






Rethinking “normal”: The role of stochasticity in the phenology of a synchronously breeding seabird

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Funding information

Pew Charitable Trusts; National Science Foundation, Grant/Award Number: 1016936 and 1341474; Office of Polar Programs, Grant/Award Number: 1255058

Handling Editor: Albert Phillimore

Abstract

1. Phenological changes have been observed in a variety of systems over the past century. There is concern that, as a consequence, ecological interactions are becoming increasingly mismatched in time, with negative consequences for ecological function.
2. Significant spatial heterogeneity (inter-site) and temporal variability (inter-annual) can make it difficult to separate intrinsic, extrinsic and stochastic drivers of phenological variability. The goal of this study was to understand the timing and variability in breeding phenology of Adélie penguins under fixed environmental conditions and to use those data to identify a “null model” appropriate for disentangling the sources of variation in wild populations.
3. Data on clutch initiation were collected from both wild and captive populations of Adélie penguins. Clutch initiation in the captive population was modelled as a function of year, individual and age to better understand phenological patterns observed in the wild population.
4. Captive populations displayed as much inter-annual variability in breeding phenology as wild populations, suggesting that variability in breeding phenology is the norm and thus may be an unreliable indicator of environmental forcing. The distribution of clutch initiation dates was found to be moderately asymmetric (right skewed) both in the wild and in captivity, consistent with the pattern expected under social facilitation.
5. The role of stochasticity in phenological processes has heretofore been largely ignored. However, these results suggest that inter-annual variability in breeding phenology can arise independent of any environmental or demographic drivers and that synchronous breeding can enhance inherent stochasticity. This complicates efforts to relate phenological variation to environmental variability in the wild. Accordingly, we must be careful to consider random forcing in phenological processes, lest we fit models to data dominated by random noise. This is particularly true for colonial species where breeding synchrony may outweigh each individual's effort to time breeding with optimal environmental conditions. Our study highlights the importance of identifying appropriate null models for studying phenology.

KEYWORDS

Adélie penguin, Antarctica, Bayesian hierarchical model, climate change, coloniality, phenological mismatch, *Pygoscelis adeliae*, stochasticity, synchrony

1 | INTRODUCTION

There is concern that ecological interactions are becoming increasingly mismatched in time as a result of climate change-driven shifts in the timing of key life-history events, such as migration, foraging and breeding (Thackeray et al., 2016). Such mismatches may result in decreased fitness (Cushing, 1974; Visser & Both, 2005) with long-term repercussions for population dynamics (Ludwig et al., 2006; McLean, Lawson, Leech, & van de Pol, 2016; Miller-Rushing, Hoyer, Inouye, & Post, 2010). These asynchronies have been observed in a diverse range of taxa, including arthropods (Both, van Asch, Bijlsma, van den Burg, & Visser, 2009; Winder & Schindler, 2004), birds (Both et al., 2009; Visser, te Marvelde, & Lof, 2012), fish (Durant et al., 2005), and mammals (Post & Forchhammer, 2008) and in a variety of ecological systems (Kerby, Wilmers, & Post, 2012 and references therein). To better understand and predict how phenological change might impact ecological systems, it is important to recognize what factors drive the timing of these life-history events.

Photoperiod has been identified as a proximate driver of the timing of key life-history events in both plants and animals (animal breeding, animal migration, plant flowering; Bradley, Leopold, Ross, & Huffaker, 1999; Hay, 1990; Helm, 2009; Temte & Temte, 1993; Zerbe et al., 2012). Studies of phenological variation (inter-annual variation and/or long-term trends), however, have focused on abiotic environmental factors, such as temperature and precipitation (Thackeray et al., 2016; Visser, Holleman, & Caro, 2009), or biotic factors, such as body condition, which may reflect environmental conditions and/or prey availability (Bêty, Gauthier, & Giroux, 2003; see review in Dawson, 2008). Variability in population-level phenology arises by some combination of three factors: (1) extrinsic drivers: changes in environmental (both abiotic and biotic) conditions, including changes in other components of the ecological community (e.g., prey, predators, mutualists); (2) intrinsic drivers: fixed differences among individuals coupled with demographic turnover within the population; and (3) stochastic variation: seemingly random variation in the timing of breeding of individuals (unrelated to known intrinsic or extrinsic factors) that propagates up to population-level metrics of phenology. Consistent with usage by Lande, Engen, and Saether (2003), we define stochasticity in this context as variability that is either truly random or, at least, appears random with respect to factors relevant to the question of interest. While numerous studies have focused on intrinsic and extrinsic drivers of phenology, there has been relatively little attention paid to the role of stochasticity. This lack of attention to stochastic factors is due, in part, to the fact that wild populations are subject to fluctuating environmental conditions, making it difficult to identify forces independent of measureable extrinsic and intrinsic factors.

