

**Reproductive phenology is a repeatable, heritable trait linked to the timing of other life history events in a migratory marine predator**

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**Electronic supplementary material (ESM)**

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**Electronic supplementary material 1: Latitudinal cline in southern elephant seal reproductive phenology**

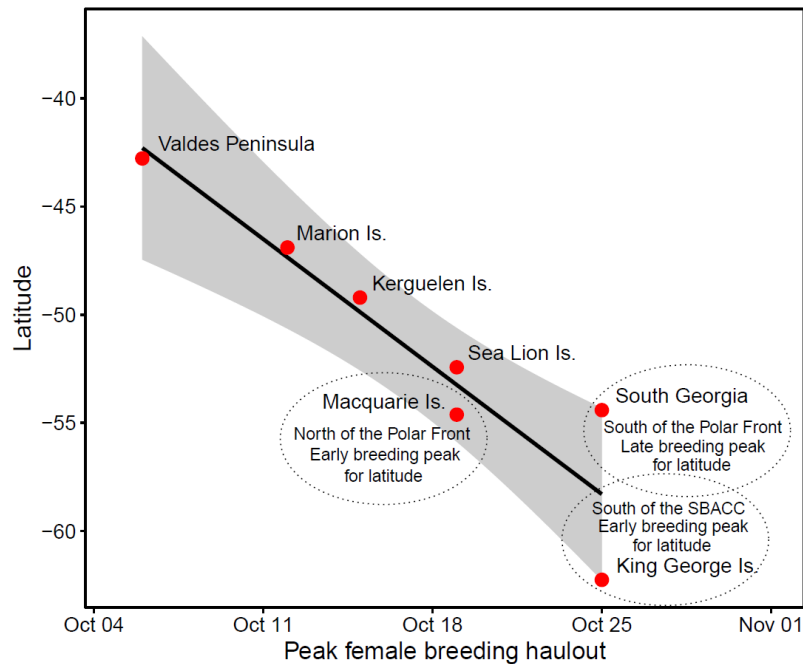


Figure S1. Southern elephant seal populations show a latitudinal cline in the timing of the breeding season, with low latitude populations breeding earlier than high latitude populations. Latitudinal gradients in photoperiod can explain the significant fit of the regression line, but fails to explain why sites at similar latitudes have the different breeding season peaks. Climate or other variables beyond day length therefore affect the timing of breeding at the individual and population level. Data sources: Valdes Peninsula (Lewis et al. 2004); Marion Is. (Oosthuizen et al. current study); Kerguelen Is. (Authier et al. 2011); Sea Lion Is. (Galimberti and Boitani 1999, Galimberti and Sanvito 2001); Macquarie Is. (Carrick et al. 1962, Hindell and Burton 1988); South Georgia (McCann and Rothery 1988); King George Is. (Vergani et al. 2004).

**Text S1**

Mammals commonly maintain seasonal reproduction through photoperiodic cueing (Goldman 2001, Forrest and Miller-Rushing 2010). Like other pinnipeds (e.g., Temte 1985, 1994), southern elephant seals (*Mirounga leonina*) are probably sensitive to changes in photoperiod, or daylength. In southern elephant seals, physiological responses to changing daylengths could be the proximate factor prompting implantation of the blastocyst and the start of gestation. Latitude and date determine photoperiod, and we may therefore expect latitudinal clines in photoperiodic traits. Southern elephant seals breed and moult over a broad latitudinal range (from about 42°S to below 62°S) and show a general latitudinal gradient in the timing of the breeding season as predicted for photoperiodic traits (Figure S1). Low latitude populations (e.g., those breeding on the Valdes Peninsula in Patagonia) breed earlier than high latitude populations (Campagna et al. 1993). Breeding earlier in the spring may help seals in Patagonia to reduce thermal stress from warmer weather. However, photoperiodic cueing fails to explain why sites at similar latitudes can have clear differences in breeding phenology (Campagna et

al. 1993). For example, the photoperiod-latitude hypothesis does not explain differences in breeding phenology between South Georgia and Macquarie Island (Figure S1). These islands are located at similar latitudes, but are climatically very different. Macquarie Island lies north of the Polar Front and has a comparatively mild climate for its latitude. Here, seals breed earlier than predicted by latitude. South Georgia, in contrast, is located south of the Polar Front and its relatively harsh polar climate is associated with later-than-predicted breeding. Variables beyond daylength, such as climate conditions, thus also seem to affect the timing of breeding at a population level. Climate conditions and individual traits may similarly underlay differences in the timing of breeding at an individual level.

