapters. Julian Evans provided assistance with producing figure 3 in chapter 2. Brett Forsyth permitted use of his gray jay photograph (chapter 3, figure 1). Erika Hutter-Burke and Julie Morand-Ferron translated the thesis abstract.

NB: Long-term data collection was permitted by Canadian Wildlife Service, conducted with permission of the Ontario Ministry of Natural Resources and in accordance with University of Guelph Animal Care Protocols (#1842, 3273).

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Chapter One

General introduction

Life-history refers to the timing and characteristics of events in an organism's life. The field of life-history study examines life-history traits, such as age at first reproduction, reproductive lifespan, fecundity, and parental investment, to better understand how these life events relate to fitness (Stearns, 1976; Freeman & Herron, 2007). Differences in life-history traits are often conspicuous among species, for example the average age at first reproduction of mice is drastically earlier than that of elephants. However, these traits can also vary among individuals of the same species and this among-individual variation can have fitness consequences (e.g. within-season timing of reproduction, Reed et al., 2013).

Annual timing of reproduction is a life-history trait that often varies among individuals, and the causes and consequences of this variation have received considerable attention. Early on, Lack (1950) proposed that birds time their breeding to match seasonal peaks in food resources to increase fitness. Over the following years, empirical studies explored the various factors underlying timing of reproduction and established that timing of reproduction within a breeding season has important fitness consequences (reviewed by Daan et al., 1989; Daan & Tinbergen, 1997; Verhulst & Nilsson, 2008). In seasonal environments, early breeders generally have higher reproductive success than late breeders (e.g. birds: Reed et al., 2006; mammals: Réale et al., 2003). Breeding early can effectively lengthen the breeding season, allowing individuals to produce more offspring by either producing more broods (Böhning-Gaese et al., 2000) or re-breeding after a failed attempt (Pakanen et al., 2014). Furthermore, the offspring produced from early breeding attempts tend to have higher fitness themselves (Green & Rothstein, 1993; Verhulst & Nilsson, 2008), possibly because they have better access to resources during development (Green & Rothstein, 1993) or more time to develop before winter (Armitage et al., 1976), relative to late-born individuals. Timing of reproduction is also a heritable trait (Réale et al., 2003; Nussey et al., 2005ab), and early breeding is often associated with other phenotypic and environmental correlates of reproductive success (reviewed by Verhulst & Nilsson, 2008).

Though early studies of reproductive timing acknowledged the importance of among-individual variation, focus has more recently shifted to within-individual variation in reproductive timing. The environment of an individual can influence its phenotype, and this phenotypic plasticity—the ability of an individual to exhibit different behaviour or morphology along a gradient of environmental conditions—became a topic of interest because it allows individuals to adjust to heterogeneous environments (Bradshaw, 1965; Stamps, 2015). The reaction norm approach, which examines individual (or genotypic) variation in phenotype over a gradient of environmental conditions, allowed researchers to quantify this within-individual variation (de Jong, 1990; Via et al., 1995). For example, a classic study by De Meester (1996) utilized the reaction norm approach to study plasticity in phototactic behaviour of *Daphnia magna*. De Meester (1996) found that individuals of the same genotype were more averse to light when tested in water with predator (fish) scent than in water never exposed to predators. With individual-based approaches like this, we can also obtain more detailed information on the drivers of classically studied population-level patterns in reproductive timing.

Adjusting to annual variation in climatic conditions through phenotypic plasticity can allow individuals to time reproduction to match environmental conditions. This flexibility in response to naturally-occurring environmental variation has critical implications in the context of climate change, because climate change increases inter-annual variation in climate and produces conditions that exceed natural variability (reviewed by Karl & Trenberth, 2003). In recent years, there has been increasing interest in the link between phenology and climate (reviewed by Parmesan, 2006), and climate change has been linked to shifts in reproductive phenology in birds (reviewed by Dunn & Winkler, 2010), mammals (Post & Forchhammer, 2008), invertebrates (Reed et al., 2013), and plants (Richardson et al., 2013). There is evidence that some populations are experiencing phenological mismatch (Visser et al., 1998), where timing of breeding does not coincide with optimal reproductive conditions because individuals are not "keeping in step" with their changing environments (e.g. Visser et al., 1998; Post & Forchhammer, 2008; Reed et al., 2013).

Temperature is one climatic factor with strong links to timing of reproduction and reproductive success in birds. Breeders may use temperature as a cue for initiation of reproduction to time the energetically-demanding nestlings with emerging food resources (Lack, 1950; Schaper et al., 2012). Alternatively, cold temperatures may impose energetic costs on breeders and therefore physiologically limit reproductive timing (Bradshaw & Holzapfel, 2010). Several studies have used a reaction norm approach to demonstrate that individuals adjust laying date in response to annual variation in temperatures prior to breeding (Nussey et al., 2005b; Brommer et al., 2005; Brommer et al., 2008; Charmantier et al., 2008; Husby et al., 2010; Porlier et al., 2012; Thorley & Lord, 2015; Bourret et al., 2015). In all of these studies, warmer temperatures were associated with earlier laying, thus warm temperatures may indirectly increase reproductive success by advancing timing of reproduction. Ambient temperatures can also influence reproductive success after reproduction is initiated (Serrano et al., 2005; Charter et al., 2007; Bentzen et al., 2010; Hallinger & Cristol, 2011; Chausson et al., 2014; Beck et al., 2015). For example, brooding females increase foraging to compensate for cold temperatures (Bentzen et al., 2010) and subsequently they and their brood may be at a higher risk of predation (DuRant et al., 2013). However, it is currently unclear whether favourable temperatures might alter the fitness costs of late reproduction.

In addition to climatic conditions, other factors can produce within-individual variation in reproductive timing, including the local environment and individual characteristics. Characteristics of an individual's local environment, such as habitat quality (Lambrechts et al., 2004; Bourret et al., 2015) and food availability (reviewed by Daan et al., 1989; Boutin, 1990), can also affect laying date. Additionally, older individuals tend to breed earlier (Lewis et al., 2012), as do individuals with more breeding experience (Saunders et al., 2012) and in good body condition (Bêty et al., 2003). Variation in these factors can lead to among-individual variation in reproductive timing within populations. However, few studies have tested whether these determinants of laying date can constrain individual plasticity in response to climatic variation (but see Bourret et al., 2015). If climatic conditions interact with other individual characteristics or environmental factors to affect laying date, this could have implications for how individuals will differentially respond to environmental variation.

The ability of populations to cope with rapid environmental changes, including climate change, largely depends on individual phenotypic plasticity (Charmantier & Gienapp, 2014). Though evolutionary changes in phenology as a response to climate change have been documented (Bradshaw & Holzapfel, 2006), these processes occur over multiple generations rather than within individual lifespans. In avian systems, there is accumulating evidence that individuals advance laying date in response to warming temperatures (Dunn & Winkler, 2010), but little evidence of microevolutionary change in laying dates (Charmantier & Gienapp, 2014). Quantifying phenotypic plasticity is necessary if we are to predict whether populations will persist with climate change (Chevin et al., 2010). However, estimating plasticity at the individual level requires large datasets (Martin et al., 2011; van de Pol, 2012) and long-term studies with sufficient data are uncommon, making it difficult to empirically predict the resilience of most populations to changing environments. Furthermore, phenotypic plasticity can vary between species, populations (Husby et al., 2010; Porlier et al., 2012), and individuals (e.g. Nussey et al., 2005ab). Thus, further work is needed to explore patterns of variation in plasticity in order to predict the resilience of populations in a changing climate.

My general aim for this thesis is to examine the role of temperature in reproductive success. Specifically, I test for environmental constraints on individual laying date plasticity and explore whether temperature can modify the benefits of early reproduction. I use 38 years of observational data from a longitudinal study, the Algonquin Gray Jay Project, which has followed the timing of reproduction and reproductive success of individually-marked gray jays, *Perisoreus canadensis*, in southern Algonquin Provincial Park, Ontario, for over 50 years. Gray jays have unique natural-history that provides an interesting context to examine these questions. These resident passerines are native to the boreal forests of North America and cache perishable food about their territory throughout late summer and autumn. Monogamous pairs breed during late winter, thus relying primarily on cached food for both winter survival and reproduction (Sechley et al., 2014; Derbyshire et al., 2015).

In chapter 2, I investigate the role of intrinsic and extrinsic determinants in the timing of reproduction. First, I test whether factors in an individual's environment can constrain or mediate that individual's response to variation in late-winter temperatures. Second, I examine the effect of laying date on reproductive success. Finally, I examine population-level patterns in laying date and demography over time. In chapter 3, I examine the interactive effect between climatic conditions during early offspring development and timing of reproduction on reproductive success. Specifically, I test whether temperatures during incubation and nestling brooding modulate the effect of laying date on brood size. This stems from a previous study on this population which indicated that warm temperatures negatively affect reproductive success via degradation of perishable food caches (Waite & Strickland, 2006). In the final chapter, I discuss new insights provided by this work and highlight what questions remain to be answered.

Chapter Two

Male experience buffers laying date plasticity in a food-hoarding, winter-breeding passerine

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ABSTRACT

Phenotypic plasticity allows individuals to adjust reproductive timing in response to variation in the environment but little is known about how other factors, such as habitat quality, social environment and experience, may influence adjustments in the timing of breeding. We evaluated intrinsic (female age), environmental and social factors influencing laying date plasticity and assessed the effect of laying date on reproductive success in a population of gray jays, *Perisoreus canadensis*, over nearly four decades (1978–2015). Gray jays rely on stored food during their late-winter nesting season, a unique life-history context to study plasticity in reproductive timing. Overall, females tended to lay eggs earlier in response to higher prelaying temperatures and advanced laying date at similar rates over their lives. Male age interacted with both temperature and female age to influence laying date. Females mated to older males were more likely to breed earlier at lower temperatures than females mated to younger males but there was little effect of male age under warmer conditions. Similarly, younger females mated to older males were more likely to breed earlier than younger females mated to younger males but there was little effect of male age when females were older. Across all years, earlier laying relative to other breeders in the population led to higher probability of nest success and summer survival for dominant juveniles. Our results suggest that individual females adjust laying date in response to temperature and provide the first evidence that male experience plays an important, and probably underappreciated, role in how females adjust their timing of breeding over their lives and with respect to annual variation in the environment.

INTRODUCTION

Timing of breeding can have important fitness consequences, particularly in seasonal environments where resources vary over time. In many species, the optimal timing of breeding appears to match the emergence of resources during times of peak food demand of developing young (Bronson, 1985; Reed et al., 2013). In other species, early breeding can be advantageous because it can provide more time to breed again after a failed attempt (Pakanen et al., 2014) or more time to produce multiple successful broods over the breeding period (Böhning-Gaese et al., 2000). Furthermore, juveniles born earlier in the season are likely to have more time to develop and acquire resources and are, therefore, more likely to survive their first year and recruit into the population (Murie & Boag, 1984; Daan et al., 1990; Nilsson, 1990; Green & Rothstein, 1993; Wauters et al., 1993; Verhulst & Nilsson, 2008).