The scale on which data are collected (i.e., population level vs. individual level) also contributes to the challenge of identifying stochasticity. Most studies of phenology in wild populations use population-level summary statistics (such as first or mean timing of a life-history event in a population) due to difficulties associated with collecting individual-level data. Metrics that capture the first instance of an

event of interest are known to be problematic due to their sensitivity to population size and sampling frequency (Miller-Rushing, Inouye, & Primack, 2008). While more robust to these influences, population mean metrics can be affected by other factors such as age (Ainley, 2002; Ainley, LeResche, & Sladen, 1983) and random variation among individuals (Crawley & Akhteruzzaman, 1988) that, through shifts in demographic composition, can impact population-level statistics. For instance, if older individuals breed earlier, an ageing population will display an apparent trend towards earlier breeding (Lewis, Nussey, Wood, Croxall, & Phillips, 2012). Similarly, any random subset of individuals may, by chance, have an earlier or later average phenology than another such random subset of individuals.

Individual-level data, in either wild or captive populations, allow us to track the role of demographic turnover (age and individual effects) on phenological response. An even more comprehensive understanding of the role for stochastic factors in driving phenological variability can be developed by pairing studies of wild populations with studies of populations under fixed environmental conditions (Dunne, Harte, & Taylor, 2003; Lambrechts, Perret, Maistre, & Blondel, 1999; Visser et al., 2009). Phenological variability in captive populations kept under fixed conditions represents a null model against which inter-annual variability in wild populations can be compared. Without such a control group, it may be difficult to determine the extent to which phenological variability is driven by environmental variability or, alternatively, inherent stochasticity. An estimate of inter-annual variation under fixed environmental conditions is, therefore, of value when interpreting phenological studies of wild populations. Assessing variability under these conditions may be particularly important for colonial breeding species that may rely on social cues to synchronize breeding (Ims, 1990b).

Here, we used data collected from both wild (representing naturally variable environmental conditions) and captive (representing fixed environmental conditions) populations of Adélie penguins *Pygoscelis adeliae*, to identify the role of stochastic factors in driving breeding phenology. Adélie penguins are a site faithful, highly colonial species that inhabit the Antarctic continent and surrounding islands. Several studies (Barbraud & Weimerskirch, 2006; Emmerson, Pike, & Southwell, 2011; Hinke, Polito, Reiss, Trivelpiece, & Trivelpiece, 2012; Lynch, Fagan, Naveen, Trivelpiece, & Trivelpiece, 2012; Youngflesh, Jenouvrier, Hinke, et al., 2017; Youngflesh, Jenouvrier, Li, et al., 2017) have sought to understand the conditions associated with breeding phenology in Adélie penguins. However, despite considerable effort to collect and analyse long-term phenological data, our understanding of what drives phenology in this species and the potential role that stochastic factors might play is limited. Our aim was to address three principal questions in this study: (1) how variable is Adélie penguin breeding phenology in the absence of environmental variability; (2) can variation in breeding phenology under fixed environmental conditions be explained by individual variation and age structure, or is there substantial residual random variation that remains unexplained; and (3) what implications do our findings have for interpreting variability in wild populations of synchronously breeding colonial species?

In sum, to what extent have we been overemphasizing the role of exogenous environmental forcing in the phenological variability in some wild populations?

2 | MATERIALS AND METHODS

2.1 | Description of data

Individual-level data on clutch initiation date (CID—the date in which the first egg is laid in each nest) were obtained for all individuals in a captive Adélie penguin population at SeaWorld San Diego from 1992 to 2015 (89 penguins in total). The number of breeding females in each year varied from 12 to 37 throughout the course of the study. The youngest birds to breed were 2 years of age, while the oldest were 45 years of age. Most penguins (67 of the 89) were born in captivity—individuals born before 1984 were taken as chicks from wild populations in the Ross Sea region of Antarctica in 1976.

