

Timing is everything: flexible phenology and shifting selection in a colonial seabird

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Summary

1. In order to reproduce successfully in a temporally varying environment, iteroparous animals must exhibit considerable behavioural flexibility across their lifetimes. By adjusting timing of breeding each year, parents can ensure optimal overlap between the energy intensive period of offspring production and the seasonal peak in favourable environmental conditions, thereby increasing their chances of successfully rearing young.

2. Few studies investigate variation among individuals in how they respond to fluctuating conditions, or how selection acts on these individual differences, but this information is essential for understanding how populations will cope with rapid environmental change.

3. We explored inter-annual trends in breeding time and individual responses to environmental variability in common guillemots *Uria aalge*, an important marine top predator in the highly variable California Current System. Complex, nonlinear relationships between phenology and oceanic and climate variables were found at the population level. Using a novel application of a statistical technique called random regression, we showed that individual females responded in a nonlinear fashion to environmental variability, and that reaction norm shape differed among females.

4. The pattern and strength of selection varied substantially over a 34-year period, but in general, earlier laying was favoured. Females deviating significantly from the population mean laying date each year also suffered reduced breeding success, with the strength of nonlinear selection varying in relation to environmental conditions.

5. We discuss our results in the wider context of an emerging literature on the evolutionary ecology of individual-level plasticity in the wild. Better understanding of how species-specific factors and local habitat features affect the timing and success of breeding will improve our ability to predict how populations will respond to climate change.

Key-words: behavioural response, climate change, environmental stochasticity, nonlinear reaction norm, phenotypic plasticity

Introduction

Organisms inhabiting seasonal environments typically face substantial variability in environmental conditions on temporal scales ranging from days to decades. The effects of climate fluctuations on the population dynamics of vertebrates are

well documented (e.g. Post & Stenseth 1999; Stenseth *et al.* 2002; Durant *et al.* 2004; Sæther, Sutherland & Engen 2004; Hone & Clutton-Brock 2007). Less well understood, however, are the mechanistic bases for these climate influences. Climate effects on demography are mediated through the behavioural, physiological and life-history responses of individuals (Sutherland 1996). Where individual-level data are available, therefore, key insights may be gained by examining individual responses to environmental variability and relating these to population-level trends. Recent studies on wild birds and mammals suggest that impacts of environmental change may

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be mitigated, at least in the short term, by individuals responding flexibly within their lifetimes through phenotypic plasticity (reviewed in Nussey, Wilson & Brommer 2007). Plastic adjustments to behaviour or life history that enhance individual fitness under the current environmental regime tend to buffer the mean fitness of the population against shifting conditions (Walther *et al.* 2002; Réale *et al.* 2003; Ghalambor *et al.* 2007; Charmantier *et al.* 2008), although adaptive plastic responses may not always prevent population declines (e.g. Both *et al.* 2006, see Visser 2008 for discussion).

One way birds cope with a fluctuating environment is by adjusting annual breeding time. By delaying or advancing breeding phenology each year, females synchronize the energy demands of offspring production and provisioning to the period of most favourable environmental conditions (Lack 1968; van Noordwijk, McCleery & Perrins 1995). Females may also be constrained by prey resources to breed at a certain time of year (Perrins 1970), so adaptive adjustments may be limited to some extent. The success of timing decisions (in terms of reproductive success of the female) will depend on the reliability of environmental cues experienced during the pre-breeding period, her ability to respond appropriately to perceived cues, and environmental conditions experienced during offspring-rearing (Nager & van Noordwijk 1995; Visser *et al.* 1998). Relationships between phenology and environmental cues and constraints, and selection pressures on breeding time, may be complex, however. Patterns will likely vary both spatially and temporally, even among populations of the same species (Lambrechts & Dias 1993; Visser *et al.* 2003; Charmantier *et al.* 2008; Silverin *et al.* 2008).

Here we explore inter-annual trends in timing of breeding of individually marked common guillemots *Uria aalge* (Pontoppidan) breeding on Southeast Farallon Island, California, in the highly variable California Current Large Marine Ecosystem (CCLME). Guillemots breed in large, dense colonies (Tuck 1961) throughout the northern Pacific and Atlantic oceans (Sibley & Monroe 1990), encompassing a range of marine environments including coastal shelf and upwelling areas, and a broad range of climates, from temperate to sub-arctic. Phenology is affected by local prey resource availability, as determined by region-specific oceanographic/climatic factors (Frederiksen *et al.* 2004), and by social factors related to coloniality (Birkhead 1977; Wanless & Harris 1988; Hatchwell 1991; Reed *et al.* 2006). While these social factors are likely to be globally important in this species, environmental conditions will be much more variable across regions. Hence, temporal patterns may not necessarily be in phase across populations, particularly those separated by large geographical distances.

The CCLME is characterized by substantial inter-annual and inter-decadal variability in oceanography and ecosystem dynamics (Hickey 1979). Ecosystem dynamics in eastern boundary current systems are driven by unpredictable coastal currents and upwelling, and guillemots breeding in the CCLME region experience much more variable conditions relative to their counterparts in the North Sea (where the above-mentioned studies were undertaken, see Appendix S1,

Supporting information). Between-year differences in oceanographic conditions are driven by broad, basin-scale atmospheric fluctuations such as the El Niño–La Niña cycle and by smaller-scale processes such as wind-generated coastal advection and upwelling (Hickey 1979). These processes play a strong role in determining annual resource availability and in certain years the CCLME can be extremely productive, while in others primary production is greatly reduced and ecological conditions degenerate (Ainley, Sydeman & Norton 1995). In extreme (e.g. El Niño) years, many seabirds in the region undergo mass breeding failure or nonbreeding (Sydeman *et al.* 2006). Under these circumstances, we expect strong selection for highly plastic breeding time responses (de Jong 1995). However, synchronization of breeding with neighbouring conspecifics is also thought to be important (Sydeman 1999), and hence individual responses may be constrained to some degree by sociality, as suggested by Reed *et al.* (2006). Given these a priori expectations derived from study of an Atlantic colony (Reed *et al.* 2006), we here make use of extensive long-term data from Southeast Farallon Island to address similar questions in a Pacific population of the same species, where guillemots breed under very different environmental conditions.

We analyse relationships between timing of breeding and environmental variability at both the population and individual levels. Explicitly, we investigate how patterns of within and among-individual variation in phenology vary across the natural range of environmental conditions encountered by this population. We adopt a reaction norm approach to quantify individual plastic responses to the environment (Via *et al.* 1995), where variation in individual trait–environment relationships is modelled statistically using random regression (Meyer & Kirkpatrick 2005, see Nussey *et al.* 2007 for a review of recent studies applying similar techniques to longitudinal data from wild vertebrate populations). We ask three key questions: (i) how does the breeding time of guillemots at Southeast Farallon Island respond to environmental variability, (ii) do females respond differently, and (iii) how does selection act on laying date in this population?

