



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



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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 grey jays, *Perisoreus canadensis*, over nearly four decades (1978–2015). Grey 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. © 2016 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

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, Jenouvrier, & Visser, 2013). In other species, early breeding can be advantageous because it can provide more time to breed again after a failed attempt (Pakanen, Rönkä, Thomson, & Koivula, 2014) or more time to produce multiple successful broods over the breeding period (Böhning-Gaese, Halbe, Lemoine, & Oberrath, 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 (Daan, Dijkstra, & Tinbergen, 1990; Green & Rothstein, 1993; Murie &

Boag, 1984; Nilsson, 1990; Verhulst & Nilsson, 2008; Wauters, Bijens, & Dhondt, 1993).

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, Clutton-Brock, Elston, Albon, & Kruuk, 2005), large-scale climatic oscillations (e.g. Wilson, Norris, Wilson, & Arcese, 2007) and temperature (e.g. Nussey, Postma, Gienapp, & Visser, 2005; Visser, van Noordwijk, Tinbergen, & Lessells, 1998). 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 Poloczanska et al., 2013; Richardson et al., 2013; Visser & Both, 2005).

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,

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1965; Stamps, 2015). There is evidence that plasticity in reproductive timing is heritable (Brommer, Rattiste, & Wilson, 2008; Husby et al. 2010; Nussey, Clutton-Brock, et al., 2005) and selection can act upon variation in plasticity (Nussey, Clutton-Brock, et al., 2005). Some studies have shown that individuals vary in their plasticity in reproductive timing within populations (Bourret, B elisle, Pelletier, & Garant, 2015; Brommer, Meril a, Sheldon, & Gustafsson, 2005; Brommer et al., 2008; Husby et al., 2010; Nussey, Clutton-Brock, et al., 2005; Nussey, Postma, et al., 2005; Porlier et al., 2012; Reed et al., 2009; Thorley & Lord, 2015), although other studies have provided evidence that individuals exhibit similar degrees of plasticity (Charmantier et al., 2008; Porlier et al., 2012; Reed et al., 2006). Despite the importance of understanding individual plasticity in the context of environmental change (Charmantier & Gienapp, 2014; Chevin, Lande, & Mace, 2010; Nussey, Wilson, & Brommer, 2007), 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, Ramsay, Boag, & Ratcliffe, 2004), and breeder experience can advance laying dates and increase reproductive success (Saunders, Roche, Arnold, & Cuthbert, 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 grey jays, *Perisoreus canadensis*, studied over 38 years in Algonquin Park, Ontario. Grey 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, Strickland, & Norris, 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 grey 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 (Derbyshire, Strickland, & Norris, 2015; Waite & Strickland, 2006). Habitat quality in the Algonquin population is linked to the proportion of conifers, potentially because conifers offer superior food storage properties (Norris, Flockhart, & Strickland, 2013; Strickland, Kielstra, & Norris, 2011). 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 1) and reproductive consequences of laying date in grey jays. Our main objectives were to determine whether (1) females adjust laying date in response to temperature, (2) laying date changes over an individual's life, (3) females vary in their rate of adjustment to temperature and (4) females vary in their rate of adjustment as they age. We also tested whether (5) the social environment (partner age), (6) habitat

Table 1
Hypotheses examined to explain variation in laying date of female grey 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	e.g. Porlier et al. (2012)
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

quality or (7) 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 grey 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 grey 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 grey 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, Nussey, Wilson, and Réale (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 Norris et al., 2013; Strickland et al., 2011). 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 Supplementary Material). 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 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 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, Mächler, Bolker, & Walker, 2015), in conjunction with package lmerTest (Kuznetsova, Brockhoff, & Christensen, 2015). Continuous fixed effects were standardized by grand mean-centring 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 \pm SD: March 23 \pm 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, $F_{1,36} = 7.97$, $P = 0.008$, $R^2 = 0.18$; Fig. 1). Over the study period, annual mean laying dates advanced (slope = -0.18 days per annum, $F_{1,36} = 7.39$, $P = 0.01$, $R^2 = 0.17$; Fig. 2a), but annual

