Variation in breeding phenology provides insights into drivers of long-term population change in harbour seals

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Phenological trends provide important indicators of environmental change and population dynamics. However, the use of untested population-level measures can lead to incorrect conclusions about phenological trends, particularly when changes in population structure or density are ignored. We used individual-based estimates of birth date and lactation duration of harbour seals (*Phoca vitulina*) to investigate energetic consequences of changes in pupping phenology. Using generalized linear mixed models, we first demonstrate annual variation in pupping phenology. Second, we show a negative relationship between lactation duration and the timing of pupping, indicating that females who pup early nurse their pups longer, thereby highlighting lactation duration as a useful proxy of female condition and resource availability. Third, individual-based data were used to derive a population-level proxy that demonstrated an advance in pupping date over the last 25 years, coincident with a reduction in population abundance that resulted from fisheries-related shootings. These findings demonstrate that phenological studies examining the impacts of climate change on mammal populations must carefully control for changes in population density and highlight how joint investigations of phenological and demographic change provide insights into the drivers of population declines.

1. Introduction

Although widespread changes in breeding phenology have commonly been interpreted as an indication of a common response to environmental variation or climate change [1–3], the literature is strongly biased towards studies of plants and primary consumers [4]. While some studies have demonstrated that certain predatory species are able to adjust the timing of breeding to avoid a mismatch with seasonal peaks in prey [5], these are typically egg-laying and income-breeding species [6–10]. For example, Thackeray et al.’s [4] analysis of phenological trends in 726 UK taxa included only four species of mammals, all of them terrestrial primary consumers. Large mammals with long gestation periods are likely to be more constrained in their response to fine-scale temporal changes in resources during their breeding season. While shifts in breeding phenology do occur in these species [11,12], they may result from a more complex interaction of factors that include both environmental variation [13–16] and population density [17]. Interpretation of population-level phenological change is further complicated in long-lived species because individual birth or laying dates are influenced by age and/or experience [13–14,18]. Thus, a population-level change in breeding phenology could result from either a common response to environmental variation or a change in population age structure.

Within marine habitats, colonial top predators can provide a valuable indicator of variation in lower trophic levels that are widely dispersed and difficult to monitor [19,20]. To date, most phenological studies of marine top predators have focused on seabirds [8,20], providing important examples of how phenological change in these income breeders reflects fine-scale changes in prey.
resources. It is unclear whether breeding phenology shows similar levels of plasticity among marine mammal predators, many of which are capital breeders [21].

Recently, it has been suggested that harbour seals (Phoca vitulina) in the southern North Sea have significantly advanced their timing of pupping over the last 35 years; a change that has been interpreted as a response to an improved forage base following fishery-induced changes in prey community structure [22]. If phenological data can offer an indication of changes in their prey base, this could provide an important tool for exploring the causes underlying unexplained pinniped population declines in other regions [23–25]. However, these investigations must be underpinned by direct individual-based estimates of pupping dates, which for harbour seals are currently available from only two populations worldwide; Sable Island, Canada [26] and the Moray Firth, Scotland [27]. At other sites, information on the presence of harbour seal pups is available only from broader scale surveys, typically from aircraft, which are used to monitor abundance trends [22, 28]. The problem with basing phenological studies on these cruder survey data is that untested proxies for the timing of pupping may be influenced by factors such as sampling frequency and population size or structure [11, 29]. Particularly when populations have experienced repeated mass mortalities, such as the northern European population [30], the direct influence of population size on breeding phenology must also be considered in such analyses [12].

To assess whether phenology can inform comparative studies of pinniped population dynamics, further work is required to confirm that year-to-year variation in the timing of breeding reflects individual responses to environmental variation rather than a change in population age structure. To maximize opportunities for using these tools in areas where individual-based studies are not possible, proxy-based estimates of the timing of pupping must also be tested in areas where direct estimates are available. Here, we use an individual-based study of Scottish harbour seals to describe inter-annual variation in the timing of pupping, and to investigate whether shifts in pupping phenology are likely to be related to resource availability by exploring parallel changes in lactation duration. These direct estimates of pupping are then used to compare different proxies that can be obtained from population-level studies. Finally, we apply the best fitting proxy to a 23-year time series of survey data to explore how the timing of pupping varied in relation to local population density, and highlight how these relationships can provide insights into the drivers underlying recent population declines.

