PHENOTYPIC PLASTICITY DRIVES PHENOLOGICAL CHANGE IN MANDT'S BLACK

GUILLEMOT (*CEPPHUS GRYLLE MANDTII)*

By

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ABSTRACT

The ability of individuals to change breeding time is predicted to be an important aspect of adapting to climate change. Changes in breeding time could occur through either behavioural adjustment of breeding time or evolution. To date, few studies have investigated these processes in Arctic environments, where temperature is rising at a greater rate than the global mean. I evaluated the contribution of behavioural adjustment of breeding time and evolution to changes in breeding time associated with annual variation in snow melt and female breeding age over a 42-year dataset from an Arctic population of Black Guillemots (*Cepphus grylle mandtii*). I used an Animal Model to decompose the variance observed in breeding time and I used three fitness metrics in a bivariate Animal Model to estimate selection on clutch initiation DOY. Finally, I examined the temporal trend in the genetic component of variation in clutch initiation date to determine if evolution contributed to the shift in breeding time. During the study period mean clutch initiation date advanced 7.8 days, snow melt date advanced 7.6 days, and the average female breeding age increased by 4.7 years. Earlier clutch initiation was associated with experienced mothers, earlier snow melt, and higher fitness. Individuals advanced clutch initiation at different rates as they aged but responded similarly to variation in snow melt. Heritability of clutch initiation date was negligible ($h^2 = 0.04$, 95% CI [0.00-0.11]), and there was no evidence of evolution contributing to the change in breeding time. My results suggest that covariation between clutch initiation date and fitness is driven by environmental, but not genetic factors. Consequently, changes of breeding time in Black Guillemots are likely driven by plastic behavioural adjustment with limited potential for evolutionary change.

CO-AUTHORSHIP

Chapter 2

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Drew M. Sauve   Organized banding data into a pedigree, performed all statistical analyses, and wrote final manuscript

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Vicki L. Friesen   Provided funding, advised on project progression, and edited drafts of the thesis.

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DOY   Day of Year

$COR_{x:y}$ Correlation between x and y

DIC   Deviance Information Criterion

GxA   Genotype by age interactions

GxE   Genotype by environment Interactions

h^2 Narrow Sense heritability

IxA   Individual by age interactions

IxE   Individual by environment interactions

E_P^2 Proportion of variance explained by permanent environment effects

r^2 Proportion of variance explained by among individual variation (repeatability)

R^2 Marginal Coefficient of determination

STS   Secondary theorem of selection or Robertson-Price Equation

USDI   United States Department of Interior (includes United States Fish and Wildlife and United States Geological Survey)

V_A Additive Genetic Variance Component

V_E Residual Variance Component

V_I Among Individual Variance Component

V_{E_P} Permanent Environment Variance Component

V_{Year} Interannual Variance Component

CHAPTER 1-GENERAL INTRODUCTION

Climate change has led to widespread changes in organism phenotypes (Parmesan 2006; Merilä and Hendry 2014). Rapid phenotypic responses associated with climate change have led to excitement that populations may be evolving in response to climate change on observable timescales (Merilä 2012). However, many phenotypic changes could be explained by phenotypic plasticity, patterns of which are understudied in wild populations (Merilä 2012; Charmantier and Gienapp 2014; Gienapp and Brommer 2014). Understanding the drivers of phenotypic change in wild populations involves characterization of both plastic and evolutionary responses to environmental change.

Mechanisms of Phenotypic Change

Phenotypic plasticity is the range of phenotypes a single genotype expresses across different environmental conditions and is widespread for most measured traits. It is commonly characterized as a genotype level function of the environment called a reaction norm, which in its simplest form is a linear function of a phenotype (from a single genotype) in response to environmental conditions (Dingemanse et al. 2010). Reaction norms are often described for labile traits, but because the same genotype may express a range of phenotypes under different developmental conditions a fixed invariant trait can also have a reaction norm (West-Eberhard 2003; Dingemanse et al. 2010). For example, genetically identical strains of *Polygonum persicaria* can express different leaf biomass in response to different light conditions (Sultan 2017). Because almost all phenotypic traits are plastic, phenotypic plasticity may explain most observed phenotypic change (West-Eberhard 2003; Anderson et al. 2014; Gienapp and Brommer 2014).

The second way a phenotype could change over time in a population could be through microevolution. Microevolution is a shift of allele frequencies in a population caused by evolutionary processes (selection, genetic drift, mutation, migration). These processes can be inferred through direct observation of changes in molecular markers over time or through quantitative genetic approaches that infer genetic changes in trait means and covariances based on relatedness among individual organisms in a population (Falconer and Mackay 1996; Lynch and Walsh 1998).

Quantitative Genetic Approaches to Predicting Evolutionary Change

Classic approaches that predict phenotypic change use the Breeder's Equation:

$$\Delta \bar{Z} = \sigma_A^2 \beta \qquad (1)$$

where the response ($\Delta \bar{Z}$) of a trait is equal to the product of the trait's additive genetic variance (σ_A^2) and the selection differential (β) (Falconer and Mackay 1996). However, in wild populations, phenotypic plasticity may often cause phenotypic traits to correlate with fitness, but not be under directional selection (Rausher 1991). For example, early breeding is often heritable and associated with high reproductive success in avian systems (Verhulst and Nilsson 2008). Therefore, the Breeder's Equation predicts an advance of the breeding time. However, this advance isn't always observed. Rather the relationship between laying date and fitness could be driven by a plastic response of breeding time to variation in individual nutrition. If it is adaptive for birds that are in a poor nutritional state to lay later the association between fitness and phenology could be driven by an correlation between breeding time and nutrition (Price et al. 1988; Bonier and Martin 2016). This so-called stasis paradox has been documented in many systems, showing that plastic responses may be common in wild populations (Merilä et al. 2001).

For example, in Red Deer (*Cervus elaphus*) larger antlers are associated with increased reproductive success however, no phenotypic change in antler size has occurred over 30 years at the Isle of Rum suggesting that the relationship between antler size and fitness might be affected by an unmeasured trait such as individual nutrition (Kruuk et al. 2002).

To accommodate the influence of multiple variables on trait expression the Breeder's Equation can be expanded to a multivariate form:

$$\Delta \bar{Z} = G\beta \tag{2}$$

where ΔZ is a vector of changes in mean trait values, G is the genetic variance-covariance matrix of these traits, and β is a vector of selection gradients. Importantly, the multivariate Breeder's Equation can control for indirect selection on a correlated trait, but if and only if the trait under selection is included in the processes of estimating of selection gradients. Variables or traits that bias estimates of selection are likely to be environmental and estimating traits such as individual quality that cause these biases will be almost impossible in natural populations.

More generally we can use the secondary theorem of selection (STS) or the Robertson-Price identity to estimate evolutionary change:

$$\Delta \bar{Z} = \sigma_A(z, w) \tag{3}$$

where $\Delta \bar{Z}$ is the expected change in the mean phenotype z between generations, and $\sigma_A(z, w)$ is the additive genetic covariance between a trait (z) and its relative fitness (w) (Robertson 1966). As the STS is a direct estimate of the relationship between fitness and a trait at the genetic level, it gives an unbiased estimate of evolution (Morrissey et al. 2010; Frank 2012; Stinchcombe et al. 2014). The Multivariate Breeder's Equation should agree with the STS when phenotypic

selection is a good representation of selection at the genetic level, but when the STS is applied to natural populations it often predicts phenotypic change in a different direction than the Breeder's Equation (Morrissey et al. 2012; Bonnet et al. 2017; Dobson et al. 2017). For example, for a 10-year study of Snow Voles (*Chionomys nivalis*) the Breeder's Equation predicted an increase in body mass over time and the STS predicted a decrease in body mass over time (Bonnet et al. 2017). Mass did not in fact change over time, suggesting that plastic responses were masking evolutionary change towards smaller voles. Similarly, in a Red Squirrel (*Tamiasciurus hudsonicus*) population in Kluane, Yukon, parturition date appears to covary with nutrition, resulting in the covariation of fitness and phenology at the phenotypic level, but not at the genetic level (Lane et al. 2018). However, in some wild populations, the STS and Multivariate Breeder's Equation yield comparable results. In Netherland populations (Vlieland and Hoge Veluwe) of Great Tits (*Parus major*), the STS and Multivariate Breeder's Equation both suggest evolutionary change should occur for earlier laying date, suggesting phenotypic selection is an unbiased estimate of selection on clutch size and laying date in these populations (Reed et al. 2016).

Both the Breeder's Equation and the STS rely on quantitative genetics to estimate the additive genetic variance of traits. Traditional quantitative genetic techniques were limited to laboratory and agricultural studies where experimental breeding crosses were possible, but statistical techniques developed in the 1950s (Henderson 1950) and computational advances in the late 1990s allowed widespread use of the Animal Model (Kruuk 2004; Charmantier et al. 2014*b*). The Animal Model is a form of mixed model that uses pedigree information to estimate the additive genetic variation of a trait. The Animal Model takes the form:

$$y_i = u + a_i + e_i \tag{4}$$

where y_i is the phenotype of individual i, u is the population mean, a_i is the breeding value of individual i, and e_i is residual error. A breeding value is a value that expresses the additive genetic difference between an individual animal and the population. If we have repeated measures of a trait we can split individual variation into an additive genetic effect and a permanent environment effect:

$$y_{i,t} = u + a_i + pe_i + e_{i,t} \tag{5}$$

where y_i, a_i, and e_i are the same as in the Animal Model above and pe_i is a permanent environment effect (environmental effects that have a persistent effect on an individual's phenotype or developmental plasticity). These models allow estimation of a breeding value or an individual's average genetic contribution to the population (Lynch and Walsh 1998). The variance of the breeding values of a trait is the additive genetic variance of the trait. Trends in the breeding values of a population can be used as a signal of evolutionary change (Hadfield et al. 2010; Houslay and Wilson 2017). However, trends in breeding values need to be used cautiously as they can be very biased towards environmental trends if 1) interannual variation is not included in an Animal Model and 2) error is not carried forward from the estimation of breeding values to the statistical assessment of temporal trends in breeding values. Trends in mean population breeding values have been used in Snow Voles to indicate that individuals are becoming genetically lighter over time, and in Big Horn Sheep (*Ovis canadensis*) to indicate that hunting pressures drive an evolutionary change towards shorter horns (Pigeon et al. 2016; Bonnet et al. 2017).

