Survival vs. reproduction: dimorphic life history strategy in Heermann's gulls during warm ocean temperature anomalies

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ABSTRACT: Seabirds have thrived over time in marine environments with highly variable productivity. Life history strategies favored by natural selection consist of late sexual maturation, few offspring per breeding event, high adult survival, long lifespan, and deferred breeding when food availability is low. Heermann's gull *Larus heermanni*, with 95% of its world population breeding on Isla Rasa, Gulf of California, follows this common pattern, including poor breeding performance during periods of low food availability often associated with high sea surface temperatures. Our interest was to characterize individual variations in this general pattern and assess its consequences for lifetime number of fledglings produced. We compared life history parameters from a set of known-age females banded during 1984–1993 and recaptured during 1989–2013 and found that most (85%) followed the general pattern (hereafter 'conservative') of laying ≤2 eggs and fledging no chicks during anomalously warm years. However, 15% of the females (hereafter 'bold') laid eggs during all anomalously warm years and fledged chicks in most of those years. Throughout their lifespan, conservative females lived significantly longer and produced significantly more eggs, but the total number of fledglings was not significantly different between strategies. Both strategies coexist over time, persisting within the population under conditions that were common until the late 20th century. If conditions continue to vary, with the occurrence of heatwaves and increases in the frequency of anomalously warm years, bold females may have a selective advantage over conservative females, which might help mitigate the impacts of ocean warming on future populations.

KEY WORDS: Breeding strategies · Global warming · Gulf of California · *Larus heermanni* · SST anomaly

1. INTRODUCTION

1.1. Life history strategies

The theory of life history strategy is based on the principle of resource allocation and trade-offs, and it assumes that if an organism devotes resources to one biological process, resources available for another process will be reduced. The theory attempts to explain how life history strategies are shaped by natural selection, and how an individual can maximize its contribution to the next generation by differentially allocating resources to a series of demands along its lifetime (Darwin 1859, Williams 1966, Stearns 1977, Roff 1992, Stearns 1992). Individual variability, when present, provides populations with the basis to respond to natural selection.

The decisions that individuals make among different alternatives may depend on environmental conditions. Organisms exhibit a suite of life history strate-

gies that contribute to their individual survival, breeding success, and the long-term permanence of their populations (Roff 1992, Mourocq 2017). The basic components of an organism's life history strategy are its age at independence and maturity, survival by age category, longevity, and breeding strategy (parental investment and the number of offspring produced according to parent's age and environmental conditions) (Williams 1966, Lack 1968, Weimerskirch 2001, Roff 2002, Reznick 2014).

1.2. Seabirds and their environment

Seabirds inhabit environments with fluctuating food availability that may vary between and within nesting seasons (Anderson 1989) according to variations in regional- and/or global-scale phenomena, such as sea surface temperature (SST) (Velarde et al. 2004, Velarde & Ezcurra 2018), which is in turn affected by atmospheric conditions (Sánchez-Velaso et al. 2000) and ocean currents (Hoefer 2000), among other drivers. The relationship between environmental parameters and food availability to seabirds is mediated — with some exceptions (Durant et al. 2003, Domínguez-Hernández et al. 2020) — by the effect of SST on phytoplankton and zooplankton production and then the productivity of higher trophic levels such as forage fish, which are food for larger marine species such as seabirds and other ecosystem components (i.e. larger fish, marine mammals) (Ainley et al. 1995, Velarde 1999, Vieyra et al. 2009). In seabirds, this environmental variability selects a tendency for deferred sexual maturation, production of small clutch sizes, and skipping reproduction in years of low food availability (Ashmole 1971, Anderson 1989).