All captive penguins were associated with unique identifiers, and metrics for each individual were tracked through time. Temperature at the facility was kept at a constant -4°C to -2°C year-round. Feeding regime of the captive birds did not change over the study period. Nesting materials (stones) were provided at the same time in each year. Photoperiod for the exhibit lighting mimicked that of 77°S latitude (though minimal exhibit lighting is required during the winter period), representative of the southern limit of the Adélie penguin breeding range. Seasonal variations in lighting are accounted for in the lighting regime and are constant from year to year. The viewing area is setup in such a way to minimize light exposure to the penguin enclosure. The penguin exhibit at SeaWorld underwent a 6-month renovation in 2005. The captive penguin population used in this study was kept in a separate enclosure during this renovation, which may have impacted breeding phenology in this year.

Data on CID were also obtained for a unique set of 100 individuals each year in a wild population of Adélie penguins located at Admiralty Bay, Antarctica (62.2°S , 58.4°W) from 1986 to 2012 using methodologies outlined in Hinke et al. (2012). Individual-level data across years were not available for the wild population. Wild penguins are typically younger than those in captivity, generally less than 20 years of age (Ainley, 2002; Ainley et al., 1983).

2.2 | Statistical analysis of individual phenology in marked captive penguins

For the captive Adélie penguin time series, a hierarchical Bayesian approach was used to model CID (y_{ij}), with year (i) and individual (j) as random effects (α and β , respectively) and age as a fixed effect (γ):

$$y_{ij} = \mu + \alpha_i + \beta_j + \gamma * \text{AGE}_{ij} + \varepsilon_{ij} \quad (1)$$

$$\alpha_i \sim N(0, \sigma_{\text{year}}^2)$$

$$\beta_j \sim N(0, \sigma_{\text{individual}}^2)$$

$$\varepsilon_{ij} \sim N(0, \sigma_{\text{model}}^2)$$

where μ represents the intercept, AGE represents the age of the female and ε represents the error term. This model was used to determine whether variation in y_{ij} was driven by the α parameter (variance attributed to a colony-wide effect that varies among years), the β parameter (variance attributed to fixed differences between individuals), the AGE covariate or the error term (ε). Individual data used in this statistical framework allowed us to account for potential confounding factors related to differences in phenology due to individual identity (or quality) and age, and these provide a more complete understanding of these processes than is possible using population-level summary statistics.

Models were fit using the R package “rjags” (Plummer, 2013), an interface to JAGS (Plummer, 2003), in the R statistical environment (R Core Team, 2016). Normal priors were used for α , β , γ and ε . Broad Gamma priors were used for all precision ($\tau = \frac{1}{\sigma^2}$) parameters (shape = 0.01, rate = 0.01). Posterior distributions were derived from three chains with 5,000 samples (after thinning every other draw) following a “burn-in” period of 40,000 draws and an adaptation period of 5,000 draws. Model convergence was assessed through a visual analysis of the posterior chains, in addition to the use of the Gelman-Rubin convergence diagnostic (Brooks & Gelman, 1998). All models unambiguously converged. Parameter estimate plots were generated using the “MCMCvis” package (Youngflesh, 2016), while other plots were generated using the “ggplot2” package (Wickham, 2009) in the R statistical environment.

2.3 | Statistical analysis of population-level phenology in captive and wild penguins

No information on individual phenology across years was available for the wild population (i.e., no information on the β parameter or AGE covariate), leaving it ambiguous as to which component was contributing to the variability in y_{ij} (CID of individual j in year i). Therefore, to directly compare the captive and wild Adélie populations, we considered population-level aggregate summaries of phenology in both populations. The median colony CID in each year (median across individuals; denoted y_{\cdot}) was calculated for both the captive and wild Adélie penguin populations. Between-year variation in median phenology, $\sigma_{\text{between}}^2 = \text{var}(y_{\cdot})$, included variation from all sources (year, individual, age and unexplained variance as captured by ε). Note that in contrast to σ_{model}^2 in Equation 1, $\sigma_{\text{between}}^2$ includes variation due to age and individual identity as well as residual stochastic variation unrelated to these factors. For both the captive and wild populations, variation within year i , $\sigma_{\text{within}}^2 = \text{var}(y_{ij})$, was used as a measure of year-specific, within-population breeding synchrony. We also note that while differences in (simulated) latitude may have generated a fixed difference in photoperiod between the captive and wild populations, our analysis examined only within-site inter-annual variability in breeding phenology.

