Título: Breeding phenology in a marine top-predator: individual and population response to environmental variation

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ABSTRACT

An emerging consequence of global climate change is a shift of seasonal biological events. In animals, climatic divers have always been found to guide population trajectories and individual life-history tactics, but it is not clear whether individuals will be able to adapt to the fast pace at which temperature and rainfall are changing. The analysis of long-term data sets reveals different degrees of plasticity in the phenological responses of individuals, within and between species, but the pattern and the payoff of this plasticity are not always known. Understanding individual responses is essential to reveal the mechanisms and implications of climate-related changes on population dynamics and individual life-history tactics. We used longitudinal data collected over eighteen breeding seasons (2001-2018) on the laying date of Cory’s shearwaters Calonectris diomedea, at Pantaleu islet at Dragonera Natural Park, Mallorca (Balearic Archipelago, Spain). The Cory’s shearwater is a trans-equatorial migratory seabird that spends the winter (October-March) into the Atlantic Ocean before returning into the Mediterranean Sea to breed (April-September). Individuals breed in colonies and egg laying occurs more synchronous than in other seabirds, however, the laying date at population as well as individual level change every year, possibly as a response to winter ocean state (e.g. through carrying over effects) and/or conditions at the breeding grounds. We first considered the winter North Atlantic Oscillation index (wNAO) as a proxy of environmental variability and assessed whether its variation correlated with the variation in the average laying date at population level. Subsequently we used longitudinal data to investigate whether individuals were consistent in their laying date relative to the population average, i.e. repeatability of laying date. Finally, using mother-daughter data we assessed whether the laying date has a heritable component. We found that reproductive onset at population level correlated positively with the climatic index. This was fully explained by individual plasticity because, despite a change in the average laying date, individuals were consistent in their trait expression. Indeed, the repeatable of this trait was high ($R = 0.517$), with some birds breeding consistently earlier than others.
Interestingly, trait repeatability was higher for those females born at the colony (R = 0.653) compared with all females. The heritability of laying date assessed using 29 half parent-half offspring pairs was high, but the value suffered of a large uncertainty due to a relatively small sample size ($h^2 = 1.14$, $R^2 = 0.12$, $p=0.07$). We thus used another approach and sorted females into two groups, namely ‘early’ and ‘late’ breeders, according to whether laying date occurred before or after the median of the population respectively. We compared the proportion of each combination through a 2x2 contingency table. Results showed a statistically significant difference ($X^2 = 7.79$, $p<0.01$) confirming a high heritability of laying date. Results from general linear mixed models indicated that early breeding birds had 27% more chance to breed successfully than late breeders (breeding success: 0.83 and 0.60, for the earliest and the latest laying date, respectively; $z = -2.68$, $p<0.01$). In conclusion, our work showed that changes in the laying date correlate to environmental conditions and that despite a high plasticity, individual repeatability is high as it is the heritability of this trait. Despite this, the advantage of an early breeding seems small suggesting that inter-individual variability is probably the result of differences in phenotypic quality intrinsic to the population.

*Keywords:* laying date, environmental variation, plasticity, heritability, shearwater
1. INTRODUCTION

Climatic variations and reproductive onset

Climatic variations have an important role on the population dynamics of vertebrates through their influence on demographic parameters, such as survival and breeding success (Coulson et al., 2001; Stenseth et al., 2002; Genovart et al., 2013). One of the most commonly reported effect of climatic variations is the influence on seasonal processes and in particular on the onset of the reproduction. Many studies have shown that the start of the reproduction of birds has advanced considerably during recent decades (Crick & Sparks, 1999; Dunn & Winkler, 1999; Przybylo, 2000; Sheldon & Merilä, 2000; Sanz et al., 2003; Sheldon et al., 2003; Pulido & Berthold, 2004; review in Dunn 2004). These changes are often linked directly to spatio-temporal changes in the patterns of climatic conditions (Dunn & Winkler, 1999; Sanz, 2002, 2003; Sæther et al., 2003; Visser et al., 2003; Both et al., 2004), providing evidence of fine-scale patterns of phenology matching fine-scale patterns of climate change as local spring temperature (Brown et al., 1999) and snowmelt date (Dunne et al., 2003). Evidence on current climate changes have led ecologists to ask which climatic drivers are affecting reproductive onset and which consequences this will have on the population and individual life-history tactics, i.e. whether animals would be able to adapt to a fast-changing climate (through a plastic response or selection; Charmantier et al., 2008). Reproductive onset has been found to be related to internal (hormonal) but mainly external cues such as photoperiod, food abundance and climate (Gwinner, 1986). All these environmental changes influence population dynamics of seabirds, for which external conditions have stronger effects than on terrestrial species (e.g. Frederiksen et al., 2008; Barbraud et al., 2011). The question is whether and how individuals will respond to the fast-changing climatic scenario.