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**Electronic supplementary material 2: Detection probability during weekly surveys and discovery curves**

**Text S2**

Oosthuizen (2016) used a multistate open robust design (MSORD) model to calculate detection probability of individually marked female southern elephant seals during the breeding season at Marion Island (1986 to 2013). Primary sampling periods were represented by  $t = 28$  annual breeding seasons. Each primary sampling period comprised  $j = 8$  secondary sampling periods – the weekly island-wide surveys conducted throughout the breeding season (mid-September to mid-November). Breeding season detection probabilities for this period are given in Figure S2. The current study analysed data collected during the 1989 to 2019 breeding seasons, except for 1998. A subset of animals (those that were seen in both the preceding moult and in the breeding season) were included in the current study, meaning that the detection probabilities in Figure S2 are approximate for the sample data analysed in this study.

Discovery curves were also drawn to show sampling coverage based on the rate of accumulation of new individuals during each southern elephant seal breeding season (1989 - 2019) at Marion Island (Figure S3).

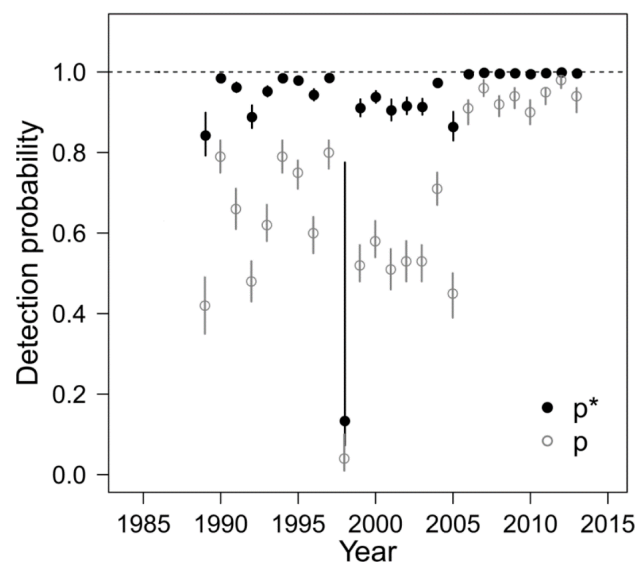


Figure S2. Estimated annual probability (mean and 95% CI) of detection of tagged female southern elephant seals during the breeding season at Marion Island (1989 – 2013). Open grey symbols ( $p_t^B$ ): mean detection probability in each of eight secondary surveys conducted at weekly intervals. Solid black symbols ( $p^*$ ): effective capture probability in the entire breeding season.

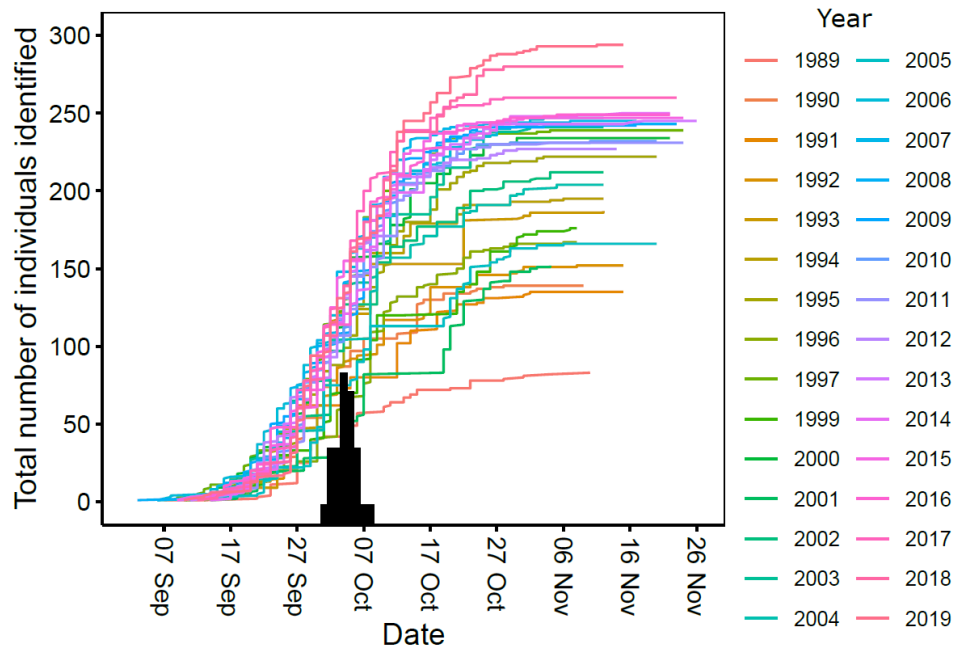


Figure S3. Discovery curves, illustrating sampling coverage based on the rate of accumulation of new individuals during each southern elephant seal breeding season at Marion Island. The discovery curves level off in late October each year as few new individuals is encountered. There is annual variation in the number of individuals identified as the sample of marked animals present in the population increased over time. The histogram shows annual variation in the observed median arrival date (1 to 8 October).