To investigate whether individual breeding dates within a colony were distributed symmetrically around a population mean, as might be expected a priori if individuals were acting independently, CID values

in each year were standardized ($z_i = \frac{y_i - \bar{y}_i}{sd(y_i)}$) and aggregated across years to be analysed for skewness using a D'Agostino skewness test (D'Agostino, 1970). All analyses were performed in the R statistical environment (R Core Team, 2016).

3 | RESULTS

3.1 | Inter-annual and intra-annual variance in CID

Inter-annual variance of median colony CID was similar between the captive ($\sigma_{\text{between-captive}}^2 = 15.8[SE=3.7]$) and wild ($\sigma_{\text{between-wild}}^2 = 13.5[SE=3.7]$) populations (Figure 1). This degree of phenological variability is comparable to that seen in other taxa (Appendix S1). Within year, individual birds were relatively synchronous in both populations, with greater synchrony among individuals in the wild population compared to the captive population ($E[\sigma_{\text{within-wild}}^2] < E[\sigma_{\text{within-captive}}^2]$; Welch two-sample *t* test, $t = 4.99$, $df = 28.5$, $p < .001$; Figure 1; Appendix S1).

3.2 | Individual phenology in marked captive penguins

A strong year effect (α) on CID was apparent for the captive penguin population (Figure 2a; median (σ_{year}^2) = 13.81; Appendix S1). Significant year to year variation was found, even when accounting for the effects of age and individual. Inter-annual variation is still substantial when accounting for first-order autocorrelation (Appendix S2). Random effects due to individual (β) were notable (as evidenced by the spread of β parameter estimates), with some individuals breeding consistently earlier/later than other individuals (Figure 2b; median ($\sigma_{\text{individual}}^2$) = 13.66; Appendix S1). Over the 24-year study period, 16 different individuals were the first to lay eggs in a particular year (in 3 of these years, multiple individuals laid eggs on the same day). No biologically significant effect of age

(γ) on CID was found (median posterior estimate = 0.06 days/year); the 95% credible interval overlapped 0 (Figure 2c). Variance unaccounted for by the model is represented by median (σ_{model}^2) = 34.96 (Appendix S1).

3.3 | Intra-annual variance in CID

The distributions of CID for both captive and wild populations (Figure 3) had a small but statistically significant right skew ($g_1^{\text{captive}} = 0.54$, $SE = 0.10$; $g_1^{\text{wild}} = 0.79$, $SE = 0.04$; D'Agostino test, $p < .001$).