Responses to environmental change: phenotypic plasticity, selection and trait heritability

Responses to environmental changes measured at population level might result from two, not exclusive, processes: a selection against maladaptive phenotypes and a change in trait value due to phenotypic plasticity, defined as the ability of a single genotype to alter its phenotype in response to environmental conditions (Møller & Merilä, 2004; Pulido & Berthold, 2004; Charmantier & Gienapp, 2014; Figure 1). Phenotypic plasticity it is an ubiquitous characteristic of individuals in all animal populations and allow individuals to respond rapidly to changes in ecological conditions (Pigliucci, 2001; Scheiner, 1993; Via et al., 1995).
Selection and plastic responses are not mutually exclusive processes. Indeed, a plastic response is possible only within a given range of trait values and individuals might differ in the range amplitude. Changes in the reproductive onset are commonly resulting from phenotypic plasticity and optimal breeding choices (Charmantier & Gienapp, 2014). Since breeding is energetically costly, animals should attempt to initiate breeding at a time that ensures optimal overlap between nutritional requirements and food availability. Within a population, early laying birds tend to be consistent in being the first to start breeding. However, repeatability of laying date in birds differs markedly across taxa, with some species showing considerable repeatability (Wanless & Harris, 1988; Wiggins, 1991; Van der Jeugd & McCleery, 2002), whilst other species less (Korpimäki, 1990; Potti, 1999; Sydeman & Eddy, 1995). The presence of high repeatability does not preclude the presence of plasticity, and various studies have directly tested for, and found, high levels of phenotypic flexibility in laying date (e.g. Pryzbylo et al., 2000; Reed et al., 2006; Charmantier et al., 2008; Porlier et al., 2012).

The importance of assessing the influence of climatic variations on the phenological response is especially relevant in the context of global warming. Environmental changes due to global temperatures that have risen considerably in the past century (0.98°C since 1901, IPCC 2013) and the widespread advancements towards earlier mean laying dates during the latter few decades of this period (Crick et al., 1997; Møller & Fiedler, 2010; Knudsen et al., 2011) has stimulated a discussion about the pervasiveness of phenotypic plasticity for laying date in bird populations. This debate has emphasized that phenotypic plasticity is probably common and frequently adaptive. The incidence of evolutionary responses, however, remains unquantified.

Fig. 1: Schematic illustration of individual response to a shift in environmental conditions (black arrows). Bell-shaped curves indicate the frequency distribution of a trait at population level. The observed shift (blue arrows) can result from a change in the values expressed by individuals (plasticity) or by the selection against individuals exhibiting non-optimal values (selection).
Considering all these aspects, we examined how a long-distance migrant seabird, the Cory’s shearwater (Calonectris diomedea), has responded to recent climate change, using data from a long-term individual-based study in Pantaleu, Dragonera Natural Park (Balearic archipelago, Spain). Shearwaters belong to the family of Procellariiformes and, as all other members, are long-lived, lay only one egg and have a long breeding period (Warham, 1992). Optimal breeding time in shearwater seems to be determined by pre-breeding conditions and individual quality rather than by the need to adjust the current reproduction to future conditions (Sanz-Aguilar et al., 2008) because selective pressure on breeding parameters in long-lived birds is low (Lebreton & Clobert, 1991). Given this, a shift in the onset of reproduction due to an evolutionary response seems unlikely. Yet, results in other long-lived species provided evidence that laying date is a repeatable and heritable trait, which are necessary (but not sufficient) characteristics for an evolutionary response to occur. The aim of this study was to assess whether average laying date of Cory’s Shearwater at Pantaleu islet changed according to an environmental driver, to investigate within- and among-individual variation and to measure trait heritability. Finally, we investigate a potential association between laying date and breeding success to investigate the strength of a possible selective force.

