

1 **Responding to environmental change: plastic responses**  
2 **vary little in a synchronous breeder.**

3

4 **Thomas E. Reed**<sup>1\*</sup>, **Sarah Wanless**<sup>2</sup>, **Michael P. Harris**<sup>2</sup>, **Morten**  
5 **Frederiksen**<sup>2</sup>, **Loeske E.B. Kruuk**<sup>1</sup> and **Emma J.A. Cunningham**<sup>1</sup>

6 <sup>1</sup>*Institute of Evolutionary Biology, King's Buildings, University of Edinburgh, Edinburgh,*  
7 *EH9 3JT, UK.*

8 <sup>2</sup>*CEH Banchory, Hill of Brathens, Banchory, Aberdeenshire, AB31 4BW, UK*

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10 The impact of environmental change on animal populations is strongly influenced by the  
11 ability of individuals to plastically adjust key life-history events. There is therefore  
12 considerable interest in establishing the degree of plasticity in traits and how selection  
13 acts on plasticity in natural populations. Breeding time is a key life-history trait that  
14 affects fitness and recent studies have found that females vary significantly in their  
15 breeding time-environment relationships, with selection often favouring individuals  
16 exhibiting stronger plastic responses. In contrast, here we show that although breeding  
17 time in the common guillemot, *Uria aalge*, is highly plastic at the population level in  
18 response to a large-scale environmental cue (the North Atlantic Oscillation), there is very  
19 little between-individual variation - most individuals respond to this climate cue very  
20 similarly. We demonstrate strong stabilising selection against individuals that deviate  
21 from the average population-level response to NAO. This species differs significantly  
22 from those previously studied in being a colonial breeder, in which reproductive

1 synchrony has a substantial impact on fitness; we suggest that counter selection imposed  
2 by a need for synchrony could limit individuals in their response and the potential for  
3 directional selection to act. This demonstrates the importance of considering the relative  
4 costs and benefits of highly plastic responses in assessing the likely response of a  
5 population to environmental change.

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7 \*Author for correspondence (tom.reed@ed.ac.uk)

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1 **1. INTRODUCTION**

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3 The need to understand how individuals respond to environmental variation has become  
4 critical as large scale environmental processes, such as climate change, continue to have  
5 demonstrable ecological effects in many natural systems (Walther et al. 2002).  
6 Determining how individuals base key life-history decisions on environmental cues is  
7 therefore crucial to predicting how these changes will affect fitness. Phenotypic plasticity,  
8 defined as the ability of a single genotype to modify its phenotype under heterogeneous  
9 environmental conditions (Houston & McNamara 1992), is fundamental to an animal's  
10 ability to deal with environmental change. However, little is known about the nature of  
11 plastic responses in wild populations or how natural selection acts on such responses  
12 (Nussey et al. 2005a; Pigliucci 2005).

13

14 The seasonal timing of reproduction is an important fitness-related trait that varies with  
15 changes in climate and temperature regimes across taxa – birds: (Crick et al. 1997;  
16 Winkel & Hudde 1997; McCleery & Perrins 1998), amphibians: (Beebee 1995),  
17 mammals: (Réale et al. 2003). Population-level changes in the timing of breeding could  
18 come about through several mechanisms: (1) changes over time in the pool of individuals  
19 constituting the breeding population arising through immigration of better-adapted  
20 individuals, (2) microevolutionary processes occurring, where changes in gene frequency  
21 across generations result from selection or genetic drift, bringing about changes in  
22 population characteristics, or (3) individuals altering their timing of breeding in response  
23 to environmental cues within their reproductive lifetimes, leading to within-individual

1 phenotypic plasticity (Przybylo et al. 2000). Distinguishing between these alternatives  
2 and determining the relative importance of plasticity are both essential to understanding  
3 how individuals cope in a changing environment and has important implications for  
4 population dynamics and evolutionary processes (Przybylo et al. 2000; Réale et al. 2003;  
5 Nussey et al. 2005a).

