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Small-scale spatial variation in evolvability for life-history traits in the storm petrel

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The evolutionary potential in the timing of recruitment and reproduction may be crucial for the ability of populations to buffer against environmental changes, allowing them to avoid unfavourable breeding conditions. The evolution of a trait in a local population is determined by its heritability and selection. In the present study, we performed pedigree-based quantitative genetic analyses for two life-history traits (recruiting age and laying date) using population data of the storm petrel over an 18-year period in two adjacent breeding colonies (only 150 m apart) that share the same environmental conditions. In both traits, natal colony effect was the main source of the phenotypic variation among individuals, and cohort variance for recruitment age and additive genetic variance for laying date were natal colony-specific. We found significant heritability only in laying date and, more specifically, only in birds born in one of the colonies. The difference in genetic variance between the colonies was statistically significant. Interestingly, selection on earlier breeding birds was detected only in the colony in which heritable variation in laying date was found. Therefore, local evolvability for a life-history trait may vary within a unexpectedly small spatial scale, through the diversifying natural selection and insulating gene flow. © 2012 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2012, **106**, 439–446.

ADDITIONAL KEYWORDS: adaptability – animal model – evolution – heritability – laying date – recruiting age – selection.

INTRODUCTION

The adaptability of a local population to changing environments depends on the amount of heritable variance expressed in traits related to fitness (Roff, 2002). For example, evolutionary potential in recruiting age and timing of reproduction (egg-laying date) may be crucial for the ability of populations to buffer against climate changes, allowing them to avoid unfavourable breeding conditions (Walther *et al.*, 2002; Brommer *et al.*, 2005; Husby *et al.*, 2010). Therefore, local adaptation occurs through the interaction between ecological and evolutionary dynamics over different spatial and time scales. Particularly, spatial variability in quality of habitat generates different population dynamics and selection pressures, and thereby results in phenotypic differentiation (Hendry, Day & Taylor, 2001). However, spatial variation in the amount of genetic variance of phenotypes (heritability) will also generate differential evolutionary responses and, when gene flow is not common, evolutionary change can be rapid (Schoener, 2011).

Some recent population studies have shown that the pattern of phenotypic variation can vary over unexpectedly small spatial scales. For example, the

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*Corresponding author. E-mail: yeonkim@uvigo.es additive genetic effect on laying date differed between two local populations of the blue tit *Cyanistes caeruleus* in which the timing of local maximum food availability differed (Caro *et al.*, 2009), suggesting the diversifying effect of selection on laying date. Garant *et al.* (2005) showed that genetic variance for nestling body mass was spatially variable even within a population in the great tit *Parus mayor*, possibly as a result of spatial heterogeneity in density-related habitat quality (Garant *et al.*, 2005). Nevertheless, evidence for between-population variation in the heritability of quantitative traits is scarce, and it is necessary to integrate knowledge about fine-scale ecological heterogeneity and dynamics to understand how evolutionary differentiation can occur between adjacent populations.

Heritability of quantitative traits can vary in space for various reasons: differential environmental conditions (Hoffmann & Merilä, 1999; Charmantier & Garant, 2005), heterogeneous gene flow (Garant *et al.*, 2005) and changes in gene frequencies through different selection pressures (Endler, 1986). Both theoretical and empirical studies have suggested that there are no universal trends for the eco-evolutionary influences on heritability. For example, unfavourable environmental conditions may either increase or decrease the heritability (Hoffmann & Merilä, 1999), and there is no consensus as to how the heritability is sensitive to environmental conditions (Charmantier & Garant, 2005).

In the present study, we use the ‘animal model’ (Kruuk, 2004) to test whether phenotypic variation in recruitment age and egg-laying date has a heritable component in two adjacent breeding colonies (two caves in Benidorm Island) of a long-lived seabird, the European storm petrel *Hydrobates pelagicus* Linnaeus. Studies of some long-lived wild populations have shown that recruiting age and timing of reproduction in the season are heritable traits (Kruuk *et al.*, 2000; Charmantier *et al.*, 2006a, b; Kim *et al.*, 2011a). In the present study, we compare genetic and environmental variation in life-history traits between two local populations of the storm petrel (Fig. 1).