One of the primary factors influencing interannual variation in the timing of reproduction in animal populations is corresponding variation in climatic conditions. Population level variation in timing of breeding has been associated with annual variability in precipitation (Nussey et al., 2005a), large-scale climatic oscillations (e.g. Wilson et al., 2007) and temperature (e.g. Visser et al., 1998; Nussey et al., 2005b). Climate change has induced shifts in timing of breeding in multiple taxa, and many populations have shown trends of advancing reproductive phenology over time (reviewed by Visser & Both, 2005; Poloczanska et al., 2013; Richardson et al., 2013).

One way that individuals are able to cope with annual variation in the environment, including climate change, is through phenotypic plasticity (Charmantier & Gienapp, 2014). This is the ability of an individual to adjust its behaviour, morphology or physiology in response to variation in environmental conditions (Bradshaw, 1965; Stamps, 2015). There is evidence that plasticity in reproductive timing is heritable (Nussey et al., 2005a; Brommer et al., 2008; Husby et al. 2010) and selection can act upon variation in plasticity (Nussey et al., 2005a). Some studies have shown that individuals vary in their plasticity in reproductive timing within populations (Nussey et al., 2005ab; Brommer et al., 2005; Brommer et al., 2008; Reed et al., 2009; Husby et al., 2010; Porlier et al., 2012; Thorley & Lord, 2015; Bourret et al., 2015), although other studies have provided evidence that individuals exhibit similar degrees of plasticity (Reed et al., 2006; Charmantier et al., 2008; Porlier et al., 2012). Despite the importance of understanding individual plasticity in the context of environmental change (Nussey et al., 2007; Chevin et al., 2010; Charmantier & Gienapp, 2014), the mechanisms driving differences in plasticity between individuals within a population are not fully understood. This is partly because there are few long-term studies on marked populations able to estimate variation in plasticity.

Although individuals may be able to adjust their timing of breeding in response to variation in climate, other factors may mediate the degree of plastic response. For example, Bourret et al. (2015) provided evidence that tree swallows, *Tachycineta bicolor*, in low-density populations altered their timing of breeding in response to changes in spring temperature less than individuals in high-density populations, for which the habitat was assumed to be of higher quality. In addition to local environmental conditions, one intriguing possibility is that the social environment of breeders may affect the relationship between the timing of breeding and climatic conditions. Several studies have shown that males can influence female nest site selection (e.g. Jones & Robertson, 2001; Mennill et al., 2004), and breeder experience can advance laying dates and increase reproductive success (Saunders et al., 2012). However, the role of male age or experience in a female's response to environmental conditions remains unexplored. For example, a female's ability to adjust timing of breeding according to temperature may be influenced by the experience of her mate. Although such effects could influence the ability to respond to environmental change, the interactive effects between partner experience and individual laying date plasticity have not yet been examined.

We examined the influence of temperature, habitat characteristics, and age of breeders on timing of breeding in a marked population of gray jays, *Perisoreus canadensis*, studied over 38 years in Algonquin Park, Ontario. Gray jays occupy large, permanent territories (ca. 160 ha) and breed during late winter (Strickland & Ouellet, 2011). They store perishable food on their territory in late summer and autumn (Strickland & Ouellet, 2011) and rely on cached food during the reproductive period (Sechley et al., 2014). Nesting typically begins in late February or early March, but breeding is asynchronous and the laying date is broadly variable (annual ranges varied from 16 to 51 days). Breeding pairs are monogamous; only females incubate, and both male and female provide parental care. Male gray jays also provision females with food during the prelaying and incubation periods as well as the first week of the nestling period (Strickland & Waite, 2001). Females advance their laying date when food-supplemented (Waite & Strickland, 2006; Derbyshire et al., 2015). Habitat quality in the Algonquin population is linked to the proportion of conifers, potentially because conifers offer superior food storage properties (Strickland et al., 2011; Norris et al., 2013). Juvenile dispersal typically takes place in one of two phases. In June, ca. 6 weeks postfledging, the dominant juvenile within a brood actively ejects subordinate siblings from the territory and remains with the parents on the natal territory until, and sometimes beyond, the following breeding season (Strickland, 1991).

We tested a suite of alternative hypotheses to explain variation in female laying date plasticity (Table 2.1) and reproductive consequences of laying date in gray jays. Our main objectives were to determine whether (i) females adjust laying date in response to temperature,

(ii) laying date changes over an individual's life, (iii) females vary in their rate of adjustment to temperature and (iv) females vary in their rate of adjustment as they age. We also tested whether (v) the social environment (partner age), (vi) habitat quality or (vii) food supplementation modulated individual plasticity in laying date. Finally, we examined the relationship between laying date and reproductive success.

METHODS

Study system

We used 38 years (1978–2015) of longitudinal, individual-based reproductive data from a marked population of gray jays located along the Highway 60 corridor in southern Algonquin Provincial Park, Ontario, Canada (45°N, 78°W) that has been monitored since 1964. The number of breeding pairs monitored each year ranged from nine to 24 (mean = 17). The population has been declining over the last three decades (Waite & Strickland, 2006) but occupancy of territories with low proportions of conifer coverage has declined more rapidly relative to territories with high proportions of conifer coverage and pairs occupying high-conifer territories are more likely to produce fledglings (Strickland et al., 2011). Park visitors regularly feed gray jays in some of these areas and this supplementation is associated with earlier laying, as well as larger clutches and brood sizes (Derbyshire et al., 2015).

Monitoring of laying date

Nests were located through behavioural observation, offering nesting materials and following flight paths of jays carrying material. Once located, nests were visited every 2–5 days to observe laying date and whether the nest remained active. Female gray jays sit on their nests beginning with the first egg (Strickland & Ouellet, 2011) and, except in low nests whose contents could be easily examined, we defined laying date as the midpoint between the earliest and latest possible dates the female began sitting on the nest. Relative laying dates were calculated as the timing of laying relative to the annual mean laying date of the population. First breeding attempts from 1978 to 2015 were included in the analysis. First clutches accounted for 94% of breeding attempts during this period. We excluded second and third clutches, which occurred only in the event of an incubation period failure of a previous attempt and were infrequent (5% and <1% of breeding attempts, respectively), as well as nests that were associated with an unmarked parent and territories for which we lacked data on habitat quality. Nests found during the incubation or nestling period were excluded because we did not observe laying dates for these breeding attempts. Nest records from females experimentally food-supplemented in 2013 and 2014 were also excluded ($N = 16$ nest attempts; Derbyshire et al., 2015). Nest records for females and males with only one observed breeding attempt were included in the analysis to increase our power to detect variation in random slopes, as recommended by Martin et al. (2011). The final data set included 626 nests with laying dates from 179 females and 175 males over 38 years.

Monitoring of reproductive success

We used two measures of reproductive success: nesting success and summer survival of the dominant juvenile. We defined nesting success as the presence of at least one nestling in the nest at banding age (ca. 11 days old). Successful dominant juvenile survival was defined as the presence of a ca. 6-month-old juvenile offspring in October on the natal territory. Although some dominant juveniles replace disappeared breeders elsewhere in their first summer and some ejected subordinates attach to unrelated adults (Strickland, 1991), we are unable to quantify these aspects of reproductive success in our study system. Breeding success was not observed for all breeding attempts because safety issues prevented some nests from being accessed. Hence, we used a subset (93%) of the laying date data set to model reproductive success ($N = 592$ nest records, 175 females).

Territory characteristics

Habitat quality was divided into three classes (low, medium, high) according to the proportion of conifers on the territory (see methods in Strickland et al., 2011; Norris et al., 2013). The level of food supplementation by park visitors was classified as low when territories were located in areas rarely visited by the public, intermediate when members of the public fed the birds during autumn, or high when either a permanent feeder was located on the territory or visitors fed jays during both autumn and winter (see also methods in Derbyshire et al., 2015).

Temperature data

Historical temperature data were obtained from Environment Canada for two weather stations: one in the study area (Algonquin Park East Gate, Ontario, 45°32'N 78°16'W; 2004–2015) and one west of the study area (Dwight, Ontario, 45°23'N 78°54'W; operated 1977–2005). Station operation overlapped from September 2004 to December 2005; we used reduced major axis regression of mean daily temperatures from this period to transform mean daily temperatures from the weather station west of the study area to estimate temperatures within the study area for 1978–2004. Mean daily temperatures recorded at the two weather stations were highly correlated in winter ($R^2 = 0.91$) and consistent between stations (slope = 1.02, 95% confidence interval, CI = 0.97–1.08, $P < 0.001$).

We used a sliding window approach to determine the temporal window of mean daily temperature that best predicted annual mean laying dates of the population. Mean daily temperature was calculated across windows varying in length (15–25 days) and start date (30 January–20 March). For each window, mean daily temperature was regressed against annual mean laying dates of the population and the temporal window with the highest coefficient of determination was used as the fixed effect in subsequent models of laying date.

Statistical analyses

We followed the methods of van de Pol and Wright (2009) to partition the effects of prelaying temperature and female age into within- and between-subject components (see example calculations in Appendix I). Nonpartitioned prelaying temperature and age terms could mask opposing effects within a mixed model and do not explicitly address questions of within-individual plasticity (van de Pol & Wright, 2009). Ambient temperature during the prelaying period was partitioned into within-female temperature (i.e. prelaying temperature in year of breeding attempt minus the mean prelaying temperature in the study area across all years the female bred) and between-female temperature (i.e. mean prelaying temperature in the study area across all years the female bred) components. Female age was partitioned into within-female age (i.e. age in year of breeding attempt minus mean age of female) and between-female age (i.e. mean age of female) components.

All fixed variables and random intercepts predicted to influence laying date based on a priori knowledge were included in a linear mixed-effects model. We tested for two-way interactions between these within-female variables and other factors predicted to influence laying date to determine whether potential constraints acted on within-individual plasticity or adjustment of laying date with age (Table 2.1). A backward stepwise procedure using type III analysis of variance (ANOVA) with Kenward–Roger approximation of degrees of freedom was used to remove nonsignificant interactions until only significant interactions and all main effects remained.

We evaluated random effects by comparing alternative models with increasingly complex random structure while keeping the fixed effect structure constant. We examined whether individual females vary in their laying date plasticity in response to prelaying temperature (Female ID*temperature, generally referred to as I*E) by adding to female identity a random slope term of prelaying temperature. We tested whether individual females vary in their adjustment of laying date over their life (Female ID*age) by adding to female identity a random slope term of female age (Table 2.1).