Specifically, our work was motivated by the following questions:

1. Does the average laying date correlate with a climatic index?
2. Are Pantaleu individuals consistent with their laying date?
3. Is this trait heritable?
4. Is laying date associated with breeding success?
2. METHODS

2.1 | Study species, study area, field methods and data sets

The Mediterranean Cory's shearwater or Scopoli's Shearwater, *Calonectris diomedea diomedea* (Figure 2) is a pelagic seabird of the family Procellariformes, which includes albatrosses, shearwaters and petrels. It has been recently suggested to be a separate species from its formerly conspecific Atlantic Cory's Shearwater *Calonectris diomedea borealis* (Sangster et al., 2012; but see Genovart et al., 2013). The Atlantic and the Mediterranean Cory's Shearwaters exhibit little morphological differences except for a size difference of about 20% and the degree of genetic separation is still a matter of debate (Genovart et al., 2013). For the sake of simplicity here I will refer to the Mediterranean species using its former name 'Cory's Shearwater'. However, if the taxonomic separation is confirmed, it would be an endemic species of the Mediterranean.

Cory's Shearwaters are long-lived migratory seabirds that spends the winter in the tropical and southern regions of the Atlantic Ocean (González-Solís et al., 2007). Populations are difficult to census, and their status can only be assessed by monitoring trends on survival and fecundity from individual-based data (Igual et al., 2009; Anselme & Durant, 2012). In several monitored populations of the Western Mediterranean, annual adult survival seems too low to secure the
long-term viability of these colonies (Jenouvrier et al., 2008; Igual et al., 2009). Therefore, the species has recently been listed as vulnerable by the Spanish government. It is sexually dimorphic, with males about 10% heavier than females (Thibault et al., 1997). The species lays a single-egg clutch and chicks develop slowly, with an average nestling period of about 90 days. Nestlings attain maximum weight at age 50–60 days. Cory’s shearwaters feed mostly on fish, squid and crustaceans, but individuals also exploit fishing discards (Karris et al., 2016; Oro & Ruiz, 1997).

![Figure 3. Localization of Cory's shearwater nests in Pantaleu (JM Igual unpublished data)](image)

The data I used here have been collected at Pantaleu Islet, Dragonera Natural Park (Mallorca; Balearic Archipelago; 39°34’N, 2°21’E; Figure 3), a 2.5 ha legally protected and predator free islet, which hosts a Shearwater colony of ca. 200 breeding pairs (Sanz-Aguilar et al., 2016). Exhaustive nest and individual monitoring during a long-term program (2001–2018) at Pantaleu carried out by the Animal Demography and Ecology Unit (IMEDEA-CSIC/UIB) allowed a robust estimate of local demographic parameters (Genovart et al., 2013a; Sanz-Aguilar et al., 2011, 2016) and provided reliable data on temporal variation in breeding numbers (Tenan et al., 2014) and reproductive onset. Cory’s shearwaters breed in burrows under boulders or thick vegetation. Accessible nests were tagged and visited during the incubation and chick rearing period to record nest occupancy and breeding success.

Every year, about a hundred nests (~ 60% of the entire colony; Sanz-Aguilar et al., 2016) are followed throughout the breeding period from May to September. Nest monitoring began in May, few days before the expected laying date of the earliest birds. Each monitored nest is visited every 2-3 days until egg laying was confirmed and both members of the pair captured.
Laying date was taken as the first day at which egg was first observed and has a 1-2 days error. Captured birds were marked with stainless rings with a unique alphanumeric code to allow individual identification. Individuals were sexed based on morphometrical measures and calls (own data). In July, nest with eggs were revised to confirm hatching. Chicks are ringed at the end of the summer. A nest with a fledgling chick was considered as successful (nests whose success / failure was doubtful were discarded; Genovart et al., 2013a).