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### **Electronic supplementary material 3: Environmental covariates**

#### **Text S3**

Important physical and biological changes have occurred in the Southern Ocean marine ecosystem over the last century (Constable et al. 2014). Changing environmental conditions have driven, and will continue to drive complex biological responses in the Southern Ocean. Although biological responses may be regionally specific and not well understood across many regions of the Southern Ocean, changes in primary production will affect zooplankton, and have ecological consequences for higher trophic level consumers, including marine predators (Pinkerton et al. 2021). Since the 1950s, mid-depth Southern Ocean temperatures have warmed at a faster rate than that of the global ocean (Gille 2002). Most of this warming occurs in the Antarctic Circumpolar Current, between 45° and 60°S (Gille 2002), in the latitude range of foraging southern elephant seals from Marion Island (Oosthuizen et al. 2015). Antarctic sea ice extent has slightly increased since the 1970s (Simmonds 2015), but trends in sea ice extent is spatially very heterogeneous. Sea ice have strongly decreased in West Antarctica (the Antarctic Peninsula, southern Bellingshausen Sea and Weddell Sea) (Stammerjohn et al. 2008, Turner et al. 2020), in association with decadal changes in atmospheric circulation. The Southern Annular Mode (SAM) has displayed an unprecedented positive mean state in the last several decades, with implications for Southern Ocean atmospheric and ocean circulation (Thompson and Wallace 2000, Marshall 2003). During positive phases of SAM, stronger westerlies between 50°S and 70°S enhance the northward Ekman transport of cold Antarctic water, leading to cold sea surface temperature anomalies at these latitudes. The Ekman drift generates upwelling near the Antarctic Polar Front (60°S), where Marion Island elephant seals forage, increasing diatom abundance (Lovenduski and Gruber 2005, Hauck et al. 2013). In addition, because of greater wind stress, increased eddy activity follows positive SAM phases (Meredith and Hogg 2006, Screen et al. 2009). Mesoscale processes such as eddies significantly enhance primary productivity and several predator species, including elephant seals, appear to forage preferentially in association with these features (Bailleul et al. 2010, Dragon et al. 2010).

Regionally specific linkages between the Southern Oscillation Index (SOI), an index of the El Niño–Southern Oscillation (ENSO), and Southern Ocean anomalies (e.g., sea ice extent and sea surface temperatures) are also evident (Kwok and Comiso 2002). ENSO has its origins in the tropical Pacific but propagates westward with oceanographic transport (Turner 2004) or through atmospheric teleconnections (Klein et al. 1999). In the mid-latitudes of the South Atlantic Ocean, northwards of where Marion Island elephant seals forage, ENSO-induced wind anomalies are an important driver of upper ocean temperatures and Ekman pumping (Colberg et al. 2004). Substantial evidence of Southern Ocean marine predator responses to ENSO exists (e.g., Barbraud et al. 2012 and references therein for southern Atlantic and Indian Ocean examples). However, marine predator responses to ENSO are not uniform across species and areas, and it is unresolved how ENSO conditions affect the foraging behaviour of southern elephant seals breeding at Marion Island.

To test hypotheses about environmental influences on the phenology of southern elephant seals at Marion Island, we fitted year, population density and climatic variables as linear continuous covariates. We used the breeding female population size on 15 October each year as a proxy of population density. The breeding female population size decreased during the 1980s and early 1990s but has grown in size since the mid-1990s (Figure S4). For climate-driven environmental variation, we calculated annual means of the Southern Oscillation Index (SOI – an index of ENSO) (Figure S5) and Southern Annular Mode (SAM) (Figure S6) from monthly data (during the pre-breeding period; March to September) (Albers 2020). Large-scale climatic modes such as ENSO and SAM incorporate several different climate components and reducing complex space and time variability characteristics of local weather variables (Hallett et al. 2004, Stenseth and Mysterud 2005). These indices showed annual variation during the study period, but no

temporal trend. Therefore, SOI and SAM may explain annual variation in breeding phenology, but any correlation with southern elephant seal breeding phenology would not result in shifts towards earlier or later breeding in during the study period. Because shifts towards earlier or later breeding may also be driven by other unidentified environmental factors, we finally used a simple linear regression to test whether breeding phenology changed over time.