We tested the effect of relative laying date, female age, male age, food supplementation and habitat quality on nesting success and dominant juvenile survival. The random structure of these models included year and female identity because models including male identity failed to converge.

All linear and generalized mixed-effect models of laying date and reproductive success were performed in R Version 3.2.3 (R Core Team, 2015). Linear mixed-effects models were fitted using restricted maximum likelihood through the 'lmer' function in the package lme4 (Bates et al., 2015), in conjunction with package lmerTest (Kuznetsova et al., 2015). Continuous fixed effects were standardized by grand mean-centering prior to analysis (Pinheiro & Bates, 2000). Significance of random effects was assessed through log-likelihood ratio tests on models fitted with maximum likelihood and significance of fixed effects in the final model of laying date was determined using type III ANOVA with Kenward–Roger approximation of degrees of freedom (Bolker et al., 2009). Generalized mixed-effects models of nesting success and dominant juvenile survival were fitted using maximum likelihood (Laplace approximation) through the 'glmer' function in the package lme4 (Bates et al., 2015). Significance of fixed effects in the generalized mixed-effect models was assessed using type II ANOVA with Wald chi-square tests (Bolker et al., 2009).

Ethical note

This research was conducted under approval of the University of Guelph Animal Care Committee (protocols 1842, 3273). The Canadian Wildlife Service provided permits for capturing and banding. Adults were trapped using walk-in Potter's traps and removed immediately upon capture. Nests were accessed only once to minimize disturbance.

RESULTS

Population level diagnostics and trends

Laying dates ranged from 19 February to 26 April (mean ± SD: March 23 ± 10). Mean daily temperatures in the prelaying window ranged from -12.4 °C to 0.8 °C (-6.8 ± 3.1 °C). Age of breeders ranged from 1 to 16 years for both sexes; the mean female and male ages were 4.7 years (± 3.3 SD) and 5.0 years (± 3.2 SD), respectively.

The temporal window of mean daily temperature that best predicted annual mean laying dates of the population was a 23-day period beginning on 28 February and ending on 22 March. Annual mean laying dates were later in years of lower prelaying temperatures and earlier in warmer years (slope = -0.64 days/°C, $F_{1,36} = 7.97$, $P = 0.008$, $R^2 = 0.18$; Figure 2.1). Over the study period, annual mean laying dates advanced (slope = -0.18 days per annum, $F_{1,36} = 7.39$, $P = 0.01$, $R^2 = 0.17$; Figure 2.2a), but annual prelaying temperatures did not increase (slope = 0.07 °C per annum, $F_{1,36} = 2.10$, $P = 0.16$, $R^2 = 0.06$; Figure 2.2b). The mean age of breeding females did not increase significantly over time (slope = 0.01 years per annum, $F_{1,36} = 2.48$, $P = 0.12$, $R^2 =$

0.06; Figure 2.2c), but that of breeding males did (slope = 0.05 years per annum, $F_{1,36} = 28.89$, $P < 0.0001$, $R^2 = 0.45$; Figure 2.2d).

Models of laying date

Using a fixed-effect structure of main effects with a priori predictions and two interactive effects that remained significant in the backward stepwise procedure (within-female temperature*male age and within-female age*male age), we evaluated the random effects hypothesized to explain female laying date. Model comparisons (see Appendix II) showed that inclusion of Female ID ($\chi^2_1 = 112$, $P < 0.0001$) and Male ID ($\chi^2_1 = 28.08$, $P < 0.0001$) as random intercepts significantly improved the model. We found that females did not significantly vary in their adjustment of laying date in response to prelaying temperature ($\chi^2_2 = 0.91$, $P = 0.63$). The Female ID*temperature model was unable to estimate the correlation between the random slope and random intercept (i.e. singular fit with -1.0 correlation). This singular fit could indicate insufficient power to properly test for variation in slope between females, possibly resulting in a type II error. However, this model showed very little between-female variation in random slope (variance = 0.011, 95% CI calculated with parametric bootstrap, 1000 iterations = 0.014–0.49). Thus, if we made a type II error by rejecting a model with Female ID*temperature, the small variation in Female ID*temperature should not greatly influence our estimates of fixed effects. Finally, females did not vary significantly in the slope of their adjustment of laying date with age ($\chi^2_2 = 1.28$, $P = 0.53$).

Using the random intercept model that included Female and Male ID, we proceeded to examine the fixed effects of laying date (Table 2.2). Individual females laid eggs earlier when they experienced higher prelaying temperatures. A marginally nonsignificant effect of between-female prelaying temperature indicated females that experienced higher average prelaying temperatures throughout their lives did not have earlier average laying dates. Females advanced laying dates with age and laid earlier when partnered with older than younger males. Females that lived longer had earlier laying dates than short-lived individuals. Laying dates also advanced with high food supplementation. A Tukey post hoc test found that females occupying highly food-supplemented territories laid earlier than females on territories with low ($P < 0.0001$) and medium ($P < 0.0001$) levels of food supplementation, whereas laying dates of females occupying territories with medium and low food supplementation did not differ ($P = 0.25$). Habitat quality (the proportion of conifers on the territory) did not significantly influence laying date.

The final model included two significant interactions with partner age. We found a negative interaction between within-female prelaying temperature and male age (Table 2.3, Figure 2.3a). Females breeding at lower temperatures had earlier laying dates when paired with older males than when paired with younger males but there was little to no influence of male age on laying date at higher prelaying temperatures (Figure 2.3a). We also found a negative interaction between within-female age and male age (Table 2.3, Figure 2.3b). Females in early life had earlier laying dates when paired with older males than when paired with younger males but there was little effect of male age on laying date when females were older (Figure 2.3b).

Models of reproductive success

We found that earlier laying females had greater nesting success and higher survival of dominant juveniles over the summer than later breeders (Figure 2.4). In the final model (Table 2.3), earlier relative laying dates resulted in higher nesting success (Figure 2.4a) and dominant juvenile survival (Figure 2.4b) than later laying dates. Older females also had higher nesting success than younger females but female age did not predict juvenile survival. Food supplementation increased nesting success and juvenile survival. Tukey post hoc tests found that high food supplementation resulted in higher reproductive success than low supplementation (nesting success: *P* = 0.03; juvenile survival: *P* = 0.005), but juvenile survival did not differ significantly between high and medium supplementation (nesting success: *P* = 0.092; juvenile survival: *P* = 0.091) or medium and low supplementation (nesting success: *P* = 0.80; juvenile survival: *P* = 0.42).

DISCUSSION

Our results demonstrate that the timing of reproduction, which is an important factor influencing reproductive success in gray jays, is influenced by a number of intrinsic and extrinsic factors. At both the population and individual level, females tended to lay earlier in warm years and later in cold years. Although this pattern of laying date plasticity along a gradient of temperatures has been reported in a number of species, it has only been observed in temperate, spring-breeding birds (e.g. Brommer et al., 2008; Husby et al., 2010; Bourret et al., 2015). Our study is the first to examine laying date plasticity in a species that breeds during the late winter and also relies on stored food during the reproductive period. Importantly, breeder experience can influence timing of reproduction (Saunders et al. 2012) and we have shown that partner experience interacted with both temperature and female age to influence laying date, neither of which has been reported for any species previously.

There are several mechanisms by which temperature could limit timing of breeding in gray jays. Low temperatures may inhibit reproductive physiology (Bradshaw & Holzapfel, 2010), and could also limit laying date through energetic constraints. The advancement of laying date in our population in response to experimental food supplementation (Derbyshire et al., 2015) also suggests an underlying energetic limitation associated with breeding in winter. The wide intra-annual variation in laying dates may reflect individual variation in energetic constraints between gray jays. Early reproduction and its associated fitness benefits may be possible only for individuals in good condition (e.g. body condition, adequate stored food) or individuals of high quality that are less limited by low temperatures than individuals in poor condition or of low quality. Alternatively, increasing temperatures may signal an optimal time to initiate reproduction (Grieco et al., 2002; Schaper et al., 2012). However, under this hypothesis we would expect high synchrony in laying date among breeders in the population, along with stabilizing selection around the population mean laying date if increasing temperatures signal optimal breeding conditions (e.g. Reed et al., 2013). Instead, we observed asynchronous breeding (i.e. wide intra-annual variation in laying date) and directional selection for early laying.

It is clear from our results that nesting early confers fitness benefits in gray jays. Early laying relative to other breeders in the population was associated with higher reproductive success before nestlings fledged and this pattern held until approximately 6 months later, when we determined whether dominant juveniles survived the summer. The advantage to breeding early relative to other breeders in the population may be driven by the role of interbrood competition in the juvenile dispersal system of gray jays (Strickland, 1991). Juveniles from early broods are developmentally advanced relative to younger juveniles, with two potential benefits: dominant juveniles from early broods that stay on the natal territory are unlikely to be ejected by intruding juveniles, and subordinate juveniles from early broods that are ejected from the natal territory are more competitive in interbrood competition to join unrelated breeders (Strickland, 1991).

Female age influenced both timing of breeding and nesting success, possibly through development, experience or changes in reproductive investment strategies over time. Females advanced laying date as they aged, and nesting success was higher for older than younger females. An experience-derived increase in foraging efficiency could reduce food limitation and therefore advance female laying date (Sechley et al., 2014) and ability to provision young. Alternatively, advancing laying date over time could be due to changing reproductive investment strategies (Winkler, 1987). Older breeders may invest more in current reproductive success due to reduced impact of this investment on future reproductive success. Although it is difficult to separate whether patterns of age-specific reproductive success are due to constraints or restraint, early life improvements in birds with relatively long life spans are probably due to changing constraints because differences in residual reproductive value are small early in life (Forslund & Pärt, 1995; Reid et al., 2003).

Males influenced female laying date, indicating that characteristics of an individual's social environment can influence timing of breeding and/or plasticity. We found consistent individual differences in timing of reproduction between males (i.e. random effect of male identity). Moreover, females laid earlier when partnered with older males at low temperatures than when partnered with younger males, whereas females bred at a similar time with either old or young partners at high temperatures. Thus, a feature of the female's social environment (partner age) could modulate female laying date plasticity in response to temperature. Similarly, young females bred earlier when partnered with older males than when partnered with younger males, and the effect of male age on laying date was reduced for late-life females. This result suggests that older male partners may buffer the effects of female inexperience. These patterns may be driven by changes in male behaviour with age via increasing experience, foraging efficiency and parental investment (see above). Mechanistically, this could occur through males reducing food limitation by storing more food on the territory as they age, which could improve female condition in the prebreeding season. Male gray jays also feed females during courtship, egg laying and incubation. Mate feeding may have evolved to counteract nutritional limitations of the female during reproduction and increase fitness (Galván & Sanz, 2011). For example, courtship feeding by male black-legged kittiwakes, *Rissa tridactyla*, is positively associated with clutch size (Helfenstein et al., 2003). Furthermore, Brommer et al. (2015) found that male tawny owls, *Strix aluco*, can indirectly affect timing of breeding, possibly via courtship feeding, which has fitness consequences when timing of breeding is associated with reproductive success. Regardless of the exact mechanism, the important role of males in the timing of reproduction challenges the usual assumption that females alone influence reproductive timing (Ball & Ketterson, 2008).