Including Phenotypic Plasticity in an Animal Model

Quantitative genetic techniques rely on decomposing the variance components of a trait (Falconer and Mackay 1996; Lynch and Walsh 1998). However, if we are interested in the potential for adaptation we also need to evaluate the suite of plastic responses available to a population (Sultan 2015; e.g. Chevin et al. 2010; Anderson et al. 2014). We can incorporate plasticity into a quantitative genetic approach by decomposing the variance of reaction norm components. Using a simple linear reaction norm as an example we would split the intercept and slope of a reaction norm into additive genetic and environmental components. To estimate individual-level reaction norms, we would use:

$$y_{i,t,E} = u + bE_t + f_{ind}(i, x, E_t) + \epsilon_{i,t,E} \tag{6}$$

where u is the fixed effect mean, E_t is the environmental value at observation t, and b is the population level change in mean responses(y) with the environment (E). This model specifies the residual error for each instance of t and value of E ($\epsilon_{I,t,E}$). The function $f_{ind}(i,x,E_t)$ specifies a polynomial of order x at the level of the individual (Gienapp and Brommer 2014). If pedigree information is available, we can extend this model by splitting a trait into additive genetic and permanent environment components:

$$y_{i,t,E} = u + bE_t + f_a(i, x, E_t) + f_{pe}(i, x, E_t) + \epsilon_{i,t,E} \tag{7}$$

where u, y, E_t, and b are the same as in equation 6, and $f_a(i,x,E_t)$ and $f_{pe}(i,x,E_t)$ specify a polynomial function of order x at the level of additive genetic effects or permanent environment effects (Gienapp and Brommer 2014).

If the plasticity (slopes) of these reaction norms have significant additive genetic variation, plasticity is heritable. Importantly, traits may respond faster to environmental change if plasticity itself is heritable (Kopp and Matuszewski 2014). Importantly, GxE interactions could change the heritability of a trait across environmental conditions, but heritability will also depend on how the environmental variance of the trait changes across environments. Evidence from early studies of heritability under favourable and unfavourable environmental conditions suggested that traits were more heritable under favourable environmental conditions (Charmantier and Garant 2005). Most (~70%) of the observed increases in heritability from unfavourable to favourable environments was not due to an increase in additive genetic variance but to decreases in residual variance (Charmantier and Garant 2005). Interestingly, many studies have identified GxE interactions in laboratory experiments of plants and animals, but examples in wild animal populations are scarce (Gienapp and Brommer 2014; Hayward et al. 2017). Patterns of GxE in existing studies of wild animal populations contrast with studies of selection across environmental conditions, which suggest that selection commonly varies across environmental conditions in wild populations (Wood and Brodie 2016; Hayward et al. 2017). If genetic variance does not change across environments but selection pressures do, variance in environmental contributions to a trait and/or selection pressures may be the major determinants of the rate of evolutionary change.

Presence of GxE in experimental, but not in natural populations suggests that patterns are difficult to detect in natural populations and we are unable to detect patterns of GxE with current methodology. Alternatively, natural conditions may not be extreme enough for GxE interactions to be observed. Climate change may reveal more GxE interactions in wild populations as it continues to alter environmental conditions. If we wish to predict how genetic variation changes

with climate change, more experimental studies replicating climate change conditions will be necessary.

How Might Plasticity Interact with Evolution?

Traditionally evolutionary biologists thought plasticity did not play a significant role in evolutionary responses, but more recent theory suggests it may potentially help evolutionary responses. Whether phenotypic plasticity assists evolutionary change is contingent on how adaptive plastic responses are under novel environmental conditions (Ghalambor et al. 2007). Adaptive plasticity increases an organism's fitness across environmental conditions. In the context of novel environmental conditions, adaptive plasticity moves the organism's phenotype closer to the new fitness optimum. Under conditions where plasticity is adaptive but does not entirely match a new environment, it may allow populations to persist long enough for new genetic variants to arise and respond to selection (Baker 1974; West-Eberhard 2003; Pfennig et al. 2010). For example, two benthic and limnetic stickleback species (*Gasterosteus* spp.) that were fed each other's diet became phenotypically similar to each other (Day et al. 1994). Plasticity could be flexible enough to allow an organism to match its phenotype completely to the new fitness landscape. In this case evolutionary change may not occur because plasticity will mask genotypes from selection.

Maladaptive Plasticity

Plastic responses to novel environmental conditions may reduce fitness (Ghalambor et al. 2007; Reed et al. 2010; Morris and Rogers 2013). For instance, freshwater snails (*Physella virgate*) raised in the presence of fish exhibit the same phenotypic response whether fish are molluscivorous or non-molluscivorous (Langerhans and DeWitt 2002). The response is adaptive

in the presence of molluscivorous fish as it increases the probability of survival, but maladaptive in response to non-molluscivorous fish because it reduces fecundity without any benefit. Similarly, observations at a colony of Common Terns (*Sterna hirundo*) in Lake Bant, Germany indicate that plasticity is maladaptive. Terns are delaying breeding time in response to poor foraging conditions during the non-breeding season, which is resulting in later mean laying dates over 17-years despite possible genetic-level selection for earlier breeding (Dobson et al. 2017). While reduced fitness may lead to an increased probability of extinction, the evolutionary consequences of maladaptive plasticity are not always certain. Maladaptive plasticity could potentially increase the speed of adaptation by exposing to selection phenotypes that are only expressed under stressful conditions. In Atlantic silversides (*Menidia menidia*) maladaptive plasticity has lead to the evolution of faster intrinsic growth rates in northern populations (Conover and Present 1990). Northern and southern fish have the same body size in their respective environments, but in a common garden the northern populations grow faster and to a larger size, suggesting the evolution of compensatory genetic responses in northern populations.

Whether plasticity is adaptive or maladaptive, we still do not know how it will interact with evolutionary processes. Empirical evidence suggests that both maladaptive plasticity and adaptive plasticity are common (Hendry 2016). Plasticity is beginning to be incorporated into predictive models of population persistence, but we are far from being able to predict population outcomes in wild populations (Chevin et al. 2010, 2013)

Senescence and Age-Related Change

Changes in trait variation could also occur over an organism's lifespan. Many iteroparous animals exhibit initial increases in reproductive success over their lives followed by a plateau and eventual decline in fitness, and many studies have found evidence of changes in genetic

variation with age (Charmantier et al. 2014*a*). But, many of these studies used statistical techniques that can upwardly bias variation explained by genotype by age (GxA) interactions. Many studies fixed residual variances or did not estimate individual by permanent environment effects, both of which could inflate estimates of GxA. Observations of GxA interactions are widespread in laboratory populations, but if we exclude studies of wild animal populations that possibly inflate estimates of GxA, little evidence for GxA exists in wild populations (Charmantier et al. 2006*a*, 2014*a*). Additionally, numerous studies have identified environmental effects of early life conditions that predict rates of senesence later in life. Therefore, if we are to gain an understanding of the ubiquity of GxA interactions in wild populations (and whether they influence evolution), we need to reanalyze existing datasets using updated practices, and to design more studies testing for the presence of GxA.

Phenology and Climate Change

A widespread phenotypic change in response to climatic change is the advance of breeding time (phenology) (Parmesan 2006). Phenological shifts tend to occur more rapidly at lower trophic levels, causing mismatches between higher and lower trophic levels (Stenseth et al. 2002; Both et al. 2009). Populations unable to track shifts in resources often experience fitness declines (Moller et al. 2008). Therefore, the ability of populations and individuals to change reproductive timing in response to climate change can affect population demographics. Broadly, change in phenology could occur through phenotypic plasticity or microevolution. Evolutionary processes are likely to be important when the scale of environmental change outpaces the plastic potential of a trait. Phenological traits are often plastic, but evidence for heritability of these responses is rare (Gienapp and Brommer 2014; Hayward et al. 2017).

Age and Phenology

In addition to altering phenology to match environmental cues in a given season, iteroparous individuals may adjust their breeding time over their lives due to senescence and experience (e.g. Lewis et al. 2012). Adjustments over individuals' lifespans could have important implications for population growth. For example, if experienced individuals breed earlier and early breeding is associated with higher reproductive success, as it is in many populations (Verhulst and Nilsson 2008), a population with a higher proportion of experienced breeders may have higher population growth. Further, genetic variation in the adjustment may mean that traits may be more heritable at different life stages (Charmantier et al. 2014*b*), which also may affect the evolution of a trait. Importantly, in organisms that form long-term pair bonds the breeding experience of a mate may also affect the timing of reproductive events (e.g. Whelan et al. 2016).

Early breeding date often correlates with reproductive success in avian systems. Correlations of breeding time and fitness could be a direct effect of environmental conditions, individual quality, or both (Verhulst and Nilsson 2008). If most breeding time variation is the result of individual quality, breeding time will not evolve (Price et al. 1988). As with any trait, to assess whether microevolution contributes to phenological change over time, plastic phenological responses need to be separated from evolutionary responses.

Constraints on Breeding Time at High Latitudes

Organisms living at high latitudes may be constrained in their timing of breeding because of shorter breeding seasons. For example, in Emerald Damselflies (*Lestes sponsa*) additive genetic variance for life history traits declines with increasing latitude (Sniegula et al. 2018). Strong historical selection associated with a constrained breeding season might have eroded

genetic variation related to the timing of life history events. As genetic variation for the timing of breeding is limited, organisms living at high latitudes might rely on plastic changes to adjust to interannual variation. Therefore, Arctic-breeding species may need to be particularly plastic in response to conditions on their breeding grounds (Wingfield and Hunt 2002; Charmantier and Gienapp 2014).While many studies have identified variation among individuals in responses to environmental variation, these studies are biased towards lower latitudes (Both et al., 2009; Brommer et al., 2008; Charmantier et al., 2008).

