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# 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.


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, Bijnens, & 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, Bélisle, Pelletier, & Garant, 2015; Brommer, Merilä, 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 |