The two local populations used in the present study have experienced different ecological dynamics during the last decades, although environmental conditions in climate, food availability, and density-dependent processes (e.g. competition) in each breeding season were the same as a result of the geographical proximity of the two caves (Tavecchia *et al.*, 2008). Phenotypic divergence within a close proximity can be possible through the balance between diversifying natural selection and insulating gene flow (García-Ramos & Kirkpatrick, 1997; Garant *et al.*, 2005; Friesen *et al.*, 2007), which may be the case in our study population. Natal philopatry to the local populations in the study is very high (95% of the marked birds recruited into their natal colony; Sanz-Aguilar *et al.*, 2009) and predation risk differs between the two sites (Sanz-Aguilar *et al.*, 2008, 2009). Interestingly, the two local populations differ in some important life-history traits, recruiting age and laying date (see Results). Therefore, in the present study, we explore quantitative genetics of these two life-history traits, and test whether the phenotypic difference among individuals in a heritable trait influences their breeding success. The study aimed: (1) to examine whether recruiting age and laying date have heritable variations, which enable evolutionary changes under directional selection; (2) to examine between-population variation in environmental and genetic components of these two life-history traits; and (3) to test whether an evolutionary change will be possible in a trait in which heritable variation was encountered by estimating selection differential.

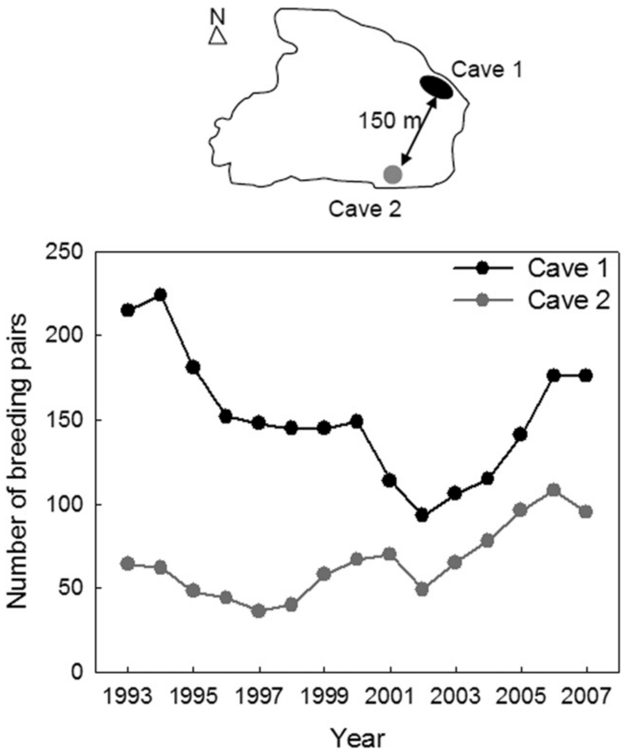

Figure 1. Locations and changes in breeding population size between 1993 and 2007 of two breeding colonies of storm petrels at Benidorm Island: cave 1 and cave 2.

MATERIAL AND METHODS

STUDY SYSTEM AND DATA COLLECTION

We studied colonial storm petrels at Benidorm Island on the Mediterranean coast of Spain (38°30′ N, 0°8′ E). The study species is a small seabird, although it has an extremely long lifespan and low fecundity, laying only one egg in a season (Sanz-Aguilar *et al.*, 2008). Data on marked birds were collected during the period 1993–2010 at two breeding colonies, caves 1 and 2, which are only 150 m apart. Most breeding petrels in the island nest in the two caves at high densities and few recruits and breeders disperse between the two cave colonies (Sanz-Aguilar *et al.*, 2008, 2009). In 1996, a number of artificial nest boxes were installed in both colonies, although they were mainly occupied in only cave 2 (de León & Mínguez, 2003). The population size of cave 2 has increased substantially since 1997 as a result of the increased availability of high quality nest sites (i.e. artificial nest boxes). Although the population of cave 1 was not nest-site limited, it did not show the same population dynamics as cave 2 (Fig. 1) (de León & Mínguez, 2003; Sanz-Aguilar *et al.*, 2009). Survival probability of adults was slightly higher in cave 2 but, historically, there have been more breeding pairs in cave 1 because there are more natural nesting sites available (Sanz-Aguilar *et al.*, 2008, 2009, 2010; Tavecchia *et al.*, 2008).