Study System and Objectives

Few studies have investigated phenotypic variation associated with climate change in species resident in the Arctic. Therefore, I focussed on a long-term dataset of breeding phenology in Mandt's Black Guillemots (Charadriiformes : Alcidae : *Cepphus grylle mandtii*) on Cooper Island, Alaska. Black Guillemots are medium (~400g) sized alcids with a circumpolar distribution. Black Guillemots breeding on Cooper Island belong to the subspecies *mandtii* which appears to be adapted to high Arctic conditions (Divoky et al. 2015). Tracking data from geolocators from Mandt's B.G. on Cooper Island suggest they remain in the Arctic year-round and track prey species along the sea ice edge (Divoky et al. 2016), and molecular genetic work suggests that the subspecies is genetically distinct from other subspecies at both mitochondrial and nuclear loci (Kidd and Friesen 1998; Harkness, 2017). Investigations of the genetic and environmental contributions to clutch initiation date in this subspecies gives a unique perspective of patterns of phenotypic plasticity and genetic variation in a phenological trait. Long-lived species such as guillemots provide powerful systems to study plasticity because repeated measures of labile traits can be made over the lifespan of an individual. However, a disadvantage is that power to estimate additive genetic variance comes from kinship, and organisms with long

generation times take many years to generate observations of relatives. The extensive data collection on Cooper Island over 43-years (Divoky 1998) provides a rare dataset that can be used to estimate quantitative genetic parameters in a long-lived Arctic organism.

I had three main goals for my thesis: 1) test whether individuals vary in timing of reproduction either in response to snow melt or with age, and whether responses are heritable; 2) assess the relationships between fitness and phenotypic, environmental, and genetic components of clutch initiation and plasticity of clutch initiation; 3) determine the amount of phenotypic change in clutch initiation date that can be explained by plastic versus evolutionary responses over time. I tested a range of hypotheses related to plasticity of clutch initiation (Table 1) and selection acting on clutch initiation (Table 2). Lastly, I evaluated the contribution of plasticity to clutch initiation date by using the slopes in population plasticity and evaluated the contribution of microevolutionary change to clutch initiation date by examining temporal trends in breeding values for clutch initiation date.

Table 1: Hypotheses tested to explain variation in clutch initiation date of Black Guillemots.

Hypothesized Effect	Prediction
1. Snow melt either limits or acts as a cue for clutch initiation date. Individuals lay earlier when snow melt is earlier.	Snowmelt correlates with timing of reproduction
2. Experienced females lay earlier as they age because of experience or changes in reproductive strategy.	Breeding experience correlations with the timing of reproduction
3. Genetic and/or environmental differences result in differences in responses to variation in snow melt.	Individuals vary in plastic responses to snow melt
4. Genetic and/or environmental differences cause individual variation in rate of clutch initiation date adjustment with experience	Individuals vary in the adjustment of clutch initiation date with experience
5. Genetic differences result in differences in response to snow melt	Plastic responses to snow melt are heritable
6. Genetic differences result in variation in rate of clutch initiation date adjustment with experience	Adjustment of clutch initiation date with breeding experience is heritable

Table 2: Hypotheses to test for selection on clutch initiation date and plasticity of clutch initiation date at phenotypic, environmental, and genetic levels in Black Guillemots.

Hypothesized Effect	Prediction
7. Individuals who lay earlier have higher fitness	Environmental variation and/or genetic variation covaries with variation in fitness
8. Clutch initiation date covaries with relative fitness at the residual level.	Association of clutch initiation date and fitness is driven by environmental factors (such as individual nutrition).
9. Additive genetic variance in clutch initiation date covaries with additive genetic variance in fitness	Individuals who are genetically predisposed to laying early have increased fitness.

CHAPTER 2 METHODS

Study System

I used 42 years (1976-2017) of data on individual reproduction from a colony of banded Mandt's Black Guillemots (Divoky et al. 1974, 2015). The colony is located on Cooper Island (71° 20′ N, 155° 41′ W), a sand and gravel bar 35 km southeast of Point Barrow, Alaska. Individual life histories are available for most of the birds breeding at the colony. Every chick fledging from the colony is banded with a United States Department of Interior (USDI) numbered aluminum or stainless-steel band before fledging and given a unique colour ring combination when captured as an adult. Recruiting immigrants are banded with a USDI band and a unique color combination at first capture.

All Black Guillemots on Cooper Island nest in manmade nest cavities, whereas guillemots at most other populations nest in natural cavities in scree or talus along rocky shorelines (Harris and Birkhead 1985). Nest sites were created by investigators from 1975-1986, allowing the colony to grow from 10 breeding pairs in 1972 to 220 in 1988. The colony has since declined to 84 pairs in 2017 and the number of available nest sites have remained constant since 1986. In the majority of years daily nest checks starting in early June continued until 90 percent of chicks had fledged. Clutch initiation was reported as the date an egg was found at a nest site. The identity of the pair breeding at a nest site was determined by direct observation or images from motion-sensitive cameras. Nest-site ownership was determined by observations of individuals regularly attending and defending a site, incubating eggs, or feeding nestlings. The pair-bond status of the owners was confirmed through observation of courtship behaviours and copulations (Divoky 1998).

Pedigree Construction

I constructed a social pedigree (using an R script) by matching the parents entering a nest box (individuals breeding at a site) with the chicks fledging from that site each year. The social pedigree is arguably a good approximation of the genetic pedigree in this species because Black Guillemots in northern Norway exhibit low rates of extra-pair paternity (0 observed occurrences with an upper limit of 6.2%) (Anker-Nilssen et al. 2010). Behavioural observations of nest defense, nest attendance, and copulations were used to sex individuals. During the pre-breeding period, male guillemots remain at nest sites later in the daily period of colony attendance than females do (Nelson 1987) and are typically involved in nest-site defense. Female breeders have greatly reduced nest attendance during egg formation, and reverse mounting (female superior) is not common in the genus. In addition to behavioural sexing, 60 birds were sexed genetically (Griffiths et al. 1998). Mates paired with behaviourally or genetically sexed individuals were scored as the opposite sex. Fifty-nine of the 60 birds that were sexed genetically matched the behavioural observations of sex. I pruned the pedigree using the 'pedantics' R package 'prune' function to mothers with known clutch initiation days (Morrissey and Wilson 2010). The pruned pedigree included 1000 mothers with 204 known maternities, 204 known paternities, 61 maternal siblings (37 full siblings, 24 half siblings), 53 paternal siblings (37 full siblings, 16 half siblings), 37 maternal grandmothers, 38 maternal grandfathers, 60 paternal grandmothers, and 61 maternal grandfathers.

Changes in Clutch Initiation and Predictor Variables

I used unstandardized clutch initiation date for all univariate Animal Models and plasticity analyses. Clutch initiation date was scored as the Day of the Year (DOY, Jan 1st = 1) of

the first egg laid and did not include relay attempts. Snow melt data was collected from a nearby weather station in Utqiagviq, Alaska (Temperature Station, http://climate.gi.alaska.edu/acis_data; 71°N, 156°W, 40km from Cooper Island) and was converted to DOY and mean centered (mean snow melt date was subtracted from each observed snow melt date). The date of snow melt was defined as the date at which snow depth was reported as zero. I estimated breeding experience as the number of years since an individual first bred at the Cooper colony (Rattiste 2004; Brommer et al. 2008). I excluded founding (birds discovered in 1975) individuals from the analysis, because the breeding experience of founding individuals banded at the beginning of the study is unknown. I only included mothers with known clutch initiation dates and fitness estimates in downstream analysis. I tested changes in mean clutch initiation date, snow melt date, and mean breeding experience over time by running each variable in a linear model as a function of year of the study. Because there was a shift in the Arctic Oscillation in 1989 to a warmer phase, which resulted in a step change in atmospheric conditions, I also tested for a shift in mean snow melt between 1975-1988 to 1989-2017 (Overland and Adams 2001). Changes over time were evaluated in linear models (without any random effects) implemented in the R package 'MCMCglmm' (Hadfield 2010). Confidence intervals (CI, 95%) and pMCMC values were used to evaluate significance of slopes.

Individual and Additive Genetic Variation in Clutch Initiation

I fit linear mixed models using a Bayesian framework implemented in the R package MCMCglmm (Hadfield 2010). MCMCglmm uses Gibbs sampling, slice sampling, and Metropolis-Hastings updates to stochastically move through parameter space to estimate the posterior distribution of a parameter (Gelman 2006; Hadfield 2010). Priors for univariate and multivariate models are specified below, but in all cases I used parameter expanded priors

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because these priors allow the estimation of variance components close to zero. I did not use default priors because they partitioned the variance equally among all variance components in the model. Parameter expanded priors speed up the convergence and mixing properties of a chain by introducing parameters that are not identified in the likelihood. These priors are from the non-central scaled F-distribution (Gelman 2006).

I assessed whether the variance of random effects was significant by comparing the deviance information criterion (DIC) of all possible combinations of random effects. I tested random effects of dam, sire, and year. Random effects in this case are predictors for which the variance is estimated in the model instead of being fixed to a large value (as is the case for fixed effects) (Hadfield 2010). I assessed the random effect structure in models with and without fixed effects. I selected the random effect structure resulting in the lowest DIC. Confidence intervals of variance components cannot be used to assess significance of effects because they are constrained to being positive in MCMCglmm (Hadfield 2010). However, I rounded variance components to the nearest hundredth of a decimal point and estimates below 0.01 were reported as 0.