6

7 Recent studies have shown that population-level changes in breeding time result from  
8 individuals responding to changing environmental cues e.g. collared flycatchers, *Ficedula*  
9 *albicollis*, in relation to the North Atlantic Oscillation (Przybylo et al. 2000) and red  
10 squirrels, *Tamiasciurus hudsonicus*, in relation to pine cone abundance (Réale et al.  
11 2003). However, only three studies have considered the possibility of between-individual  
12 variation in plasticity and explicitly tested whether individual females respond in similar  
13 or different ways to climate and food conditions (two short-lived passerine birds:  
14 Brommer et al. 2005; Nussey et al. 2005b; one ungulate: Nussey et al. 2005a). All found  
15 that females differed significantly in their breeding time-environment relationships, with  
16 some evidence for selection in favour of highly plastic individuals. However,  
17 evolutionary pressures on breeding time will vary greatly between different animal  
18 systems. In social or colonial species, breeding synchronisation can be an important  
19 determinant of breeding success and selection may therefore disfavour traits that generate  
20 asynchrony (Emlen & Demong 1975; Findlay & Cooke 1982; Ims 1990; Westneat 1992;  
21 Foley & Fitzgerald 1996; Sillero-Zubiri et al. 1998). This is true of many seabirds, a  
22 group of long-lived organisms commonly used as bio-indicators of change in the marine  
23 environment (Furness & Monaghan 1987). Synchronisation of the timing of breeding and

1 social factors are often assumed to play an important role in determining seabird  
2 reproductive success (Darling 1938; Birkhead & Harris 1985; Hatchwell 1991; Murphy  
3 & Schauer 1996). Potential benefits of synchronous breeding include a dilution of the  
4 predation risk (Birkhead 1977; Hatchwell 1991) and lower risk of egg and/or chick losses  
5 due to interference from conspecifics when neighbouring birds are at the same stage of  
6 breeding (Murphy & Schauer 1996). Selection against asynchrony may limit the potential  
7 fitness advantage that could be gained from a large shift in response to environmental  
8 change and this, in theory, should decrease variation in plastic responses among  
9 individuals, thereby creating a very different arena for the evolution of plasticity than that  
10 seen in less social breeding systems.

11

12 Here, we use data from a well-studied seabird, the common guillemot, *Uria aalge*, to  
13 investigate phenotypic plasticity in breeding time in a colonially breeding species. Where  
14 a population shows an average plastic response to an environmental gradient, there are  
15 two possible scenarios: either individuals respond in the same way, or there is variation in  
16 individual plastic responses and reaction norms (Pigliucci 2005). These scenarios can be  
17 distinguished statistically by quantifying the interaction between individual responses and  
18 environmental cues, using the linear reaction norm approach (de Jong 1995); Brommer et  
19 al. 2005; Nussey et al. 2005a&b). We use records from a long-term intensive study of  
20 common guillemots to test (i) whether the population shows, on average, a plastic  
21 adjustment of laying dates in response to a large-scale atmospheric phenomenon known  
22 to be an important predictor of likely spring conditions, the winter North Atlantic  
23 Oscillation (NAO) index; (ii) whether females differ in their individual plastic responses

1 to this environmental variation and (iii) whether stronger plastic responses lead to higher  
2 breeding success and hence if selection acts on this plasticity. We show that, contrary to  
3 previous findings, virtually no between-individual variation in plasticity could be  
4 detected in relation to NAO, despite an overall plastic response at the population level.  
5 This suggests that females respond in a remarkably similar fashion to this environmental  
6 cue. We then demonstrate that stabilising selection appears to act against females  
7 deviating from the average population-level response, given that breeding  
8 synchronisation is an important component of fitness in this highly social and colonial  
9 species.