A total of 1452 fledglings of age 20–50 days and 1115 adults were marked with steel rings since 1993 and 103 marked fledglings have been recruited into the study population so far. A total of 56 birds from cave 1 and 47 birds from cave 2, which were marked as fledglings between 1993 and 2007, were recruited to the study population. Among those, only four recruits from cave 1 and two from cave 2 dispersed to the other cave. Each year, breeding birds (i.e. breeders at nests with an egg) were captured for identification only once at their nests during the incubation and most breeding nests were inspected once every week (or a maximum of every 2 weeks in some nests) to record hatching and breeding success in both colonies. The recruits from cave 1 and cave 2 nested repeatedly up to maximum age of 17 years, performing 140 and 121 breeding events, respectively.

The age of recruitment of each bird comprised the age at first observation in the breeding colony, although some birds could have bred earlier but remained undetected (Sanz-Aguilar *et al.*, 2009). The sex of most recruits was unknown (males: $N = 34$, females: $N = 19$, unknown: $N = 50$), and recruitment age did not differ between males and females (mean ± SE recruitment age: males 4.9 ± 0.4 years, females 4.3 ± 0.3 years; Mann–Whitney test: $U = 270.00$, $P = 0.31$). Therefore, we did not account for sex in data analyses of recruiting age. Laying date (i.e. timing of reproduction) of the only egg in each nest was estimated from observed hatching date or recorded when it occurred (i.e. median date of two consecutive visits) in the two caves. Laying date was Z-transformed using the annual population mean to account for variation among years. Timing of reproduction was analyzed for male, female, and unknown sex breeders in the same model to assure sufficient sample size. We assumed that the female laying date also reflects the timing of reproduction of her partner, which is based on timing of arrival to the breeding colony, pre-reproductive condition, and pair-bond.

QUANTITATIVE GENETIC ANALYSIS

The animal model estimates the additive genetic variance and heritability of a trait by assessing the phenotypic covariance between all pairs of relatives in the pedigree (Kruuk, 2004). We prepared the pedigree to contain only links that were informative for the available data used in the present study (Morrissey & Wilson, 2010). The combined pedigree for individuals from caves 1 and 2 was based on 230 individuals, including 71 paternal and 75 maternal identities. Parents with unknown sex from the two caves (28%) were assigned to either a sire or a dam in the pedigree. Among the study birds, 27% from cave 1 and 30% from cave 2 were related to one or more samples in each data set (i.e. full sib, half sib, parent or offspring). Individuals without any known relative in the pedigree were included in the analyses for a better estimation of the total phenotypic variance although they cannot influence the estimate of genetic variance. We used the R package PEDANTICS for information from the pedigrees of the two caves (Morrissey & Wilson, 2010), (Table 1). Mean pairwise relatedness of ≥ 0.25 (i.e. the lowest relatedness in the pedigree used in the study) was slightly stronger in the pedigree of cave 2.

Animal models with a restricted maximum likelihood were fitted for recruiting age and laying date, using ASREML, version 3 (VSN International; Gilmour *et al.*, 2008). In the univariate animal models

Table 1. Pedigree statistics of informative individuals from caves 1 and 2 at Benidorm Island

	Cave 1	Cave 2
Number of individuals	132	98
Number of maternities	45	30
Number of paternities	41	30
Maximum pedigree depth	2	2
Pairwise relatedness		
≥ 0.25	0.011	0.014
≥ 0.5	0.010	0.013

Note that 0.25 is the lowest relatedness in the pedigrees used in the present study.

fitted to recruits from the 1993–2007 cohorts, recruiting age of an individual *i* is modelled as:

$$r_i = \mu + a_i + nc_i + c_i + e_i$$

In the model, the population mean (μ) was included as a fixed effect. As random effects, we included additive genetic effect (a_i, effect of the *i* genotype relative to μ), a residual term (e_i), and common environmental effects (nc_i and c_i). Natal colony-specific (cave 1/cave 2) and cohort-specific effects (nc_i and c_i, respectively) were included to quantify the covariance amongst individuals sharing common environments.