Only random intercepts were evaluated in the initial evaluation of among individual and additive genetic variance. After the random effect structure was selected, I split the among dam variance into permanent environment and additive genetic components by including pedigree information in a mixed model framework (Lynch and Walsh 1998; Kruuk, 2004; Wilson et al., 2010). Decomposing among individual variation is done by retaining the random effect of individual identity (dam in this case) and adding an additive genetic effect that estimates covariation among individuals based on the relatedness information in a pedigree. Once an additive effect is included in the model, the individual component now represents permanent

environmental effects, or any persistent effects that are not from genetic variation shared among relatives. Significance of repeatability and heritability was determined by whether addition of individual or additive genetic variance components improved model fit (resulted in a decrease in DIC values). I included fixed effects of male breeding experience, female breeding experience, snow melt date, and mate status (first time breeding, mate switched from previous year, or mate retained from previous year) to control for breeding experience, snow melt, and mate switching effects on clutch initiation date.

I used pMCMC values to estimate the significance of fixed effects. Fixed effects of female breeding experience and snowmelt were separated into within and among individual components to control for non-independence of predictor variables (van de Pol and Wright 2009). Within individual components were calculated by subtracting each snowmelt date an individual experienced by the average snowmelt date an individual experienced, and between individual effects were calculated as the mean snowmelt date an individual experienced. Separation of within and among individual fixed effects is necessary because while random effects in a mixed model control for among individual effects in the response, fixed effects do not necessarily represent within-individual effects (van de Pol and Wright 2009). This is particularly true in studies of wild populations where the range of environments an individual experiences is not controlled.

I ran all models with a burn-in period of $5x10^7$ iterations followed by a $4.5x10^8$ iterations with a thinning interval of 1000. Parameter expanded priors ($V = 1$, $v = 0.002$, $\mu_\alpha = 0$, $V_\alpha = 1000$) were used to allow estimation of variance components close to zero (Hadfield 2010). I visually inspected the variance component chains to determine convergence of the MCMC sampling and checked to make sure autocorrelation between variables was less than 0.05. I determined that the

chain had converged when there was no trend in the time-series of the sampled posterior distribution.

Plasticity of Clutch Initiation

I tested for among individual variation in responses by fitting models that allowed slopes to vary among individuals and comparing DIC values to models fit with just random intercepts (Table 1; Hypotheses 1-4). I allowed slopes to vary among individuals by adding an interacting fixed effect of female breeding experience or snowmelt date with the among individual component of variance. Individuals with only one observed clutch initiation date were retained in the analysis as these observations can improve the power to estimate individual variance in plasticity (Martin et al. 2011). I fit the random slopes models with unadjusted snowmelt DOY and years of breeding experience, or an interaction between both terms. Significance of random slopes was evaluated by determining whether model fit improved (measured as a lower DIC) when a random slope effect was added and compared to a model without the random slope. If individual level reaction norms were significantly different from the population response, I tested whether random slopes at the additive genetic level were different from the population slope while retaining random slopes at the permanent environment level (Table 1; Hypotheses 5&6). This was evaluated by first testing the significance of the interaction between the fixed effect of interest with the permanent environment variance component first and then testing the significance of the interaction between the fixed effect of interest and the additive genetic variance component.

Selection on Clutch Initiation

I fit six bivariate models in MCMCglmm to estimate the covariance between aspects of fitness and clutch initiation date. I estimated fecundity using the annual sum of fledglings (0,1,2), and the annual sum of recruits (0,1,2). I scored recruits as breeding adults that returned to Cooper Island. I used annual survival to the next year (0,1) to estimate survival. Annual measures of fitness were mean standardized within their respective year. Annual recruit estimates do not distinguish individuals that have permanently emigrated from those that have died. However, for my investigation I was interested in recruitment at a population level. Emigration and death have the same consequences at the population level of analysis.

Clutch initiation date was scaled to units of standard deviation to allow for convergence of these models. Bivariate models allow the estimation of covariance between two responses at separate random effect levels. I evaluated the significance of (co)variance terms by whether they overlapped zero. Covariance terms can be evaluated by confidence intervals because they are not constrained to positive values like variance terms. I evaluated covariance at among individual, permanent environment, additive genetic, and residual levels (Table 2; Hypotheses 7-9). I first ran three mixed models with each of the fitness metrics covarying with clutch initiation date at the among individual level. Next, I ran three Animal Models with each fitness metric (fledglings success, recruits, and survival) covarying with clutch initiation DOY at the additive genetic and permanent environment levels.

I ran all bivariate models with a burn-in period of 5×10^7 iterations followed by 9.5×10^8 iterations with a thinning interval of 1000. Parameter expanded priors (V = $\begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$, $\nu = 0.002$, $M_\alpha = (0,0)$, $V_\alpha = \begin{bmatrix} 1000 & 0 \\ 0 & 1000 \end{bmatrix}$) were used to allow estimation of variance components close to

zero (Hadfield 2010). I visually inspected the variance component chains to determine convergence of the MCMC sampling and checked to make sure autocorrelation between variables was less than 0.05. I determined that the chain had converged when there was no trend in the time-series of the sampled posterior distribution.

Plastic and Evolutionary Contributions to Changes in Phenology

To determine the contribution of 1) plastic responses to snowmelt date and 2) breeding experience to changes in phenology, I multiplied the slopes for snowmelt date, female breeding experience, and male breeding experience estimated in the univariate linear models by the estimated mean population level change over time for each variable. For example, if my analysis suggests clutch initiation date advances 0.4 days for every day that snowmelt advances, and snowmelt has advanced 4 days over the study period, I would conclude that 1.6 days of the advance in clutch initiation date might be driven by an advance in snowmelt. Similarly, if a trend in breeding values exists I can use the slope of this trend to estimate the contribution of evolutionary change to the observed phenotypic change. For example, if the change of breeding values is equal to 0.01 days per year we could multiple this by the number of years of observation (42 years) to conclude that 0.42 days of the observed phenotypic trend might be due to a change in allele frequencies in the population.

CHAPTER 3-RESULTS

Changes in Clutch Initiation and Predictor Variables

The data set included 3751 records of clutch initiation and annual fitness measures from 1000 mothers (mean number of records per female = 3.75, range = 1-21). The mean clutch initiation DOY across all years was 179.9 (95% Confidence Interval (CI) [179.0,180.7]). During the study period mean clutch initiation DOY advanced 7.8 days (N = 42, β = -0.19 CI[-0.27, -0.12] days per year, pMCMC<0.001, R^2 = 0.42; Figure 1A), snowmelt DOY advanced 7.6 days (N = 42, β = -0.22 CI[-0.47, 0.03] days per year, pMCMC = 0.08, R^2 = 0.07; Figure 1B), and average female breeding experience increased by 4.7 years (N = 42, β = 0.12 CI[0.10, 0.14] years per year, pMCMC<0.001) R^2 = 0.82; Figure 1C). Because known-age females varied in their age at first breeding (mean: 5.02, range:2-13 years) I tested for an effect of female age at first breeding on clutch initiation DOY. Using a subset of the data with known-age birds, after controlling for male breeding experience and snowmelt DOY I found that older females laid earlier (N = 201, β = -0.40 days per year, CI[-0.80, 0.04], pMCMC = 0.06, R^2 = 0.17). The increase in breeding experience may be the result of a decrease in the proportion of first time breeders on Cooper Island over time (Males, N = 43, β = -0.77% CI[-1.0%, -0.4%] per year, pMCMC<0.001, R^2 = 0.44; Females, β = -0.81% CI[-1.1%, -0.5%] per year, pMCMC<0.001, R^2 = 0.42; Figure 1A). The change in snowmelt DOY was not statistically significant, likely because of high interannual variation, but from 1990 to 2017 the average snowmelt DOY was 7.3 (CI[1.2, 13.0], pMCMC = 0.02) days earlier than the snowmelt DOY during 1975 to 1989.

Individual and Additive Genetic Variation in Clutch Initiation

In models including fixed effects, clutch initiation DOY was significantly repeatable (r^2 = 0.14; CI [0.11-0.17], V_I = 3.1; CI [2.3,3.8]; Table 3). But adding an additive genetic component

to univariate models including fixed effects did not improve model fit (h^2 = 0.04; CI [0.0-0.11], V_A=0.9; CI [0,2.2]; Table 3). Similarly, repeatability of clutch initiation DOY was significant in models with only random effects (r^2 = 0.11; CI [0.07-0.14], V_I = 3.4; CI [2.5,4.2]; Table 3), but clutch initiation DOY was not significantly heritable (h^2 = 0.03; CI [0.0-0.09], V_A = 0.07; CI [0.0,2.6]; Table 3). Only models without fixed effects had a significant (but small) proportion of the phenotypic variance explained by permanent environment effects (E_P^2 = 0.09; CI [0.02-0.14], V_{E_P} = 2.6; CI [0.6-4.14]; Table 4). In models both with and without fixed effects, random effects of year and mate improved model fit and were included in the final model of clutch initiation DOY (Table 3). In all models most of the variation in clutch initiation DOY was explained by interannual variation and residual variation (Table 4)

Plasticity of Clutch Initiation

Both within and among individual fixed effect components of breeding experience and snowmelt DOY were associated with clutch initiation DOY (Table 5). Early snowmelt correlated with earlier clutch initiation, and females that experienced earlier average snowmelt DOY over their breeding lives laid earlier (Table 5). Females laid earlier as they age, and females that bred for more years laid earlier (Table 5). Individuals advanced clutch initiation DOY at different rates as they aged (Figure2A, B; Table 3; Table 4) but similarly in response to snowmelt (Figure 2C, D). Further, females who laid earlier when inexperienced tended to advance clutch initiation DOY more slowly than those who laid late when inexperienced ($COR_{int:slope}$ = -0.82; CI [-98.2,-64.2]). As my estimate of additive genetic variance was small and did not improve models based on DIC (Table 3) I did not test for heritability of within-individual plasticity of breeding experience.