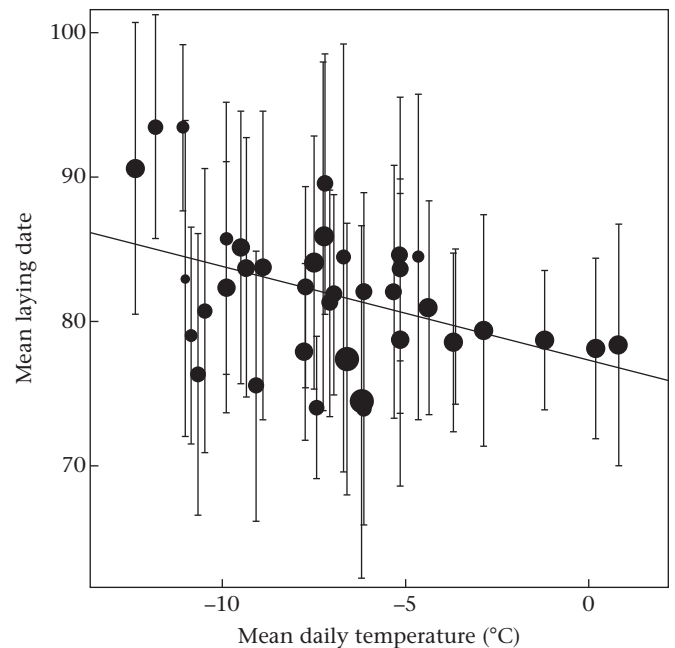


Figure 1. Relationship between mean daily temperature (°C) during the prelaying period (28 February–22 March) and annual mean laying dates (\pm SD) of grey jays in Algonquin Park, ON, over 38 years (1978–2015). Each point represents 1 year; point size corresponds to the number of first nest attempts 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.

prelaying temperatures did not increase (slope = 0.07 °C per annum, $F_{1,36} = 2.10$, $P = 0.16$, $R^2 = 0.06$; Fig. 2b). The mean age of breeding females did not increase significantly over time (slope = 0.01 years per annum, $F_{1,36} = 2.48$, $P = 0.12$, $R^2 = 0.06$; Fig. 2c), but that of breeding males did (slope = 0.05 years per annum, $F_{1,36} = 28.89$, $P < 0.0001$, $R^2 = 0.45$; Fig. 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 Supplementary Material, Table S1) 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