Variation in the environment can contribute to variation in plasticity (Brommer, 2013) and we found evidence that a variable component of the social environment (partner age) modulated female plasticity. From our model of laying date, we can infer that a female gray jay that partners only with old males will have low laying date plasticity in response to temperature and with age, relative to a female that partners only with young males. Consequently, a less plastic female (i.e. flatter reaction norm) is predicted to have higher reproductive success than a more plastic female (i.e. steeper reaction norm) because there is directional selection favouring early laying. Thus in our system, plasticity may be driven by necessity, rather than capacity, according to variation in the social environment, although females can also vary in plasticity due to developmental and genetic differences (see below). In contrast, Bourret et al. (2015) provided evidence that low laying date plasticity in tree swallows was associated with suboptimal environmental conditions, whereas high plasticity was associated with better environmental conditions. Plasticity is therefore not synonymous with quality or condition, and can reflect constraints of the environment.

Our study joins a minority of studies that found nonsignificant individual variation in laying date plasticity with respect to variation in climate (Reed et al., 2006; Charmantier et al., 2008; Porlier et al., 2012; but see Husby et al., 2010). Although the drivers of individual variation in plasticity are not entirely clear, homogeneous and predictable environments are associated with lack of individual variation in plasticity (Porlier et al., 2012; Brommer, 2013). The predictability of resources due to reliance on stored food during reproduction and directional selection for early laying may underlie the lack of I*E in this population of gray jays. Although previous work found that variation in habitat quality and food supplementation has important reproductive consequences (Strickland et al., 2011; Derbyshire et al., 2015), we did not find evidence that these factors influenced laying date plasticity itself. Thus, heterogeneity in these environmental conditions is unlikely to drive individual variation in plasticity. However, we found evidence that between-female variation in age of male partners could potentially produce variation in plasticity, although we did not find evidence that females differed in their rate of adjustment to temperature. Testing for variation in random slopes requires large data sets (see Martin et al., 2011; van de Pol, 2012) and we may have failed to detect individual variation in plasticity due to too few observed nesting attempts.

Testing for individual variation in plasticity alone does not identify the drivers of this variation. Individual variation in plasticity can be due to individual differences in genotype (G*E) and permanent environment (PE*E; reviewed by Brommer, 2013). There is evidence that individual differences in permanent environment account for individual variation in plasticity, but to date there is no evidence that interactions between genotypes and the environment underlie individual variation in laying date plasticity (Brommer et al., 2008; Husby et al., 2010; Brommer, 2013). Here, we tested for interactive effects between individual responses to temperature and breeder experience to determine whether features of an individual's environment modulated plasticity. We found that variation in partner age, which constitutes part of the between-female variation in the permanent environment, could potentially produce individual variation in laying date plasticity of female gray jays. Previous studies suggested that local environmental factors, such as population density or environmental quality, could influence individual plasticity (Wilson et al., 2007; Bourret et al., 2015). These interactive effects may account for some variation in plasticity (see I*Age approach by Lewis et al., 2012), suggesting that one link between environmental heterogeneity and variation in plasticity may be differential environmental constraints on individuals.

Laying dates in the population advanced by 0.18 days per annum over the 38-year study period, although this is unlikely to be due to increasing temperatures in the prelaying period. Most long-term studies of avian reproductive timing have found advancing reproductive phenology over time, probably in response to climate change (Dunn & Winkler, 2010). Although we observed laying date plasticity in response to temperature, our results suggest that plasticity did not drive the shift in reproductive timing because temperatures in the prelaying period did not increase over the study period. Alternatively, the advance in laying date may be due to phenotypic plasticity in response to an unmeasured environmental variable that covaries with time. However, shifts in phenology can occur not only through phenotypic plasticity, but also via changes in demography and micro-evolution (Dunn & Winkler, 2010; Merilä & Hendry, 2014).

Population level trends within the data suggest a potential driver of the observed shift towards earlier laying. Although the average age of female breeders did not increase over time, the average age of breeding males increased by nearly 2 years over the study period. Given this demographic shift towards older males, our model of laying date predicts that a gradual increase in breeding male age over time would result in a corresponding advance in female laying date. Reduced juvenile recruitment into the breeding population over time (Strickland & Norris, n.d.), rather than increased male longevity, may underlie the increase in mean age of breeding males but a long-term demographic model is required to separate these factors, as well as link the effects of earlier breeding to population growth rates.

Understanding the factors that drive and modulate individual phenological plasticity is increasingly important in the context of climate change. Although phenotypic plasticity can allow populations to persist under changing climatic conditions (Charmantier & Gienapp, 2014), timing of breeding is a complex phenotype that is influenced by other environmental factors. Furthermore, conditions in the local environment may constrain plasticity in response to climate (Wilson et al., 2007; Bourret et al., 2015), and we provide new evidence that an individual's social environment can also modulate individual plasticity.

TABLES AND FIGURES

Table 2.1 Hypotheses examined to explain variation in laying date of female gray jays in Algonquin Park, ON.

Hypothesized effect	Hypothesized mechanism(s)	Predictor variable	Source
Temperature limits timing of reproduction	Females breed earlier in warmer years and later in colder years because temperature either limits or acts as a cue for reproduction	Within-female temperature	Bourret et al., 2015
Age influences timing of reproduction	Individual females lay earlier as they age because experience increases and/or reproductive investment strategies change	Within-female age	Lewis et al., 2012
Individuals vary in plastic responses to temperature	Genetic and/or environmental differences cause variation in laying date plasticity along a gradient of prelaying temperature	Female ID*temperature	Porlier et al., 2012; Brommer, 2013
Individuals vary in laying date adjustment with age	Genetic and/or environmental differences cause variation in rate of laying date adjustment with age	Female ID*age	Lewis et al., 2012
Plasticity modulated by age	Female experience buffers effects of low temperatures on laying	Within-female temperature*within-female age	None

Plasticity modulated by partner age	Male experience buffers effects of female inexperience on laying	Within-female temperature*male age	None
Plasticity modulated by habitat quality	Habitat quality buffers effects of temperatures on laying	Within-female temperature*habitat quality	None
Plasticity modulated by anthropogenic food sources	Food supplementation buffers effects of low temperatures on laying	Within-female temperature*food supplementation	None
Adjustment of laying date with age modulated by partner age	Male experience buffers effects of female inexperience on laying	Within-female age*male age	None
Adjustment of laying date with age modulated by habitat quality	Habitat quality influences the rate at which females advance laying with age	Within-female age*habitat quality	None
Adjustment of laying date with age modulated by anthropogenic food sources	Food supplementation influences the rate at which females advance laying date with age	Within-female age*food supplementation	None

Table 2.2 Final model to explain laying date of female gray jays in Algonquin Park, ON in response to fixed and random effects (see Table 2.1).

Term	Estimate ± SE	*F*	*P*	SD
Random effects				
Year				3.3
Female ID				4.1
Male ID				4.1
Residual				5.5
Fixed effects				
Intercept	86.6 ± 1.42			
Within-female prelaying temperature	-0.69 ± 0.20	12.15	0.001	
Between-female prelaying temperature	-0.51 ± 0.30	2.82	0.095	
Within-female age	-0.81 ± 0.14	31.36	<0.0001	
Between-female age	-0.52 ± 0.19	7.89	0.005	
Male age	-0.44 ± 0.12	14.14	0.0002	
Habitat quality				
M	-2.17 ± 1.39			
H	-1.89 ± 1.33	1.32	0.27	
Food supplementation				
M	-2.00 ± 1.26			
H	-7.68 ± 1.26	20.52	<0.0001	
Within-female prelaying temperature*male age	0.07 ± 0.03	5.84	0.02	
Within-female age*male age	0.14 ± 0.04	13.50	0.0003	

N=179 females, 175 males, 626 nest records, 38 years. Levels for the factors ‘habitat quality’ and ‘food supplementation’ are: L = low (reference category), M = medium, H = high (see Methods for details).

Table 2.3 Models of nesting success and dominant juvenile survival in response to fixed and random effects for gray jays in Algonquin Park, ON, between 1978 and 2015.

	Nesting success (Y/N)					Dominant juvenile survival (Y/N)				
Term	Estimate ± SE	χ^2	*df*	*P*	SD	Estimate ± SE	χ^2	*df*	*P*	SD
Random effects										
Year					0.57					0.40
Female ID					6.7×10^{-4}					3.8×10^{-5}
Fixed effects										
Intercept	0.21 ± 0.36					-0.38 ± 0.33				
Relative laying date	-0.068 ± 0.013	27.1	1	<0.0001		-0.058 ± 0.013	19.4	1	<0.0001	
Female age	0.072 ± 0.033	4.74	1	0.03		0.00011 ± 0.030	0.00	1	1.0	
Male age	0.057 ± 0.034	2.92	1	0.087		-0.0088 ± 0.030	0.088	1	0.77	
Food supplementation										
M	-0.16 ± 0.24	7.24	2	0.03		-0.29 ± 0.23	9.7	2	0.008	
H	-0.69 ± 0.27					-0.81 ± 0.26				
Habitat quality										
M	0.64 ± 0.29	4.87	2	0.088		-0.087 ± 0.28	0.093	2	0.95	
H	0.45 ± 0.27					-0.056 ± 0.27				

N = 592 nest records, 175 females. Levels for the factors ‘habitat quality’ and ‘food supplementation’ are: L = low (reference category), M = medium, H = high (see Methods for details).

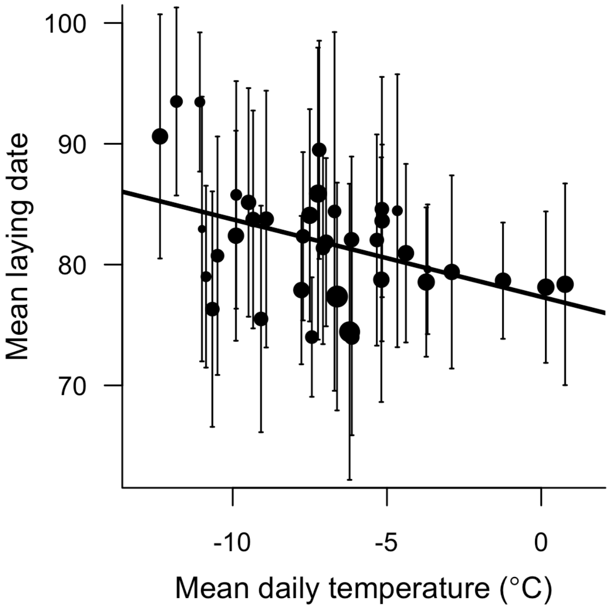

Figure 2.1 Relationship between mean daily temperature (°C) during the prelaying period (28 February–22 March) and annual mean laying dates (± SD) of gray jays in Algonquin Park, ON, over 38 years (1978–2015). Each point represents 1 year; point size corresponds to the number of first nest attempts found each year (range 9–24 nests/year). Line of best fit represents population level laying date plasticity in response to mean daily temperature in the prelaying period.