Figure 1: Variation during the study period (1978-2017) in A) clutch initiation DOY of Black Guillemots on Cooper Island, Alaska, B) snowmelt DOY at a temperature station 40km from Copper Island in Utqiagviq, Alaska, and C) mean years of Black Guillemot female breeding experience. Lines of best fit from linear regressions are displayed.

Table 3: Comparisons of random effects structure and associated Deviance information criteria (DIC) of models saturated with fixed effects and those without any fixed effects (mean only). Fixed effects models include all tested fixed effects (within female and male breeding experience, within female snowmelt DOY, among female breeding experience, among female snowmelt DOY, and mate status). Models are in increasing order of DIC value.

Random effects structure	Fixed effect DIC	Mean only DIC
~(breedexp|dam)+(1|sire)+(1|year)	21921.76	NA
~(breedexp*snowmelt|dam)+(1|sire)+(1|year)	21958.43	NA
~(1|dam)+(1|sire)+(1|year)	21960.09	22088.87
~(1|dam)+(1|animal)+(1|sire)+(1|year)	21962.03	22090.37
~(snowmelt|dam)+(1|sire)+(1|year)	21962.44	NA
~(1|dam)+(1|year)	22065.89	22199.13
~(1|dam)+(1|sire)	22950.83	23951.17
~(1|dam)	23029.33	24036.85

Table 4: Variance components estimated from mixed effect models with only an individual component (Model = Ind) and from models with individual effects split into additive genetic and permanent environment effects (Model = Gen). Models are further split into models that exclude fixed effects (Fixed Effects = Mean) and models that include all fixed effects (Fixed Effects = All). Raw variance components for individual (V_{Ind}), additive genetic (V_A), permanent environment (V_{E_P}), interannual variation (V_{Year}), mate effects (V_{Sire}), and residual variance (V_E) are presented. The proportion of variance explained (posterior distribution of each variance component divided by the total phenotypic variance) by among individual variation (Ind^2), additive genetic (h^2), permanent environment (E_P^2), interannual variation ($Year^2$), and among mate variation ($sire^2$) for each model is displayed. Numbers in parenthesis are 95% confidence intervals. NA indicates that the component was not evaluated in that model.

Model	Fixed Effect	Mean	V_{Ind}	V_A	V_{E_P}	V_{Year}	V_{Sire}
Ind	Mean	179.1 [177.9,180.2]	3.4 [2.5,4.2]	NA	NA	14.0 [8.3,20.8]	1.6 [1.0,2.3]
Ind	All	180.1 [179.2,181.0]	3.1 [2.3,3.8]	NA	NA	6.3 [3.6,9.6]	1.3 [0.7,1.9]
Gen	Mean	179.1 [178.0,180.3]	NA	0.7 [0.0,2.6]	2.6 [0.6,4.15]	14.1 [8.0,20.9]	1.6 [1.0,2.3]
Gen	All	180.1 [179.2,181.0]	NA	0.9 [0.0,2.2]	2.2 [0.1,3.4]	6.3 [3.7,9.5]	1.3 [0.7,1.9]

Model	Fixed Effect	V_E	Ind^2	h^2	E_P^2	$Year^2$	$sire^2$
Ind	Mean	12.75 [12.1,13.5]	0.11 [0.08,0.13]	NA	NA	0.42 [0.33,0.55]	0.05 [0.03,0.07]
Ind	All	12.4 [11.8,13.1]	0.13 [0.10,0.17]	NA	NA	0.26 [0.18,0.37]	0.05 [0.03,0.08]
Gen	Mean	12.75 [12.1,13.5]	0.10 [0.07,0.14]	0.03 [0.0,0.09]	0.09 [0.02,0.14]	0.42 [0.33,0.55]	0.05 [0.03,0.07]
Gen	All	12.4 [11.7,13.1]	0.11 [0.07,0.19]	0.04 [0.0,0.11]	0.11 [0.0,0.15]	0.26 [0.18,0.37]	0.05 [0.03,0.08]
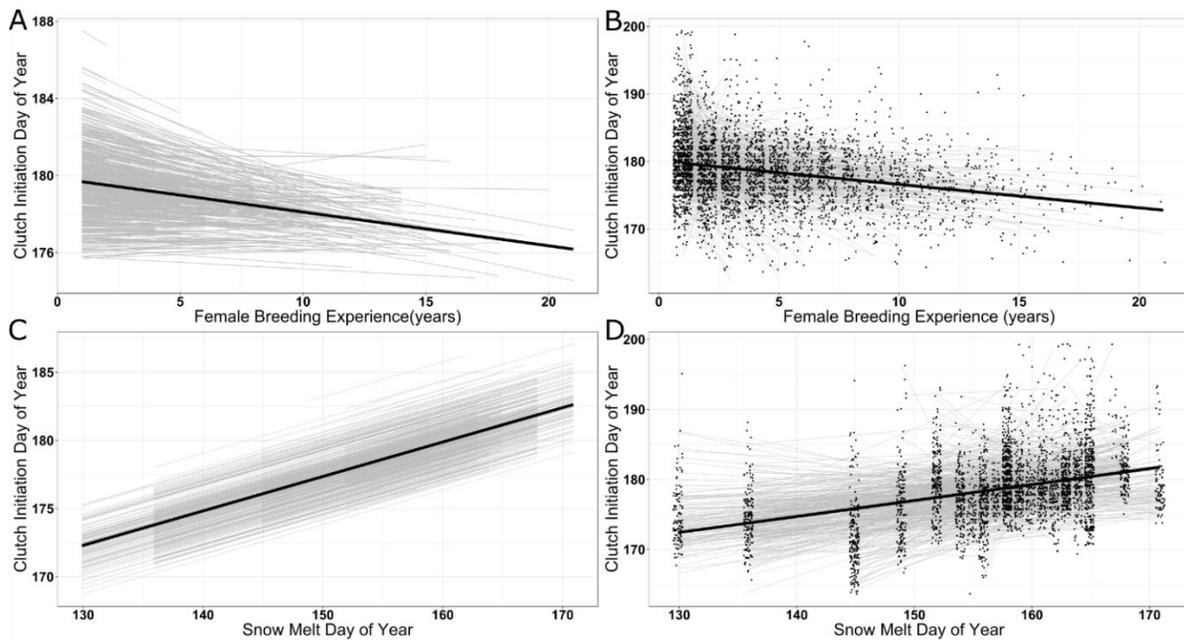
Figure 2: Model predicted and raw variation of clutch initiation DOY of female Black Guillemots predicted by years of female breeding experience (A,B) and snow melt DOY (C,D). Each individual grey line is the clutch initiation of a single female and the thicker black line is the population level variation. Partial regressions from model predicted clutch initiation dates are displayed on the left (A,C) and raw variation of clutch initiation dates are plotted on the right (B,D). Y-axis of partial regression predictions are on different scales to highlight variation in predicted responses (A,C).

Table 5: Final model including fixed and random effects used to predict clutch initiation DOY

of Black Guillemots on Cooper Island, Alaska.

Term	Estimate	Variance	95% Confidence Intervals
Random Effect			
Year		6.15	3.57, 9.23
Sire		1.39	0.78, 2.02
Dam		4.48	3.01, 5.98
Breeding Experience*Dam		0.03	0.01, 0.06
Residual		12.46	11.81, 13.17
Fixed Effects			
(Intercept)	179.81		178.9, 180.6
Within Female Snowmelt	0.26		0.17, 0.35
Among Female Snowmelt	0.23		0.13, 0.32
Within Female Breeding Experience	-0.14		-0.19, -0.09
Among female breeding experience	-0.26		-0.34, -0.18
Within Male Breeding experience	-0.20		-0.27, -0.14
Among Male Breeding Experience	-0.19		-0.13, -0.22
Mate Status			
Retain	-0.35		-0.61, -0.2
Switch	0.19		-0.18, 0.57

Selection on Clutch Initiation

Bivariate models split into environmental and individual level components gave similar estimates of repeatability as univariate models (Table 5; Appendix Tables A1, A2, A3). My bivariate Animal Models gave a similar estimate of additive genetic variance as univariate models, but with larger confidence intervals (Table 5; Appendix Table 1,2,3). Estimates of additive genetic variance approached zero for both relative annual fledging success ($V_A = 0.02$; CI [0.0,0.06]) and relative annual recruits ($V_A = 0.09$; CI [0.00-0.30]) but was significant for relative annual survival ($V_A = 0.03$; CI [0.03-0.05]). Additive genetic and permanent environment covariance between clutch initiation DOY and all fitness metrics was negligible (Figure 3). Residual covariance was the only significant level of covariance between fitness metrics and clutch initiation DOY (Figure 3).

Plastic and Evolutionary Contributions to Changes in Phenology

There was no significant trend in breeding values for clutch initiation DOY over years (slope = -7.2×10^{-5} days year^{-1}, CI [-0.02, 0.01]; Appendix Figure 2). Therefore, my analysis suggests that a negligible amount of the observed phenotypic change was driven by evolutionary change or a change in breeding values for clutch initiation DOY. Estimates of breeding experience indicate that for every year of female breeding experience, clutch initiation DOY is 0.14 days earlier; for every year of male breeding experience, clutch initiation DOY is 0.20 days earlier; and for every day advance in snowmelt DOY, clutch initiation DOY is 0.26 days earlier. Given an estimated change over the 42 years of study of 4.7 years in mean female breeding experience, 5.0 years in mean male breeding experience, and 7.3 days in snowmelt DOY, changes in female breeding experience, male breeding experience, and snowmelt DOY to

explain 0.66 days, 1 days, and 1.9 days respectively for a total of 3.56 days in clutch initiation.