10

## 11 **2. MATERIALS AND METHODS**

12

### 13 **(a) *Study area and population***

14 The common guillemot (hereafter guillemot) is a long-lived seabird occurring in both the  
15 North Atlantic and North Pacific and the most abundant seabird in the UK. The data used  
16 here were collected on the Isle of May, Firth of Forth, Scotland (56°11'N, 2°33'W) each  
17 breeding season from 1981 to 2005. The study population occupies six topographically  
18 discrete areas dispersed along c.100 metres of cliff. All 1412 unique breeding sites in the  
19 areas were followed each year, though not all sites were occupied in every year, to give a  
20 total of 23,258 breeding records (see Harris & Wanless 1996 for a full description of  
21 breeding site characteristics). A subset of 245 individually colour-ringed females were  
22 followed in five of the areas from 1982 to 2005. Laying dates at all sites were recorded in  
23 each year. The species has a single egg clutch but will lay a replacement egg if the first

1 one is lost. Here we consider only the laying of the first egg. Approximately 75% of all  
2 first eggs are laid during a 7-10 day period. Details of the study population and data  
3 collection methods are given in Harris & Wanless (1988).

4

5 ***(b) Plasticity of laying date in relation to NAO***

6 The phenology of common guillemots on the Isle of May up to 2002 correlated with the  
7 winter North Atlantic Oscillation Index (NAO), with laying tending to be earlier in  
8 positive NAO years (Frederiksen et al. 2004). Winter NAO strongly predicts large-scale  
9 climatic conditions and weather patterns in the northern Atlantic and adjoining  
10 landmasses (Hurrell 1995). Positive NAO values indicate warm, wet winters dominated  
11 by westerly winds in north-western Europe and vice versa. NAO has been used in many  
12 ecological studies of a range of species as an environmental correlate of biological traits  
13 (Stenseth et al. 2003). In species such as guillemots that spend the winter far from the  
14 breeding grounds, winter NAO may act as a useful signal that allows birds to anticipate  
15 likely spring conditions in the breeding areas in advance of returning (Frederiksen et al.  
16 2004). No significant linear or cyclical trends in NAO were apparent over the time period  
17 considered in this study (NAO data taken from  
18 <http://www.cru.uea.ac.uk/cru/data/nao.htm>, see (Jones et al. 1997)). We also examined  
19 the effects of sea surface temperature (SST) as a more local environmental cue on laying  
20 date; there was no correlation at the population level between SST and laying date  
21 (Frederiksen et al. 2004), nor any evidence for individual variation in slopes (unpublished  
22 data). SST was therefore not considered further.

23

1 The cross-sectional analysis (i.e. considering mean laying dates of all individuals each  
2 year) was first updated using all records up to 2005 by regressing annual mean Julian  
3 laying date against winter NAO. Mean laying dates each year were calculated from the  
4 full dataset of all breeding sites followed. Birds breeding for the first and second time  
5 (circa 5-7 years of age) lay later in the season than more experienced birds (Hedgren  
6 1980) so, to remove any possible initial age-dependent variation in phenology, first and  
7 second breeding records for all individuals, regardless of actual age, were excluded from  
8 analyses using individually known birds. Breeding experience, or number of years since a  
9 female was first recorded as a breeder, was then entered into analyses as a covariate.

10

11 To test whether the observed correlation between laying date and NAO represented a  
12 plastic adjustment of phenology by female guillemots, the following restricted maximum  
13 likelihood linear mixed-effects model (LMM):

14

15  $\text{Laying date} = \text{NAO} + \text{area} + \text{NAO} * \text{area} + \text{breeding experience} + \text{ID} + \text{year}$

16

17 where NAO, area and breeding experience were fixed effects and ID (female identity)  
18 and year were multi-level random effects, was fitted to the data in a longitudinal analysis  
19 (i.e. where the laying dates each year of individuals breeding in multiple years are  
20 considered).

21

22 Only laying dates of females breeding in 4 or more years were considered. NAO and  
23 breeding experience were entered as continuous fixed effects. Laying patterns tended to



1 vary consistently between areas (Wanless & Harris 1988); hence, area was entered as a  
2 factor in the fixed model and an interaction between NAO and area was included to  
3 determine whether birds in different areas responded differently. The random factor ID  
4 accounts for the cumulative effects of individual-specific properties, such as genes,  
5 maternal effects and developmental factors, thereby allowing the main effect of NAO on  
6 laying date to be estimated independently (Przybylo et al. 2000). It also accounts for  
7 repeated measures on individual females.