1.3. Ecological/oceanographic situation

Some of Pacific Ocean climatic and oceanographic phenomena, such as El Niño–Southern Oscillation (ENSO), the Pacific Decadal Oscillation, and, recently, the occurrence of local warm SST anomalies, have been increasing in frequency and intensity (Springer et al. 2007, Velarde et al. 2015, Cai et al. 2018, Velarde & Ezcurra 2018). These changes modify selective pressures, affecting the adaptive value of the current life history strategies and observed trade-offs for different species. ENSO, an important inter-annual climatic/ oceanographic phenomenon with noticeable effects in the Gulf of California (Soto-Mardones et al. 1999), may occur every 3–7 yr (White & Tourre 2003) and

significantly impact the entire food web, from the primary producers to the highest trophic levels (Catry et al. 2013). The Midriff Island Region (MIR) exhibits the lowest SSTs in the entire gulf, and SST changes may be intense at the local level and independent of ENSO events, while pigment concentration is highest in this area of the gulf, indicating high primary productivity (Santamaría-del-Ángel et al. 1994, Soto-Mardones et al. 1999). Several authors have found that SST is negatively correlated with chlorophyll concentration and prey abundance and, thus, can be used as a proxy for food availability (Ainley et al. 1995, Velarde 1999, Vieyra et al. 2009). While we are confident about using SST as a proxy for food availability in our study area, we note that a few studies in extreme low or high latitudes have found different relationships, where food availability may be low in areas with extremely low SST (Durant et al. 2003) or, conversely, areas with high SST may exhibit high primary productivity (Domínguez-Hernández et al. 2020).

1.4. Our study

In this study, we used breeding parameters and longevity data of Heermann's gulls *Larus heermanni* nesting in Isla Rasa, a protected area (DOF 1964) located in the MIR, in Mexico's Gulf of California (28° 49′ 24″ N, 112° 59′ 03″ W), to assess individual variability in life history strategies (focusing on longevity and number of offspring produced) and compare its outcome in individual lifetime reproductive success. Since we have observed a shift in climatic regime, particularly in the most recent decades, we used these observations as a natural experiment in which different individual life history strategies could be evaluated, and hypothesized that individuals exhibiting certain life history strategies may be at an advantage under these new conditions. The questions that guided our investigation were (1) can individuals be classified into distinctive lifetime breeding strategies under warm anomaly conditions, and (2) what is the lifetime reproductive success of individuals of these different breeding strategies and longevities, compared to other individuals?

2. MATERIALS AND METHODS

2.1. Data acquisition

We banded 3500–4000 Heermann's gull fledglings per year between 1984 and 1993 (except in 1988 and

1992, which were breeding failure years). Individuals returning to the island to breed as 4 yr old adults and older were recaptured between 1989 and 2013. Details of banding and monitoring methods are found in Vieyra et al. (2009) and Velarde & Ezcurra (2018). In this study, we only used data from females with at least 4 recaptures in normal years and at least 1 recapture in anomalous years. Although the total number of tracked females was large, the use of these criteria reduced our sample size to 39 females followed for 22 yr along a time span of 25 yr.

2.2. Individual variables

The variables that we used for each female were (1) total number of eggs laid per female, (2) total number of chicks surviving to fledgling per female, (3) breeding success, defined as the total number of surviving fledglings/number of eggs laid per female, and (4) longevity, defined as the maximum age recorded for each female the last time she was observed nesting on the island when ≥5 yr had passed without her being resighted.

2.3. SST

We calculated the mean values of SST anomaly in degrees Celsius (°C) from 1989 to 2013 between the months of January and April, in a 1° lat. × 1° long. (~111 km^2) cartographic quadrat located in the Gulf of California (29–30°N, 113–114°W) from National Oceanic and Atmospheric Administration's Climate Program and Columbia University's International Research Institute for Climate and Society 'ENSO Monitor' website (http://iridl.ldeo.columbia.edu/SOURCES/ .Indices/ensomonitor.html). In this study, we considered 'anomalous years' those with temperatures >1°C above the historical average record for the last 50 yr (SST positive anomaly) and 'normal years' those with SST <1°C above the historical average record for the last 50 yr, according to Velarde et al. (2015).