The model fitted to timing of reproduction measured repeatedly from the recruits is modelled as:

$$t_i = \mu + age_i + a_i + nc_i + c_i + pe_i + e_i$$

In the model, age of individual (age_i) was included as a fixed effect (fitted as a covariate, age between 3–14 years) to account for its negative association with timing of reproduction in the season. Although a quadratic effect of age on reproductive performance as a result of senescence is often observed in long-lived bird species, there was no evidence for a nonlinear relationship between age and laying date in our data set (Berman, Gaillard & Weimerskirch, 2009). Individual identity (pe_i) was included as an additional random effect to account for permanent environmental effect on individual's phenotype as a result of constant differences in the conditions experienced by different individuals throughout their lives or the long-term effects of conditions experienced during early development.

The distribution of all random effects, additive genetic (a_i), permanent environment (pe_i), common environment (nc_i and c_i) and the residual term (e_i), is assumed to have a mean of zero and a variance to be estimated (V_A, V_{PE}, V_{Cave}, V_{Cohort} and V_R). Total phenotypic variance was calculated as: $V_P = V_A \ (+ V_{PE}) + V_{Cave} + V_{Cohort} + V_R$, then heritability and environmental effects were calculated as $h^2 = V_A/V_P$, $pe^2 = V_{PE}/V_P$, $nc^2 = V_{Cave}/V_P$ and $c^2 = V_{Cohort}/V_P$. The statistical significance of each variance component was assessed using a likelihood ratio test (LRT) that compares models based on –2 times the difference in REML log-likelihood scores distributed as chi-squared, where the degree of freedom equals the number of variance terms removed.

We tested explicitly whether the size of the variance components differ significantly between the two caves by using bivariate animal models fitted to the data from both local populations (Husby *et al*., 2010). Recruiting age and timing of reproduction in the two local populations were analyzed in two separate bivariate models (i.e. recruiting age in caves 1 and 2 in one bivariate model, and timing of reproduction in another). All covariances, including residual covariance, were constrained to zero because the dispersal rate between the two adjacent local populations was low. The same fixed effect as in the univariate analysis was included in the bivariate analysis (i.e. age in the model fitted to timing of reproduction). The comparison between the two populations was performed by constraining the variance components in the two local populations to be equal then using a LRT to compare the likelihood of this model with the unconstrained model (Husby *et al*., 2010).

To ensure between-population variation in quantitative genetic parameters of the timing of reproduction (i.e. standardized laying date) estimated by animal models (see Results), we additionally used a classic approach based on parent–offspring and full sibling regressions (Falconer & Mackay, 1996). These two types of relationship with the same level of genetic relatedness ($r = 0.5$) were included in a single linear regression analysis for each local population to ensure sufficient sample size. Related individuals of similar age (difference, ≤ 2 years) were paired to regress their phenotypic values. Heritability (h^2) was estimated as twice the slope of regression (r^2).

SELECTION ANALYSIS FOR LAYING DATE

We used standard selection analyses (Arnold & Wade, 1984) to correlate timing of reproduction with the breeding success (1 = fledge a chick; 0 = fail to hatch or fledge) as a measure of annual fitness. Laying date was standardized within each natal colony, and fitness was converted to relative fitness, in accordance with standard procedures for selection analyses. Directional selection differential (S') for each natal colony was estimated by fitting a generalized linear model with a binomial error distribution and a logit link (SAS Institute, 2002). There was no evidence for nonlinear selection on laying date, and so only the linear selection differentials are presented. We did not perform selection analysis for recruiting age, which did not show a heritable variation (see Results). Although selection on recruiting age can be adequately analyzed by using lifetime reproductive success as a measure of fitness (and not by annual fitness, which cannot account for a lifetime trade-off between early and late reproductions), it was difficult to calculate lifetime fitness in the present study as a result of the extremely long lifespan of the study species.