8

9 Because females have such long breeding lifespans (mean = 10.7 breeding records per  
10 female, range = 4 -25 in this dataset), they will experience a wide range of NAO  
11 conditions across years. One can infer, therefore, that trends will be present within  
12 females as well as across females: if the longitudinal analysis revealed a significant  
13 overall main effect of NAO of similar magnitude to the cross-sectional analysis, the  
14 population-level correlation would be largely due to phenotypic plasticity, rather than to  
15 different females experiencing different NAO conditions. The first model assumed that  
16 females all responded in a similar fashion to NAO, i.e. that the variation due to  
17 differences between females in their individual responses to NAO was zero. To test  
18 whether females varied in their individual responses, a second LMM was fitted:

19

20  $\text{Laying date} = \text{NAO} + \text{area} + \text{NAO} * \text{area} + \text{breeding experience} + \text{ID} + \text{year} + \text{ID} * \text{NAO}$

21

22 This time a random interaction term for ID\*NAO was included. ID estimates the variance  
23 component due to differences between females in their mean trait values in the average

1 environment (elevations), while the random interaction term estimates the variance  
2 component resulting from differences between females in their laying date – NAO  
3 relationship (slopes). Comparing the deviance of models with and without this interaction  
4 term allows one to test whether females differ significantly in their plastic responses.  
5 Again, only females which bred in four or more years were used for the analysis, in order  
6 to generate meaningful slopes. Further restricting the analysis to females with at least five  
7 or six observations yielded very similar results.

8

### 9 **(c) Selection analysis**

10 If selection favours increased plasticity, females that show a greater than average  
11 response should achieve higher fitness. However, if synchrony is important, a plastic  
12 response that takes individuals too far from the average response could decrease the  
13 success of these individuals and be counter-selected for. Stabilising selection would thus  
14 act to reduce any variation in plasticity that might exist in the population. To quantify  
15 individual plastic responses, coefficients for elevation and slope were obtained from a  
16 linear regression model, where a separate regression of residual laying date against NAO  
17 was calculated for each female (n=245). Residual laying dates were the residuals from an  
18 ANCOVA model of laying date against year and area, with year as a covariate and area  
19 as a factor. (Using residual laying date controls for the effects of year and area on laying  
20 date, allowing laying date to be modeled against NAO independently; however, using  
21 residuals from a model of laying date against area only (i.e. ignoring the effect of year) or  
22 simply modeling raw laying dates against NAO (i.e. ignoring the effects of year and area)  
23 produced very similar results to those presented here, both qualitatively and

1 quantitatively). Separate regressions for each female generate individual estimates for  
2 *elevation*, a female's expected laying date response in the average environment and *slope*,  
3 which measures the strength of her plastic response to the NAO (Nussey et al. 2005c).  
4 Again, only females that bred in four or more years were used, to remove potential  
5 extreme values.

6

7 A generalised linear model (GLIM) with a logit link function and binomial errors was  
8 constructed to test for a statistically significant relationship between breeding success and  
9 the estimates of slope and elevation in a weighted logistic regression:

10

$$11 \text{ breeding success} = \text{elevation} + (\text{elevation})^2 + \text{slope} + (\text{slope})^2 + \text{elevation} * \text{slope}$$

12

13 where breeding success was a binomial proportion consisting of a vector of 'successes'  
14 (i.e. number of breeding attempts in which a chick was successfully raised to fledging)  
15 and 'failures' (i.e. number of failed breeding attempts). The quadratic terms test for non-  
16 linear selection and the interaction for correlational selection between slope and  
17 elevation. If these two traits are highly correlated then selection on elevation could also  
18 cause a correlated response in slope, even if selection does not act directly on slope itself.  
19 For comparison with other studies, standardised selection gradients were subsequently  
20 obtained using relative breeding success, where breeding success, expressed as the  
21 proportion of breeding attempts per individual that were successful, was standardised by  
22 dividing by the mean for all individuals. Elevation and slope were standardised to have a  
23 mean of zero and a standard deviation of one and then entered into a linear regression,

1 weighted by the total number of breeding attempts per female, assuming a normal error  
2 distribution (Lande & Arnold 1983). This gives parameter estimates which can be taken  
3 to be the standardised selection gradients; these are the selection gradient values reported  
4 in the results, whereas the significance of terms is obtained from the formal GLIM that  
5 tests for selection on elevation and slope.