2. Material and methods

(a) Data collection

The study was carried out in the Loch Fleet National Nature Reserve in the Moray Firth, northeast Scotland [31], where individual harbour seals hauling-out onto the main sandbank in the estuary could be recognized using photo-identification techniques [27]. Data were collected daily during the pupping season (1 June to 22 July) from 2006 to 2011, with fewer regular surveys in late May and late July. Surveys were started approximately an hour after low tide and were continued for 2–3 h to ensure that photographs were obtained of all individuals using the main sandbank. Photographs were taken of the head and neck region using a digital camera (Nikon Coolpix 5100 or Canon 60D) and a telescope (20–60 × 80 mm Swarowski HD-ATX 80), and matched against a catalogue of the best images of all seals photographed during the study. Photographs were also used to record whether or not individually identified females were seen with or without a pup. At the start, during and at the end of surveys, haul-out counts were also made of the total number of adults and pups present both on the main sandbank and other smaller haul-out sites within Loch Fleet (1–6 counts per survey).

(b) Estimation of the timing of pupping and lactation duration

Daily sightings and re-sightings of individual seals were recorded in a capture history matrix, which included information on the status of individual females (whether she was seen or not seen, and if seen, whether or not she was with a pup). From this capture history, pupping date was calculated as the midpoint between the day that the female was last seen alone and the day that she was first seen with pup [27]. If this period was less than or equal to 3 days, then the pupping date was defined as accurate, if the period was longer than 3 days, the pupping date was excluded from the analyses (x̄ = 9.5 yr−1, σ = 3.3). All pupping dates were converted to day of the year (Julian day; see the electronic supplementary material, appendix A). During lactation, females and pups spend a significant amount of time in the water where they cannot be observed. Because weaning in harbour seals is abrupt, and the female often leaves the breeding site to undertake a long foraging trip, lactation durations were defined as the number of days between the pupping date and the day that the female was last seen with the pup. Lactation durations were therefore only estimated for females with accurate pupping dates (see the electronic supplementary material, appendix A). To ensure lactation durations were representative of weaned pups, and not simply movement of mother–pup pairs to other sandbanks, we only used lactation durations where the females were seen again without a pup within 10 days of the last sighting with her pup. Pups born prior to 1 June either died at birth or had very short lactation durations. Typically, these early pups were also seen with some lanugo indicating that they were born prematurely, so pups born before 1 June were also excluded from the analysis.

Generalized linear mixed modelling (GLMM) was used to understand whether there was annual variation in pupping dates and to determine the relationship between repeated measurements of pupping dates and lactation durations from individual females using the nlme package in R v. 2.15.0 [32]. For the first analysis, we tested the strength of a non-mixed model, a mixed model with individual identification number (ID) included as a random effect in order to account for repeated measures. The Akaike information criteria correcting for small sample size (AICc) score was lowest for the mixed model (AICc = 21) and this was then used to assess a model with year as a covariate against a model without (null) using the AICmodavg package. To understand the relationship between lactation duration and pupping date, pupping dates were centred on the annual median (relative pupping dates). We first tested the strength of a non-mixed model, a mixed model with random intercept and a mixed model with a random intercept and slope. The AICc score for the mixed model with a random intercept and slope was lowest, followed by that for the mixed model with a random intercept (ΔAICc = 3). The random intercept and slope model was then used to undertake model selection of four different models, including relative pupping date and year, relative pupping date, year and the null model. For both analyses, AICc scores were used to...
compare models in order to correct for small sample size (154 observations from 51 individual females; [33]). Model averaging of the top models accounting for 0.95 of the AICc weight was used to extract $\beta$-estimates of model parameters. The 95% confidence intervals (CIs) around the $\beta$-estimates were used to assess the relationship between the specific model parameter and the response variable.

(c) Population-level proxy for the timing of pupping

We compared our individual-based estimates of median pupping date with different proxies that were based upon the crude count data collected simultaneously at this site. As well as using Reijnders et al.’s [22] proxy (date of maximum pup count), we explored the use of two other proxies that could be obtained from population-level studies, namely the date of first offspring (which is commonly used in studies of seabirds [34]) and the date on which 50 per cent of the maximum number of pups counted were seen (which we anticipated would be less influenced by sampling frequency and variability). Although premature pups were observed in May, estimates of the date of first offspring only used data from 1 June once daily surveys were undertaken.