RESULTS

In the model fitted to all individuals, natal cave and cohort explained significant proportions of the total phenotypic variance for $\log_{10}$-transformed recruiting age (Fig. 2A, Table 2) ($nc^2 = 0.120 \pm 0.168$,

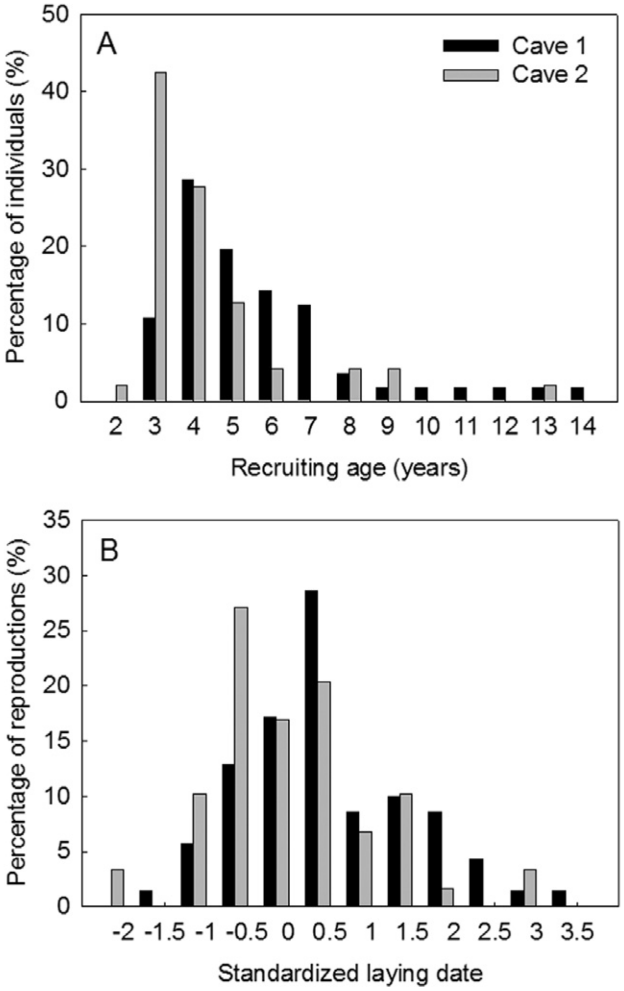

Figure 2. Distribution of (A) recruiting age (years) and (B) laying date (*Z*-transformed by year) in storm petrels from cave 1 and cave 2. Birds from cave 1 recruited on average 1.4 years later (mean ± SE recruiting age: cave, 1 5.7 ± 0.3 years; cave 2, 4.3 ± 0.3 years) and laid eggs 6.9 days later than those from cave 2 (mean ± SE laying date, expressed as number of days from 1 April = 1: cave 1, 50.0 ± 1.7 days; cave 2, 43.1 ± 2.0 days).

$c^2 = 0.268 \pm 0.132$). Note that SEs of V_{Cave} and nc^2 are relatively high despite statistical significance, as is also the case in the model of laying date (see below), possibly because natal cave is an only two-level variable (caves 1 and 2). The estimated SE of natal cave as a random factor depends on the variation between the two caves, as well as the sum of the individual residuals (Littell *et al.*, 1996). When models were fitted for recruits from caves 1 and 2 separately, only recruits from cave 2 showed statistically significant cohort variance (Table 2) (cave 1: $c^2 = 0.142 \pm 0.142$, cave 2: $c^2 = 0.660 \pm 0.130$). Additive genetic variance for recruiting age was null in all models. Therefore, only cohort variance was compared between the

Table 2. Decomposition of phenotypic variance in recruiting age (years, $\log_{10}$ transformed) and laying date (standardized by year) in storm petrels from the 1993–2007 cohorts