Methods

Breeding success, phenology, population size and diet of common guillemots have been monitored at Southeast Farallon Island (hereafter SEFI) continuously since 1972. During this period, laying dates and breeding success were monitored in a plot that varied in size from 75–225 breeding sites. Laying dates were determined to within 2 days (in 89% of cases to within 1 day), and the breeding attempt was considered successful if the chick survived to at least 18 days post-hatching (the male parent takes the chick to sea at this stage, when chicks are still flightless). Guillemots lay a single-egg clutch but can re-lay if the first egg is lost. For the purpose of this study, we only considered laying dates for the first breeding attempt, since this was more likely to reflect an adaptive response than subsequent attempts in the same season. From 1986 onwards, adult birds of unknown age were captured and marked with unique colour ring combinations to allow individual identification. Between 1986

Table 1. Functional relationships between average annual laying date and each environmental variable: results of model selection procedure. For each variable, the model with the lowest AICc (highlighted in bold) was chosen. AICc was calculated by taking AIC and adding a correction-factor to account for small sample sizes: $2*k*(n + 1)/(n - k - 1)$, where k = the number of parameters and n = sample size

Environmental variable	Model	d.f. (model, error)	AICc	R ²	P
SST	Null	0,19	140.09		
	Main effect	1,18	132.96	38.37%	0.004
	Quadratic	2,17	120.48	71.45%	< 0.001
	GAM smooth spline	2.49, 16.51	122.78	70.40%	< 0.001
UI	Null	0,19	140.09		
	Main effect	1,18	137.02	24.51%	0.027
	Quadratic	2,17	137.29	33.85%	0.140
	GAM smooth spline	2.49, 16.51	133.49	59.10%	0.018
NOI	Null	0,19	140.09		
	Main effect	1,18	130.10	46.59%	< 0.001
	Quadratic	2,17	128.38	57.62%	0.050
	GAM smooth spline	4.58, 14.42	127.58	75.10%	< 0.001
Log(rockfish abundance)	Null	0,19	140.09		
	Main effect	1,18	130.02	46.80%	0.001
	Quadratic	2,17	132.89	46.91%	0.852
	GAM smooth spline	1,18	130.02	46.80%	< 0.001
Multivariate measure (PC1)	Null	0,19	140.09		
	Main effect	1,18	124.79	59.04%	< 0.001
	Quadratic	2,17	116.81	74.11%	< 0.001
	GAM smooth spline	4.45, 14.55	121.00	69.50%	< 0.001

and 2005, a total of 89 colour-ringed females, each recorded as having bred in at least 2 years (range 2–16 breeding attempts per female), were studied. This information was used in individual-level analyses of timing responses to fluctuating environmental conditions. We utilized data from all breeding sites followed between 1972 and 2005 (including marked and unmarked birds) to examine temporal patterns of selection on breeding time across years at the population level. For full details on the study population and methods, see Boekelheide *et al.* (1990), Sydeman (1993), Sydeman & Eddy (1995) and Sydeman (1999).

POPULATION-LEVEL CORRELATIONS BETWEEN BREEDING TIME AND ENVIRONMENTAL VARIABLES

Ocean climate is extremely variable in the California Current System (CCS). While many environmental parameters are linked to the El Niño–La Niña cycle, not all of these may be important in terms of influencing phenology in this population. Our first aim, therefore, was to isolate relevant environmental variables associated with variation in the phenology of guillemots at SEFI. Mean laying date was calculated each year from 1986–2005 (the years for which both environmental and individual-level data were available) from the sample of colour-ringed females (sample sizes each year given in Table 3). We tested for functional relationships between average annual laying date and four separate indices of environmental conditions: (i) average spring sea surface temperature (SST) at SEFI, (ii) an index of the strength of upwelling in the Gulf of the Farallones (upwelling index, UI), (iii) a large-scale atmospheric phenomenon, the Northern Oscillation Index (NOI), and (iv) an index of juvenile rockfish (*Sebastes* sp.) abundance in Central California, a key prey species on which breeding guillemots rely (Mills *et al.* 2007). Details regarding data collation on each of these variables are given in Appendix S1. In order to reduce the dimensionality in environmental variability, we also derived a multivariate summary measure

based on principal components analysis (PCA) on the above four variables. The first principal component, PC1, accounted for almost 62% of the variation and was subsequently used as the basis for testing functional relationships (see Appendix S1 for more details).

We tested for significant relationships between annual average laying date and each of the above indices of environmental variability. In each case, we fitted increasingly complex models, beginning with the null model (fitting an intercept only), then a linear model, next a quadratic model and finally a generalized additive model (GAM) with a smoothing spline function (Crawley 2002). The best models for each variable were chosen on the basis of Akaike's information criteria, corrected for small sample sizes (AICc) (Burnham 2002). We tested for correlations among the four environmental variables contributing to the multivariate summary measure. We also tested for population-level correlations between annual productivity (mean number of chicks fledged per breeding pair) and laying date, and productivity and PC1. To test the influence of extreme years (defined as years when productivity fell by >1 standard deviation from the long term average (0.73)) on population-level trends, we repeated these latter analyses excluding the years 1992, 1998 and 2005 (productivities of 0.08, 0.39 and 0.51, respectively). Finally, we tested for a temporal trend in laying date over the entire study period (1972–2005) using linear regression.

INDIVIDUAL VARIATION IN BREEDING TIME RESPONSES

Linear reaction norms are defined by two parameters: an intercept, which reflects the individual's expected trait value in the average environment (if the environmental covariate is first mean-centred) and slope, which describes the amount by which the trait changes per unit change in the environment i.e. the plasticity of the trait (Pigliucci 2005). Nonlinear reaction norms contain extra parameters which describe in more detail the way the phenotype changes across