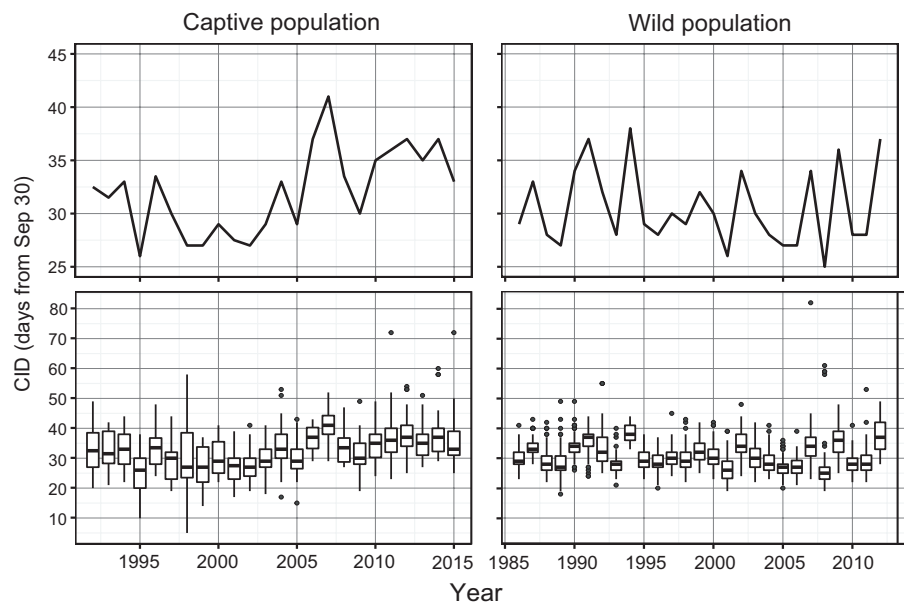
4 | DISCUSSION

Despite prior expectations of lower inter-annual variance in breeding phenology under fixed environmental conditions, we found that both the captive and wild Adélie penguin populations exhibit a similar degree of inter-annual fluctuation in breeding phenology. Stochasticity appears to play a substantial role in determining the timing of Adélie penguin breeding within the window of time dictated by biological and physical constraints. We suggest that stochasticity at the individual level is amplified by the importance of breeding synchrony among individuals, producing the observed inter-annual variance.

4.1 | Inherent inter-annual variation

Previous studies have suggested that photoperiod (Dawson, 2008), abiotic conditions such as rainfall (Deviche, Small, Sharp, & Tsutsui, 2006; Leitner, Van't Hof, & Gahr, 2003) and temperature (Both et al., 2004; Torti & Dunn, 2005; Visser et al., 2009), biotic conditions such as food availability (Reynolds, Schoech, & Bowman, 2003), or some combination of these factors are important in regulating phenology in a number of bird species. While these conditions may define a larger

FIGURE 1 Mean colony breeding phenology (top panels) and distribution of individual clutch initiation date (CID) in each year (bottom panels). The bold lines in the box-and-whisker plots represent the median CID, while boxes represent the 25th and 75th quantiles. The top and bottom of the whiskers are $1.5 \times$ interquartile range from the upper and lower boxes, respectively. Data beyond this range are plotted as points. The number of data points per year in the captive population ranged from 13 to 38. One hundred data points were collected for each year in the wild population



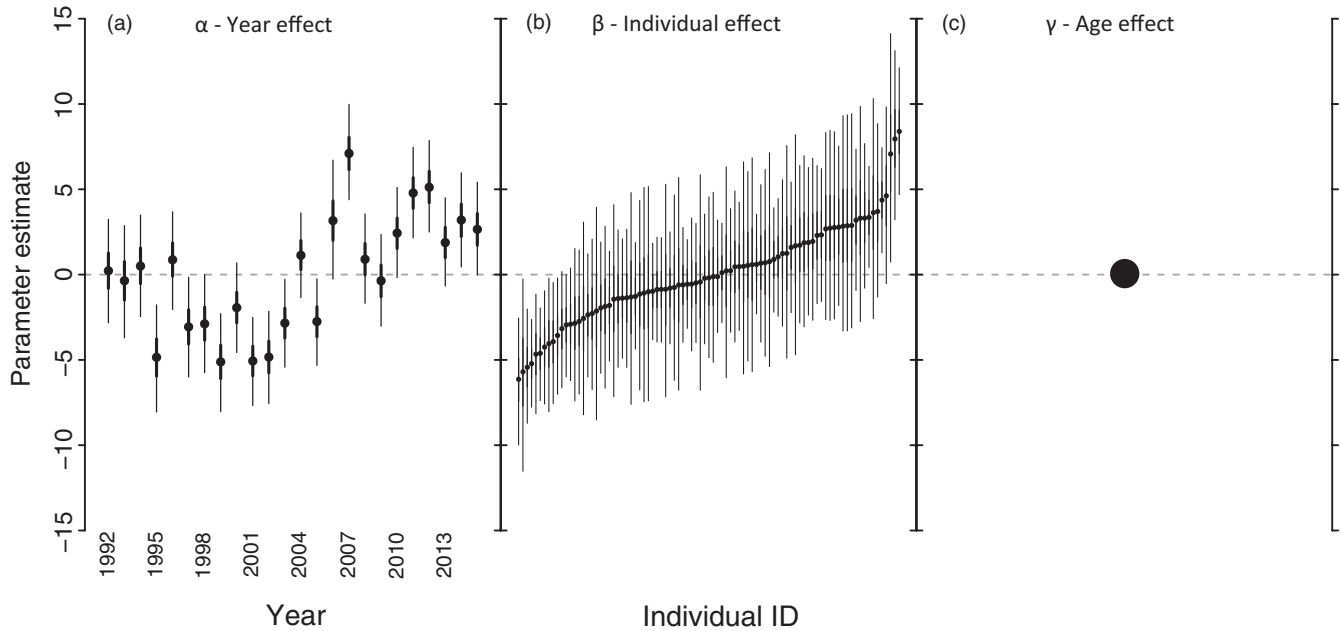


FIGURE 2 Posterior estimates for the captive population parameters: (a) year effect— α ; (b) individual effect— β ; and (c) age effect— γ parameters (see Equation 1). Black circles represent posterior medians. Thicker lines represent 50% credible intervals while thinner lines represent 95% credible intervals. Error bars for the γ parameter are obscured by the point itself