2.2 | Statistical analyses

- **Environmental conditions**

We considered winter NAO (December–March) values as an indication of yearly environmental conditions in the North Atlantic ocean (Hurrell, 1995), taken from the station-based measures available at [https://climatedataguide.ucar.edu/sites/default/files/nao_station_djfm.txt](https://climatedataguide.ucar.edu/sites/default/files/nao_station_djfm.txt) (last visited 06/09/2019). Positive values of winter NAO (hereafter, wNAO) lead to windy and warmer conditions in the North Atlantic and Western Europe, whereas the Mediterranean basin experiences drought during these phases. On the other hand, negative values of NAO result in colder winters in Western Europe and wetter conditions in the Mediterranean. NAO phases are known to influence marine biological processes in the western Mediterranean (Lloret et al., 2004) but it is unknown how these processes act in shearwaters. Also, Genovart et al. (2013) found that wNAO values correlated with breeding success at Pantaleu islet. However, the mechanisms underlying this association is unknown. After assessing normality of laying date values, we investigated a possible relationship between wNAO values and laying date through linear regressions in program R. Note that we have eliminated from the original dataset values collected in year 2001 because the laying date was not reliable, and we discarded data from nests initiated after the 8th of June (Julian date >160) because considered as outliers.

- **Mixed effects models of laying date and estimates of repeatability**

A necessary, but not sufficient, aspect for an evolutionary response to occur is that individuals show consistency in their trait value, i.e. repeatability. Formally, the common measure of repeatability, R, can be defined as the proportion of the total variance accounted for by differences among groups (Sokal & Rohlf, 1995):
\[ R = \frac{\sigma^2_{\alpha}}{\sigma^2_{\alpha} + \sigma^2_{\varepsilon}} \]

Where \( \sigma^2_{\alpha} \) is the between-individual variance and \( \sigma^2_{\varepsilon} \) is the within-individual variance (see Nakagawa & Schielzeth, 2010). Confidence intervals for repeatability in this model were estimated using parametric Bootstrap methods discussed in Nakagawa & Schielzeth (2010).

As can be seen from equation, repeatability is a function of both the within-group variance \( \sigma^2_{\varepsilon} \) and the between-group variance \( \sigma^2_{\alpha} \). Therefore, individual consistency will only be evident in the repeatability if there is between-individual variation in the population (i.e. \( \sigma^2_{\alpha} > 0 \)). It is important to bear in mind that the repeatability can be low if within-individual is high but also if between-individual variation is low, i.e. when individuals have random trait values over time or when all individual are consistently exhibiting the same trait value, respectively (Nakagawa & Schielzeth, 2010).

The most general approach to estimate repeatability is through general linear mixed-effects models (GLMM) using individual identity as a random effect, because GLMMs directly estimate \( \sigma^2_{\alpha} \) and \( \sigma^2_{\varepsilon} \). However, because laying date distribution changes every year, we calculate the value in relation the population mean of the same year. In this case negative values corresponded to early-than-average breeders while positive values to birds laying after the average laying date. The repeatability of laying date is estimated here for females with the rptR package in R (available at http://r-forge.r-project.org/projects/rptr, Nakagawa & Schielzeth, 2010) using female identity as a random effect. The final dataset was made by 1571 laying events by 404 females. I also estimated the repeatability of the relative laying date for those females born at Pantaleu colony only (n=29).

**Mother-daughter regression**

A second necessary but not sufficient condition for an evolutionary response to occur is that the trait should be heritable. Character heritability is a concept that summarizes how much of the variation in a trait is due to the variation in genetic factors. Often, this term is used in reference to the similarity between parents and their descendants. In this context, high heritability implies a great similarity between parents and offspring with respect to a specific trait (Wray, N. & Visscher, P. 2008). However, trait expression is not only a function of genetic factors and it may vary in relation to environmental conditions (Hoffmann & Merilä, 1999; Charmantier & Garant, 2005). For example, unfavourable environmental conditions may increase or decrease heritability (Hoffmann & Merilä, 1999), although there is no consensus on how heritability is
sensitive to environmental conditions (Charmantier & Garant, 2005). In the present study, we used the parent-offspring regression, methods like those of Åkesson et al. (2008), to estimate the heritability, $h^2$, of laying date. Because we only used data from mothers and daughters this type of regression estimates only half of the additive genetic variance and heritability corresponds to twice the slope of regressions (Falconer, 1989; Visscher et al., 2008). We used 29 daughter-mother paired values. Mothers’ value was taken the year of birth of the daughter while daughters’ values was averaged over the (sometimes) multiple breeding events.