6

7 All models were fitted using restricted maximum likelihood (REML) methods in  
8 GENSTAT 8<sup>th</sup> edition (VSN International) or R version 2.1 (R development team 2005).  
9 Continuous explanatory variables were centred on their mean values prior to inclusion in  
10 the models (Pinheiro & Bates 2000).

11

### 12 **3. RESULTS**

13

#### 14 **Plasticity in relation to NAO**

15 The cross-sectional analysis showed that annual mean laying date was negatively  
16 correlated with NAO (Figure 1). The results (Table 1) showed that this negative main  
17 effect of NAO persisted in the full LMMs after other significant terms had been  
18 accounted for (model 1,  $b = -1.43 \pm 0.59$ ). Birds in different areas also responded slightly  
19 differently to NAO, as evidenced by the significant interaction between NAO and area,  
20 but in each area NAO always had a negative effect. There was no effect of breeding  
21 experience on laying date, though there were strong effects of year and female identity  
22 (Table 1).

23

1 In the second LMM, a random interaction term ID\*NAO was included to determine  
2 whether females varied significantly in their plastic responses. This model estimated a  
3 non-significant variance component for this random interaction term, which was very  
4 close to zero ( $0.01 \pm 0.06$ ), indicating very little variation between females in their  
5 responses to NAO. Inclusion of this random interaction term resulted in a very slight drop  
6 in deviance and did not significantly improve the explanatory power of the model, nor did  
7 it have any effect on the fixed effects (change in deviance = 0.03, d.f.=1,  $P = 0.86$ ).

8

### 9 **Selection analysis**

10 Once all non-significant terms were removed from the GLIM, the only terms that  
11 remained significant were elevation and the square of slope. This indicates directional  
12 selection on elevation (Figure 2b), favouring earlier laying dates on average, as evidenced  
13 by a negative selection gradient (Table 2). The fact that there was no direct selection on  
14 slope but there was selection on the square term for slope shows that stabilising selection  
15 acted on plasticity, where the average slope has optimal breeding success and breeding  
16 success declines as one moves away from this optimum in either direction (Figure 2a&b),  
17 i.e. there was selection against females whose plastic responses deviated strongly from  
18 the average response. The interaction between elevation and slope was not significant,  
19 indicating that selection on slope was not affected by whether individuals were on  
20 average late or early breeders over their lifetime.

21

### 22 **3. DISCUSSION**

23

1 Here we show that population-level changes in phenology, in response to a large scale  
2 atmospheric phenomenon, arose from individuals plastically adjusting their laying date.  
3 However, in contrast to previous studies, we found very little between-individual  
4 variation in plasticity, indicating that individuals responded in a remarkably similar  
5 fashion to the North Atlantic Oscillation. We demonstrate that stabilising selection acts  
6 on plasticity and suggest that selection against asynchronous breeding may prevent  
7 individuals deviating too far from the population mean response, despite potential  
8 benefits of early breeding.

9

10 Breeding was on average earlier in years when NAO was positive, indicative of warmer  
11 and wetter winter conditions. In winter, guillemots from the Isle of May disperse  
12 throughout the North Sea and thus the onset of reproduction in spring is expected to be  
13 informed by cues operating both over large distances and during a period well in advance  
14 of when birds actually return to the colony, allowing birds to adequately predict likely  
15 conditions (Frederiksen et al. 2004). Alternatively, NAO could act as a constraint on the  
16 timing of breeding, whereby climatic conditions determine food supply and hence body  
17 condition in the pre-breeding period. Although the actual mechanisms by which  
18 individual birds respond are unclear, the overall population-level response to NAO was  
19 largely explained by individual phenotypic plasticity. Other explanations that could  
20 underlie this type of population shift in breeding time, such as immigration of more  
21 adapted individuals, microevolutionary processes or some association between different  
22 values of NAO and the average laying date (Przybylo et al. 2000) could be discounted.