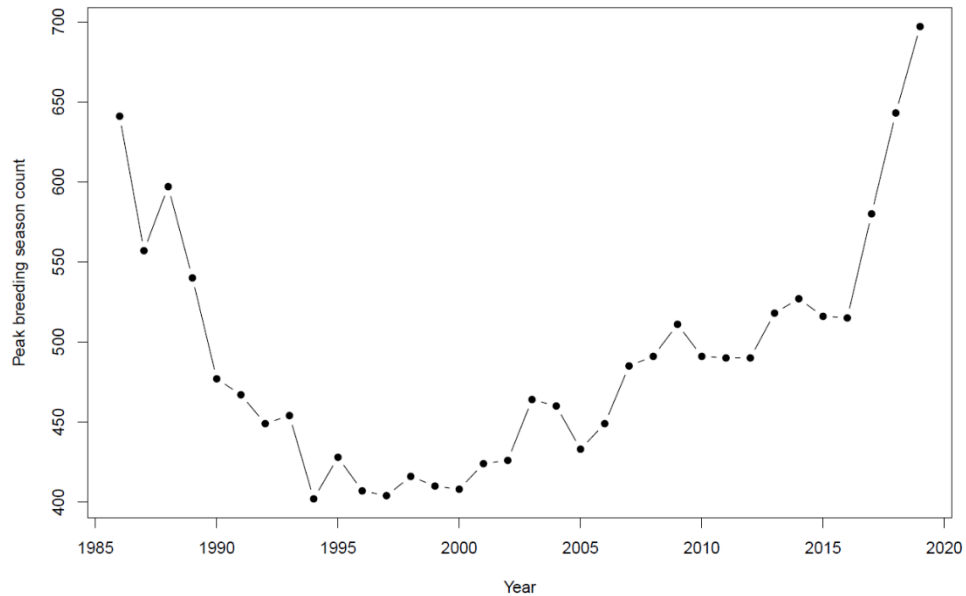


Figure S4. Change in the breeding female population size on 15 October during the study period as a proxy of population density.

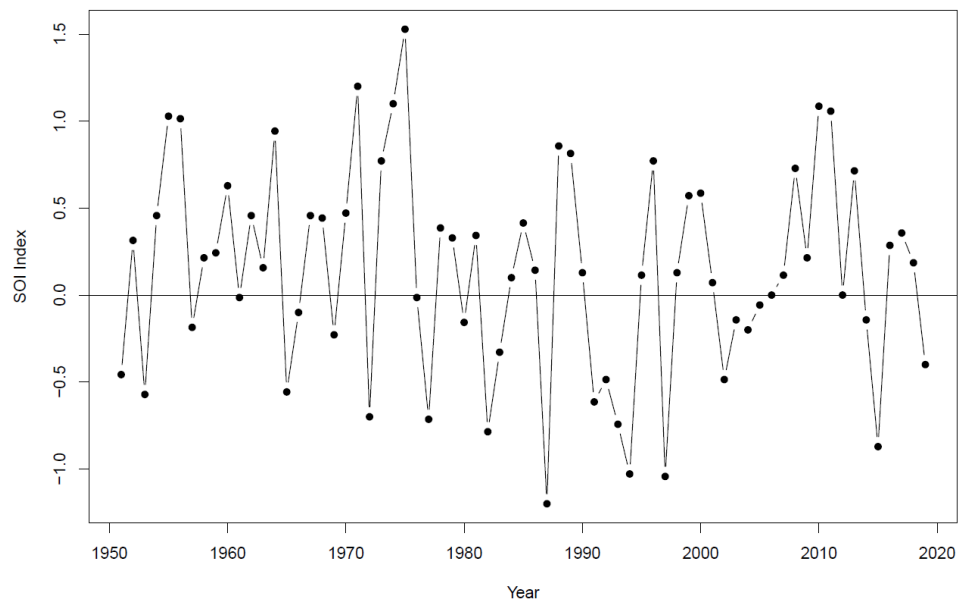


Figure S5. Annual means of the Southern Oscillation Index (SOI) from monthly data (during the pre-breeding period; March to September) since the 1950s. Source: <https://www.ncei.noaa.gov/access/monitoring/enso/soi>