This is about 45% of the total observed phenotypic change of 7.8 days in clutch initiation DOY.
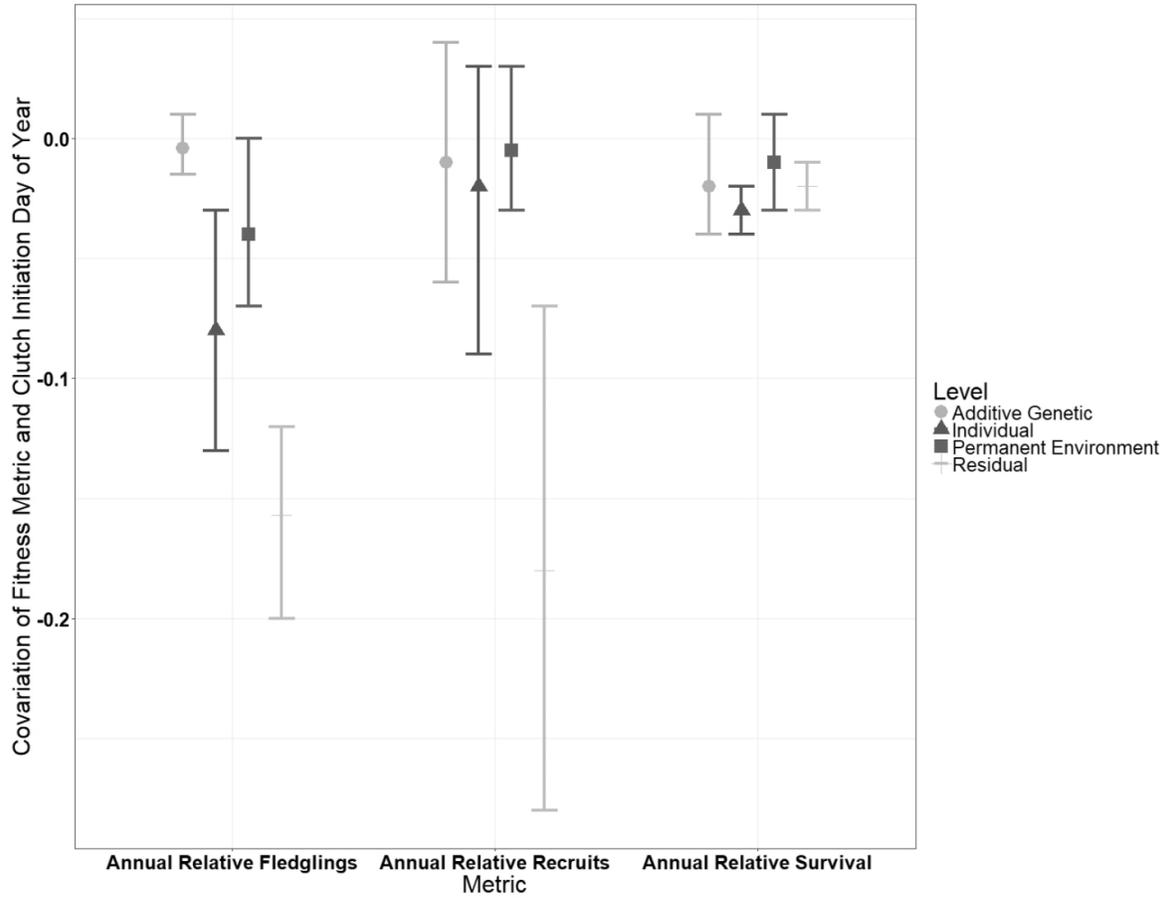
Figure 3: Additive genetic, individual, permanent environment, and residual covariation estimates between clutch initiation and relative annual sum of fledglings, annual relative sum of recruits, and annual relative annual survival of Black Guillemots on Cooper Island, Alaska.

CHAPTER 4-DISCUSSION

Variation in Clutch Initiation

Mandt's Black Guillemots, like many organisms, are adjusting the timing of life-history traits in concert with human-driven climatic changes (Divoky 1998; Parmesan 2006; Cox et al. 2017). The Black Guillemots on Cooper Island have advanced mean clutch initiation by 7.8 days over 42 years of study. While many examples of phenological changes exist, few datasets can characterize the individual responses and genetic changes that underlie these phenotypic changes. To understand how organisms are responding to climate change, these responses need to be characterized in different populations and species. Because the cues used for plastic responses and the selection acting on phenological traits will differ among environments and species, different constraints on responding or potential to respond to climate change will exist (Pujol et al. 2018). My analyses suggest that phenological changes in clutch initiation DOY in Mandt's Black Guillemot represent a plastic, not evolutionary, response to environmental and demographic changes at the Cooper Island colony. My study is the first to decompose plastic and evolutionary contributions to phenology in a high Arctic animal population. I found that, in addition to climatic driven changes in snowmelt, demographic changes in male and female breeding experience predict some of the observed phenological change. However, much of the change in clutch initiation DOY remains statistically unexplained, suggesting that unmeasured traits or environmental variables are affecting clutch initiation DOY in Black Guillemots.

I observed low among individual variation and negligible additive genetic variation in clutch initiation DOY in Black Guillemots on Cooper Island. Low additive genetic variation in clutch initiation DOY has three implications: that natural selection or genetic drift has depleted additive genetic variation for clutch initiation DOY (e.g. Kristensen et al. 2005); that clutch

initiation DOY has limited evolutionary potential; and that most of the variation in clutch

initiation DOY is the result of phenotypic plasticity. Theory predicts that traits closely associated

with fitness will have lower additive genetic variation (Falconer and Mackay 1996; Kruuk et al.

2000). Strong historical selection for phenological timing could have depleted additive genetic

variance for clutch initiation DOY in Black Guillemots. Reduction in variation via genetic drift

or inbreeding is also possible, but the Black Guillemots on Cooper Island do not have lower

genetic diversity at mitochondrial or genome-wide markers than other North American Black

Guillemot populations (Kidd and Friesen 1998; Harkness, 2017). Therefore, the low additive

genetic variance I observed is more likely to be due to historical selection on clutch initiation

DOY rather than low genetic variation caused by a bottleneck or drift.

Most studies of avian phenology have identified a moderate heritability (0.15-0.30) of

phenological traits, and selection experiments on laying date of Great Tits indicate that

evolutionary change of laying date is possible (Postma et al. 2007; Charmantier and Gienapp

2014). Therefore, if genetic selection were operating on phenology there is potential for

evolutionary change (Price et al. 1988; but see, Pujol et al. 2018). However, I observed

negligible heritability or additive genetic variance in clutch initiation DOY of Black Guillemots.

An absence of additive genetic variance in clutch initiation DOY may suggest a limited ability to

adapt via a microevolutionary response to selection. Similarly to the Black Guillemots, studies of

Mute Swans (*Cygnus olor*) and Red-Billed Gulls *(Chroicocephalus novaehollandiae scopulinus)*

report heritabilities of zero for laying date, suggesting limited evolutionary potential in laying

date in these species (Charmantier et al. 2006*b*; Teplitsky et al. 2010). Consequently, the

proportion of variation in clutch initiation DOY caused by variation in additive genetic variation

is minor. Any change we observe in these traits over time is likely representative of a plastic adjustment to environmental conditions rather than an evolutionary change.

I found some evidence that among individual variation in clutch initiation is caused by permanent environment effects. This suggests that persistent effects of an individual's environment explain some of the among individual variation observed. For example, permanent environment effects could arise from development conditions or from constant differences in the environment an individual experience (habitat selection). In my analysis, permanent environment effects are only apparent in models without any fixed effects which suggests that these permanent environment effects might stem from fixed effects in my mixed effects models. Permanent environment effects would be captured by the among individual fixed effects included in fixed effects models. For example, an individual that experiences earlier average snowmelts than another individual might have an earlier average clutch initiation.

Snowmelt

Snowmelt DOY predicts some of the clutch initiation DOY variation in Black Guillemots. In Arctic bird species, snowmelt can be a predictor of clutch initiation and a snow-free period during the breeding season is often required for Arctic species to breed (Meltofte et al. 2007; Grabowski et al. 2013; Liebezeit et al. 2014). The relationship between snowmelt DOY and breeding time may exist because snowmelt predicts the timing of food resources. For instance, because snowmelt often predicts insect abundance, insectivorous species may use it as a cue for food abundance (Meltofte et al. 2007). However, the timing of snowmelt may be less likely to be an accurate cue for the timing of fish abundance. As piscivores, Black Guillemots may be less able to use snowmelt as a cue for resource abundance. Alternatively, patterns of snow cover in Utqiagviq, Alaska, indicate that the after the majority of snowmelt occurs, snow

cover is ephemeral until snow accumulation in late August or September (Cox et al. 2017). Therefore, the DOY of first snowmelt may be a good cue for the suitability of nesting habitat. Although, historical records indicate that the area near Cooper Island might not have been snow free long-enough (~80 days) for Black Guillemots to breed until recently (Divoky 1998). Snowmelt DOY may also be related to breeding time because snow cover physically blocks nesting sites. Whether snowmelt is used as a cue or restricts breeding, there would be strong selection against laying when snow still covers the ground.

Strong selection may explain low variation in female responses to snowmelt. In a few long-lived seabird species that have been studied individual females adjust clutch initiation DOY to environmental conditions similarly to each other. In Rock Hopper Penguins (*Eudyptes chrysocome chrysocome*), Common Murres (*Uria aalge*), and Common Terns, strong plastic responses are found at the population level, but there is no among individual variation in these responses (Reed et al. 2006; Dehnhard et al. 2015; Dobson et al. 2017). Because Common Murres are colonial and experience selection for synchronous breeding, strong breeding synchrony might explain the low variation among female responses to environmental conditions in this species (Reed et al. 2006). However, even within a synchronously breeding species different populations display different patterns of variation in female responses to environmental conditions (Reed et al. 2009). Black Guillemots are in the same family as Common Murres (Alcidae) but tend to aggregate in smaller colonies than Murres (Harris and Birkhead 1985). As Black Guillemots are less colonial than many alcids, the constraints of a short breeding season, rather than breeding synchrony, likely explain the consistent, but plastic, response to snowmelt among females.