We applied the best fitting proxy for the timing of pupping to a time series of available historical (1988–2011) counts of pups from breeding sites within the Moray Firth, namely the Cromarty Firth (1988–2004; [35]) and in more recent years Loch Fleet (2006–2011). Prior to the development of Loch Fleet as a breeding site in the late 1990s [31], the Cromarty Firth had been the most accessible regional breeding site for behavioural observations and counts of mothers and pups [36,37], therefore providing the best time series of counts to investigate long-term variation in the timing of pupping. Regular counts of adults and pups were made using a telescope from shore-based vantage points during the breeding season (1 June–31 July) as described in Thompson et al. [35]. The number of Cromarty Firth surveys per breeding season ranged from 3 to 64 ($\chi^2 = 20.5$). Variations in the timing of pupping were related to local population size by using the annual mean count of adults at all sites within the inner Moray Firth [35,38]. Estimates of local population size since 2006 have been collected using aerial surveys by the Natural Environment Research Council Sea Mammal Research Unit and are taken from Cordes et al. [31] and the 2011 Special Committee on Seals report [39].

Since phenological responses to changes in population abundance may be delayed, we used a cross-correlation to determine when the relationship between the timing of pupping and mean population count was strongest. The cross-correlation indicated that this relationship was strongest at minus 1-year lag, that is, indicating that the timing of pupping responded to changes in mean population count after 1 year. As mean count and year were collinear, we investigated the factors contributing to variation in the timing of pupping by testing three single parameter models (mean count, year and null) using linear regression. As above, the 95% CIs of the $\beta$-estimates of model predictors were used to assess their relationship with the timing of pupping.

\[ \text{Figure 1. Consistency in the timing of pupping of individual females with greater than or equal to five accurate pupping dates. Triangles represent the median pupping date with interquartile ranges (bars), while dots indicate actual pupping dates.} \]

3. Results

(a) Inter-annual variation in the timing of pupping and lactation durations

Over the course of the study, 186 accurate pupping dates and 154 lactation durations were obtained from 51 females (table 1). Pupping dates ranged from 1 June to 9 July, although 90 per cent of pups were born within 13–17 days in each year. Individual females with at least five accurate pupping dates puffed within a range of 7 days ($\sigma = 4.4$; figure 1). GLMM of pupping dates revealed that the model with year accounted for all of the AICc weight (table 1), indicating that there was annual variation in the timing of pupping. More specifically, pupping was delayed in 2006 and 2011 and early in 2009 and 2010 compared with 2007, the year that was most similar to the overall median (figure 2).

<table>
<thead>
<tr>
<th>year</th>
<th>no. pups</th>
<th>pupping date</th>
<th>90% range (days)</th>
<th>lactation duration (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2006</td>
<td>34</td>
<td>170 (19 June)</td>
<td>17</td>
<td>19.0</td>
</tr>
<tr>
<td>2007</td>
<td>37</td>
<td>168 (17 June)</td>
<td>17</td>
<td>19.4</td>
</tr>
<tr>
<td>2008</td>
<td>41</td>
<td>168 (16 June)</td>
<td>13</td>
<td>19.9</td>
</tr>
<tr>
<td>2009</td>
<td>49</td>
<td>164 (13 June)</td>
<td>15</td>
<td>21.1</td>
</tr>
<tr>
<td>2010</td>
<td>51</td>
<td>165 (14 June)</td>
<td>13</td>
<td>23.4</td>
</tr>
<tr>
<td>2011</td>
<td>45</td>
<td>168 (17 June)</td>
<td>14</td>
<td>18.6</td>
</tr>
</tbody>
</table>

*Leap year.
Table 2. Model selection results using (a) GLMM to investigate annual variation in pupping dates, (b) GLMM to investigate the contributing factors to variation in lactation duration, and (c) linear regression to investigate the contributing factors to the long-term variation in the date of 50% of maximum pup count.