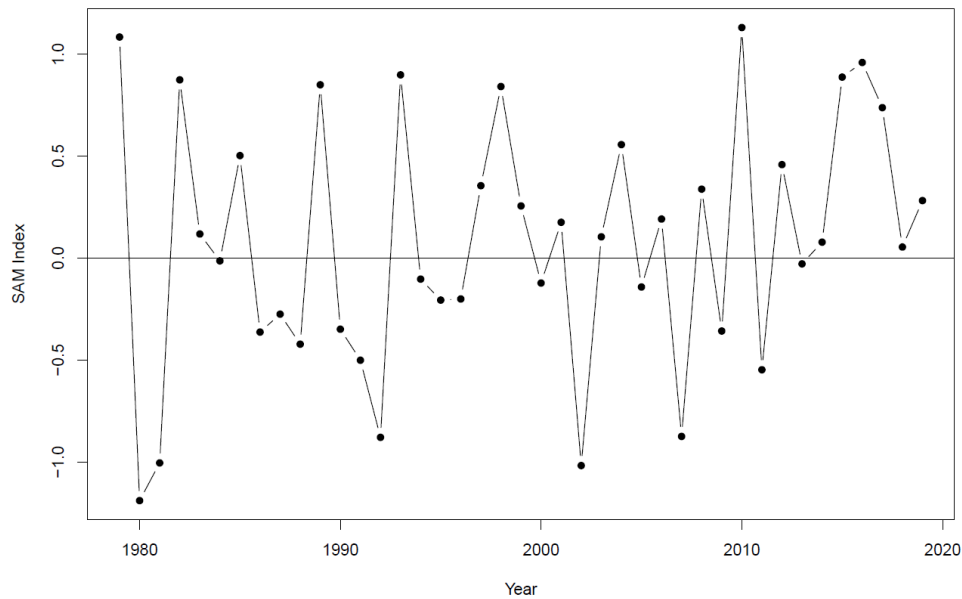


Figure S6. Annual means of the Southern Annular Mode (SAM) from monthly data (during the pre-breeding period; March to September) since 1979. Source: [https://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily\\_ao\\_index/aao/aao.shtml](https://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/aao/aao.shtml)

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## Electronic supplementary material 4: Model diagnostics

Linear mixed models make allowance for non-independence of observations (e.g., multiple arrival date observations per female) but explanatory variables are still assumed to be independent. Multicollinearity (when explanatory variables are correlated) can cause problems in model fitting and interpretation. We estimated correlation coefficients (Figure S7) and variance inflation factor (VIF) values (Table S1) that confirmed that multicollinearity was low.

Table S1. Variance Inflation Factor (VIF) multicollinearity test for the most parsimonious model (Table 1, main text) used for inference. The VIF values indicate low correlation (VIF < 5).

Model term <sup>1</sup>	VIF	VIF 95% CI
age*state	1.29	[1.25, 1.33]
moult	1.29	[1.25, 1.34]
wean	1	[1.00, 2.66]

<sup>1</sup> age: All individuals aged 21 to 26 were considered to be 21; state: first-time and experienced breeders were separated at ages 4 to 7. moult: date of the last observation in the preceding moult haulout; wean: the individual's weaning date as a pup

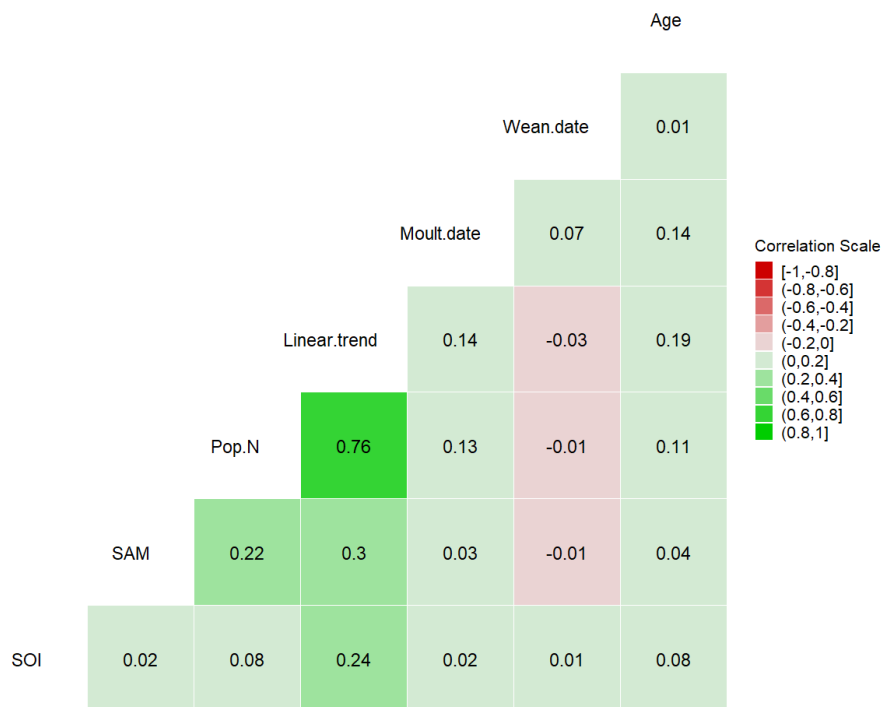


Figure S7. Pearson correlation coefficient matrix of continuous covariates used to model the breeding phenology of southern elephant seals at Marion Island. The population size (Pop.N) of breeding elephant seals decreased early in the study period, but steadily increased since the mid-1990s, leading to high correlation (correlation coefficient > 0.7) with the linear temporal trend variable.

We used the R package ‘performance’ (Lüdtke et al. 2021) to perform graphical (visual) model checking of assumptions and model fit for the most parsimonious model (Table 1, main text) used for inference (Figure S8).