2.4. Data analyses

From field data recorded for each female, we estimated the mean number of eggs laid, mean number of surviving fledglings, and mean breeding success for both normal and anomalously warm years, without separating females by strategy (which was done later in the analysis process; see below). We used a Mann-Whitney *U*-test in RStudio (version 3.6.0) to estimate if the values of these parameters were significantly different between normal and anomalously warm years (see Table 1). As a second step, we determined differences between the females' tendency to lay eggs and raise chicks in anomalously warm years and observed the following pattern:

Conservative: females who laid eggs in <70% of the anomalously warm years in which they were studied and raised chicks at the most in 2% of these years.

Bold: females who laid eggs in 100% of the anomalously warm years in which they were studied and raised chicks in at least 50% of these years.

Using field data, we determined if these patterns were significantly different between strategies, using a Mann-Whitney *U*-test in RStudio to compare the mean number of eggs laid and surviving fledglings produced per female (only for anomalous years). We used the resulting categories to establish 2 different breeding strategies for these females: conservative and bold.

2.5. Estimation of eggs and fledglings when data were not available

Not all females were resighted every breeding season. To enable a more robust data set for each female, we estimated the number of eggs laid and number of surviving fledglings for the years when no data were available from age 4 (sexual maturity of the species) to the last year when each female was observed in the nesting area, according to the method described in Lescroël et al. (2009). Once we had these estimates and data gaps were eliminated, we built generalized linear mixed models (GLMMs) with logit link and a Poisson error distribution in the statistical program RStudio. In all models, each female was included as an independent variable, identified by band number (random nested effect), age in each study year (linear and quadratic term), year type according to SST as 'normal' or 'anomalous', and breeding strategy as a factor 'conservative' or 'bold'. We selected the most parsimonious models as adequate as well as those that had the best fit of the variables according to Akaike's information criterion (AIC; Akaike 1973, Burnham & Anderson 2002). Based on the selected models for each dependent variable (number of eggs laid and number of surviving fledglings), we used the function 'predict' in RStudio to create a table with all the estimated values of these variables for each female from

age 4 yr (age of sexual maturity) to the maximum recorded age (longevity); we used estimated data from that table only for years in which no field record was available.

2.6. Differences between breeding strategies

To determine significant differences between females in the total number of eggs laid, chicks fledged (sum of observed plus estimated), and longevity, we ran 3 linear regressions — one per parameter. In all cases for these linear regression analyses, the breeding strategy was used as an independent variable, and the other 3 parameters were used as dependent variables according to the analyzed parameter. All regressions were run in RStudio.

3. RESULTS

3.1. SST variation and relationship to reproductive success

Mean clutch size, number of surviving fledglings per breeding attempt, and breeding success (Table 1, Fig. 1) were significantly higher during normal years compared to anomalously warm years ($U = 256$, $U = 50$, and $U = 78$, respectively, n = 39, p < 0.001 in all cases), considering values obtained in the field for all females, regardless of strategy.

Table 1. Female Heermann's gull breeding parameters (mean ± SE) obtained in the field under normal and anomalously warm year conditions for all nesting females, conservative females, and bold females (strategy descriptions in Section 2.4). Breeding success was calculated as the mean eggs-to-fledglings ratio

	Normal year	Anomalous year
All females		
No. of eggs	2.09 ± 0.04	1.13 ± 0.11
No. of fledglings	1.12 ± 0.05	0.12 ± 0.04
Breeding success	0.52 ± 0.02	0.07 ± 0.03
Conservative females		
No. of eggs	2.08 ± 0.05	1.02 ± 0.12
No. of fledglings	1.12 ± 0.06	0.02 ± 0.02
Breeding success	0.53 ± 0.02	0.01 ± 0.01
Bold females		
No. of eggs	2.13 ± 0.13	1.77 ± 0.15
No. of fledglings	1.14 ± 0.13	0.66 ± 0.16
Breeding success	0.52 ± 0.06	0.38 ± 0.11

3.2. Female breeding strategies

Using only data obtained in the field, from 39 females analyzed, we found that 33 exhibited the conservative strategy (85%) and only 6 showed the bold strategy (15%). Mean values of clutch size, number of fledged chicks per breeding attempt, and breeding success for the females of each strategy during both normal and anomalously warm years are shown in Table 1. We found significant differences (using only actual field data and only from anomalously warm years) for the mean number of eggs laid and chicks fledged between breeding strategies. Bold females laid a significantly larger clutch and fledged significantly more chicks in anomalously warm years than conservative females ($U = 152.2$, p = 0.03 and $U = 198.0$, p = 0.01, respectively; Table 1).