Breeding Experience

I found that individual Black Guillemots with more years of breeding experience laid earlier. An advance of clutch initiation DOY with breeding experience/age is observed also in other long-lived bird species (Charmantier et al. 2006*b*; Lewis et al. 2012) and two main hypotheses for this advance of breeding time with age have been proposed. An advance could be caused by shifts in reproductive strategies with age (Winkler 1987). Theory suggests that older individuals will invest in immediate reproduction because future reproduction is less certain. Alternatively, advances in clutch initiation DOY could be an indication of increasing experience with age (e.g. Sechley et al. 2014). Whether advances of clutch initiation DOY are caused by a change in reproductive strategy or by increased breeding experience, an increase in the proportion of experienced breeders at a colony suggests that reproductive output of the colony might increase and clutch initiation DOY will advance. Because the number of first-time breeders at Cooper Island has declined (Figure 1A), we might predict an improvement in reproductive output at Cooper Island. However, there has been a decline in breeding success at Cooper Island. This decline has been linked to reduction in the primary prey of Mandt's B.G. and recession of Arctic sea-ice (Divoky et al. 2015). Perhaps, the decline in breeding success would have been more severe had the colony not been composed of a high proportion of experienced individuals.

I showed that not all females advanced clutch initiation DOY at the same rate with experience. Variation in female breeding adjustment with age could be caused by females using different breeding cues or different responses to the same environmental cues (Nager and Noordwijk 1995). However, I did not find evidence for a heritable basis to these differences, as estimates of additive genetic variation approached zero for clutch initiation DOY. Therefore, the

variation in rates of clutch initiation advance is likely environmentally based. Some of the variation in individual adjustment with breeding experience could be caused by variation in the age of first breeding. My analyses on a subset of females indicates that females that lay early when they are naïve breeders tend to advance clutch initiation DOY more slowly with breeding experience. We do not know the ages of many individuals in our dataset, so I cannot account for variation in age at first breeding. If some females breed earlier because they started breeding when older, they are more likely to have a slower advance in clutch initiation DOY over their lives while females that breed while young might have a more rapid advance of clutch initiation DOY with breeding experience. Unaccounted for variation in age at first breeding could translate into variation in the rates at which females advance clutch initiation DOY with breeding experience.

Unaccounted for Plastic Responses

Residual variance represented the largest proportion of the variation in clutch initiation DOY. Residual variance is variance in a trait that is caused by an unmeasured trait or measurement error. For example, if individual quality influenced clutch initiation DOY, quality would appear as residual or interannual variation in my model because we have no metric of individual quality. The residual variation is significant because it indicates that ~%42 of the variation we see in clutch initiation DOY is unmeasured individual responses to environmental conditions. In other words, individuals are responding plastically to environmental variables not included in our models.

Phenotypic plasticity is predicted to evolve when organisms experience a broad range of environmental conditions (Ghalambor et al. 2007). Plasticity of a trait then allows an organism to

maximize fitness across a range of environmental conditions. Black Guillemots may have evolved plasticity to cope with the environmental variation they experience over their lives.

Selection on Phenology

Estimates of phenotypic selection on clutch initiation DOY indicate that Black Guillemots that breed earlier have higher fitness than late breeders. My decomposition of this covariance pattern indicates this pattern is a result of statistical covariance at the residual level. Residual covariance indicates that an unmeasured trait affects both fitness and clutch initiation DOY. Residual covariance of fitness and clutch initiation DOY agrees with expectations that apparent selection on fitness could be driven by a trait such as individual quality (Price et al. 1988). The absence of permanent environment covariance suggests that the residual covariance is temporary. The factors that determine individual fitness may be determined by luck rather than persistent difference among individuals. The results of our selection analyses are very similar to a selection analysis of parturition date in Red Squirrels in Kluane, Alaska, where only residual variation was found to underlie phenotypic selection (Lane et al. 2018). However, unlike Black Guillemots, a significant proportion of the variance in phenology was explained by additive genetic variance in Red Squirrels. Therefore, Red Squirrels may evolve if selection operates on phenological traits while Black Guillemots are unlikely to do so.

Mechanisms of Plasticity and the Potential to Adjust Phenology

Phenological advance in Black Guillemots is itself interesting because a review of 145 seabird species indicated that on average seabird populations are not adjusting phenology either over time or in response to sea-surface temperatures (Keogan et al. 2018). A lack of a general response to sea-surface temperature might indicate the inability of seabirds to respond to changes

in sea-surface temperature but a high amount of interannual and residual variation in phenological advances of nonmigratory and short-distance migrant seabird species was identified (Keogan et al. 2018). High interannual and residual variation suggests that unmeasured environmental variables could be driving phenological changes in nonmigratory seabirds. Local environmental conditions not measured in the meta-analysis could explain some of the residual variation. Black Guillemots are one of the resident species included in the study by Keogan et al (2018). I have found that some of this residual variation may indeed be explained by local snowmelt conditions and demographic structure in the population.

Birds use cues such as photoperiod to provide a rough timing mechanism that can be fine-tuned by local conditions to accelerate or delay breeding (Carey 2009). The breeding conditions and local cues that Black Guillemots experience have changed over time on Cooper Island (Divoky 1998; Divoky et al. 2015; Cox et al. 2017). Importantly, while I was able to predict some of the advance in clutch initiation using changes in snowmelt and breeding experience, much of the change in clutch initiation is not explained by my model and is in response to unmeasured cues that are transient or vary interannually. Given that genetic variation for clutch initiation DOY in Black Guillemots is apparently low, a better understanding of the predictors of phenological change in Black Guillemots will come from identification of more environmental cues, investigations of how individuals within the population are responding to these cues, and how the cues are changing or are predicted to change over time.

Conclusions

Anthropogenic climate change is occurring at the same time as widespread phenological changes across taxonomic groups. However, we do not have a thorough enough understanding of the mechanisms animals are using to track these changes. I found evidence that phenotypic

plasticity is the primary mechanism that predicts phenological changes in a long-lived Arctic seabird. This study on phenology of Black Guillemots is joining a majority of research suggesting phenotypic plasticity is the primary predictor of phenological change. Understanding the conservation and evolutionary implications of phenological plasticity will require climate change research to focus on the limits of phenotypic plasticity and its potential interactions with evolutionary processes.

SUMMARY

1. Phenological responses are occurring in concert with anthropogenic climate change and are occurring across taxa and around the globe. Evolutionary and conservation biologists are interested in whether evolutionary change or phenotypic plasticity is driving these phenological responses

2. I used 42 years of banding data for Black Guillemots (*Cepphus grille mandtii*) on Cooper Island, Alaska, to reconstruct a pedigree. Using the pedigree information in an Animal Model approach, I was able to partition the contribution of genetic and environmental factors to variation in clutch initiation DOY. I was able to characterize the individual plasticity in clutch initiation DOY in response to snowmelt DOY and female breeding experience.

3. I found that some of the change in phenology was predicted by patterns of snowmelt and changing demographics in the population, but none could be explained by evolutionary changes. Further, clutch initiation had a negligible genetic component, suggesting historical selection on the trait.

4. Selection analyses indicated that selection was only acting on the residual or environmental component of clutch initiation.

5. My research indicates that phenological changes in Black Guillemots are likely driven by plastic changes with little potential for evolutionary change, and that a further understanding of phenological change in this species will come from investigations of the environmental and interannual determinants of clutch initiation.

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APPENDIX

Table 1A: Estimates of (co)variance and correlations of and between relative annual recruits and clutch initiation DOY for female Mandt's Black Guillemot. Variances are displayed on the diagonal, covariance are below the diagonal, and correlations are above. Year variance, and sire variance was only estimated for clutch initiation DOY. Estimates of residual and individual (co)variance components were estimated in the individual model and additive genetic, permanent environment, and residual (co)variance components were estimated in the additive genetic model.

Individual Model

Variance Component	Clutch Initiation DOY	Relative Annual Recruits
Residual		
Clutch Initiation DOY	0.48 [0.46,0.53]	-0.06[-0.10,-0.02]
Relative Annual Recruits	-0.18 [-0.28, -0.07]	14.26 [13.49,15.02]
Year		
Clutch Initiation DOY	0.27 [0.15,0.42]	0.004[0-0.01]
Individual		
Clutch Initiation DOY	0.14 [0.10,0.17]	-0.23[-0.95,0.47]
Relative Annual Recruits	-0.02 [-0.09,0.03]	0.08 [0.0,0.28]
Sire		
Clutch Initiation DOY	0.05 [0.3,0.08]	0.01[0-0.01]

Additive Genetic Model

Variance Component	Clutch Initiation DOY	Relative Annual Recruits
Residual		
Clutch Initiation DOY	0.49 [0.46,0.53]	-0.07 [-0.11, -0.03]
Relative Annual Recruits	-0.18 [-0.28 ,-0.07]	14.26 [13.49,15.02]
Year		
Clutch Initiation DOY	0.19 [0.09,0.32]	0.003[0-0.01]
Permanent Environment		
Clutch Initiation DOY	0.11 [0.02,0.18]	-0.31 [-0.91,0.47]
Relative Annual Recruits	-0.01 [-0.03,0.03]	0.09 [0.0,0.29]
Additive Genetic		
Clutch Initiation DOY	0.04 [0.0,0.12]	-0.11 [-0.94,0.76]
Relative Annual Recruits	-0.01 [-0.06,0.04]	0.09 [0.0,0.3]
Sire		
Clutch Initiation DOY	0.05 [0.3,0.08]	0.01[0-0.01]

Table 2A: Estimates of (co)variance and correlations of and between relative annual fledglings and Clutch Initiation DOY for female Mandt's Black Guillemot. Variances are displayed on the diagonal, covariance are below the diagonal, and correlations are above. Year variance, and sire variance was only estimated for Clutch Initiation DOY. Estimates of residual and individual (co)variance components were estimated in the individual model and additive genetic, permanent environment, and residual (co)variance components were estimated in the additive genetic model.