<table>
<thead>
<tr>
<th></th>
<th>$K$</th>
<th>$\Delta AIC_c$</th>
<th>AIC_weight</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(a)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>year</td>
<td>8</td>
<td>0</td>
<td>1.00</td>
</tr>
<tr>
<td>null</td>
<td>3</td>
<td>22.5</td>
<td>0</td>
</tr>
<tr>
<td>(b)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>relative pupping date</td>
<td>6</td>
<td>0</td>
<td>0.54</td>
</tr>
<tr>
<td>relative pupping date + year</td>
<td>11</td>
<td>0.9</td>
<td>0.34</td>
</tr>
<tr>
<td>null</td>
<td>5</td>
<td>3.5</td>
<td>0.09</td>
</tr>
<tr>
<td>year</td>
<td>10</td>
<td>6.0</td>
<td>0.03</td>
</tr>
<tr>
<td>(c)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>year</td>
<td>3</td>
<td>0</td>
<td>0.56</td>
</tr>
<tr>
<td>mean count</td>
<td>3</td>
<td>0.5</td>
<td>0.44</td>
</tr>
<tr>
<td>null</td>
<td>2</td>
<td>21.6</td>
<td>0</td>
</tr>
</tbody>
</table>

GLMM of lactation duration revealed two top models, including relative pupping date and relative pupping date and year, accounting for 0.54 and 0.34 of the $AIC_c$ weight, respectively (table 2b). Model averaging revealed a negative $\beta$-estimate for relative pupping date of $-0.46$ (95% CI: $-0.81/-0.11$), highlighting that females which pupped early nursed their pups longer compared with females that pupped late. For example, females on the 95% per cent boundary of early (relative pupping date: -8) and late breeding (relative pupping date: 9) nursed their pups for 24 (95% CI: 23–26) and 17 (95% CI: 15–19) days, respectively. The amount of variation around the intercepts (4.58$^2 = 20.98$) was considerable larger than the amount of variation around the slopes (0.74$^2 = 0.53$), and the correlation between the random intercepts and slopes was $-0.15$. Residuals plotted against fitted values and all explanatory variables showed reasonably good model fit.

(b) Population-level proxy for the timing of pupping
There was a weak negative association between median pupping date and day of maximum pup count, which was not significant (Spearman’s rank order, $r_s = -0.358$, $S = 47.54$, $p$-value = 0.5). Similarly, there was a negative although non-significant association between median pupping date and the day of first offspring (Spearman’s rank order, $r_s = -0.591$, $S = 55.68$, $p$-value = 0.217). By contrast, the correlation between median pupping date and the day of 50 per cent of maximum pup count revealed a strong positive and significant association (Spearman’s rank order, $r_s = 0.934$, $S = 2.17$, $p$-value = 0.006), and this was chosen as the optimal population-level proxy when using crude count data.

We applied this population-level proxy to the longer time series of pup counts (figure 3) to investigate the contributing factors to variation in the timing of pupping. Model selection showed that year and mean count accounted for similar amounts of the $AIC_c$ weight, 0.56 and 0.44 (table 2c), respectively, and models only differed by 0.5 $AIC_c$, suggesting that both year and population density are contributing to the temporal variation in the timing of pupping (figure 4). The confidence interval from the model averaged $\beta$-estimate of mean count did not overlap zero and revealed a strong positive relationship with day of 50 per cent of maximum pup count ($F_{20} = 39.11$, $R^2 = 0.64$; $\beta$-estimate = 0.02 (95% CI: 0.01/0.04)). Similarly, the $\beta$-estimate for year did not overlap zero and indicated a negative relationship between date of 50 per cent of maximum pup count and year ($F_{20} = 44.40$, $R^2 = 0.65$; $\beta$-estimate = $-0.55$ (95% CI: $-0.71/-0.40$)).

4. Discussion
This study provides, to our knowledge, the first direct estimates of variability in the timing of pupping in European harbour seals. Results show a highly synchronized pupping season where individual females were generally consistent in their annual timing of pupping, indicating that the inter-annual variation in pupping phenology that we recorded was the result of individuals responding in a consistent manner, as observed in other colonial breeders [40]. This supports previous work that demonstrated individual consistency in the timing of pupping both in captivity [41], and in the only other individual-based study of breeding phenology in wild harbour seals on Sable Island, Canada [26]. The negative relationship between pupping dates and lactation durations suggests that variation in breeding phenology is condition dependent, as observed in other mammals and birds where the timing of breeding was delayed during years of low food availability [14–16,18,42].