Trait	Natal site	N	$V_{\mathrm{Cave}} \pm$ SE	$V_{\mathrm{A}} \pm$ SE	$V_{\mathrm{Cohort}} \pm$ SE	$V_{\mathrm{PE}} \pm$ SE	$V_{\mathrm{R}} \pm$ SE	$V_{\mathrm{P}} \pm$ SE
Recruiting age*	Caves 1 and 2	103	0.401 ± 0.630 ($P = 0.012$)	$<10^{-6}$	0.895 ± 0.526 ($P = 0.001$)	–	2.044 ± 0.310	3.340 ± 0.842
	Cave 1	56	–	$<10^{-6}$	0.391 ± 0.426 ($P = 0.205$)	–	2.366 ± 0.500	2.757 ± 0.564
	Cave 2	47	–	$<10^{-6}$	2.273 ± 1.121 ($P < 0.001$)	–	1.173 ± 0.291	3.445 ± 1.119
Laying date†	Caves 1 and 2	129	0.170 ± 0.272 ($P = 0.028$)	0.220 ± 0.129 ($P = 0.045$)	$<10^{-6}$	$<10^{-6}$	0.790 ± 0.131	1.180 ± 0.302
	Cave 1	70	–	0.346 ± 0.202 ($P = 0.043$)	$<10^{-6}$	$<10^{-6}$	0.707 ± 0.166	1.053 ± 0.197
	Cave 2	59	–	0.088 ± 0.159 ($P = 0.507$)	0.029 ± 0.098 ($P = 0.705$)	$<10^{-6}$	0.862 ± 0.199	0.979 ± 0.190

*Variance components and their SEs: $\times 10^{-2}$.

†Age of breeder was included as a fixed effect in the models ($P < 0.02$).

recruits from the two caves in a bivariate model fitted to $\log_{10}$-transformed recruiting age. Despite the apparent difference in c^2 estimated using the univariate analyses, the bivariate analysis showed no statistically significant difference in recruiting age between the two caves ($\chi^2 = 2.680$, d.f. = 1, $P = 0.102$).

There was significant natal cave and additive genetic effects on the phenotypic variation in timing of reproduction, standardized laying date (Fig. 2B, Table 2) ($nc^2 = 0.144 \pm 0.198$, $h^2 = 0.187 \pm 0.110$). When analyzed separately for recruits from caves 1 and 2, only those from cave 1 had significant additive genetic variance (Table 2) (cave 1: $h^2 = 0.329 \pm 0.159$, cave 2: $h^2 = 0.090 \pm 0.159$). Permanent environmental variance and cohort variance for laying date was null or nonsignificant in all models (Table 2). Therefore, additive genetic variance in standardized laying date was compared between caves 1 and 2 in a bivariate model. V_A in laying date in birds from cave 1 was significantly higher than in birds from cave 2 ($\chi^2 = 7.452$, d.f. = 1, $P = 0.006$). The h^2 estimates from combined parent–offspring and full sibling regressions (cave 1: $h^2 = 0.724$, $F_{1,13} = 8.954$, $P = 0.010$; cave 2: $h^2 = 0.112$, $F_{1,11} = 0.365$, $P = 0.558$) were higher than those estimated by animal models possibly because the regression method failed to account for the increased covariance between relatives generated by shared environments (Kruuk, 2004). However, these two different approaches detected the same pattern of between-population difference in h^2.

Linear selection analyses showed significant negative directional selection on timing of reproduction in birds from cave 1 ($S' = -0.560 \pm 0.268$, $P = 0.037$) but not in those from cave 2 ($S' = -0.030 \pm 0.274$, $P = 0.912$).

DISCUSSION

We explored the source of phenotypic variation in two life-history traits, recruitment age and laying date, in two adjacent local populations of the storm petrel by using long-term data collected over an 18-year period. Although the use of animal models allowed us to estimate additive genetic variance (V_A) based on all relatives in the pedigree, downward bias in V_A estimates as a result of the limited sample size is possible. Moreover, the long lifespan and low fecundity of storm petrels possibly weakened the power of the quantitative genetic analyses, which depends on the pedigree structure (Wilson *et al.*, 2009). Nevertheless, low gene flow between the two local populations as a result of strong philopatry to the natal colony in the study system provided a rare opportunity to compare V_A between two neighbouring colonies.

In long-lived animals, trade-offs between early and late reproductions shape individual phenotype for recruitment age, and different early environments encountered by different cohorts affect the trade-offs through differential costs of early reproduction (Kim *et al.*, 2011b). This may explain significant common environmental variance of recruitment age assigned to cohort (V_{Cohort}) in the study population in which climate and food availability in early life vary among cohorts (Sanz-Aguilar *et al.*, 2009). The apparent difference in V_{Cohort} between caves 1 and 2 ($c^2 = 0.142 \pm 0.142$ and $c^2 = 0.660 \pm 0.130$, respectively) was unexpected, given that cohort-specific environmental conditions (e.g. climate, food availability) should have been the same for birds from the two caves as a result of the close proximity (Tavecchia *et al.*, 2008). The phenotypic variation of birds from cave 1 might be influenced by other environmental factors such as stochastic predation risk by breeding yellow-legged gulls *Larus michahellis* and local population density (Fig. 1) (Oro *et al.*, 2005). Nevertheless, our result obtained from a bivariate animal model showed that the between-population difference in V_{Cohort} of recruiting age was not statistically significant. Hence, our results from univariate and bivariate animal models suggest the need for caution when comparing the estimates of common environment effects between different local populations.