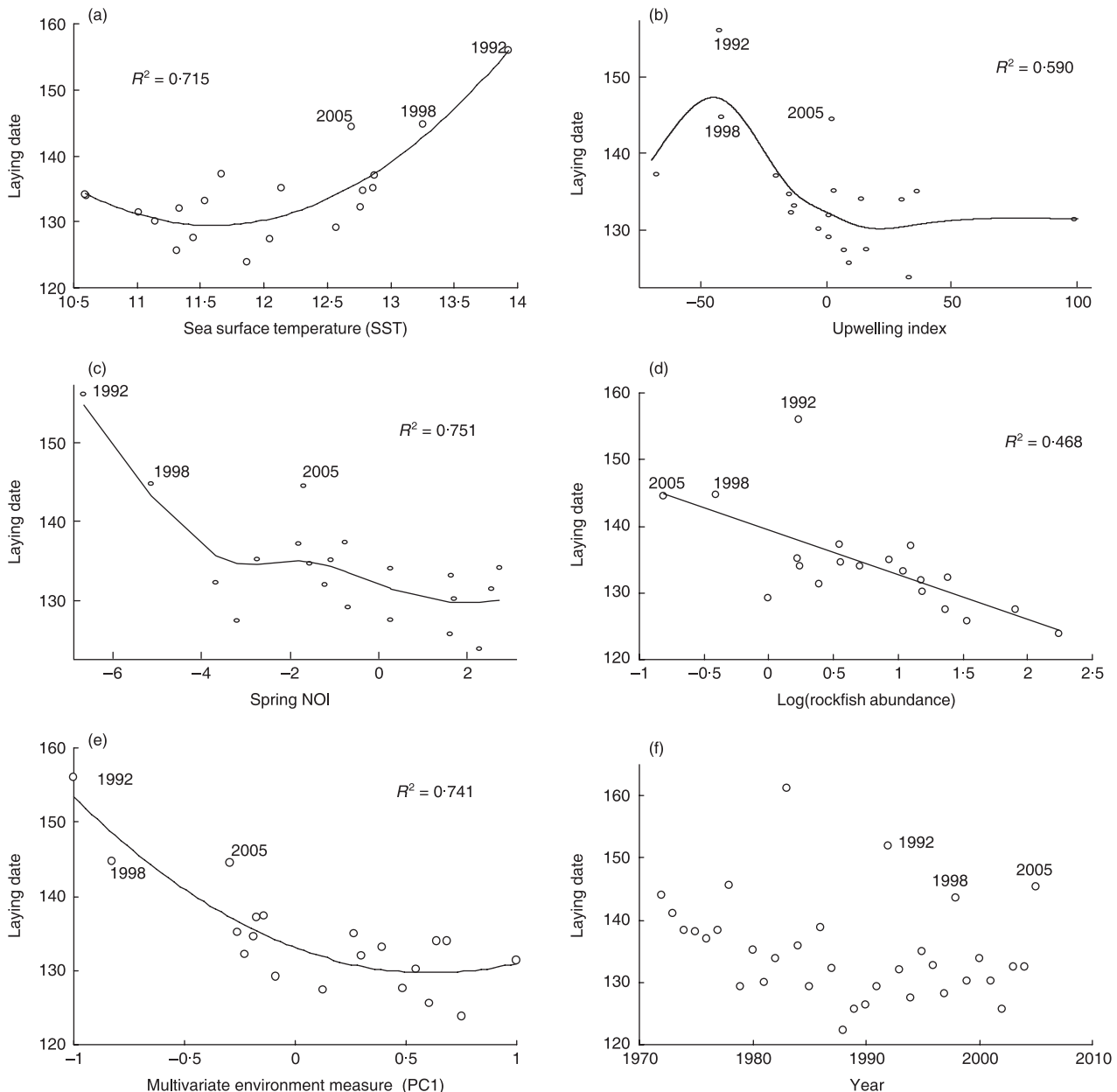


Fig. 1. (a–f) Functional relationships between average annual laying date at the population level and environmental variables. (a) Laying date = $782.48 - 112.5 \cdot \text{SST} + 4.86 \cdot \text{SST}^2$ (b) GAM smoothed spline for UI (c) GAM smoothed spline for spring NOI (d) Laying date = $139.43 - 6.69 \cdot \text{Log}(\text{rockfish abundance})$. (e) Laying date = $131.79 - 2.97 \cdot \text{PC1} + 1.04 \cdot \text{PC1}^2$ (f) Laying date versus year (nonsignificant negative linear trend).

environments. With random regression, increasingly complex functions of the environmental gradient can be fitted as random effects in a mixed-model; that is, regression coefficients are allowed to vary freely across individuals (Meyer & Kirkpatrick 2005). If a significant improvement to model fit is achieved by allowing slopes and/or quadratic coefficients to vary (compared to models where they are kept constant), this implies statistically significant variation among individuals in these reaction norm parameters.

Our goal was to explore broadly how individuals respond to environmental variability per se, rather than speculate on the exact cue to which individuals respond. For this reason, we used the multivariate measure PC1 as our environmental axis in the random regressions. A quadratic fixed effect of PC1 was modelled, to reflect the population-level response (see Fig. 1e). Among and within-individual

variation in laying date were simultaneously analysed in relation to PC1 in a linear mixed-effects model (LMM), where the laying date of a given female i in a given environment E was specified as:

$$\text{Laying date}_{iE} = \mu + (\text{PC1} + \text{PC1}^2)_E + \text{year} + f(p_i, n_x, E) + e_{iE},$$

where μ was the population mean laying date in the average environment, the term $(\text{PC1} + \text{PC1}^2)_E$ was a fixed effect describing the mean population response to PC1 across all environments E , year was a random effect (included to account for any sources of environmental covariance among individuals measured in each year additional to that explained by PC1), and $f(p_i, n_x, E)$ was the random regression function, on orthogonal polynomials of E (the values of PC1 in each environment) of order n_x (taking potential values 0, 1,

2, 3), where p_i represented the phenotypic deviation of individual i from the population mean in each environment. Finally, e_{iE} was the residual error term for each individual in each environment, which was assumed to be uncorrelated across records within individuals.

We fitted a series of increasingly complex random regressions, each time retaining the same fixed effect structure and a random year effect. We began with a zero order polynomial function, where individual deviations were effectively held constant across the range of environmental conditions. Next, we fitted a first order polynomial function ($n_x = 1$), which allowed females to have different reaction norm slopes. We subsequently tested for nonlinearity in reaction norms by fitting models with second order ($n_x = 2$) and third order ($n_x = 3$) polynomial functions, with corresponding 3×3 and 4×4 symmetrical variance–covariance matrices, respectively. We used a forward model selection procedure to assess the fit of each successively more complex model using likelihood-ratio tests: two times the difference in log-likelihood scores between successive models were compared against a χ^2 distribution, with one degree of freedom for each additional (co)variance component in the more complex model.