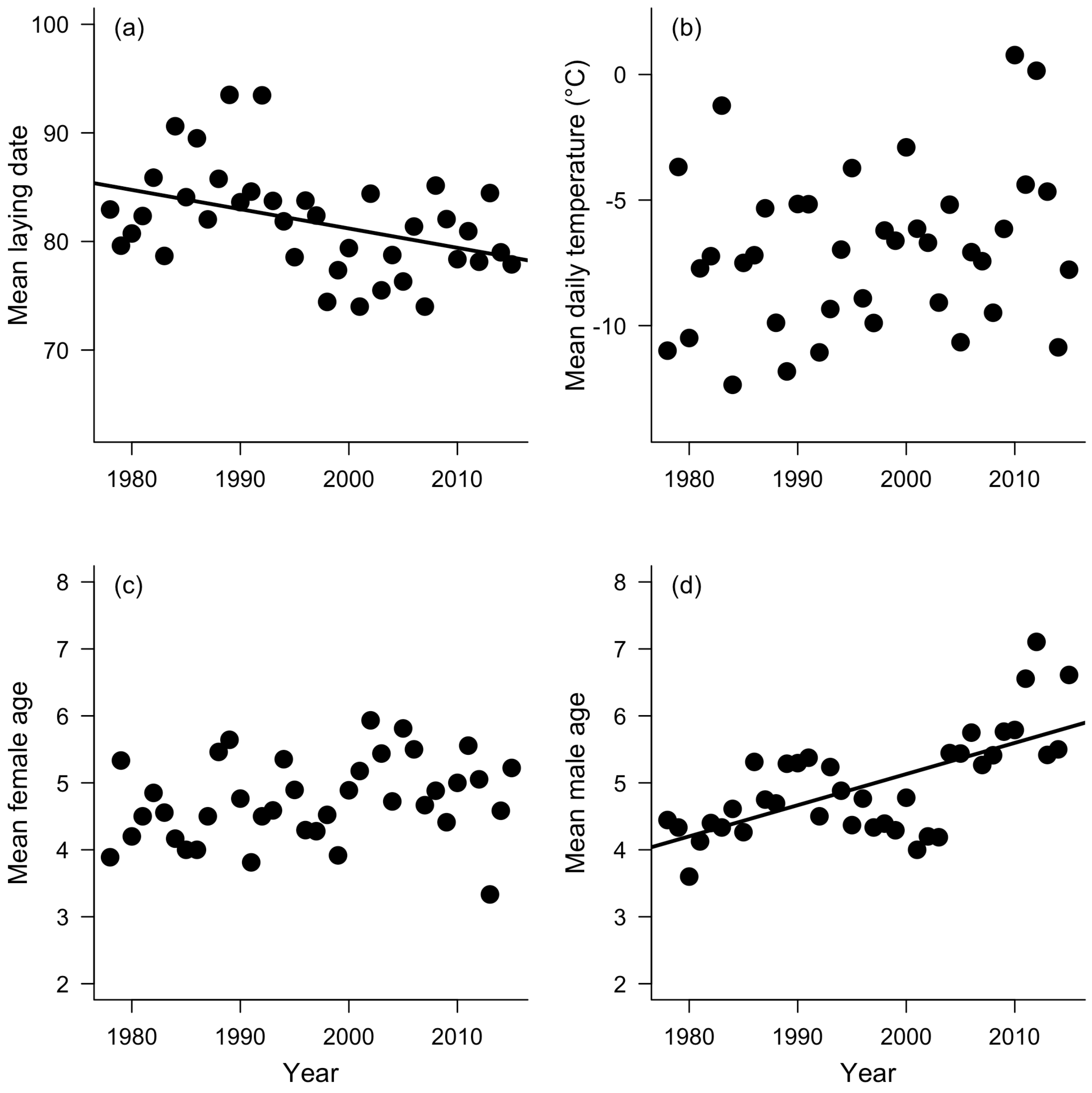

Figure 2.2 Variation during the study period (1978–2015) of (a) laying dates of gray jays in Algonquin Park, ON, (b) mean daily temperature during the prelaying period (28 February–22 March), (c) mean age of breeding females and (d) mean age of breeding males. Lines of best fit are shown for significant linear regressions over time.

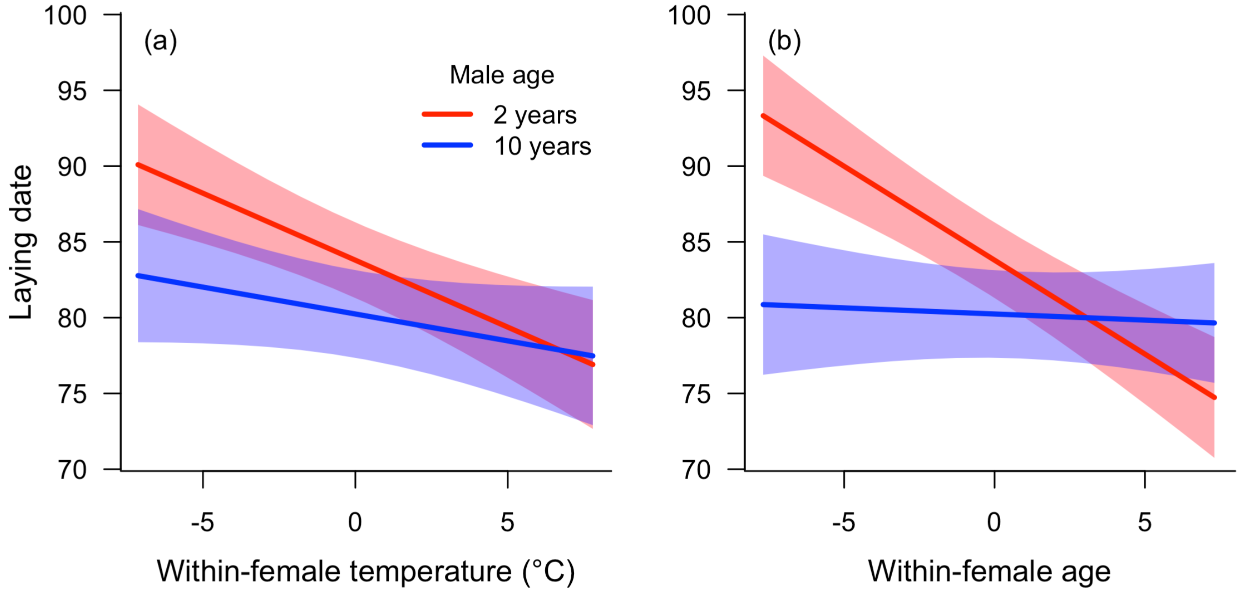

Figure 2.3 Model estimates showing the interactive effects between (a) within-female prelaying temperature and male age and (b) within-female age and male age, based on results from a mixed-effects model on laying date of gray jays in Algonquin Park, ON (Table 2). Lines represent predicted values for males aged 2 years (red, N = 255) and 10 years (blue, N = 371), with 95% confidence intervals (shaded area), with all other continuous covariates held at their mean and categorical predictors (low, medium, high) held at ‘medium’.

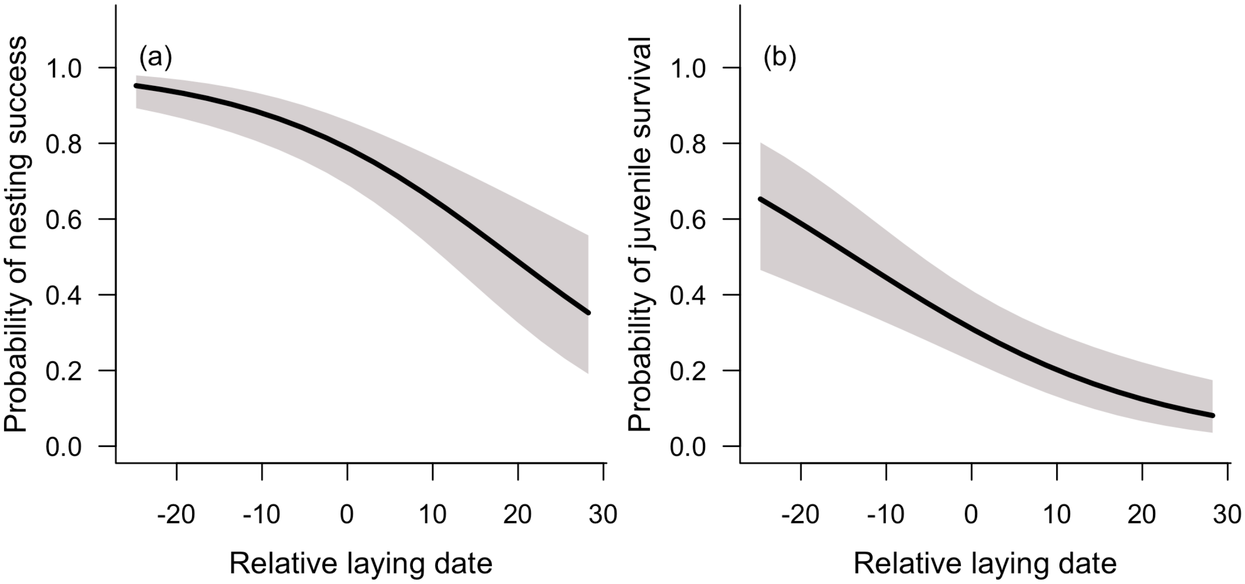

Figure 2.4 Model estimates for relative laying dates in relation to (a) nesting success and (b) survival of dominant juveniles. Lines represent predictions based on mixed-effects models of gray jay reproductive success in Algonquin Park, ON (Table 3), with all other continuous covariates held at their mean and categorical predictors (low, medium, high) held at 'medium'. Shaded areas show 95% confidence intervals.