23

1 Analysis of data from females who had bred for at least 4 years revealed that females  
2 behaved in an extremely similar manner in relation to NAO, with very little variation in  
3 their plastic responses. The formal mixed model indicated that this variation was not  
4 significantly different from zero, implying that the variance due to any differences in  
5 plasticity between individuals was not large enough to be statistically significant relative  
6 to other sources of variance in the model: individuals therefore appeared to respond very  
7 similarly. This represents a novel result since previous studies that have considered  
8 between-individual variation in plasticity in breeding time have all found significant  
9 differences between individuals: in collared flycatchers in Sweden (Brommer et al. 2005;  
10 Nussey et al. 2005b), great tits *Parus major* in the Netherlands (Nussey et al. 2005b) and  
11 red deer *Cervus elaphus* in Scotland (Nussey et al. 2005a). In contrast, we have shown  
12 that the opposite is true for guillemots, with females exhibiting a strong response to NAO  
13 but all to a similar extent.

14

15 This may arise from their colonial lifestyle. Breeding guillemots are characterised by a  
16 high degree of breeding synchrony; they typically breed at extremely high densities (in  
17 this population, often >40 pairs per m<sup>2</sup>) and low mortality and high levels of site and  
18 mate fidelity mean that pairs are likely to breed alongside the same neighbours from year  
19 to year (Harris et al. 1996). Reproductive synchrony appears to have a number of social  
20 benefits: actively breeding close neighbours may be less likely to flush and dislodge eggs  
21 when disturbed than non-breeders or late breeders not yet settled on eggs or brooding  
22 chicks (Murphy & Schauer 1996) and synchronisation of breeding between groups of  
23 neighbouring pairs may accrue benefits via a dilution of predation risk – this may be

1 important for the advantages of predator swamping to apply throughout the season  
2 (Birkhead 1977; Hatchwell 1991). The general importance of reproductive synchrony in  
3 guillemots may therefore limit selection on an ability to respond to environment cues; in  
4 this study, the average plastic response, which appears to be closely followed by the  
5 majority of females, has optimal fitness. Guillemots laying consistently early or  
6 consistently late shift their laying date by the same amount when the environment  
7 changes, maintaining the ranking of individuals' laying dates relative to each other  
8 (repeatability of individual laying dates, expressed relative to area means, equals 0.494 in  
9 this colony). This is despite evidence for significant directional selection for earlier  
10 breeding (females with earlier average laying dates, relative to others in the colony, had  
11 higher breeding success than later breeding females). Stabilising selection thus acts to  
12 reduce between-individual variation in plasticity. We suggest that for a colonially  
13 breeding seabird, the ability to modify the phenotype in line with the rest of the  
14 population and to remain synchronous may be of primary importance, rather than the  
15 strength of plastic response *per se*, which is more likely to be determined by the level of  
16 environmental variation. This stabilising selection may explain our observation that the  
17 component of variance due to differences in slopes in a mixed model was not statistically  
18 significant, in marked contrast to previous studies (Brommer et al. 2005; Nussey et al.  
19 2005a; Nussey et al. 2005a).

20

21 A number of environmental factors could in general explain this type of result; indeed  
22 recent evidence from great tits in Southern England would also seem to suggest a lack of  
23 significant variation in plastic responses, for reasons as yet undetermined (A.



1 Charmantier, pers. comm.). In some species, environmental conditions could impose a  
2 limited time window during which successful reproduction is possible; if the timing of  
3 this window varies among years then this could also limit selection away from an average  
4 response and individuals would follow the same reaction norm. However, the short time  
5 window hypothesis seems unlikely for our particular result, as guillemots are not  
6 necessarily constrained by external conditions to breed in such a contracted period. For  
7 example, other seabird species breeding on the Isle of May, such as shags (*Phalacrocorax*  
8 *aristotelis*), also rely on lesser sandeels (*Ammodytes marinus*) as their main prey items  
9 and face similar conditions, but have a much more extended breeding season; shags do  
10 not breed in dense colonies like guillemots and therefore synchrony may not be as  
11 important. The social constraints argument rather seems more plausible, given the highly  
12 social and colonial lifestyle of guillemots. If the increased need for reproductive  
13 synchrony in guillemots plays a key role in determining selection pressures, this may  
14 limit the expression of highly variable responses. Evidence from recent studies of free-  
15 living vertebrate populations suggests that there is an underlying heritable component to  
16 breeding time plasticity (Brommer et al. 2005; Nussey et al. 2005a; Nussey et al. 2005b);  
17 from an evolutionary standpoint, therefore, stabilising selection and the consequent  
18 erosion of variation could be important phenomena to take into account when  
19 investigating the evolution of plastic responses. This is a crucial aspect to consider in  
20 social species and highlights the importance of evaluating the costs as well as the benefits  
21 of a highly plastic response when analysing how populations of animals might respond to  
22 climatic and other types of environmental change.