For each of these random regressions, we also modelled the residual error structure (the e_{iE} term) in one of two ways. First, we assumed a simple univariate error structure, where residual errors were assumed to be uncorrelated across environments. Second, we modelled a multivariate error structure, by splitting our environment measure into three groups (low, intermediate and high values of PC1, corresponding to thirds of the distribution) and estimating the variance in e_i (the residual variance component, V_i) separately for each environmental grouping. Following model selection to determine the most appropriate functional form of the individual reaction norm, the variance–covariance matrix of random regression coefficients was transformed to yield environment-specific estimates of the among-individual variance (V_{ind}) in laying date. For $n_x > 0$, V_{ind} will change across environments, implying individuals vary in plasticity (Nussey *et al.* 2007).

PATTERNS OF SELECTION ON LAYING DATE

Absolute (calendar) laying date

We quantified the strength of selection on laying date each year by regressing breeding success (binary variable, successfully raised a chick or unsuccessful) against laying date using generalized linear models (GLM) with binomial errors and logit-link functions. Data from all numbered breeding sites (i.e. including those occupied by unknown individuals) were used in this case, as these data were available for the entire period of study (1972 to 2005). GLMs testing for linear and nonlinear selection on laying date were performed on each year's data. Nonlinear selection was tested for by including a quadratic effect of laying date, which was dropped from the model if not significant. Annual selection gradients were calculated using procedures outlined in Lande & Arnold (1983). We tested for temporal trends in the strength of directional selection by linear regression against year.

Relative laying date

We next examined a relative timing measure, where the laying date of females was expressed relative to the population mean that year, i.e. by subtracting annual mean laying dates from individual laying dates. These deviation scores provide a standardized measure of the extent to which females tracked (or failed to track) the mean population response over time. We related the success of each breeding

attempt (whether the female raised a chick that year or not) to these deviation scores using logistic regression. Here, a generalized linear mixed-effects model (GLMM with binomial errors and a logit-link function) was used.

$$\begin{aligned} \text{Breeding success} = & \text{deviation score} + (\text{deviation score})^2 \\ & + \text{PC1} \times (\text{deviation} + \text{deviation}^2) \\ & + \text{female identity} + \text{year} \end{aligned}$$

Breeding success was a binary response variable (1 = successful, 0 = unsuccessful). Female identity and year were included as random effects. Data from 1986–2005 were used for this analysis, as known individuals were not followed pre-1986. The first two explanatory terms were continuous fixed effects. The linear term tested for directional selection and the quadratic term for nonlinear selection. Interactions between PC1 and deviation score and its square were included to test whether the strength of linear and/or nonlinear selection varied across years in relation to environmental conditions.

Statistical analyses were performed using restricted maximum likelihood procedures implemented in ASREML and GENSTAT Edition 8 (VSN International, Hemel Hempstead, UK).

Results

POPULATION-LEVEL RELATIONSHIPS

Significant relationships were detected at the population level between average annual laying date and each of the environmental indicators (SST, UI, NOI and \log_{10} -transformed rockfish abundance). Table 1 shows the results from the model selection procedures for each variable. A quadratic fit best described the relationship between laying date and SST (Fig. 1a), explaining over 71% of the variation. 1992 was the warmest year for spring SST during the study period and this was also the year in which laying was latest (mean laying date 4 June). The best model in the case of upwelling index was a GAM with a smoothed spline function, which explained 59% of the variation in laying dates (Table 1, Fig. 1b). The general trend was for laying to be earlier in years where upwelling was stronger, at least for intermediate values of UI (at extremely high values of UI breeding was delayed). A GAM smooth spline also best described the relationship between laying date and spring NOI ($r^2 = 0.751$, Table 1, Fig. 1c). Laying was generally earlier in strongly positive NOI years (Fig. 1c). A negative linear fit best described the relationship between laying date and log-transformed rockfish abundance ($r^2 = 0.468$, Table 1, Fig. 1d). Thus, in years where juvenile rockfish were plentiful, laying was earlier. The four environmental variables were inter-correlated to some degree (Appendix S1). A quadratic fit to the data best explained the relationship between laying date and the multivariate measure PC1 (74.1% of the variation explained, Table 1, Fig. 1e). Laying was earlier in years in which PC1 was positive, which corresponded broadly to years in which SST was intermediate to low, UI was high, NOI was positive and rockfish were abundant. Conversely, laying was late in strongly negative years (high SST, low UI, negative NOI and low rockfish abundance). A negative linear relationship persisted when the three extreme years were removed from the analysis ($t = -2.09$, $r^2 = 0.17$, $P = 0.05$).

Table 2. (a) Forward model selection procedure for random regression model. For each order of orthogonal polynomial specified in the random regression, the error structure was modelled as either univariate or multivariate. All models had the same fixed effects structure and a random effect for year. The fit of each successively more complex model was assessed using likelihood ratio tests. Each model was compared with the one immediately preceding it in the table, except where a decrease in log-likelihood resulted, in which case it was compared with the model two rows up from it (i.e. 2a was compared with 1a rather than 1b). Multivariate models were only preferred if their univariate version was better than the previous simpler model. (b) Output of model 3b, the most preferred random regression model

Model	Random regression function	Error structure	Log likelihood	d.f. (random effects)	Models compared	Chi prob
1a	Zero order polynomial	Univariate	-1399.49	2		
1b	Zero order polynomial	Multivariate	-1388.12	4	1a v 1b	< 0.001
2a	1st order polynomial	Univariate	-1394.16	4	2a v 1a	0.005
2b	1st order polynomial	Multivariate	-1385.22	6	2b v 2a	< 0.001
3a	2nd order polynomial	Univariate	-1377.6	7	3a v 2b	< 0.001
3b	2nd order polynomial	Multivariate	-1373.68	9	3b v 3a	0.020
4a	3rd order polynomial	Univariate	-1375.52	11	4a v 3a	0.385
4b	3rd order polynomial	Multivariate	-1370.42	13	4b v 3b	0.164

(b)

Preferred model = 3b		d.f.	F	P
Fixed effects:	PC1	1	49.90	< 0.001
	PC1 ²	1	6.65	0.020
Random model:	Year	Component	SE	
	Var(Intercept)	11.48	4.40	
	Cov(intercept:slope)	66.8474	12.01	
	Var(slope)	-0.29392	4.20	
	Cov(interc:quadratic)	6.84878	2.78	
	Cov(slope:quadratic)	4.82924	3.08	
	Var(Quadratic)	-5.10107	1.61	
Multivariate error structure	Environmental grouping	Residual variance	SE	
	1	32.8416	3.81	
	2	27.9414	3.11	
	3	19.4462	2.31	

Highly significant quadratic relationships were detected between annual productivity and laying date ($F_{2,17} = 63.89$, $P < 0.001$, Fig. 2a), and productivity and PC1 ($F_{2,17} = 48.59$, $P < 0.001$, Fig. 2b). These trends disappeared, however, when the three extreme years were removed from each analysis (effect of laying date on productivity, excluding these 3 years: $t = -1.76$, $r^2 = 0.12$, $P = 0.10$; effect of PC1 on annual productivity, excluding these 3 years: $t = 1.27$, $r^2 = 0.04$, $P = 0.22$ quadratic effect NS). There was a nonsignificant trend towards earlier laying over the entire study period (Fig. 1f, $b = -0.212$, $t = -1.59$, $P = 0.121$).