3.3. Estimate of missing values for clutch size and surviving fledglings

For the estimation of clutch size, the best model included female age squared, SST for the year (normal or anomalous), and the female's strategy. For the estimation of the number of surviving fledglings, the best model included female age, female age squared, SST for the year (normal or anomalous), and the female's strategy. We obtained 4 GLMMs from the resulting analysis to estimate clutch size and number of surviving fledglings. From each of these models, we selected the best to estimate the values of each of the 2 variables (Table 2).

3.4. Differences within the life history strategy

The regression analyses included the values obtained in the field and the values obtained from the selected GLMM, both for clutch size and number of surviving fledglings during each female's lifespan. We found a significant positive linear relationship between longevity and number of eggs laid ($r^2 = 0.90$, p < 0.001), as well as a significant linear positive relationship between longevity and number of surviving fledglings ($r^2 = 0.68$; p < 0.001; Fig. 2).

Throughout their lifespan, females following the bold strategy laid 6 fewer eggs, produced 2 fewer surviving fledglings, and lived 4 yr less than conservative females (Table 3). Despite the low number of bold females (n = 6) observed compared to conservative females (n = 33), differences between total number of eggs laid and longevity were significant (p =
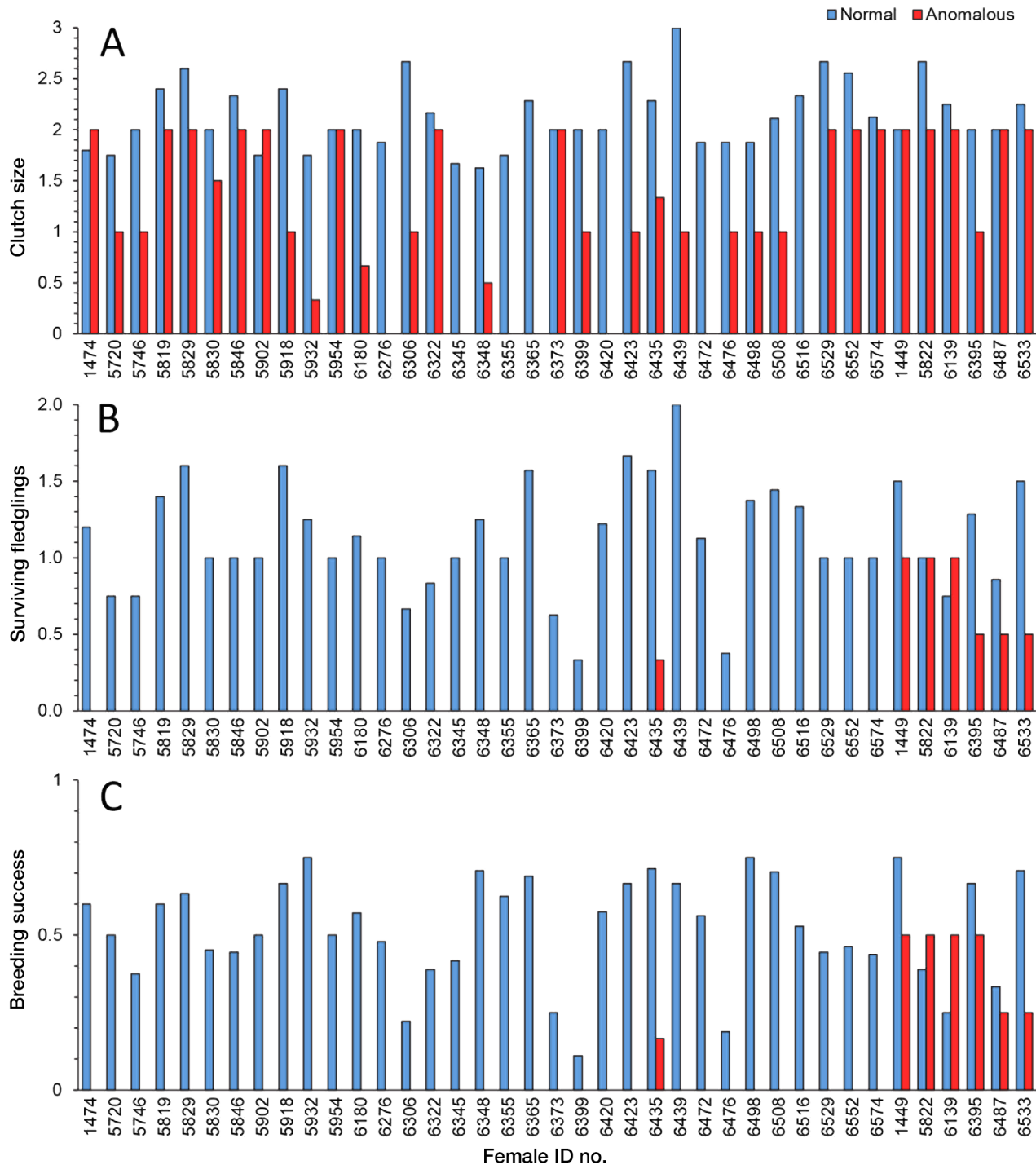
Fig. 1. Mean value of breeding variables (A) clutch size, (B) surviving fledglings, and (C) breeding success for each female Heermann's gull during normal and anomalously warm years. The last 6 females follow a bold strategy