23

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1 **Table 1.** Linear mixed effects model of laying date with random effects for year and (a)  
 2 female identity only, where females are all assumed to respond in the same way to NAO  
 3 and (b) female identity plus a female identity\*NAO random interaction term, which  
 4 allows for different individual responses to NAO (n = 2,597 breeding records for 245  
 5 females). The significance of adding each subsequent random effect to the models was  
 6 assessed using log-likelihood test statistics, where the change in deviance (-2logLik) is  
 7 compared to a Chi-squared distribution with appropriate degrees of freedom. Only  
 8 significant fixed effects are shown, as when added last to the model (Type III tests). \*\*\*  
 9  $P < 0.001$ . Year and NAO had independent effects in both models.

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Variance components for random effects in final model:					
	Component	SE	Df	Deviance	Log likelihood test statistic
year	10.60	3.32	2582	10221.32	
(a) female identity	8.72	0.91	2581	9303.94	917.38***
(b) female identity*NAO	0.01	0.06	2580	9303.91	0.03

  

Fixed effects:	Coefficient	SE	Df	Wald statistic	P-value
NAO	-1.434	0.586	1		0.013
area	129.3	0.8	4	37.88	<0.001
NAO*area	-	-	4	7.96	<0.001

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1 **Table 2.** Results of selection analysis GLIM using individual regression coefficients for  
 2 elevation, slope, their squared terms and interaction for n=245 females. Significance of  
 3 terms was assessed using *F* deletion tests to compensate for overdispersion;\* p-values of  
 4 significant terms are from final model where non-significant terms have been removed.  
 5 An intercept was also fitted but is not shown. Coefficient estimates and their standard  
 6 errors are standardised selection gradients from a linear regression (see Methods for  
 7 details).

8

Coefficient	Estimate	SE	<i>P</i> – value
elevation	-0.05	0.01	0.001
elevation <sup>2</sup>	-0.006	0.01	0.773
slope	-0.01	0.02	0.193
slope <sup>2</sup>	-0.02	0.007	0.019
elevation x slope	-0.01	0.01	0.607

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10 \* There was some overdispersion in the data, as a result of the residual scaled deviance  
 11 being larger than the residual degrees of freedom by a factor of 1.68; this was overcome  
 12 by specifying quasi-binomial errors that makes use of a scaled deviance parameter  
 13 (Crawley 2002).

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1 **Figure 1.** Annual mean laying date in the colony, in number of days since January 1 ( $\pm$   
2 s.e.), plotted against NAO values for each year, showing a significant negative  
3 relationship ( $b = -1.56 \pm 0.59$ ,  $R^2 = 0.24$ ,  $P = 0.015$ ). This effect of NAO on laying date is  
4 independent of year.

5

6 **Figure 2. (a)** Results from the selection analysis showing how breeding success,  
7 measured as the proportion of total breeding attempts per female where a chick was  
8 produced, depends on slope (actual slopes used in GLIM and not standardised values).  
9 Each data point ( $n = 245$ ) represents an individual female. The curved line shows the  
10 relationship between breeding success and slope as predicted by the GLIM, where  
11 elevation is held constant at the average value. The average slope has optimum breeding  
12 success, as indicated by the dashed lines, and breeding success declines as you move  
13 away from this optimum in either direction. **(b)** 3-D surface plot showing the relation of  
14 both elevation and slope to breeding success, as predicted by the GLIM, indicating  
15 directional selection on elevation and stabilising selection on slope.

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