Chapter Three

Reduced reproductive performance associated with warmer ambient temperatures during incubation in a winter-breeding, food-storing passerine

Whelan, S., Strickland, D., Morand-Ferron, J., & Norris, D. R. (n.d.). Reduced reproductive performance associated with warmer ambient temperatures during incubation in a winter-breeding, food-storing passerine. *Ecology and Evolution, In revision.*

ABSTRACT

Early breeders tend to have higher reproductive success than late breeders. However, the fitness costs of later breeding may also be influenced by favourable environmental conditions after the commencement of breeding. We tested whether ambient temperatures during incubation and nestling brooding modulated the effect of laying date on brood size in gray jays, *Perisoreus canadensis*, a sedentary boreal species whose late-winter nesting depends on caches of perishable food. Previous evidence has suggested that warmer temperatures degrade the quality of these food hoards, and we asked whether warmer ambient temperatures during incubation and nestling brooding would be associated with reduced reproductive success. We used 38 years of data from a range-edge population of gray jays in Algonquin Provincial Park, Ontario, where the population has declined over 50% since the study began. We found that ambient temperatures during nestling brooding had little effect on reproductive success for females breeding early in the season but, consistent with the "hoard-rot" hypothesis, cold temperatures were associated with larger brood sizes in later-breeding females. This is the first evidence for an interactive effect of laying date and temperature during incubation on reproductive success in any bird species. Our findings provide further evidence that warming temperatures are associated with reduced reproductive success of a species that is reliant on cold temperatures to store perishable food caches, some of which are later consumed during the reproductive period.

INTRODUCTION

Individuals that initiate reproduction earlier in the breeding season tend to have higher reproductive success than late breeders (Daan et al., 1989; Green & Rothstein, 1991; Réale et al., 2003; Reed et al., 2006; McKellar et al., 2013). Early breeders are more likely to initiate breeding again after a failed attempt (Pakanen et al., 2014) and have a higher probability of breeding multiple times in a season (Böhning-Gaese et al., 2000; Gil-Delgado et al., 2005). Early breeders also tend to produce more offspring (Daan et al., 1989; Rowe et al., 2005) that are in better condition (e.g. Green & Rothstein, 1991; Stier et al., 2014). Furthermore, offspring from early reproductive attempts are more likely to survive (Naef-Daenzer et al., 2001) and recruit into the breeding population (Green & Rothstein, 1991; Descamps et al., 2006), increasing the fitness benefits for early breeders.

Although early reproduction can confer fitness benefits, climatic conditions during offspring development can also influence reproductive success regardless of when individuals begin reproduction. Incubation and brooding of nestlings are energetically expensive behaviours, (Williams, 1996; Sanz & Tinbergen, 1999), and this energetic expenditure can be influenced by food availability and ambient temperature (e.g. Tinbergen & Dietz, 1994). In extreme cases, parents will abandon a nest due to poor weather conditions (Elkins, 2010) or insufficient food (Anderson, 1989). Furthermore, ambient temperature is often linked to food availability, which in turn influences the ability of parents to successfully rear offspring (e.g. van Noordwijk et al., 1995; Reed et al., 2013). Parents may increase their time spent foraging to compensate for low food availability or poor weather during incubation (Bentzen et al., 2010) and nestling brooding (Johnson & Best, 1982). Subsequently, both parents and offspring may be at a higher risk of predation (DuRant et al., 2013), or reduce incubation constancy, which can lower offspring condition and survival (Bentzen et al., 2010; DuRant et al., 2013).

Although there is evidence that timing of breeding and climatic conditions during incubation and the nestling brooding period can both affect reproductive outcomes, little is known about how these two factors may interact to influence reproductive success in birds. Our objective was to determine whether ambient temperatures during nestling brooding modulate the effect of timing of breeding on reproductive success in a population of gray jays, *Perisoreus canadensis* (Figure 3.1) breeding in Algonquin Provincial Park, Ontario. Gray jays are year-round residents of North American boreal and subalpine forests that store perishable food (e.g. berries, mushrooms, invertebrates, vertebrate carrion) during late summer and autumn (Strickland & Ouellet, 2011). Pairs initiate breeding in mid to late winter, when temperatures are typically below freezing and fresh food resources are scarce (Strickland & Ouellet, 2011). Males provision females during incubation and nestling brooding (Strickland & Waite, 2001), though females also leave the nest occasionally to retrieve cached food during incubation and increase time spent away from the nest as nestlings develop (D.S., pers. obs.).

In Algonquin Park, gray jay reproductive success is higher for pairs that breed earlier in the breeding season (chapter 2). Timing of reproduction and reproductive success are food-limited in this population; females advance laying and have larger brood sizes when food-supplemented (Derbyshire et al., 2015). Waite and Strickland (2006) linked warming autumn temperatures to a long-term population decline, and proposed warm temperatures in late autumn degrade the quality of perishable food stores. Using an experimental approach, Sechley et al. (2015) found that cold temperatures better preserved artificial food caches than warm temperatures, providing further indirect evidence that warm temperatures may degrade gray jay food stores. Although there is strong evidence that laying date influences reproductive success in Algonquin gray jays (chapter 2), and warmer autumn temperatures are associated with reduced clutch size (Waite & Strickland, 2006), we do not know whether temperatures during incubation and/or the nestling brooding period alter the fitness costs of late reproduction.

We examined an extension of the "hoard-rot" hypothesis (Waite & Strickland, 2006) to test whether ambient temperature during incubation and the nestling brooding period might affect reproductive success through its influence on cached food availability. Specifically, we hypothesized that the costs of later laying would be enhanced (lower reproductive performance) under warm ambient temperatures during incubation and the nestling brooding period under the assumption that warmer temperatures do not preserve cached food as well as colder temperatures. In contrast, there may be little or no costs of later laying when temperatures are cold during incubation and nestling brooding. Following this hypothesis, we predicted an interaction between laying date and ambient incubation and nestling brooding period temperature such that, at later laying dates, brood sizes would be larger under colder temperatures but that temperature would have no effect on brood size at earlier laying dates. The effect of ambient temperature on reproductive success could also depend on which phase of offspring development is examined. The female is largely dependent on male provisioning during incubation, but is able to independently forage and retrieve caches as nestlings develop. Furthermore, fresh food resources may become available in the nestling brooding phase due to melting of snow cover. Therefore incubation and nestling brooding are behaviourally distinct periods in gray jay reproduction, thus we separately tested for the effect of ambient temperatures for three different time periods: incubation only, incubation + nestling brooding, nestling brooding only.

METHODS

Study system

We studied a marked population of gray jays in southern Algonquin Provincial Park, Ontario (45°N, 78°W) from 1978 to 2015. Gray jay pairs in this population typically initiate breeding between late February and March, when ambient temperatures are below 0°C. Pairs rely on stored food for winter survival and during reproduction (Strickland & Ouellet, 2011; Sechley et al., 2014). Only females incubate but males provision females during the incubation and nestling brooding periods (Strickland & Ouellet, 2011).

Population monitoring

We located nests through behavioural observations and revisited them every 2-5 days to determine laying date and reproductive success. We considered laying date to be the midpoint between the earliest and latest possible dates of clutch initiation, and calculated *relative laying date* as the female's laying date relative to other females breeding in the population that year (Reed et al., 2009; Lewis et al., 2012; chapter 2). Female gray jays sit from their first egg but usually initiate incubation only when the clutch is complete, resulting in an apparent incubation period of 20 days for a typical 3-egg clutch (i.e., 18 days of true incubation plus 2 days from the laying of the first egg to the laying of the third egg; Strickland & Ouellet, 2011). We banded nestlings approximately 11 days after the estimated hatching date (laying date of first egg + 20 days of incubation) and recorded brood size (i.e. number of nestlings that survived to banding age).

Ambient temperature during incubation and nestling brooding

We obtained historical temperature records from Environment Canada for two weather stations: one operated west of the study area (Dwight, Ontario, 45°23' N 78°54' W) from the beginning of the study period until 2005 and the second (Algonquin Park East Gate, Ontario, 45°32' N 78°16' W) began operation within the study area in 2004. We used reduced major axis regression for the period of overlapping station operation to estimate winter temperatures within the study region from 1978-2004 by transforming mean daily temperatures from the western weather station with the regression equation (see chapter 2). We calculated *mean incubation temperature* as the mean of mean daily temperatures between egg-laying and the estimated hatching date, *mean incubation/nestling brooding temperature* as the mean of mean daily temperatures between egg-laying and 11 d post-hatch, and *mean nestling brooding temperature* as the mean of mean daily temperatures between the estimated hatching date and 11 d post-hatch.

Food supplementation

Food supplementation by park visitors has been shown to advance laying date and increase clutch and brood sizes in this study population (Derbyshire et al., 2015), thus we accounted for level of food supplementation on territories in all models. Territories were classified as a low (little or no public access to territory), medium (public feeding during autumn only), or high (public feeding during autumn and winter or permanent feeder on territory) level of supplementation (see also Derbyshire et al., 2015; chapter 2).

Final dataset

For our analyses, we used all first nest records of marked pairs for which we observed laying dates and brood size. We excluded nests that were experimentally food supplemented in 2013 and 2014 (Derbyshire et al., 2015). The final dataset included 597 nest records from 175 females monitored between 1978 and 2015.

Statistical analyses

We fit generalized linear mixed models with maximum likelihood (Laplace approximation) using the statistical package *lme4* (Bates et al., 2015) in *R* (version 3.2.3, R Core Team, 2015). We tested for overdispersion because brood size followed a Poisson distribution, and we used variance inflation factors (VIF) to test for collinearity between all predictor variables (Zuur et al., 2009). We examined variation in brood size using fixed effects of relative laying date, female age, food supplementation, mean ambient temperature, and an interaction between relative laying date and mean ambient temperature. Significance of the effect of ambient temperatures and an interaction between ambient temperatures and relative laying date was tested using log-likelihood ratio tests for each of the three ambient temperature periods. Random effects of female identity and year were included in the model. All continuous predictor variables were standardized by grand mean centering and dividing by one standard deviation.

RESULTS

Mean incubation temperatures ranged from -11.8°C to 10.8°C (mean = -0.7°C ± 3.6 SD), incubation/nestling brooding temperatures ranged from -8.0°C to 11.3°C (mean = 0.6°C ± 3.3 SD), and nestling brooding temperatures ranged from -8.3°C to 13.8°C (mean = 3.2°C ± 3.6 SD). The mean ambient temperatures did not increase significantly over the study period (incubation: slope = 0.0051°C/a, $F_{1,36} = 0.024$, $P = 0.88$, $R^2 = 0.0007$; incubation/nestling brooding period: slope = 0.0054°C/a, $F_{1,36} = 0.032$, $P = 0.86$, $R^2 = 0.0009$; nestling brooding period: slope = 0.0076°C/a, $F_{1,36} = 0.060$, $P = 0.81$, $R^2 = 0.002$). Brood size varied from zero to five nestlings (mode = 3) and was not overdispersed ($\chi^2 = 569$, df = 588, p = 0.71). As the VIFs of all fixed predictors were < 3, we proceeded to fit the brood size model with all predictor variables (Zuur et al., 2009).