INDIVIDUAL VARIATION IN BREEDING TIME RESPONSES

The results from the random regression model selection procedure are shown in Table 2. The most preferred model was one with a second order polynomial function and a multivariate error structure (details of the forward model selection procedure are given in the Table 2a legend). This model showed that there was statistically significant among-

individual variation in plasticity, and that individuals exhibited variable nonlinear (quadratic shaped) reaction norms. To visualize this, we plotted how the among-individual component of total phenotypic variance (V_{ind}) changed with PC1 (Fig. 3a). V_{ind} was highest in years where PC1 was strongly negative, i.e. when environmental conditions were poor, and declined to a constant level in medium (PC1 \approx 0) and good environments (positive PC1). A schematic representation of the variation in reaction norms for five hypothetical individuals is also given, consistent with this pattern of changing V_{ind} across PC1 (Fig. 3b). Residual variance (V_r) was also not constant across environments: V_r was highest in the poorest environments, lower in average environments and lowest in the best quality environments (Table 2b).

PATTERNS OF SELECTION ON LAYING DATE

Calendar laying date

The results of the GLMs examining selection on laying date each year are summarized in Table 3. Negative directional

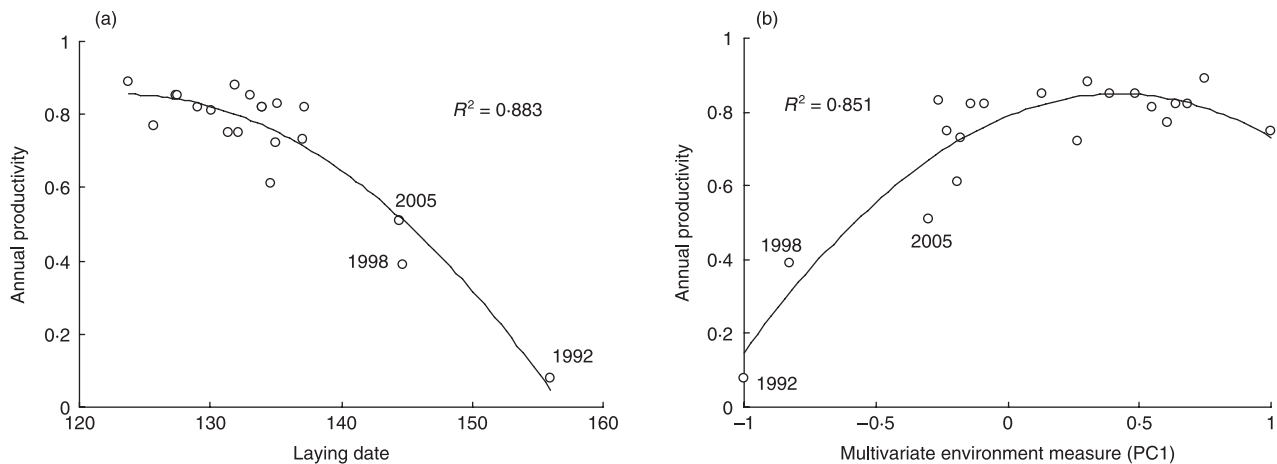


Fig. 2. (a) Relationship between annual productivity (mean number of chicks fledged per breeding pair) and mean laying date of all pairs that year. (b) Relationship between annual productivity and environmental quality, as indexed by PC1.

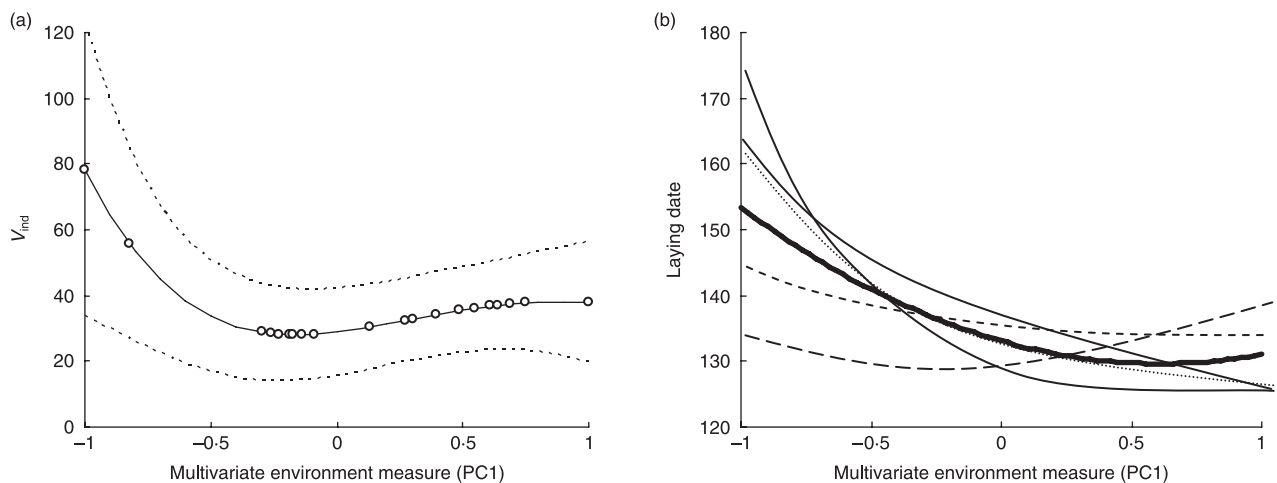


Fig. 3. (a) Changes in the among-individual component of variance, V_{ind} , across the natural range of environmental conditions experienced (PC1). Each data point (open circle) represents a year. The solid line represents V_{ind} predicted continuously across PC1, and dashed lines are 95% confidence intervals. (b) Schematic representation of among-individual variation in reaction norms, showing the expected pattern for five hypothetical individuals (not actual data), given the results of the random regression. Dark line shows the mean population-level response to PC1, from which individuals are expected to deviate. Individuals also differ in the shape of their reaction norms.

selection was detected in 26 out of 34 years (21 of these selection gradients were significant after Bonferroni sequential correction, Rice 1989). Significant nonlinear selection was also detected in 6 years, all in the latter part of the study (1990's onwards). Selection was stabilizing in 1996 and 1997 and disruptive in 1999. There was substantial inter-annual variation in the strength of directional selection, but no systematic temporal trend (correlation between linear selection gradients and year, $r = 0.02$, $P = 0.91$).