0.04 and p = 0.02, respectively). However, although conservative females produced more fledglings throughout their total lifespan than bold ones, the differences were not significant (p = 0.22; though this lack of significance could be due to the small sample of bold females; see Table 3).

4. DISCUSSION

Many studies of marine ecosystems have reported a strong inverse relationship between SST and food availability for seabirds (Ainley et al. 1995, Velarde 1999, Vieyra et al. 2009). This relationship is medi-

Table 2. Generalized linear mixed models generated and intervening independent variables used to estimate clutch size and number of surviving fledglings for each Heermann's gull female for years when data were missing. **Bold** letters indicate the most adequate and significant (p < 0.05) model for each breeding parameter. CS: clutch size; age^2: age as a quadratic term; year: sea surface temperature condition (normal/anomalous) represented as a factor; SF: surviving fledglings; strategy: female strategy (conservative or bold) represented as a factor; AIC: Akaike's information criteria

Model	Clutch size	Log	SE	SD	p	AIC	z
1	**CS ~ age^2 + year*strategy**	**−379.7**	**0.259**	**759.4**	**0.002**	**771.4**	**2.974**
2	CS ~ age + age^2 + year*strategy	−378.8	0.408	757.5	0.391	771.5	0.856
3	CS ~ age + age^2 + year + strategy	−380.2	0.346	760.4	0.871	772.4	−0.162
4	CS ~ age^2 + year + strategy	−381.3	0.169	762.6	0.028	772.6	2.197

Model	Surviving fledglings	Log	SE	SD	p	AIC	z
5	**SF ~ age + age^2 + year*strategy**	**−284.3**	**0.665**	**568.59**	**0.027**	**582.6**	**−2.215**
6	SF ~ age^2 + year*strategy	−286.8	0.422	573.68	0.367	585.7	−0.902
7	SF ~ age + age^2 + year + strategy	−292.1	0.644	584.11	<0.001	596.1	−4.76
8	SF ~ age^2 + year + strategy	−294.9	4.13E−01	589.8	<0.001	599.8	−4.765

ated through the effect of low SST on increased primary productivity (increased phytoplankton production followed by increased zooplankton production). The next step is an increased productivity of higher trophic levels such as forage fish, which are food for the next trophic level such as seabirds, larger fish, and marine mammals (Hoefer 2000, Catry et al. 2013, Velarde et al. 2015).