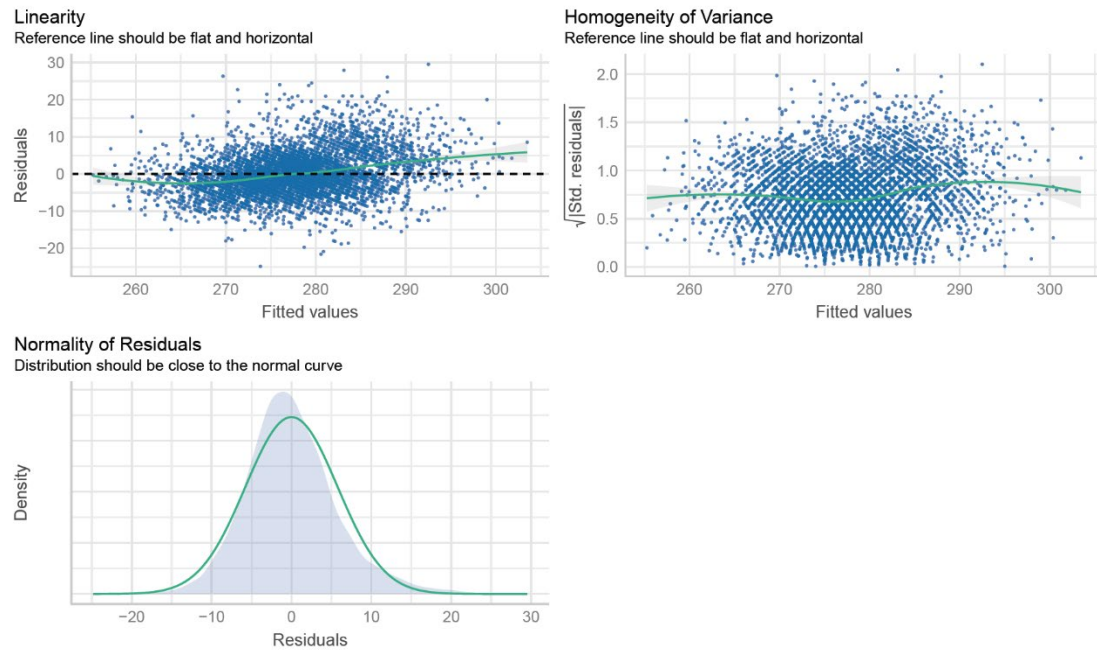


Figure S8. Model diagnostic plots for the most parsimonious model (Table 1, main text) used for inference. The Linearity panel (top left) evaluates the assumption of linear relationship between arrival dates and the explanatory variables. The spread of dots indicates slight heteroscedasticity (i.e., non-constant variance) also visible in the Homogeneity of Variance panel (top right). The Normality of Residuals panel (bottom left) showed residuals approximated a normal distribution.

## References

Lüdtke, D., M.S. Ben-Shachar, Patil, I., Waggoner, P., Makowski, D. 2021. performance: An R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software* 6: 3139.

**Electronic supplementary material 5: Models with trait-trait and trait-environment reaction norm slopes**

Table S2. Testing for individual plasticity in the breeding arrival dates of female elephant seals at Marion Island (1989 – 2019) via models that specified trait-trait and trait-environment reaction norm slopes. Model 1 is a random intercept linear mixed-effect model, with all fixed effects considered in this study (age, beeding state, breeding state and age interaction, moult date, weaning date, population density, Southern Annular Mode, Southern Oscillation Index, linear time trend). All other models in Table S2 have the same fixed-effect structure as model 1, but also includes a random slope term that allows individual-specific deviations around the population slope. Models 2 to 5 were compared to model 1 using likelihood ratio tests with associated difference in degrees of freedom ( $\Delta df$ ). A significant p-value indicates that the more complex random slope model fits the data better than the random intercept model. Model 2 allows the strength and/or direction of breeding responses (i.e., the slope of the relationship) to moult date to differ between individuals (a trait-trait reaction norm). Models 3 to 5 allow the strength and/or direction of breeding responses to population density and climate covairates to differ between individuals (environment-trait reaction norms). The ‘delta’ in the random effect structure of models 3 to 5 indicate that we are testing the within-subject mean slopes for population density (deltaN), Southern Oscillation Index (deltaSOI) and Southern Annular Model (deltaSAM). The model degrees of freedom, delta Akaike information criterion ( $\Delta AIC$ ) and log likelihood (log[L]) are given. The model with the best random effect structure is indicated in bold.