Relative laying date

The GLMM of breeding success in relation to relative laying date (individual deviation scores) provided evidence for both directional and stabilizing selection (Table 4). On average, females breeding earlier than the mean had higher breeding success (significant negative effect of 'deviation score'). There

was also an overall significant negative quadratic (deviation score²), such that breeding success was lower for both strongly negative and strongly positive deviations, and was highest at intermediate values close to zero. The strength of stabilising, but not directional, selection depended on environmental quality as indexed by PC1 (interaction effect: PC1 \times deviation score²: $\chi^2 = 5.73$, $P = 0.017$). To explore the nature of this quadratic interaction in more detail, PC1 was split into three categories, corresponding to thirds of the distribution ('poor', 'average' and 'good' quality environments, as in Table 2b) and the same model was run for each environmental grouping. In the poorest environments, there was no evidence for any selection, either directional or stabilising (Fig. 4a, linear effect: $\chi^2 = 0.04$, $P = 0.838$, quadratic effect: $\chi^2 = 0.12$, $P = 0.730$). In average environments, there was significant directional selection (Fig. 4b, linear effect: $\chi^2 = 12.83$, $P < 0.001$) but no stabilising selection (quadratic effect:

Table 3. Temporal patterns of selection on laying date. LD = mean laying date across all sites. N = number of breeding sites each year (includes sites with colour-ringed birds). n = number of colour-ringed females followed each year (89 in total followed since 1986, with repeat measures on each across years). Linear terms (β) indicate the strength of directional selection and quadratic terms (γ) the strength of non-linear selection (stabilizing if negative and disruptive if positive). Quadratic terms included in table only if significant. P values are actual values from logistic regressions; asterisks denote values significant at $\alpha = 0.05$ after Bonferroni sequential correction

Year	LD	N	Linear term (directional selection)					Quadratic term (non-linear selection)			
			n	β	SE	t	P	γ	SE	T	P
1972	23-May	116		-0.325	0.040	-4.91	< 0.001*				n.s.
1973	20-May	130		-0.141	0.071	-1.94	0.052				n.s.
1974	17-May	139		-0.205	0.057	-3.19	0.001*				n.s.
1975	17-May	137		-0.141	0.057	-2.30	0.021				n.s.
1976	16-May	164		-0.292	0.065	-3.78	< 0.001*				n.s.
1977	17-May	122		-0.076	0.065	-1.16	0.246				n.s.
1978	24-May	123		-0.400	0.111	-3.04	0.002*				n.s.
1979	8-May	135		0.093	0.086	1.10	0.272				n.s.
1980	14-May	142		-0.278	0.059	-3.68	< 0.001*				n.s.
1981	9-May	145		-0.259	0.037	-3.95	< 0.001*				n.s.
1982	13-May	70		-0.451	0.073	-3.13	0.002*				n.s.
1983	9-Jun	45		-0.001	0.054	-0.02	0.988				n.s.
1984	15-May	91		-0.114	0.058	-1.86	0.063				n.s.
1985	8-May	110		-0.339	0.068	-3.49	< 0.001*				n.s.
1986	18-May	145	6	-0.090	0.063	-1.42	0.155				n.s.
1987	11-May	167	5	-0.175	0.054	-2.91	0.004				n.s.
1988	1-May	204	27	-0.143	0.040	-3.04	0.002*				n.s.
1989	5-May	214	31	-0.178	0.036	-5.06	< 0.001*				n.s.
1990	5-May	219	30	-0.166	0.039	-3.37	< 0.001*				n.s.
1991	8-May	217	50	-0.257	0.039	-4.81	< 0.001*				n.s.
1992	31-May	152	30	-0.060	0.027	-2.11	0.035				n.s.
1993	11-May	206	40	-0.233	0.045	-4.38	< 0.001*	-0.162	0.027	-2.52	0.012
1994	6-May	216	41	-0.317	0.041	-5.12	< 0.001*				n.s.
1995	14-May	230	46	-0.348	0.073	-3.29	< 0.001*	-0.328	0.060	-1.97	0.049
1996	12-May	232	48	0.122	0.064	1.88	0.060	-0.16	0.035	2.10	0.036
1997	7-May	228	37	-0.059	0.023	-2.90	0.004	-0.172	0.048	-2.07	0.038
1998	23-May	185	30	-0.121	0.055	-2.02	0.043				n.s.
1999	9-May	189	20	-0.156	0.038	-3.75	< 0.001*	0.08	0.022	2.18	0.029
2000	13-May	179	28	-0.232	0.041	-4.42	< 0.001*				n.s.
2001	9-May	215	29	-0.214	0.039	-4.10	< 0.001*				n.s.
2002	5-May	207	23	-0.271	0.052	-4.45	< 0.001*				n.s.
2003	11-May	203	21	-0.189	0.052	-3.36	< 0.001*				n.s.
2004	11-May	218	18	-0.141	0.042	-1.86	0.063				n.s.
2005	24-May	242	23	-0.736	0.139	-4.74	< 0.001*	0.288	0.040	3.39	< 0.001

Table 4. Results of the GLMM testing for directional (linear effect) and stabilising (quadratic) selection on individual deviations from the population mean laying date each year

Selection on individual responses to multivariate measure of the environment (PC1)

	Coefficient	SE	Wald	P
Intercept	0.977	0.047		
Deviation score	-0.064	0.023	5.72	0.017
Deviation score ²	-0.032	0.011	3.96	0.046
PC1	0.430	0.087	21.55	< 0.001
PC1 × Deviation score	-0.029	0.038	2.19	0.139
PC1 × Deviation score ²	-0.048	0.021	5.73	0.017
Random terms:	Variance component	SE		
Female identity	0.358	0.194		
Year	0.582	0.282		