As in many other studies, we found that at the population level, Heermann's gull reproductive output
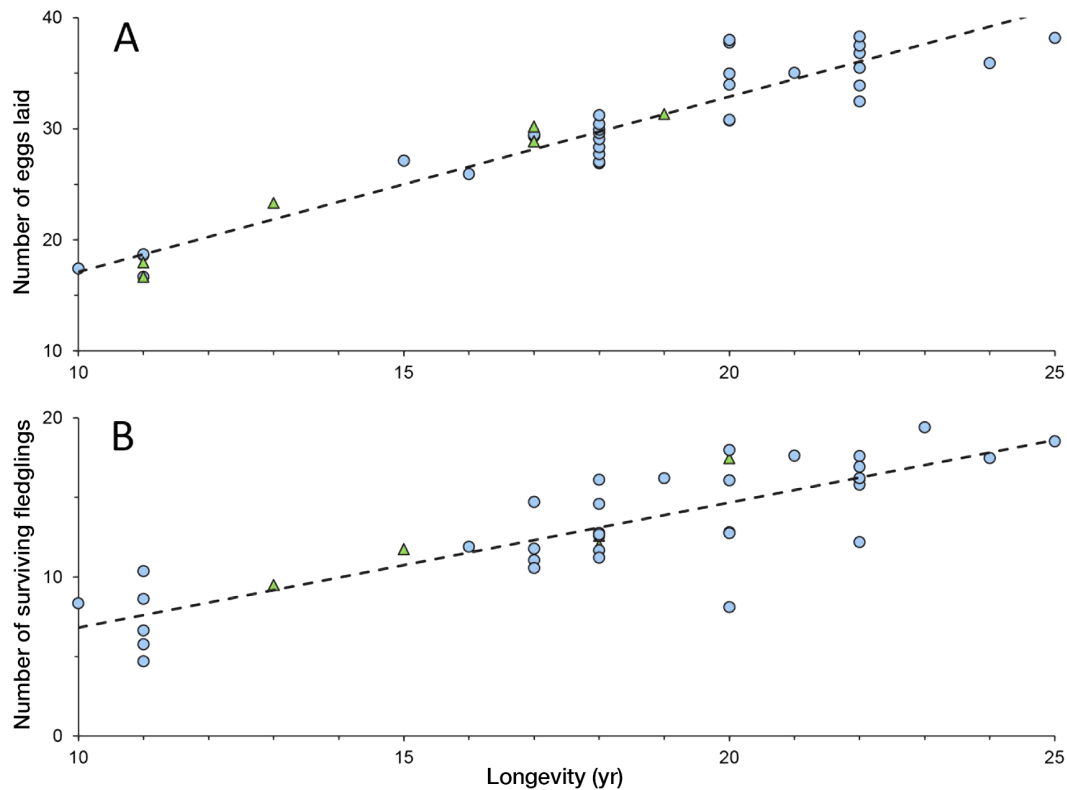

Fig. 2. Relationship between longevity and the value of 2 reproductive parameters for each female Heermann's gull during her lifespan, including values both observed and estimated (A) total number of eggs laid (r^2 = 0.90, p < 0.001) and (B) total number of surviving fledglings (r^2 = 0.69, p < 0.001). Blue circles: conservative females; green triangles: bold females

Table 3. Results of linear models showing the relationship between total number of eggs laid and total number of surviving fledglings throughout the female's lifespan along with longevity for female Heermann's gull conservative and bold strategies in Isla Rasa (n = 39, df = 37)

	Mean conservative (n = 33)	Mean bold (n = 6)	Difference	SE	r^2	p	F
Total number of eggs	30.71	24.72	5.98	6.26	0.11	0.03	4.63
Total number of fledglings	13.43	11.42	2.01	3.69	0.04	0.22	1.50
Longevity (years)	18.63	14.66	3.96	3.71	0.13	0.02	5.79

variables (clutch size, number of surviving offspring, and breeding success) are higher during normal years and lower during anomalous positive SST years (Vieyra et al. 2009, Velarde & Ezcurra 2018). This breeding strategy allows females to survive to future nesting seasons and breed successfully when food conditions are adequate to raise chicks. Reducing mortality of adults during unfavorable years by avoiding investing scarce energy in breeding and, rather, investing it in their own survival, allows the maintenance of individuals of high reproductive value in the population for future breeding seasons.