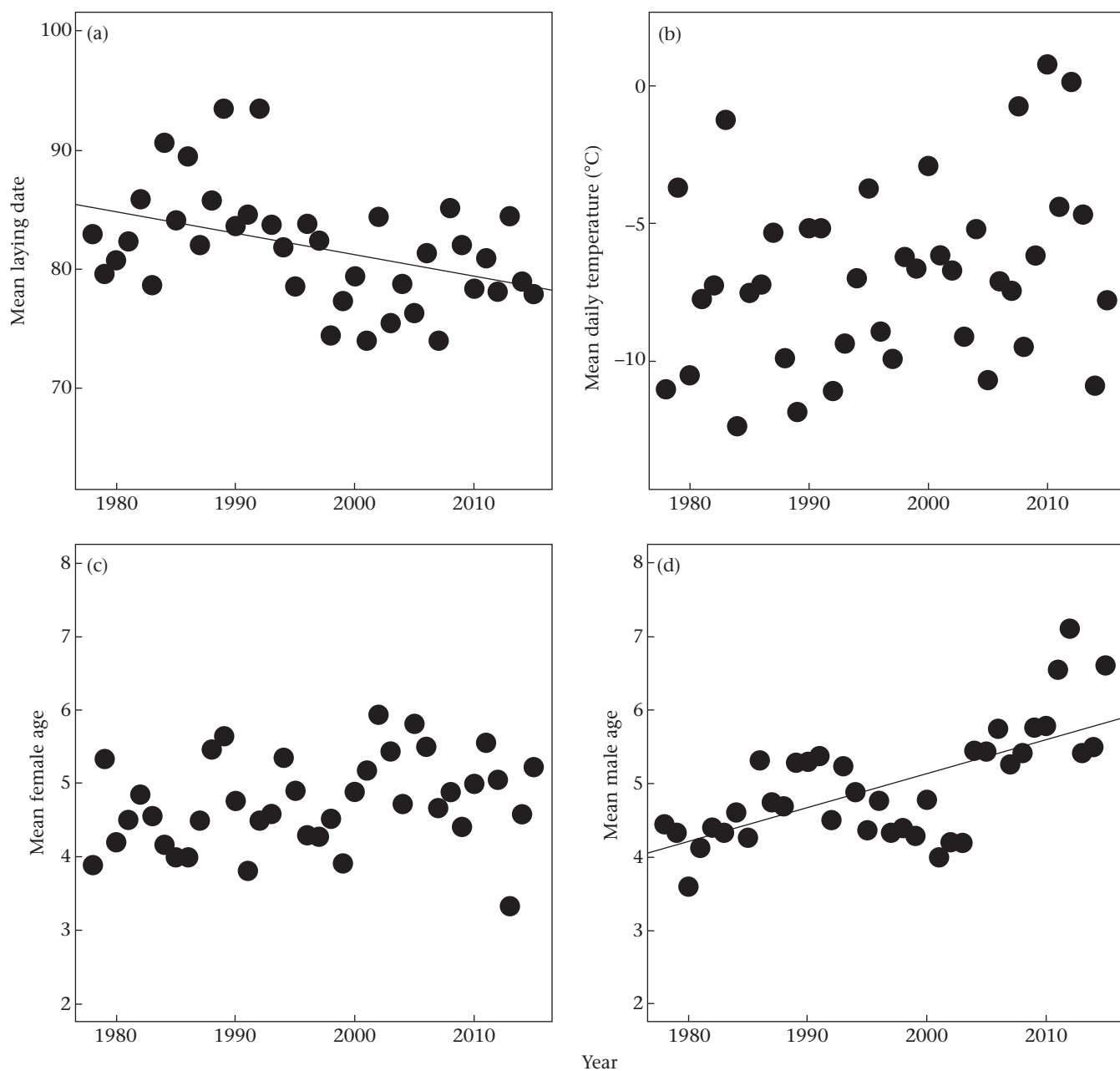


Figure 2. Variation during the study period (1978–2015) of (a) laying dates of grey jays in Algonquin Park, ON, (b) mean daily temperature during the prelaying period (28 February–22 March), (c) mean age of breeding females and (d) mean age of breeding males. Lines of best fit are shown for significant linear regressions over time.

(Table 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 3, Fig. 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 (Fig. 3a). We also found a negative interaction between within-female age and male age (Table 3, Fig. 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 (Fig. 3b).

Table 2
Final model to explain laying date of female grey jays in Algonquin Park, ON, in response to fixed and random effects (see Table 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).

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 (Fig. 4). In the final model (Table 3), earlier relative laying dates resulted in higher nesting success (Fig. 4a) and dominant juvenile survival (Fig. 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: $P = 0.42$).

Table 3
Models of nesting success and dominant juvenile survival in response to fixed and random effects for grey jays in Algonquin Park, ON, between 1978 and 2015

Term	Nesting success (Y/N)					Dominant juvenile survival (Y/N)				
	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).

DISCUSSION

Our results demonstrate that the timing of reproduction, which is an important factor influencing reproductive success in grey 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. Bourret et al., 2015; Brommer et al., 2008; Husby et al., 2010). 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 grey 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 grey 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, van Noordwijk, & Visser, 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 grey 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

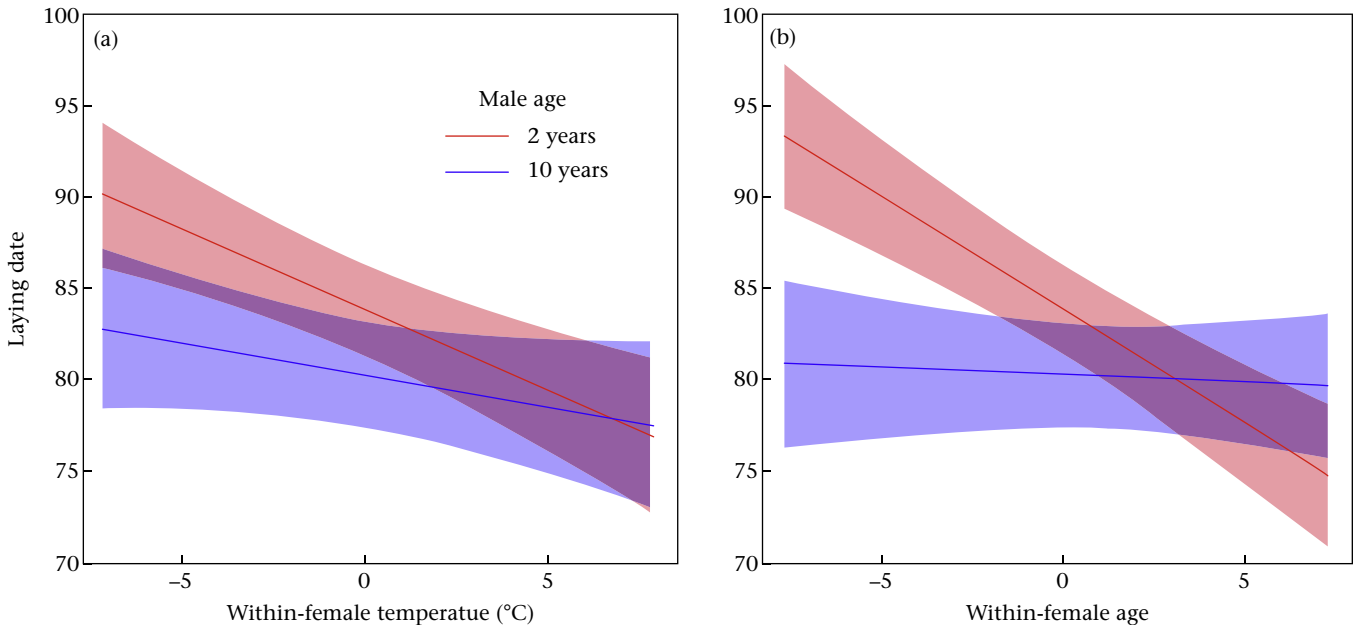


Figure 3. Model estimates showing the interactive effects between (a) within-female prelaying temperature and male age and (b) within-female age and male age, based on results from a mixed-effects model on laying date of grey jays in Algonquin Park, ON (Table 2). Lines represent predicted values for 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'.