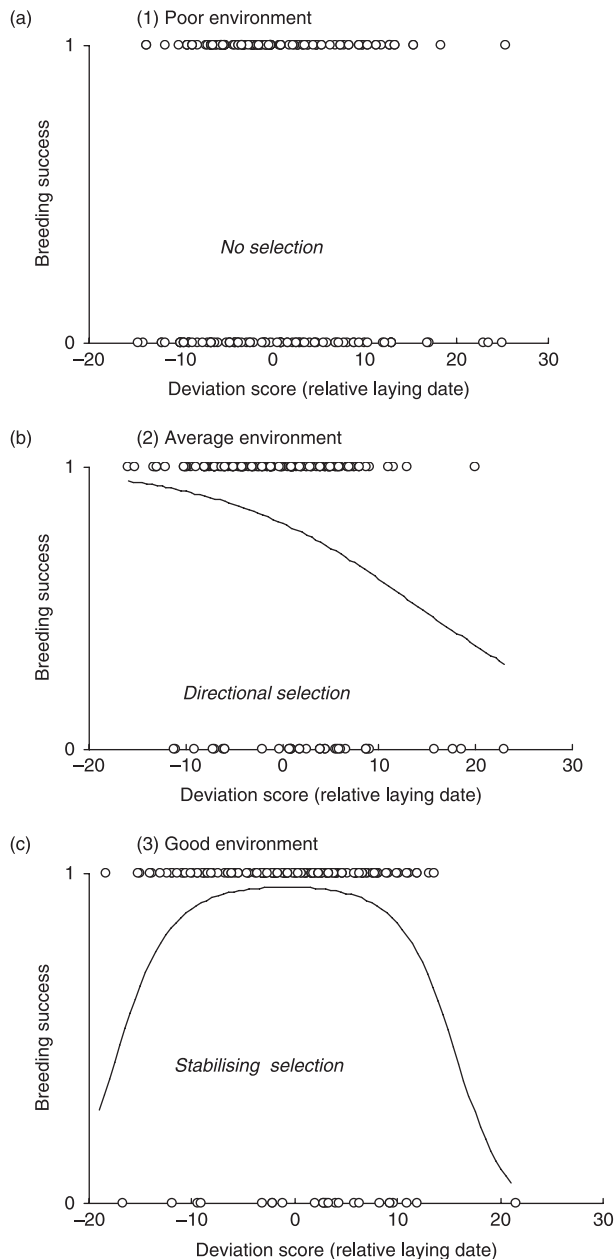


Fig. 4. Changing patterns of selection on individual deviations from the mean response each year. No selection apparent in 'poor' years (top panel), directional selection for earlier-than-average breeding in 'average' years (middle panel) and stabilizing selection in 'good' years (bottom panel). Curves are predicted fits from separate GLMMs in each environment.

$\chi^2 = 2.13$, $P = 0.144$). Finally, in the best environments, there was evidence for strong stabilising selection (Fig. 4c, quadratic effect: $\chi^2 = 19.61$, $P < 0.001$) but no overall directional selection (linear effect: $\chi^2 = 0.23$, $P = 0.634$).

Discussion

We addressed three central questions in this study: (i) how is the breeding phenology of guillemots affected by annual fluctuations in the marine environment, (ii) do females differ

in their responses to environmental changes, and (iii) what are the fitness consequences of phenology differences among females? Strong associations were documented at the population level between phenology and four separate measures of environmental variability, in particular spring SST (measured at the breeding colony) and spring NOI (measured across the entire North Pacific). Breeding was earlier in years where water temperatures were low and the NOI index was positive. Enhanced upwelling of cold, nutrient-rich water from depth in such years would have made the seas around SEFI more productive, which likely influenced the availability and/or timing of fish prey. Population-level trends were mirrored at the individual level, as revealed by mixed-model analysis of the reaction norms of individual females. This implied that the changes were attributable mostly to phenotypic plasticity, i.e. individuals altering their laying dates in response to changing conditions, rather than shifts in the demographic or genetic composition of the population (Przybylo, Sheldon & Merila 2000), although these could not be excluded entirely and may have occurred concomitantly (see below).

Rather than focussing on single environmental variables in turn, we combined information from all four variables into a multivariate summary measure, effectively reducing environmental complexity down to a single axis of variation. We believe this was justifiable due to the high degree of environmental variation captured by PC1 (62%) and the inability to ascribe guillemot phenology entirely to a single environmental variable. A quadratic effect of PC1 explained just over 74% of the variation in annual mean laying dates, and random regression analysis confirmed that individual females responded in a non-linear fashion to this multivariate measure of environmental variability. We interpret the relationship between laying dates and PC1 as predominantly reflecting adaptive behavioural and physiological responses of birds to environmental cues, but suggest that environmental constraints on the timing of egg laying may also be important, particularly in poor years. Important prey species such as krill and rockfish (Sydeman *et al.* 1997) may be less abundant around the time when birds are coming into breeding condition in these unfavourable years, forcing females to delay breeding until they accumulate sufficient body energy reserves (Stevenson & Bryant 2000). Nonetheless, aside from three extreme years (1992, 1998 and 2005), during which conditions were particularly bad and productivity in the colony fell to 51% or lower, most of the variation in environmental conditions had little effect on mean breeding success (Fig. 2b, no significant effect of PC1 on annual productivity when these 3 years are excluded). Laying date still responded to environmental variability in non-extreme years, however, suggesting that guillemots were able to maintain high breeding success across most of the range of environmental conditions by adaptively adjusting laying dates in line with cues. Behavioural adjustments during the incubation and chick-rearing periods (for example to foraging patterns) may also have contributed to the maintenance of high productivity in these less extreme (but still variable) years. When conditions deteriorated beyond a certain point, however, breeding success dropped

off dramatically (Fig. 2b, extreme negative values of PC1), and the birds also bred much later (Fig. 1e). This might indicate common constraints on both phenology and breeding success in poor years, perhaps acting through the reduced nutritional state of mothers (see below for discussion of how this likely also affected selection patterns). These constraints notwithstanding, phenological plasticity appeared to be an effective mechanism enabling the birds to track all but the most extreme fluctuations in their environment.

To determine if individual females varied in their laying date responses to climate variability, we employed a random regression analytical framework in which individual reaction norm coefficients were fitted as random effects in a mixed model (Nussey *et al.* 2007). We found a model with a second order polynomial function, where individual reaction norms were allowed to vary in degree of curvature, as well as in elevation and slope, best fit our data (Fig. 3b). To better visualize this variation in plasticity, we estimated the among-individual component (V_{ind}) of total phenotypic variance in each environmental category, and plotted how this component varied across PC1 (Fig. 3a). Individual reaction norms were distinct from each other (i.e. the variance in laying dates among individuals was higher) in the poorest environments, but converged as environmental conditions became more favourable (increasingly positive values of PC1, lower V_{ind}). Again, this suggested that many females were constrained to lay later when conditions were challenging (low values of PC1), but when conditions improved, females responded similarly to PC1 by laying more synchronously, perhaps because constraints were lifted. Mean laying date was presumably also closer to the optimal date in these more favourable years (positive values of PC1), as females laying earlier or later than the mean suffered reduced breeding success (Fig. 4c), implying that the average response was adaptive. In average environments, by contrast, constraints on the timing of egg laying may still have been important: directional selection favoured females that managed to lay earlier than the rest in these years, implying that many females laid later than otherwise optimal (Fig. 4b).