Laying date showed heritable variance in the storm petrel breeding at Benidorm Island as shown in some other long-lived bird populations (Charmantier *et al.*, 2006a). Interestingly, our analyses using two different methods, univariate and bivariate animal models, suggested that the size of the additive genetic variance was greater in cave 1 than in the other cave colony, which were only 150 m apart. This result suggests that microevolution in laying date may be possible in cave 1 if directional selection operates on this trait. However, it is unclear why laying date is more genetically variable in cave 1. Although weak pedigree structure can give rise to downward bias in V_A estimate, mean pairwise relatedness was rather (slightly) stronger in the pedigree of cave 2, suggesting that the pedigree structure was not responsible for the between-population difference in V_A. One possible reason for the spatial variability may be that environmental conditions are more heterogeneous (Falconer & MacKay, 1996) in cave 1, although it is unlikely that environmental heterogeneity alone would preserve additive genetic variation (Roff, 1997). Another possibility is that relatively small local population size in cave 2 could have resulted in loss of variation because of genetic drift (Roff, 2002). By contrast, gene flow by immigrants might impede the reduction of genetic variation (Ingvarsson, 2001) in cave 1 if gene flow as a result of immigration from other populations was not homogeneous at Benidorm populations. The study species shows strong philopatry to the natal colonies, and immigration from other populations into the study populations has never been detected, although we cannot neglect the possibility of immigration. Although the results of the present study, based on only individuals ringed as chicks in the study populations, did not account for genetic contribution of immigrants of the first generation, it is possible that their descendants contributed the maintenance of genetic variation.

Evolutionary theories predict that directional selection would reduce genetic variation for phenotypic traits (Kruuk, 2004), although the opposite pattern was observed in the present study. Our selection analysis with annual fitness showed that earlier birds bred more successfully in cave 1, although there was no selection on laying date in birds from cave 2. Breeders in cave 1 suffered stochastic predation by yellow-legged gulls, which probably functioned as a selection pressure on early reproduction in the season. The gulls breeding in the study colony specialized in predation on storm petrels, and their predation rate might have increased as the season progressed. In long-lived bird species, young or first-time breeders lay later and have lower breeding success than others as a result of inexperience and a lack of coordination between the partners (Clutton-Brock, 1988; Newton, 1989; Forslund & Pärt, 1995). In colonially breeding birds, early breeders are often competitive and experienced individuals, and occupy high quality breeding sites that provide protection against predators to the breeders and offspring (Partridge, 1978; Cody, 1985). By contrast, individuals in cave 2 could be benefited in settlement and reproduction from increased high-quality nest sites (i.e. artificial nest boxes) and low predation risk (de León & Mínguez, 2003; Tavecchia *et al*., 2008) regardless of laying date. A previous study showed that overall breeding success was higher in cave 2 than in cave 1 (Sanz-Aguilar *et al*., 2009). Low predation risk and adult mortality in cave 2 might prolong pair bonds of breeders, which in turn positively influenced their reproductive output.

The ability to adjust the timing of reproduction adaptively in response to climate-induced environmental changes should influence local population dynamics over the long-term (Walther *et al*., 2002). Our results on natal site specific heritability and selection on laying date potentially have an important eco-evolutionary implication for this population: local adaptation for the timing of reproduction is possible in cave 1 but not in cave 2. This difference may result from the interacting effects of genetic variation and demography, both potentially influenced by heterogeneity in habitat quality (e.g. predation pressure). The present study provides only fractional evidence for such an interaction, although it stresses the importance of considering eco-evolutionary dynamics over small spatial scales by opposing the general assumption that genetic variance should be constant within a small spatial scale.

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