An interactive effect between relative laying date and ambient temperature during incubation and the incubation/nestling brooding period significantly improved the model fit for brood size, but ambient temperature during the nestling brooding period alone did not improve the model (Table 1). Brood size was generally larger for breeding attempts initiated at earlier relative laying dates than later dates in all models but, consistent with the hoard-rot hypothesis, late nests incubated and brooded at colder temperatures had larger brood sizes than late nests incubated and brooded at warmer temperatures (Figure 2.2).

DISCUSSION

Our results provide, to the best of our knowledge, the first evidence that ambient temperatures during incubation can modulate the effect of laying date on reproductive success in birds. Among late breeders, colder ambient temperatures during incubation were associated with larger brood sizes than warmer temperatures. Thus, the fitness benefit of early nesting was not affected by laying date for nests incubated under cold conditions but heightened for those incubated at warmer ambient temperatures. However, ambient temperatures during nestling brooding did not appear to affect reproductive success.

These findings are consistent with Waite and Strickland's (2006) "hoard-rot" hypothesis, which reasons that warm autumn temperatures could degrade food caches, resulting in a food limitation in the subsequent breeding season. Poor quality food may require females to increase foraging trips to meet their nutritive needs, thus decreasing incubation constancy (Bentzen et al., 2010) and increasing the risk of nest and adult predation (DuRant et al., 2013). Furthermore, females with degraded food stores could deplete endogenous reserves more rapidly than females with access to high-quality food, and depletion of endogenous reserves is associated with nest desertion (Yorio & Boersma, 1994). An alternative hypothesis for an association between warm temperatures during incubation and reduced reproductive success is that nestlings and parents overheat (e.g. *Falco naumanni,* Serrano et al., 2005; *Falco tinnunculus,* Charter et al., 2007). However, gray jays incubate and brood in winter conditions, making hyperthermia an unlikely mechanism for the reduction in brood sizes at warm temperatures.

Our results indicate that ambient temperatures during incubation in particular are driving the relationship between temperature, laying date, and reproductive success. Ambient temperatures during the nestling brooding period did not significantly impact reproductive success. This may be because nesting jays increasingly gain access to terrestrial and shallow-water aquatic invertebrates as snow cover disappears and creeks open up in the nestling brooding period. Though we also have evidence that parents feed stored food to developing nestlings, some of the nestlings' diet appears to be comprised of fresh food during this time period (Strickland et al., n.d.).

Further work is needed to determine whether degradation of food stores underlies this interactive effect between ambient temperature and timing of reproduction in gray jays. It is important to note that after nest failure, renesting attempts can be quite successful (23/38 renests observed during our study produced nestlings at 11 d). However, since only early breeders can renest after a failed attempt and these individuals may have greater food stores than late breeders, early breeders may still have sufficient food stores for their second reproductive attempt despite their rapidly diminishing food quality. Additionally, the hypothesized negative impact of increased hoard rot resulting from warmer late-season temperatures could be offset by increased availability of invertebrates later in the breeding season. To improve our understanding of the role of temperature in the preservation of gray jay food caches and reproductive success, observational studies could compare cache retrieval trips of females at different times during the breeding season and determine whether ambient temperatures during incubation predicts the duration of time females spend retrieving caches. If caches do indeed degrade with warm temperatures in late winter and spring, we expect females incubating at warmer temperatures late in the season will make more cache retrieval trips than females incubating earlier in the season or at colder temperatures. To experimentally determine whether food caches degrade more at warm temperatures late in the breeding season, artificial food caches could be deployed along a temperature gradient (see Sechley et al., 2015) during late winter and spring and retrieved at different time points.

Interestingly, we now have evidence that ambient temperatures after laying have the opposite effect on reproductive performance compared to temperatures prior to laying. Female gray jays lay earlier when they experience warmer temperatures before laying, possibly because temperature imposes a physiological limitation on timing of reproduction, and early reproduction relative to other breeders in the population is positively associated with reproductive success (chapter 2). However, despite the cold temperatures at which gray jays incubate, we did not find evidence for a fitness cost to brooding nestlings at cold temperatures. Instead, we found that warm temperatures during nestling brooding had a negative effect on reproductive success later in the breeding season, but temperature did not influence reproductive success early in the breeding season. It is possible that only pairs in good condition with large amounts of stored food were capable of breeding early, and their large food stores buffered them from effects of temperature. Alternatively, the benefit of cold ambient temperatures with respect to food storage may exceed the thermoregulatory costs during incubation in gray jays. In contrast, several studies have found that reproductive success increased with ambient temperatures in the incubation and nestling periods (Hallinger & Cristol, 2011; Chausson et al., 2014; Beck et al., 2015). However, these studies did not test whether the effect of temperature on reproductive success depended on timing of reproduction. Further studies should test for an interaction between timing of breeding and incubation temperature in a species that does not rely on cached food during the breeding season. In such a system, thermoregulatory costs of cold ambient temperatures during nestling brooding could be offset by increased food availability (e.g. invertebrates) later in the breeding season.

Population declines have been documented in two areas along the southern limit of gray jay range (Waite & Strickland, 2006; Menebroeker et al., 2016), potentially due to warming temperatures associated with climate change (Waite & Strickland, 2006). Our findings bolster the evidence that a warming climate could negatively impact reproductive success in gray jays. Warming temperatures could thus lead to range loss at the southern edge of gray jay distribution, a well-documented pattern observed in several taxa (Chen et al., 2011). We did not find evidence that ambient temperatures during incubation or the nestling brooding period have increased over time in the Algonquin population. However, warming temperatures during incubation could potentially negatively affect reproductive success in other gray jay populations, or with future climate change.

We found evidence that climatic conditions during incubation can influence the relationship between timing of breeding and reproductive success. Though gray jays breed in winter, we found no evidence that colder temperatures negatively impacted reproductive success. Indeed, colder temperatures were associated with higher reproductive success in the late breeding season, potentially because cold temperatures better-preserve food caches that gray jays utilize during the breeding season. Though previous studies of other birds have indicated a positive link between ambient temperatures during incubation and reproductive success, we found, in the gray jay, further evidence consistent with an opposite and novel, indirect effect of temperature on reproductive success.

TABLE AND FIGURES

Table 3.1 Results of model comparisons, modelling brood size in response to multiple fixed predictors and random effects of year and female identity. Significance of an interactive effect between laying date and ambient temperature during three periods of offspring development (incubation, incubation and nestling brooding, and nestling brooding) was determined using log-likelihood ratio tests to compare models with and without the laying date × temperature interaction (N=175 females, 597 nest records, 38 years).

Model	Fixed effect terms	*df*	Log-likelihood	Model comparison	$\chi2$	*P*
1	relative laying date + female age + food supplementation	7	-996.08			
2	relative laying date + incubation temperature + female age + food supplementation	8	-993.48	1 vs 2	5.20	0.023
3	relative laying date + incubation temperature + female age + food supplementation + relative laying date × incubation temperature	9	-989.24	2 vs 3	8.48	0.0036
4	relative laying date + incubation/nestling brooding temperature + female age + food supplementation	8	-992.32	1 vs 4	7.52	0.0061
5	relative laying date + incubation/nestling brooding temperature + female age + food supplementation + relative laying date × incubation/nestling brooding temperature	9	-988.79	4 vs 5	7.06	0.0079
6	relative laying date + nestling brooding temperature + female age + food supplementation	8	-994.77	1 vs 6	2.61	0.11
7	relative laying date + nestling brooding temperature + female age + food supplementation + relative laying date × nestling brooding temperature	9	-993.24	6 vs 7	3.07	0.080

Figure 3.1 Female gray jay incubating during winter in Algonquin Provincial Park, ON. Photo credit: Brett Forsyth.

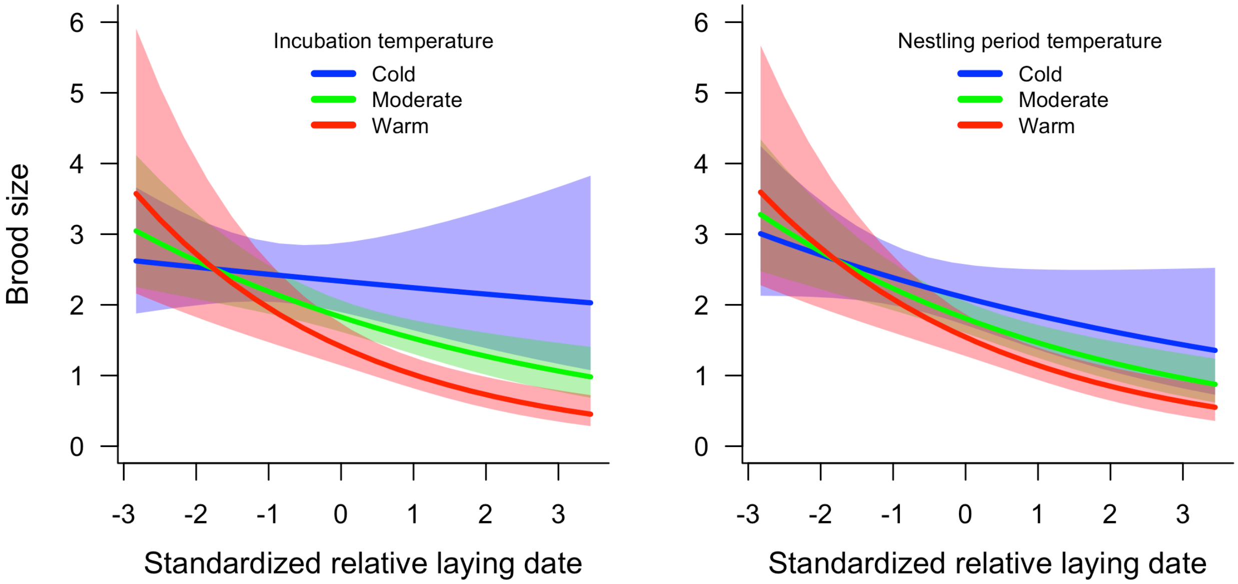

Figure 3.2 Relative laying date and mean ambient temperatures during incubation had an interactive effect on brood size (a), but an interaction between relative laying date and mean ambient temperatures during nestling brooding was not significant (b). Model predictions are based on models 3 (a) and 7 (b) presented in Table 3.1, and are shown for cold (blue; incubation = -6.5°C and nestling brooding period = -3°C), moderate (green; incubation = -0.5°C and nestling brooding period = 3°C), and warm (red; incubation = 5.5°C and nestling brooding period = 9°C) mean ambient temperatures. Shaded areas represent 95% confidence intervals.