Breeding success

If laying date was under selection, optimal laying date should have a fitness payoff. To investigate a possible link between the relative laying date and breeding success I used 1571 laying events from 404 females. I modelled the probability of nest success as a function of the relative laying date through logistic regression in general mixed models using female’s identity as a random effect to avoid pseudoreplications. I also used absolute (Julian) values of laying date to assess a possible relationship regardless the population value.
3. RESULTS

3.1 Laying date and environmental conditions

Laying occurred within a short period, about 14-18 days, but there were considerable differences in the average onset during the study period (Figure 4), with an overall median laying date on 25 May (145 julian) and average of 145.5.

![Figure 4](image)

**Figure 4.** The distribution of Cory’s shearwater laying date across the years. Boxes indicate the interquartile range in each year, with the median marked as a bold solid line. Whiskers note the upper and lower quantiles. The horizontal grey line represents the overall median of the laying date distribution (25 May).

wNAO was positively associated with the laying date accounting for nearly 45% of the variation in the average laying date at Pantaleu islet ($R^2 = 0.449$, $t=3.49$, $p < 0.01$, Fig 5-6).

![Figure 5](image)

**Figure 5:** Laying date mean (circles) and wNAO (solid line) during the 17 years of the study period (2002-2018). The large-scale index explained nearly 45% of the time-dependent variability in the Laying Date.

Positive phases of wNAO, i.e. windy and warmer conditions, wet winters dominated by westerly
winds in the Atlantic (Genovart et al., 2013), were associated with later average laying date and larger variances (Fig. 6).

![Figure 6: Relationship between winter environmental conditions (winter NAO) and the average laying date (left) and its variance (right)](image)

3.2 | Repeatability

Laying date differed across individuals (Fig 7) with some females laying systematically earlier than the average and others systematically later.

![Figure 7. Individual-based distribution of laying date refer only to females with more than 3 observations. The horizontal straight line indicates the population average values. Individual on the left side of the graph begin breeding consistently earlier than the average while those on the right do so consistently later.](image)

Indeed, the repeatability measure of the relative laying date from a model including only female identity as a random term was 0.517 (95%-CI: 0.462–0.565, n = 1571 observations from 404 females) and statistically significantly greater than zero (Fig. 8). Interestingly, repeatability of laying date was higher (n=29; R = 0.653, 95%CI=0.37-0.8) when only those females born at Pantaleu islet were considered.
3.3 | Heritability

Heritability ($h^2$) was calculated using the laying date of the mother and the averaged one of the daughters ($n=29$, Figure 8).

Note that mother laying date was taken at the year of birth of the daughter. In this respect the two measures refer to different years. Only in one case the mother bred simultaneously with...
her daughter. The slope of daughter-mother regression was 0.57 ($r^2 = 0.11$; $p = 0.07$, Fig 9).

Heritability of laying date from half-parent / sibling regression is twice this slope (Falconer, 1989), a value greater than the upper limit of heritability. This suggested a high heritability but indicated that the measure was not reliable probably due to the small dataset. Contingency table on the proportion of early daughter according to the state of the mother supports a high heritability ($X^2 = 7.79$, $p<0.01$). In specific, there was a lack of early breeding daughters from late breeding mothers (Table 1).

Table 1. Number of early/late daughters according to mother group. Individuals were classified as ‘early’ or late ‘late’ according to whether they bred before or after the average population value, respectively.

<table>
<thead>
<tr>
<th>Mother</th>
<th>Early</th>
<th>Late</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Daughter</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Early</td>
<td>12</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td>Late</td>
<td>9</td>
<td>8</td>
<td>17</td>
</tr>
<tr>
<td>Total</td>
<td>21</td>
<td>8</td>
<td>29</td>
</tr>
</tbody>
</table>

Nevertheless, only future studies with a larger sample size will shed a light on heritability processes.