A number of recent studies have employed similar methodology to quantify individual variation in plasticity in wild vertebrate populations (Brommer *et al.* 2005; Nussey *et al.* 2005a,b; Reed *et al.* 2006; Brommer, Rattiste & Wilson 2008; Charmantier *et al.* 2008). Two of these (Reed *et al.* 2006; Charmantier *et al.* 2008) found no detectable differences among females in the degree of plasticity exhibited, but here we document among-individual differences in nonlinear (as well as linear) components of the reaction norm. Brommer *et al.* (2008) also used higher order polynomial functions when examining individual variation in laying date responses of common gulls *Larus canus* (Linnaeus) to temperature, but found evidence for variation in linear responses only. These studies together reveal that plasticity patterns can differ considerably in the wild: among species with different life histories, among populations of the same species experiencing different environments and selection pressures [e.g. great tits

Parus major (Linnaeus) in the Netherlands, Nussey *et al.* 2005b, versus great tits in England, Charmantier *et al.* 2008; guillemots in Scotland, Reed *et al.* 2006, versus guillemots in California, this study], and even among individuals within a single population. Untangling the ecological causes of variability at these hierarchical levels will improve our ability to predict how species, populations and genotypes will respond differently to climate change. It is important to realize, however, that the interpretation of any differences is contingent upon whether the reaction norms measured are indeed reflective of responses to real cues, i.e. we could be measuring the wrong thing, and the organisms actually respond to something else (Lyon, Chaine & Winkler 2008). The use of coarse proxies such as temperature sum or large-scale climate indices no doubt washes over many important mechanistic details in this respect. However, basic ecological details are still lacking for the vast majority of marine vertebrate populations, making it difficult to untangle potential causal mechanisms. Identifying individual-level associations between phenology, breeding success and specific environmental factors is therefore a critical first step towards a more complete understanding of the mechanisms by which seabirds and other marine top predators respond to environmental change (Sandvik, Coulson & Saether 2008).

Relating phenotypic differences among individuals to fitness differences can also shed light on the evolutionary mechanisms affecting how organisms respond to environmental change. Several striking patterns emerged from our selection analyses. First, selection by and large always favoured earlier breeding (Table 4). In some years, selection was nonlinear, with apparent fitness costs to breeding too early (very early breeders may have had mismatched timing relative to prey availability), but the overall trend in these years was still that early breeding was better than late breeding (linear coefficients were always negative). Second, the strength of directional selection fluctuated across years. This supports a growing body of evidence indicating that selection gradients can vary considerably over time for wild populations (Kruuk, Merilä & Sheldon 2001; Coulson *et al.* 2003; Sheldon, Kruuk & Merilä 2003), or even alternate in sign from 1 year to the next (Grant & Grant 1995). The strength of directional selection did not vary systematically, however, at least not in relation to our PC1 index of environmental quality. It is interesting to note that during the first period of this study (up until circa 1989), there was consistent directional selection for earlier breeding (significant in 10 out of 18 years), and laying dates appeared to advance progressively over this period (Fig. 1f). From this point on, there was no trend in laying dates, and the pattern of selection was correspondingly less consistent (Table 4). It is possible, therefore, that the genetic composition of the population shifted somewhat during the early years, in response to selection continually favouring earlier laying genotypes. At the same time, some of the observed directional selection may have acted via the nutritional state of mothers (Price, Kirkpatrick & Arnold 1988). That is, mothers in good physical condition may have both bred earlier and been better parents, without

any causal relationship between laying date and breeding success: this type of selection (i.e. on the environmental, rather than genetic, component of breeding time) would not have resulted in an evolutionary response in laying dates (Merila, Sheldon & Kruuk 2001).

Finally, analysis of selection on relative laying dates revealed that females deviating significantly, in either direction, from the population mean laying date each year had reduced breeding success, particularly in good years. A narrow time window for successful reproduction may have selected for synchronous laying. Alternatively, selection may have favoured synchrony for social reasons (e.g. Murphy & Schauer 1996), or predation on chicks may have been greater for parents breeding earlier or later than most other breeders (Birkhead 1977; Hatchwell 1991). Social constraints may limit the general potential of this species to respond plastically to environmental changes (Reed *et al.* 2006), but the results of the current study suggest that environmental constraints also come into play, at least under certain conditions. Thus, individual reaction norms are shaped by a combination of constraints on the timing of egg laying and fitness trade-offs between the need to breed in synch with neighbours versus the need to track a fluctuating environment by responding appropriately to cues.

In conclusion, this study highlights the need to consider both proximate and ultimate influences on the timing of reproduction in a variable environment. Reaction norms reflect the degree of variability in environmental conditions historically and currently encountered, as well as the fitness costs and benefits of plastic responses. Phenotypic plasticity in ecologically important traits such as breeding time may accommodate rapid habitat changes up to a certain point (e.g. Charmantier *et al.* 2008), but existing reaction norms may not remain adaptive indefinitely (Visser 2008) – particularly if extreme events become more frequent in the future, as predicted by some climate models (e.g. Timmermann *et al.* 1999). Further studies of the ecological causes and genetic underpinnings of plasticity differences among and within populations and species will shed light on how animals will respond to climate change.

Acknowledgements

The authors wish to thank USFWS Farallon National Wildlife Refuge for supporting research on SEFI. This study was supported by USFWS, Friends of the Farallones, Gordon and Betty Moore Foundation, Bradford Foundation, ExxonMobil, and California SeaGrant. We thank previous Farallon biologists and interns for their dedicated efforts to monitor and study guillemot phenology. In particular, we thank Deborah Jaques, Larry Spear, Teya and Jay Penniman, and Harry Carter for initiating guillemot colour-banding operations in the mid 1980s. Many thanks also to Matthew Robinson, Christine Abraham, Morten Frederiksen, Loeske Kruuk, Mike Harris, Emma Cunningham, Dan Nussey and Jarrod Hadfield for helpful discussion and comments. The work was supported by a Principle's Studentship to T.E.R. from the University of Edinburgh.

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Received 20 April 2008; accepted 24 October 2008

Handling Editor: Henri Weimerskirch

Supporting information

Additional supporting information may be found in the online version of this article:

Appendix S1. (a) Comparing variability in sea surface temperatures between SEFI, California and the Isle of May, Scotland. (b) Obtaining data on environmental variables

Fig. S1. SST time series for the Isle of May and SEFI.

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