envelope of time in which successful breeding may occur, our analysis of a captive Adélie penguin population shows that external drivers neither explain nor are required to generate substantial inter-annual variability in breeding phenology (i.e., a large year effect). Inter-annual fluctuations are apparent even under constant environmental conditions and after accounting for the effects of individual variation and age (Figure 2a). Other potential factors that we thought might have influenced penguin breeding phenology, such as number of breeders in a given season, the timing of nesting material availability, and potential effects of the 2005 captive population exhibit renovation,

were investigated but ultimately determined to have only minor effects (Appendix S2).

Beyond the random effect of year, some fixed differences in the timing of breeding among individuals in the captive population do exist—that is, some individuals breed earlier than others on average (Figure 2b). However, the relatively minor shifts in the composition of the population each year cannot explain the inter-annual fluctuations in the breeding phenology of captive individuals. While previous work has suggested that age plays a role in determining Adélie penguin breeding phenology in the wild (Ainley, 2002; Ainley et al., 1983), the effect of age on breeding phenology was minimal in the captive population studied here (Figure 2c). This is not surprising, given that one hypothesized mechanism by which age might impact breeding phenology is through an individual's ability to navigate back to the breeding colony following the overwintering period. Older individuals, being more experienced, are thought to be able to find their way back to the breeding colonies more quickly, particularly through substantial sea ice (Ainley et al., 1983). With no migration in a captive population, we would expect age and experience to have a substantially smaller impact on breeding phenology.

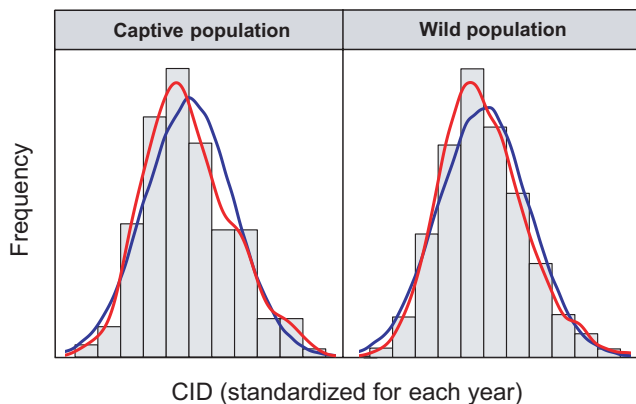


FIGURE 3 Distribution of clutch initiation dates (CIDs) for the captive (left) and wild (right) populations. Data were standardized and aggregated across years. Coloured lines depict the kernel density estimates on the distribution. Red lines represent the actual distributions of CID, while the blue lines represent the normal distributions generated using the actual mean and variance of the CID distribution

4.2 | Interplay between synchrony and stochasticity

Adélie penguins are highly synchronous breeders within a population in a given season (Figure 1; see also Ainley, 2002), and previous work has shown that increased synchrony among individuals leads to increased breeding success (Youngflesh, Jenouvrier, Hinke, et al., 2017; Youngflesh, Jenouvrier, Li, et al., 2017). Where colonial breeding is driven by predator avoidance, individuals that breed not only in the same area but also at the same time as others in the population would

be at an advantage (Darling, 1938; Young, 1994). Penguins breeding during the same time period in the same location can more easily defend nests against aerial predators, a principal threat to Adélie penguin chicks (Young, 1994). Synchronous breeding also results in an overwhelming influx of potential prey resources for species that prey on penguins; such “predator-swamping” can facilitate higher breeding success (Ims, 1990a). We hypothesize that the fitness consequences of breeding in sync with conspecifics may outweigh the importance of matching optimal environmental conditions within the environmentally-driven time envelope in which reproduction can occur successfully (as suggested in Hinke et al., 2012; Youngflesh, Jenouvrier, Hinke, et al., 2017; Youngflesh, Jenouvrier, Li, et al., 2017). We suggest that the importance of this phenomenon for any given species reflects a balance between the expected fitness advantages of synchronous breeding among conspecifics and the fitness advantages of breeding during some (environmentally determined) optimal period of time—the latter of which may be more difficult to assess for an individual with limited information.