Individual Model

Variance Component	Clutch Initiation DOY	Relative Annual Fledglings
Residual		
Clutch Initiation DOY	0.51 [0.48,0.54]	-0.08 [-0.11,-0.04]
Relative Annual Fledglings	-0.15 [-0.20,-0.12]	5.5 [5.2,5.8]
Year		
Clutch Initiation DOY	0.27 [0.15,0.42]	0.0[0.0,0.0]
Individual		
Clutch Initiation DOY	0.11 [0.02,0.19]	-0.51 [-0.81, -0.21]
Relative Annual Fledglings	-0.08 [-0.13,-0.03]	0.19 [0.05,0.34]
Sire		
Clutch Initiation DOY	0.05 [0.3,0.08]	0.04[0-0.08]

Additive Genetic Model

Variance Component	Clutch Initiation DOY	Relative Annual Fledglings
Residual		
Clutch Initiation DOY	0.51 [0.48,0.54]	-0.17[-0.21,-0.13]
Relative Annual Fledglings	-0.15 [-0.20,-0.12]	1.70 [1.61,1.79]
Year		
Clutch Initiation DOY	0.25 [0.14,0.38]	0.0[0.0,0.0]
Permanent Environment		
Clutch Initiation DOY	0.11 [0.02,0.19]	-0.49[-0.97, -0.03]
Relative Annual Fledglings	-0.04 [-0.07,0.00]	0.06 [0.0,0.11]
Additive Genetic		
Clutch Initiation DOY	0.05 [0.0,0.13]	-0.21[-0.97, 0.69]
Relative Annual Fledglings	-0.01 [-0.015,0.01]	0.02 [0.0,0.06]
Sire		
Clutch Initiation DOY	0.05 [0.3,0.08]	0.04[0-0.08]

Table 3A: Estimates of (co)variance and correlations of and between relative annual survival and clutch initiation date for female Mandt's Black Guillemot. Variances are displayed on the diagonal, covariance are below the diagonal, and correlations are above. Year variance, and sire variance was only estimated for clutch initiation date. Estimates of residual and individual (co)variance components were estimated in the individual model and additive genetic, permanent environment, and residual (co)variance components were estimated in the additive genetic model.

Individual Model

Variance Component	Clutch Initiation DOY	Relative Survival
Residual		
Clutch Initiation DOY	0.47 [0.44,0.49]	-0.08[-0.13, -0.05]
Relative Survival	-0.01 [-0.02,-0.01]	0.04 [0.03,0.04]
Year		
Clutch Initiation DOY	0.27 [0.15,0.42]	0.0[0.0-0]
Individual		
Clutch Initiation DOY	0.15 [0.12,0.18]	-0.33[-0.46, -0.19]
Relative Survival	-0.03 [-0.04,-0.02]	0.05 [0.04,0.05]
Sire		
Clutch Initiation DOY	0.05 [0.3,0.08]	0.003[0.001-0.005]

Additive Genetic Model

| Variance Component	Clutch Initiation DOY	Relative Survival
Residual		
Clutch Initiation DOY	0.60 [0.56,0.64]	-0.13[-0.18, -0.08]
Relative Survival	-0.02 [-0.03,-0.01]	0.03 [0.03,0.04]
Year		
Clutch Initiation DOY	0.25 [0.14,0.38]	0.0[0.0,0.0]
Permanent Environment		
Clutch Initiation DOY	0.12 [0.00,0.21]	-0.30[-0.99,0.69]
Relative Survival	-0.01 [-0.03,0.01]	0.01[0.0,0.02]
Additive Genetic		
Clutch Initiation DOY	0.07 [0.0,0.19]	-0.28[-0.91,0.41]
Relative Survival	-0.02 [-0.04,0.01]	0.03 [0.02,0.05]
Sire		
Clutch Initiation DOY	0.05 [0.3,0.08]	0.003[0.001-0.005]
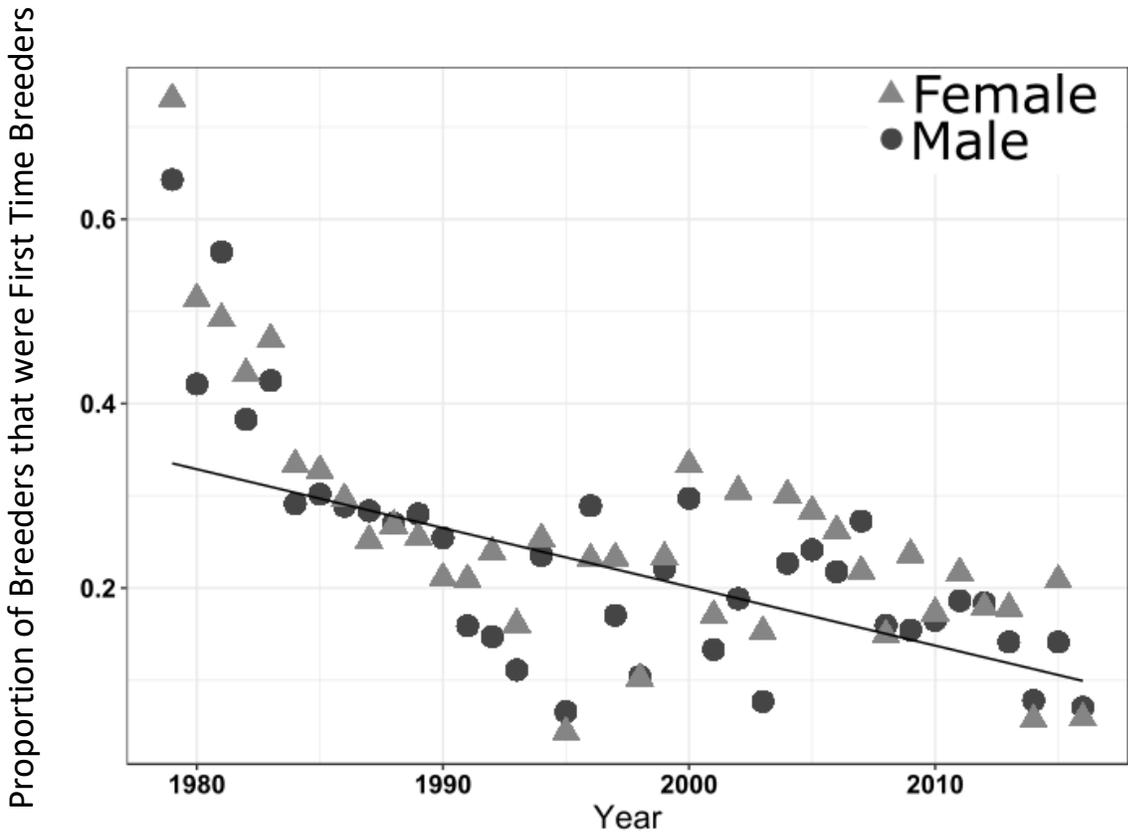
Figure 1A: Variation over time in the proportion of male and female breeders that were female

breeding Black Guillemots on Cooper Island, Alaska.

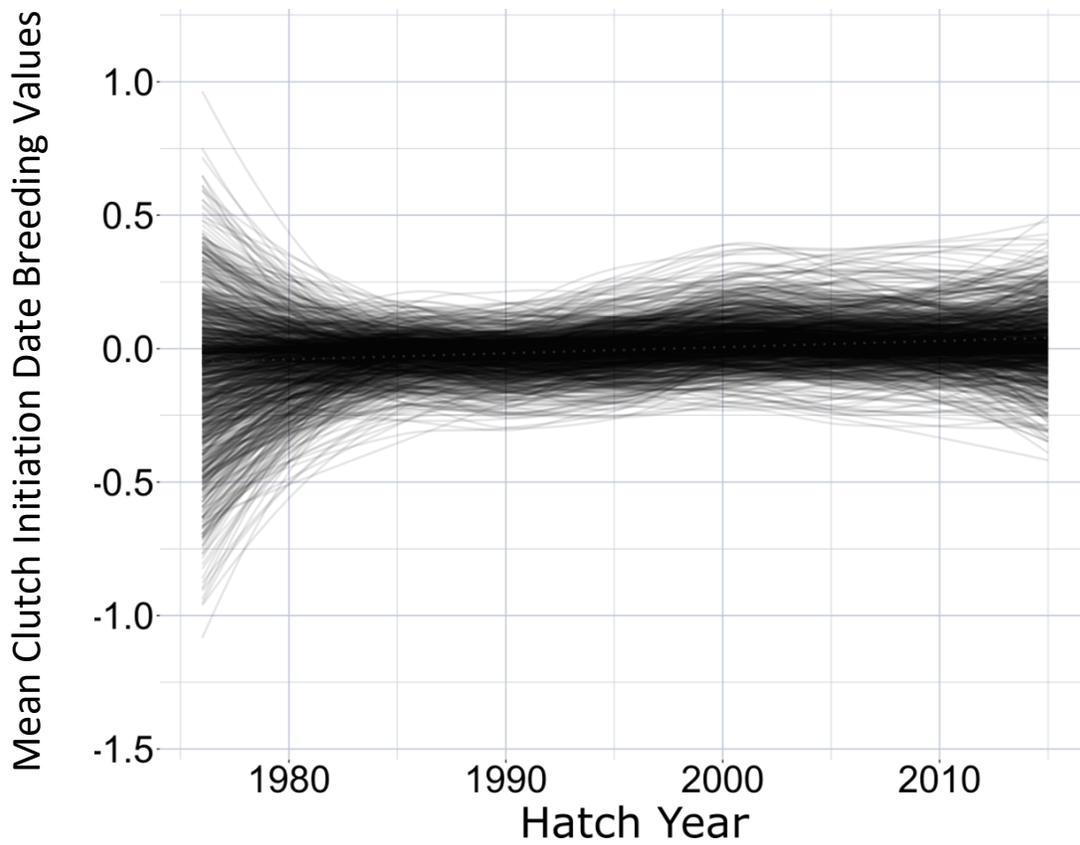**Figure 2A:** Posterior distribution of estimated clutch initiation breeding values of female Black

Guillemots on Cooper Island, Alaska over time.