Chapter Four

General conclusion

Since the pioneering work of Lack (1950, 1968) that explored life history traits in avian systems, the role of the environment in reproductive timing of individuals has been further elucidated. In this thesis, I aimed to build on and contribute to this large body of research by exploring the role of temperature in timing of reproduction and reproductive success. In chapter 2, I found that female gray jays, *Perisoreus canadensis*, plastically adjusted their laying dates in response to temperatures experienced prior to breeding. However, female plasticity was constrained by male age—a factor in the female's social environment. Breeding early relative to other pairs in the population resulted in higher reproductive success, thus male experience may indirectly increase reproductive success by advancing female laying date. In chapter 3, I built on the finding that laying early relative to other individuals in the population confers fitness benefits, along with previous work from the Algonquin study that suggested cold temperatures may preserve the perishable food stores of gray jays better than warm temperatures (Waite & Strickland, 2006; Sechley et al., 2015). I tested the hypothesis that ambient temperatures during incubation and nestling brooding modulate the effect of reproductive timing on reproductive success. Warm ambient temperatures during incubation were associated with reduced brood size in late-breeding pairs, but not early-breeding pairs. This finding is consistent with Waite and Strickland's (2006) "hoard-rot" hypothesis because warm temperatures late in the breeding season may degrade food caches, inhibiting the female's ability to incubate.

It is interesting to note that the effect of ambient temperature on gray jay reproductive success depended on timing within the breeding cycle. I found evidence that prelaying temperature was a limiting factor for timing of reproduction. Laying date was negatively associated with reproductive success, therefore cold prelaying temperatures may indirectly reduce reproductive success. Later, in the incubation period, I found evidence that colder temperatures had a positive effect on brood size, while warm incubation temperatures were associated with decreased reproductive success. Thus, cold ambient temperatures may first limit timing of reproduction, and enhance reproductive success later in the breeding cycle.

Chapter 2 emphasizes the importance of investigating potential constraints on phenotypic plasticity because individual responses to temperature variation can be buffered by social factors. Although several studies to date have found that individuals plastically adjust laying date in response to temperature (Nussey et al., 2005b; Brommer et al., 2005; Brommer et al., 2008; Charmantier et al., 2008; Husby et al., 2010; Porlier et al., 2012; Thorley & Lord, 2015; Bourret et al., 2015), I found the first evidence that a social factor (age of mate) can modulate female laying date plasticity. Importantly, I used within-subject centering to separate within-female effects of temperature from between-female effects of temperature (van de Pol & Wright, 2009) and tested for constraints on individual plasticity via the within-female effect of temperature. Previously, environmental factors that constrain individual laying date plasticity had remained unexplored (but see Wilson et al., 2007; Bourret et al., 2015). Understanding the factors that limit phenotypic plasticity is critical because plasticity is the main mechanism by which populations are able to adapt to human-induced environmental change in the short-term (Charmantier & Gienapp, 2014). Furthermore, plasticity should be considered when predicting whether populations can persist in their changing environments (Chevin et al., 2010). Longitudinal studies with sufficient data to estimate plasticity in reproductive timing are not common, and more work is needed to better understand what factors facilitate and constrain individual plasticity to refine predictions of population persistence in changing environments.

The gray jay study system brought unique perspectives to the research questions pursued in chapter 2. Despite laying in winter, when fresh food resources are scarce, gray jays responded to temperature in the same way as spring-breeding species. Until now, laying date plasticity in response to temperature had only been found in spring-breeding species that rely on emerging food resources during reproduction, specifically great tits (i.e. *Parus major*, Nussey et al., 2005b; Charmantier et al., 2008; Husby et al., 2010), collared flycatchers (*Ficedula albicollis*, Brommer et al., 2005), common gulls (*Larus canus*, Brommer et al., 2008), blue tits (*Cyanistes caeruleus*, Porlier et al., 2012; Thorley & Lord, 2015), and tree swallows (*Tachycineta bicolor*, Bourret et al., 2015). It is often suggested that birds plastically adjust laying date in response to prelaying temperatures because temperature is a cue for seasonal invertebrate emergences, which many species rely on to feed nestlings (e.g. Lack, 1950; Grieco et al., 2002; Schaper et al., 2012; Reed et al., 2013). However, peaks in invertebrates in the Algonquin study area occur well after fledging; thus, the selective factors shaping the reaction norm of laying date in response to temperature in gray jays are not entirely clear.

Chapter 3 highlights that the costs of late reproduction can be influenced by climate after the initiation of reproduction. Many studies have found that early breeders have higher reproductive success than late breeders (e.g. Green & Rothstein, 1991; Réale et al., 2003; Reed et al., 2006; McKellar et al., 2013). Other studies found that ambient temperatures during incubation or nestling brooding can influence reproductive success either positively (e.g. Hallinger & Cristol, 2011; Chausson et al., 2014; Beck et al., 2015) or negatively (e.g. Serrano et al., 2005; Charter et al., 2007). I examined the effects of both reproductive timing and ambient temperature on reproductive success together and, to my knowledge, provided the first documentation of an interactive effect between laying date and ambient temperature on reproductive success. This relationship could be due to the unique natural history of gray jays (i.e. winter reproduction, storage of perishable food). To determine the generality of this finding, future work could test whether ambient temperature and timing of reproduction interact to affect reproductive success in spring-breeding species that rely on emerging food resources during early offspring development.

The findings presented in this thesis point to additional questions to be addressed in the gray jay system. First, how might male experience buffer female laying date plasticity? The ability of individuals to store and retrieve cached food often improves as they age and gain experience (Clayton & Soha, 1999). In gray jays, Sechley et al. (2014) found that older females gained weight more rapidly and reached greater final weights than younger females. The authors suggested this positive association between age and weight gain could be due to improving caching and retrieval abilities, increasing territory familiarity, or learning cues for optimal timing of reproduction. Thus, older males may cache more food during late summer and autumn or better provide females with food during the breeding season. An empirical study could use observations of male caching and provisioning behaviour to test whether male age predicts the quantity/quality of food caches or amount of food males provide females during the breeding season. However, this study would need to control for territory quality (Norris et al., 2013). Alternatively, early breeding is often associated with other phenotypic correlates of reproductive success (Verhulst & Nilsson, 2008), and it is possible that late breeding males selectively disappear from the population (e.g. Bouwhuis et al., 2009). Thus, the relationship between male age and laying date could be due to only early breeding males remaining in the population to breed at older ages (between-male effects), rather than males breeding earlier as they age (within-male effects). The statistical approach described by van de Pol & Verhulst (2006) could be used to test for selective disappearance of late-breeding males in this population. Second, to what extent do gray jays rely on stored food during the reproductive period? While there is evidence that gray jays feed nestlings stored food (Strickland et al., n.d.) and fresh food resources become available as snow cover decreases late in the breeding season, it is currently unclear what proportions of each are fed to nestlings and whether this varies depending on timing of reproduction. Early reproduction may only be possible for pairs with sufficient food stores, while pairs with inferior food stores delay reproduction to utilize fresh food stores. However, my findings in chapter 3 suggest that delaying reproduction to access fresh food would be a costly strategy.

My findings are informative in the context of climate change. While chapter 2 suggests that gray jays may advance laying date if winter temperatures warm due to climate change, chapter 3 warns that reproductive success in gray jays could decrease due to degradation of perishable food caches. Though this population has declined by over 50% since the study began (Waite & Strickland, 2006), we did not find evidence that ambient temperatures during the prelaying period or incubation were driving this decline. In chapter 2, I found that prelaying temperatures influenced laying date and laying dates advanced over time, but found no increase in prelaying temperatures. However, it is important to note that the jays could be plastically responding to ambient temperatures at other times of the year (e.g. Williams et al., 2013). In chapter 3, I found that cold ambient temperatures during incubation were associated with larger brood sizes, but again found no temporal trend in ambient temperature during the incubation period.

Overall, this thesis highlighted that ambient temperature can influence reproductive success at different stages of the breeding cycle. Additionally, the effect of temperature on reproductive success can be modulated by social factors (chapter 2) or timing of reproduction (chapter 3). Through use of a longitudinal life-history dataset, my findings provide insights on how individuals respond to environmental variation. Furthermore, this information can be used to predict population responses to human-induced environmental change.

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APPENDIX I – Example calculations for within-subject centering

Example of within-subject centering, following the methods of van de Pol and Wright (2009), to partition prelaying temperature (°C) and age into within- and between- subject terms for one female (‘FEMALE1’), given the following sample data:

Year	Prelaying temperature (°C)	Female age (years)	Female ID
1978	-6	1	FEMALE1
1979	-3	2	FEMALE1
1980	-9	3	FEMALE1
1981	-10	4	FEMALE1
1982	-2	5	FEMALE1

Equations:

Between-subject (BS) term = mean value of variable experienced by subject.
Within-subject (WS) term = value of subject – mean value of variable experienced by subject.

Calculations:

$$\text{BS temperature} = \frac{(-6) + (-3) + (-9) + (-10) + (-2)}{5} = -6 \qquad \text{BS age} = \frac{1 + 2 + 3 + 4 + 5}{5} = 3$$

WS temperature (1978) = (-6) – (-6) = 0 | WS age (1978) = 1 – 3 = -2

WS temperature (1979) = (-3) – (-6) = 3 | WS age (1979) = 2 – 3 = -1

WS temperature (1980) = (-9) – (-6) = -3 | WS age (1980) = 3 – 3 = 0

WS temperature (1981) = (-10) – (-6) = -4 | WS age (1981) = 4 – 3 = 1

WS temperature (1982) = (-2) – (-6) = 4 | WS age (1982) = 5 – 3 = 2

Within-subject centering produces the following partitioned temperature and age variables for FEMALE1:

Year	WS temperature	BS temperature	WS age	BS age	Female ID
1978	0	-6	-2	3	FEMALE1
1979	3	-6	-1	3	FEMALE1
1980	-3	-6	0	3	FEMALE1
1981	-4	-6	1	3	FEMALE1
1982	4	-6	2	3	FEMALE1

APPENDIX II – Laying date model comparisons

Results of model comparisons, modelling female gray jay laying date with constant fixed-effects structure and increasingly complex random structure

Model	Random-effect terms	*df*	Log likelihood	Model comparison	χ2	*P*
1	Year	14	-2193.6			
2	Year + female ID	15	-2132.6	1 vs 2	112	<0.0001
3	Year + female ID + male ID	16	-2118.5	2 vs 3	28.08	<0.0001
4	Year + female ID*temperature + male ID	18	-2118.1	3 vs 4	0.91	0.63
5	Year + female ID*female age + male ID	18	-2117.9	3 vs 5	1.28	0.53

Significance of random effects was determined using log-likelihood ratio tests to compare models with and without the random effect (*N*=179 females, 175 males, 626 nest records, 38 years).