In this way, predators indirectly influence the breeding phenology of Adélie penguins—a top-down process. Abiotic (e.g., photoperiod, temperature) and/or bottom-up processes (e.g., resource availability, organism physiological condition) are typically the focus of phenological studies. However, top-down forcing (via antagonists such as predators and pathogens) has been identified as an important process in the regulation of a number of phenological processes, including absolute phenology (Elzinga et al., 2007; Galloway & Burgess, 2012), phenological synchrony (Hatchwell, 1991; Sinclair, Mduma, & Arcese, 2000) and the rate at which offspring develop (Vonesh, 2005). These processes often operate in concert with abiotic and/or bottom-up processes (as suggested by Burr et al., 2016; Varpe, Jørgensen, Tarling, & Fiksen, 2007), painting a complex picture of multiple ecological determinants of phenological processes. While the mechanisms for top-down control on phenology are diverse, these patterns may be more common among colonial breeders given the importance of phenological synchrony for predator avoidance in many species (Ims, 1990b).

While the precise mechanism that regulates this highly synchronous behaviour in Adélie penguins is unknown, social cues have been found to drive courtship and copulation (Waas, 1988, 1991, 1995; Waas, Caulfield, Colgan, & Boag, 2000) and result in more synchronized breeding patterns (Setiawan et al., 2007). This has been demonstrated in a number of birds (Burger, 1979; Danchin, 1988; Waas, Colgan, & Boag, 2005), including other species of penguins, as well as in mammals (Berger, 1992; McClintock, 1978; Scott, 1986). Vocalizations (Clark, Haseley, Van Genderen, Hofling, & Clum, 2012), exposure to courtship displays (Lehrman & Friedman, 1969) and chemical cues (McClintock, 1978) have all been demonstrated as proximate behavioural mechanisms by which this social facilitation occurs.

Slightly right skewed distributions of CID are apparent within each year—very late breeders in this right skewed distribution contribute to a relatively large residual variance in our model. This skew is also consistent with, though by no means proves conclusively, a role for social facilitation in the timing of breeding. Even a simple model in which breeding is accelerated proportional to the number

of pairs that have recently initiated breeding creates a right skewed distribution for clutch initiation (Appendix S1). This notion of facilitation is further supported by the strong relationship (70% of variance explained) between first CID (the first breeders in each year) and median CID in both the captive and wild populations (Appendix S1). Right skewed distributions of phenological events are apparent in many species of both birds and plants (Sparks et al., 2005; Thomson, 1980; Wilson, 2013) in magnitudes similar to those observed here (Appendix S1). Environmental factors may play a role in driving this pattern for many species, a hypothesis difficult to exclude if only wild data were available. In this case, however, both a right skewed distribution and a strong relationship between first breeding and median breeding are apparent under controlled conditions, despite inter-annual variability in the overall timing of breeding.

It should be noted that the captive penguin population in this study exhibited less synchrony among individuals in a given year than did the wild population (Figure 1; Appendix S1). One possible explanation for this relates to colony size; larger populations in the wild may, through increased colony noise, better facilitate the transmission of social cues (Waas et al., 2000). Other possibilities include the notion that the degree of synchrony is a plastic trait that may be relaxed under the predator-free conditions of captivity. Future work, including manipulative experiments, is required to understand the precise behavioural mechanisms regulating synchrony in this species.

To be clear, we are not suggesting that synchronous breeding is necessary to observe the impacts of stochastic factors on breeding phenology at the individual level, but rather that the importance of synchrony in colonial species may facilitate the propagation of stochasticity from the individual level to that of the population. Social cues that facilitate synchrony (see above) may encourage individuals to initiate breeding once other individuals in the colony have done so. This cascading effect of synchronous breeding may drive a shift in the average phenology of the population that is largely uncoupled from any environmental trigger.

4.3 | In ignoring the role of stochasticity, have we been modelling noise?