3.4 | Laying date and Breeding success

Individual breeding success (BS) was negatively correlated with relative laying date (GLMM: $\beta=-0.054$, $Z=-2.68$, $p<0.01$; Figure 10) with early breeder having a 29% more chance to breed successfully than late breeders, following the relationship $\logit(BS)= 1.04713-0.05402*LY$, where BS is the breeding success and LY is the individual relative laying date. A similar relationship was found when using the absolute laying date (Julian): $\logit(BS)= 7.82-0.0047*JulianDate$
4. DISCUSSION

At population level, the most common response to climatic changes is a shift of the onset of biological process, such as flowering, arriving date or reproduction (Post et al., 2001; Parmesan & Yohe, 2003). This observed shift might be the result of individual plasticity or of evolutionary processes due to the selective pressure of the new environment. Plasticity, i.e. defined as the individual capacity to express different values of a given trait in different environment (Charmantier & Gienapp, 2014), would result in a trait shift without necessarily a change in the genotype frequency. On the other hand, an evolutionary response might result from a process of selection against those individuals that show a maladjusted value of the trait, leading to a change in genotype frequency. Necessary (but not sufficient) conditions for this to occur is that i) optimal trait value should lead to fitness advantages, ii) individuals should be consistent in their trait expression (repeatability) and iii) the trait should be heritable (heritability; Falconer & Mackay, 1996). Phenotypic plasticity grants organisms a mechanism for coping with environmental change and it is therefore heavily implicated in the phenological changes induced by the changing climate across trophic chain (Parmesan & Yohe, 2003; Thackeray, 2010). These responses testify to the power of phenotypic plasticity and there is even one case where it can be shown to be adaptive (Charmantier et al., 2008). Evolutionary changes may also play a considerable role, but its quantification awaits treatment (Charmantier & Gienapp, 2014). The two processes, plasticity and selection, are however not mutually exclusive and many evolutionary biologists consider that plasticity itself is a trait under selection, i.e. individuals would vary in their capability to adapt to new environment. In this work I investigate the shift in the onset of reproduction, i.e. laying date, of the Cory's shearwater (Calonectris diomedea) over
a period of eighteen years. Using data at population level, I first evaluate the relationship between average laying date and an index of ocean state variability (the wNAO). I then used individual data to measure trait repeatability (relative to population average) and heritability. Finally, I investigated a possible association between laying date and breeding success.

A first result was that nearly half (44%) of the yearly variation in the average laying date was explained by the winter North Atlantic Oscillation (wNAO). The relationship was positive so that early average breeding dates are associated with negative wNAO phases. Cory's shearwaters stay in the Atlantic Ocean from October to March and tend to visit the North Atlantic at the end of the winter (González-Solís et al., 2007). The winter NAO index has previously been shown to be a predictor of spring phenology of, for example, flowering plants (Post et al., 2001), phytoplankton (Weyhenmeyer et al., 1999), terrestrial birds (Crick et al., 1997; Forchhammer et al., 1998; Visser et al., 1998; Brown et al., 1999; Both & Visser, 2001; Thomas et al., 2001; Sanz et al., 2003) as well as seabirds (Aebischer et al., 1990; Moller et al., 2006; Brommer et al., 2008; Votier et al., 2009). Indeed, a similar strong relationship (50%) between breeding onset and seabirds was also found by M. Frederiksen et al. (2004). In this study, however, the relationship was positive and high NAO values (i.e. mild winters) were associated with earlier breeding for black-legged kittiwake (Rissa tridactyla) and common guillemot (Uria aalge) but had no effect on European shag (Phalacrocorax aristotelis). This difference is to be expected as positive wNAO values favour mild winter in northern Europe (Durant et al., 2004; Lloret et al., 2004; Frederiksen et al., 2004; Moller et al., 2006; Reed et al., 2006) but colder winters in Western Europe and wetter conditions in the Mediterranean. Here positive phases had a negative effect on the density of small pelagic fish (the main prey of shearwater together with squid; Genovart et al., 2012). The mechanisms underlying the relationship between wNAO and laying date in Shearwaters however are still not clear. Seabirds' response probably reflects the complex nature of bottom-up effects of environmental conditions on fish population dynamics, including spatial differences in the effect of NAO on environmental conditions (Hallett et al., 2004, Stige et al., 2006) and non-linear effects of NAO (Durant et al. 2004). Also, it is possible that carry-over effects (Harrison et al., 2011) of wintering conditions are translated into the reproductive onset. However, other aspects, e.g. flying speed, prey accessibility...etc., cannot be excluded.