However, individual females were found to exhibit 2 distinctive (dimorphic) life history alternatives. (1) In the 'conservative strategy', the number of eggs laid was either reduced or eliminated entirely during anomalously warm years. Besides laying fewer eggs or not laying at all during these anomalously warm seasons, conservative females had a longer lifespan. This strategy of longer lifespan associated with reduced or skipped breeding efforts during years with conditions of poor food abundance has been observed in several seabird species (Lescroël et al. 2009, Griesser et al. 2017) and is likely related to the strategy of trade-offs incurred by the organisms, particularly those living in such variable environments such as seabirds. (2) In the 'bold strategy', females consistently laid eggs during all anomalous years and were able to fledge chicks in at least half of those years, but had a shorter lifespan. This inverse relationship between fecundity and lifespan has long been detected in birds and is particularly evident in seabirds (Cody 1966).

However, the significant differences in lifetime total number of eggs laid and longevity observed between females of each alternative dimorphic strategy did not result in a significantly different total lifetime production of fledglings between individuals exhibiting either strategy. This comparison between lifetime individual breeding strategies has rarely been conducted in other seabird studies (Lescroël et al. 2009, Ballard et al. 2010, Catry et al. 2013, Kappes

et al. 2021), largely because there are few long-term banding programs in seabird research; however, some of these studies have shown that a seabird species or population may have a mixed array of individual life history strategy morphs, allowing different types of individuals to leave more or less offspring during years of higher or lower food abundance. The existence of 2 (or more) life history strategy morphs could allow a population to respond adaptively under different environmental conditions. In this way, a certain proportion of individuals in the population will be leaving a certain number of offspring under various environmental conditions, which will allow the population to persist through times of change in these conditions. This phenomenon has been equated to the 'portfolio effect' analyzed by Schindler et al. (2015), in which the existence of diverse responses of individual organisms provides a population with varied options to leave offspring for future generations, allowing a relatively stable breeding success mediated by successful reproduction of alternate life history strategy morphs and the long-term persistence of the species.

Furthermore, individuals exhibiting a life history strategy morph that is better adapted to specific conditions will be leaving more offspring in the population under those circumstances, eventually leading to an increase of this strategy in the population. This would be the case only if the life history strategy morph is genetically inherited. Investigation of the heritability of characters such as phenotypic plasticity has only recently begun, mainly because long time series and many generations are needed to assess this phenomenon. However, some works are now beginning to show that this trend may occur in wild populations of birds such as shown for timing of reproduction by Nussey et al. (2005) for a passeriform. Even fewer works have been published for seabirds, likely since seabirds are long-lived species with longer generation times and potentially more than one generation of researchers will be necessary to unveil such adaptable characteristics (Moiron et

al. 2022). Heritability of phenotypic diversity of characters related to breeding success is a topic of increasing interest under conditions of climate change, to elucidate how wild populations will fare in future decades and centuries.

In our study, we found that 85% of the females exhibited the conservative strategy and only 15% exhibited the bold strategy. In this case, the bold female strategy may be masked by the conservative female strategy if a general analysis of the whole population is carried out. In our case, as has been observed in many other marine areas, the frequency and intensity of positive SST anomalies has recently increased (Piatt et al. 2020). This means that if anomalous warm years continue to increase in frequency, as they have been observed to increase in recent decades in the main area where Heermann's gulls nest (Velarde & Ezcurra 2018), the presence of 2 (or more) different life history strategies could allow this species to respond differently to changing environmental conditions, and certain individuals in the entire population may be able to cope with these changes in an adaptive fashion. Further studies are needed to determine if this variability in life history strategies will allow this species to cope with the magnitude of environmental changes that are occurring now at the worldwide level and, also, to identify similar polymorphic strategies in other species that may serve them in the struggle for adaptation and long-term survival.

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