In the search for causal drivers for phenology, the role of inherent stochasticity has been largely ignored in the existing phenological literature. Our study has important implications for studying patterns of phenology across all animal systems as it highlights the difficulty of teasing out the extent to which the environment may, or may not, be driving variation in phenology. The observed levels of inter-annual variability under fixed environmental conditions are of a similar magnitude to those seen in the wild (Figure 1; Appendices S1 and S2)—a surprising result. Previous studies of Adélie penguin phenology at Admiralty Bay found October mean air temperature (thought to be related to snow melt and nest site availability) to be the most important environmental determinant of CID in a model selection framework (Hinke et al., 2012; Lynch et al., 2012). Our analyses of the same CID

data (with additional years beyond what was used in the original studies) do not contradict these original findings, but suggest that environmental drivers, such as temperature, are layered on top of substantial “built-in” variability. Put another way, our null model for phenological studies should not, by default, be one of stasis.

Whether the drivers that influence a pair’s “decision” to breed are unknown, or unknowable, the implication is that phenological variability at this scale can be generated in the absence of environmental variability. This finding is of practical importance, as it highlights the difficulty in identifying external causal drivers of phenological events. Our study shows that stochastic variation in penguin breeding phenology, with respect to the environmental factors addressed here, may be the rule rather than the exception and does not require external forcing from the environment. This is similar to stochastic outcomes of individuals, whereby identical individuals, experiencing identical conditions, will differ with respect to lifespan and fecundity (Caswell, 2011). This role of stochasticity may partially explain previous findings of a relatively weak relationship between Antarctic seabird breeding phenology and environmental forcing (Barbraud & Weimerskirch, 2006).

One way to address the inherent convolution of environmental variability and inherent stochasticity is through the study of captive populations in controlled conditions. While studies focusing on plants more often include experiments in controlled environments to distinguish the role of multiple factors on phenology (Cleland, Chuine, Menzel, Mooney, & Schwartz, 2007), there are fewer studies elucidating inter-annual changes in phenology in captive animals (but see Lambrechts et al., 1999; Visser et al., 2009). Captive animal populations are not, of course, perfect replicas of wild populations. For instance, penguins in captive populations are kept in enclosed spaces and do not undergo an overwinter migration. Captive populations are also limited in size, often smaller than what might be observed in the wild. Accordingly, we must be cautious not to overextend the analogy between captive and wild populations. Nevertheless, studies focusing on populations in controlled conditions can provide a wealth of information on phenology in the absence of all environmental factors deemed potentially important in wild populations. Identification and tracking of individual animals further allows for straightforward estimation of age effects and random individual variation. Ultimately, these studies can provide a reasonable null model against which to assess factors contributing to variation in wild populations. Studies involving experimental manipulation and/or transplantation of organisms to new environments (e.g., Helm, 2009) may provide additional power to disentangle the factors controlling breeding phenology. Our study highlights the challenges of understanding the factors driving phenology in wild populations and reminds us to take caution in ascribing causality when we are unaware of the degree of inherent variation in the response variable of interest.

ACKNOWLEDGEMENTS

We acknowledge the many fieldworkers and SeaWorld staff who contributed to the collection of data used in this study. We also

acknowledge the authors of, and commenters on, the blog Dynamic Ecology for insights into stochasticity in ecological systems. Funding to H.J.L. and C.Y. was provided by the National Science Foundation Grant OPP/GSS 1255058, and to S.J., H.J.L. and C.Y. by the National Science Foundation grant 1341474. Data from Admiralty Bay were made possible with support from the US Antarctic Marine Living Resources programme, the Lenfest Oceans Program at the Pew Charitable Trusts and many prior grants from the National Science Foundation (including grant no. 1016936 to W.Z.T./S.G.T.). The authors declare no conflicts of interest.

AUTHORS’ CONTRIBUTIONS

C.Y., H.J.L. and S.J. conceived the ideas and designed the methodology; J.T.H., L.D., J.S.L., W.Z.T. and S.G.T. collected the data; C.Y. analysed the data; C.Y. and H.J.L. led the writing of the manuscript. All authors contributed to drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data used in this study are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.23sv1> (Youngflesh, Jenouvrier, Hinke, et al., 2017).

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How to cite this article: Youngflesh C, Jenouvrier S, Hinke JT, et al. Rethinking “normal”: The role of stochasticity in the phenology of a synchronously breeding seabird. *J Anim Ecol*. 2018;87:682–690. <https://doi.org/10.1111/1365-2656.12790>