Model	Model random effect structure	df	$\Delta AIC$	Log(L)	$\chi^2$	$\Delta df$	p-value
1	(1 ID) + (1 year)	35	12.80	-18747			
<b>2</b>	<b>(moult ID) + (1 year)</b>	<b>37</b>	<b>0</b>	<b>-18739</b>	<b>16.80</b>	<b>2</b>	<b>&lt; 0.001</b>
3	(deltaSAM ID) + (1 year)	37	16.49	-18746	1.95	2	0.38
4	(deltaSOI ID) + (1 year)	37	16.58	-18747	0.21	2	0.89
5	(deltaN ID) + (1 year)	37	16.37	-18747	0.43	2	0.80

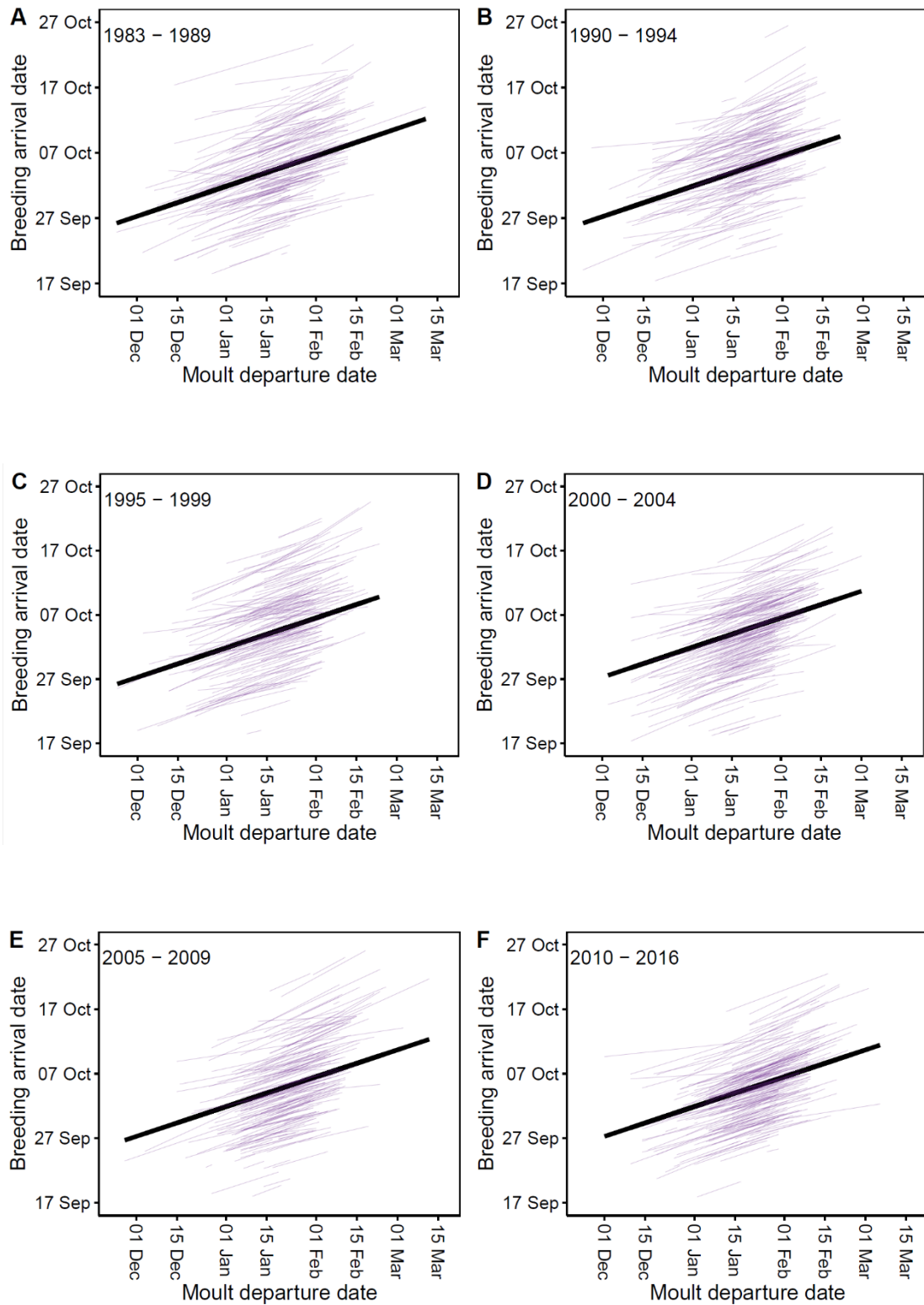


Figure S9. Plotting random intercepts and slopes by birth cohort (panels A to F) for better visualization of reaction norm slopes. The thin purple lines are the individual linear reaction norms, i.e., the across-year within-individual change in breeding arrival date as a function of a change in moult date. Individual deviations from the population intercept were larger (standard deviation  $\sigma = 6.5$ ) and explained more of the variance in the data than individual differences in slopes (plasticity) ( $\sigma = 1.6$ ). The population level effect (i.e., the average change in breeding arrival date in response to moult date) is given by the thick black regression line.