Reijnders et al. [22] suggested that there had been an advance in the timing of pupping in this species (of 25 days over 35 years) using a proxy that was based on the date of the maximum pup count. However, our analyses demonstrated that the date of maximum pup count cannot be used as a robust proxy for the timing of pupping, as the relationship between the two was not only non-significant.

Figure 2. Annual variation in the timing of pupping as signified by the $\beta$-estimates from the generalized linear mixed model with 95% CIs.
but also in the wrong direction. Similarly, the direction of the non-significant relationship between the date of first offspring and our individual-based estimate was negative. Previous studies have also demonstrated that first flowering date [29] and first arrival dates of migrants [43] are sensitive to changes in population size, which can compromise their use in phenological studies. By contrast, the date on which 50 per cent of the maximum pup count was observed performed well as a proxy, revealing a positive and highly significant association with the median timing of pupping. When applied to our long-term time series of annual pup counts, this proxy indicated that there had been significant temporal variation in the timing of pupping over the last 25 years with a general advance in the timing of pupping, which probably has been the result of changes in population density with females pupping earlier at lower densities. This finding highlights that analyses of temporal changes in breeding phenology should account for changes in population density. While this has been recognized in some single-species studies [12], it has been ignored in others [22], and neither population density nor trend has yet been considered in multi-species comparison that have explored what factors affect rates of phenological change [4]. Recent population status may be particularly important where density-independent changes in abundance owing to disease outbreaks [30], by-catch [44] or exploitation [45] can affect per capita food availability. The impact of these factors may also vary between age-classes, raising the possibility that population-level changes in breeding phenology could also be influenced by changes in population structure [11].

When used in association with appropriate data on abundance trends, our findings highlight how information on variation in breeding phenology can be used to explore the drivers of population change. Both of the harbour seal populations in which individual-based estimates of the timing of breeding are available have experienced marked declines in recent decades, but contrasting patterns of change in breeding phenology suggest that the causes underlying declines in these two populations differ. On Sable Island, Canada, there was a 7-day delay in the timing of pupping during a 7-year decline [24]. By contrast, in the Moray Firth, we observed an advance in the timing of pupping during a 15-year population decline (figure 3). Bowen et al. [24] highlight that observed changes in breeding phenology on Sable Island are likely to have resulted from nutritional stress, supporting hypotheses that the decline resulted from increasing competition with an expanding local grey seal population. By contrast, population modelling has demonstrated that reported levels of shooting by salmon fishery managers could explain declines in the Moray Firth [38]. This top-down control would have led to a reduction in intraspecific competition, and we suggest that an advance in the timing of breeding reflects a resulting improvement in female condition. While individual-based studies provide the most powerful way of assessing how breeding phenology varies in relation to population trends, many pinniped populations of interest are in remote and inaccessible areas where such work may be logistically impossible. Our analyses also highlight how individual-based studies can be used to develop and validate proxies that can be applied to data collected from broad-scale abundance surveys. Survey designs that are optimized to assess variation in both abundance and breeding phenology could now play a critical role in testing competing hypotheses about the drivers of unexplained declines in both harbour seals [25,46] and other pinniped populations [45,47].

Over our 25-year study, the timing of pupping in this North Sea harbour seal population varied within an approximate two-week window (figure 3). Comparative studies over a similar period at two nearby North Sea colonies suggest that the timing of seabird breeding was more variable [34]. This may partly be owing to the use of first egg laying in the seabird studies, as first events can be more variable [29,48]. However, income-breeding seabirds would be expected to respond more flexibly to variation in spring foraging conditions, whereas the timing of pupping in capital breeding harbour seals will be influenced by conditions prior to implantation or during pregnancy, many months earlier [15,24]. Previous discussion of the consequences of variable responses to environmental change has focused on trophic mismatches between predators and prey [49,50]. If these results reflect consistent differences in the way that seabird and marine mammal predators respond to environmental change, this could also influence competitive

Figure 3. Trend in counts of harbour seals within the Inner Moray Firth (dots with error bars) and the timing of pupping (triangles) as inferred by the proxy of 50% of maximum pup count from 1988 to 2011.

Figure 4. Relationship between mean annual counts from the Moray Firth and day of 50% of maximum pup count at minus 1 year (linear regression with 95% CIs).
interactions between these groups and their influence on marine community structure.

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