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 grey 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

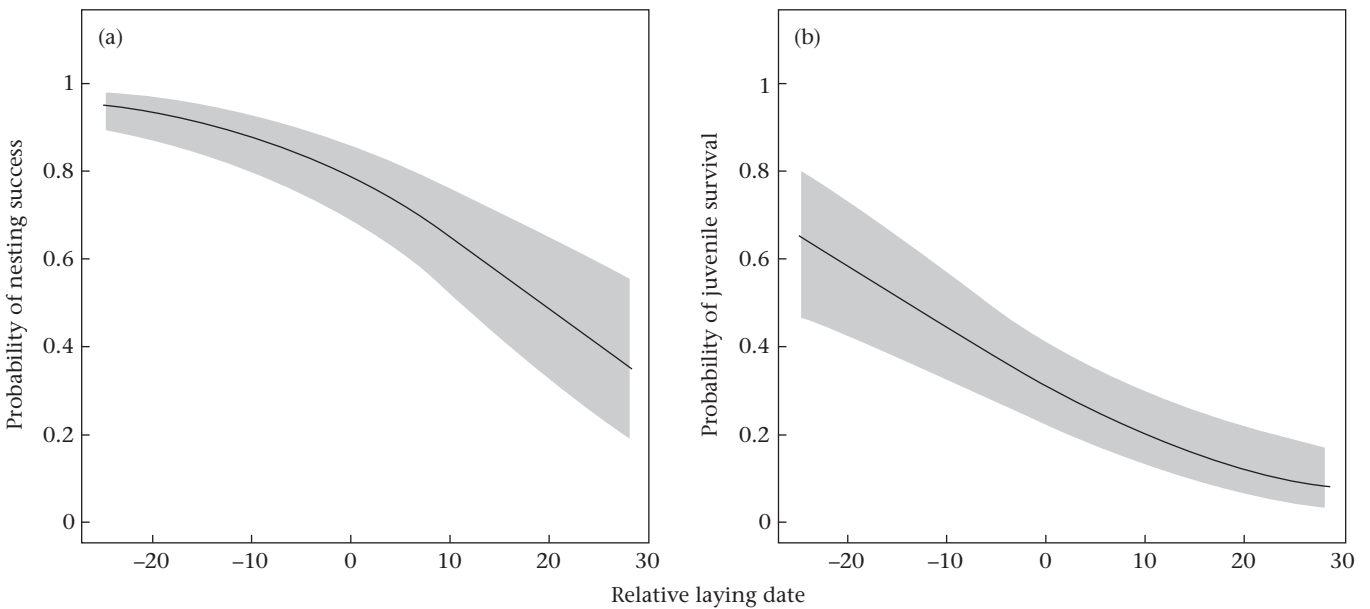


Figure 4. Model estimates for relative laying dates in relation to (a) nesting success and (b) survival of dominant juveniles. Lines represent predictions based on mixed-effects models of grey jay reproductive success in Algonquin Park, ON (Table 3), with all other continuous covariates held at their mean and categorical predictors (low, medium, high) held at 'medium'. Shaded areas show 95% confidence intervals.

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, Bignal, Bignal, McCracken, & Monaghan, 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 grey 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 male quality and clutch size (Helfenstein, Wagner, Danchin, & Rossi, 2003). Furthermore, Brommer, Karell, Aaltonen, Ahola, and Karstinen (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 grey 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 (Charmantier et al., 2008; Porlier et al., 2012; Reed et al., 2006; 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 (Brommer, 2013; Porlier et al., 2012). 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 grey jays. Although previous work found that variation in habitat quality and food supplementation has important reproductive consequences (Derbyshire et al., 2015; Strickland et al., 2011), 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, 2013; Brommer et al., 2008; Husby et al., 2010). 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 grey jays. Previous studies suggested that local environmental factors, such as population density or environmental quality, could influence individual plasticity (Bourret et al., 2015; Wilson et al., 2007). These interactive effects may account for some variation in plasticity (see I*Age approach by Lewis, Nussey, Wood, Croxall, & Phillips, 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 (Bourret et al., 2015; Wilson et al., 2007), and we provide new evidence that an individual's social environment can also modulate individual plasticity.

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Supplementary Material

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