### Electronic supplementary material 6: Permutation tests of narrow-sense heritability

Permutation tests showed that the predicted slope between arrival dates of random pairs of animals was mostly non-significant and centred around zero, and that the observed parent-offspring regression slope coefficient is higher than expected by chance (Figure S10).

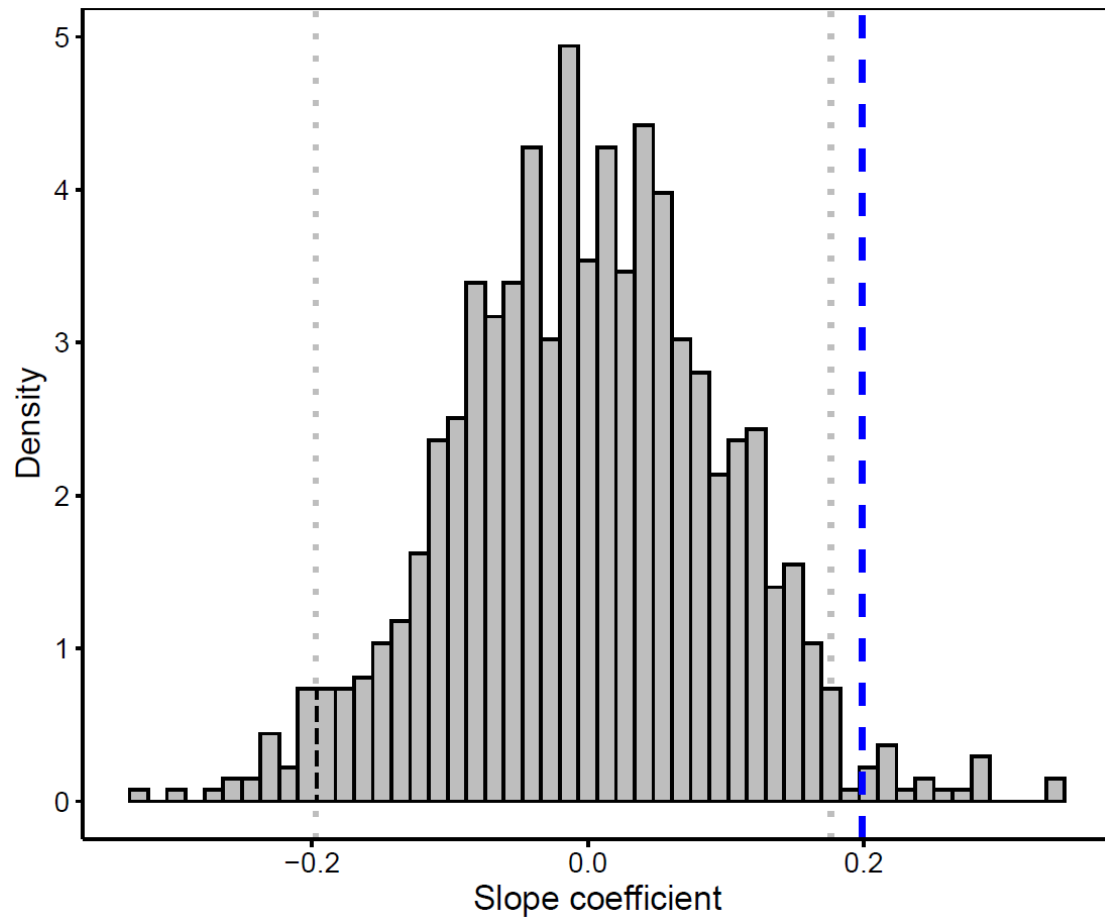


Figure S10. The histogram shows the distribution of 1000 linear regression slope coefficients of breeding season arrival dates of random pairs of animals. Grey dotted lines indicate the tail of the distribution (2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles). The blue dashed line is the observed parent-offspring regression slope coefficient.

## **Electronic supplementary material 7: Age-regression model**

### **Text S4**

Our analysis of breeding arrival timing of southern elephant seal females at Marion Island considered models specifying full age dependence (i.e., one estimate for each age). One of the benefits of the models with full age dependence is that they do not make restricting assumptions about the shape of the relationship between age and arrival date (e.g. linear, quadratic). But, although full age dependent models may explain more of the variation in the data (minimize the deviance) compared to age-regression models, they do not provide an estimate of trends (and slope parameters) in the data. Given that breeding arrival dates appeared to become earlier with increasing age from age 8, we fitted a model with age as a linear regression from age 8 to test whether the regression slope was significantly different from zero. Model results showed that from age 8, the linear regression slope of age was -0.43 (standard error = 0.07, 95% profile confidence interval = -0.57 to -0.29), supporting the statement that breeding arrival dates became earlier with increasing age from age 8.