Despite being highly variable at population level, the laying date was repeatable within individuals in agreement with other studies (Gill et al., 2014; Thorley & Lord, 2015; Moller, 2001). Laying early typically pays off in terms of reproductive success, and we found a
directional selection towards earlier breeding (Verhulst & Nilsson, 2008). In the context of repeatability, this would suggest that some aspects of phenotypic quality influence laying date. This may reflect the physiological condition of breeding females (Moreno et al., 1998), their ability to attract a higher quality mate (Sheldon, 2000) or their acquisition of a good nesting site (Daan et al., 1990). Interestingly, the repeatability of females born in Pantaleu was higher than average repeatability (0.65 and 0.55, respectively). This might indicate a certain advantage of familiarity or parenthood in the laying date. Results from mother-daughter regression suggested a high heritability of 0.57 of the relative laying date, h2=0.57x2=1.14 (see Visscher et al., 2008). A value >1 is likely to reflect a spurious relationship possibly due to the small sample size. Laying date has been proved to be an heritability trait in larger sample size of long-lived bird populations (Charmantier et al., 2006; Both & Visser, 2001; Kim et al., 2012; Liedvogel et al., 2012; Thorley & Lord, 2015). A further insight in the heritability the relative laying date of Cory’s Shearwaters at Pantaleu islet came from the 2x2 contingency table, where it was clear (and statistically significant) a lack of early laying daughter born from late laying mothers. Finally, we found a negative relationship between relative laying date and breeding success. Interestingly this was also confirmed when we used the absolute (Julian) laying date. A negative breeding performance of late laying breeders has been reported in many other birds (Hasselquist, 1998; Gill et al., 2001; Alves et al., 2012-2013; Thorley & Lord, 2015). In shearwaters earliest breeders had a 27% more change to breed successfully than late breeders. However, how much of this disadvantage is than translated into lifespan breeding success it is not clear. About 15% of Cory’s Shearwater at Pantaleu skip reproduction every year (Sanz-Aguilar et al., 2011). Reproductive skipping in long-lived species is a common strategy to trade current vs future reproduction (Igual et al., 2009; Weimerskirch, 2002; Genovart et al., 2012). As plasticity can be constrained, late breeders might skip the entire reproduction making the disadvantage higher. At present this cost is not included in our analysis which is conditional to birds that have bred. Our results are pointing to a difference in phenotypic quality across individuals because repeatability is high, meaning late breeding individuals with lower breeding success are consistently doing so.

Despite the necessary conditions for an evolutionary response in a shift in laying date are met (repeatability and heritability), our results point to a plastic response of individuals to environmental changes. Micro-evolutionary change as a response to selection acting on heritable traits is generally slower to changes due to phenotypic plasticity (Hendry & Kinnison, 1999), in particular this is because heritability estimates in natural populations are often moderate (Kruuk, 2004), and generation times can be on the order of several years.
Consequently, phenotypic plasticity might be a better way to cope with environmental change as it can allow a faster tracking of the changing environment. It is also important to notice that breeding onset in Shearwaters is highly synchronous with all birds laying within an interval of 2-3 weeks. Despite, the relative laying date is repeatable and has a consequence on breeding success.

**In summary**

Climatic changes impose a shift in the breeding onset of Cory’s shearwater demonstrated by a link between laying date and winter North Atlantic Oscillation index. Despite a clear evidence for this relationship, the mechanisms are still unknown. This study showed that the variation in laying date resulted from phenotypic plasticity, a way through which individuals buffer environmental variability. This plasticity seems to be an intrinsic characteristic of the individuals because the repeatability of laying date in relation to the average population value is very high. The high consistency, coupled with a negative association between laying date and breeding success, point to a difference in phenotypic quality across breeding females. Finally, plasticity can buffer environmental variation, but individual response might not be optimal due to physiological constrains. For example, individuals that begin reproduction too late, might skip the reproduction entirely. The negative relationship between absolute laying date and wNAO found in previous study of the same population with breeding success, might suggest an increase in skipping probability (and an average decrease in breeding success) with increasing values of wNAO.

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