Severely stressful natal environment does not impact lifetime reproductive success of adult boobies

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Abstract

Although stressful natal conditions are expected to have developmental impacts that prejudice fitness, wild animals sometimes respond to early-life adversity with phenotypic resilience or make life-history adjustments that apparently mitigate fitness penalties. Whether these adjustments enable long-lived animals to completely evade impacts of natural environmental stresses experienced during early development remains uncertain. Analysis of recruits from 18 birth cohorts of the blue-footed booby (*Sula nebouxii*) showed that El Niño (warm-water) conditions in the natal year did not prejudice annual breeding success, fledgling viability, adult lifespan or lifetime reproductive success. This equivalence of El Niño cohorts was attributed to high average quality due to overrepresentation of young + old parental pairings, known to engender high quality fledglings, and to a possible filtering effect of greater nestling and juvenile mortality, as well as documented life history adjustments. Parents of high-quality or peak reproductive age were not overrepresented in El Niño years. In this long-lived species which faces the world's most dramatic climatic oscillation, recruits from cohorts that faced the most severe climatic events are fully equivalent to those from cohorts that faced benign conditions, and self-selection of adults for breeding in such conditions may be a key adaptation for achieving this.

Keywords

Early-life stress, life history, resilience, lifetime reproductive success, El Niño Southern Oscillation, long-term effects

Introduction

Documenting the impacts of different early-life conditions on adult survival and reproduction, discerning how individuals cope with them, and tallying the effects on lifetime reproductive success is fundamental to understanding evolutionary trade-offs and life-history strategies (e.g. [1]), but seldom undertaken for long-lived vertebrates [2,3]. Early-life environmental conditions can have important effects on the physiology, metabolism and life history traits of adults in diverse taxa [4–8], and adverse early-life conditions have repeatedly been linked to negative consequences on senescence rates and on fitness components in adulthood (e.g. [5,9–11]). These include negative impacts on the quality and viability of offspring produced by animals that experience nutritional and social stress [12–14]. Nonetheless, negative effects of early adversity are not universal; wild animals sometimes respond by making life-history adjustments that seemingly neutralize fitness penalties (e.g. [15–18]).

Long-lived species should have more scope for managing the costs of early stress, for example by postponing their expression or spreading them across a longer period or over more reproductive events. Natural selection is expected to favour late expression of costs [19,20], although few studies have probed the influence of natal conditions on late-life traits or lifetime trade-offs, leaving lifetime fitness consequences of early stress unresolved. This failure occurs because individuals of long-lived species are rarely followed across their whole lifespan and dispersal of offspring commonly frustrates assessment of their viability. Comprehensive assessment of impacts of adverse early conditions on lifetime reproductive success and fitness [21] is usually unattainable (exceptions in [16], [22–24]), and it is still uncertain whether the compensatory responses and life history adjustments of long-lived animals can enable them to completely evade the impact of adversity at the start of life when development is maximally vulnerable [25].

Here, we investigated the effects of early-life conditions on life-history trajectories, fledgling quality and lifetime reproductive success in a marked population of the Blue-footed booby (*Sula nebouxii*), an apex predator of the eastern tropical Pacific Ocean that lays clutches of 1-3 eggs. Across the reproductive span of this plunge-diving specialist, warm surface waters associated with El Niño Southern Oscillation (ENSO) periodically deplete prey populations and pose a major ecological challenge, lessening breeding participation, delaying breeding, decreasing clutch and brood sizes, reducing hatching, fledging and breeding success, and depressing the growth of nestlings [26,27]. Nonetheless, annual monitoring of a population in Mexico has demonstrated its ability to minimize or sidestep potential effects of natal disadvantage. Specifically, recruits from

cohorts born under warm water conditions make life history adjustments, bringing forward their age of first reproduction and breeding less frequently. Over the first ten years, slightly longer than the average lifespan of recruits (mean ± SD; males: 8.05 ± 3.49 years, n = 1319; females: 8.02 ± 3.99 years, n = 1105; unpublished data), these adjustments along with the boobies' developmental resilience allowed recruits to match the survivorship and accumulated breeding success (fledgling production) of boobies born under favourable cold-water conditions [15]. But do fitness penalties manifest themselves afterwards or elsewhere; for example, in unexplored life history variables such as survival and reproduction in old age, and viability of offspring produced at different ages? We tested these possibilities and asked whether the adjustments and developmental resilience of recruits neutralize comprehensively the impact of early adversity on lifetime fitness, and also whether the costs of being born under harsh conditions are paid in the juvenile stage.

Using longitudinal data on 18 birth cohorts of recruits marked with steel bands at fledging, we investigated whether natal warm water ENSO conditions (sea surface temperature anomalies, SSTA) influence annual breeding success or fledgling viability (probability of eventual recruitment) at any age over a breeder´s lifespan. Secondly, to achieve an integrative assessment of fitness impacts, we tested whether natal warm water conditions affect either adult lifespan or lifetime reproductive success (production of recruits). Thirdly, to capture more comprehensively the fitness costs of developing under harsh conditions, we analysed whether natal conditions affect the lifetime reproductive success of fledglings, thus incorporating failure to recruit, which is greater in juveniles from warm water years (Ancona et al. 2018), in the computation of fitness. Finally, in an effort to explain minimal and non-existent effects of warm water natal conditions on fitness of fledglings and recruits, we asked whether in warm years boobies of high quality or favourable ages, or born in cool years, increase their representation among breeders. The necessary observations were possible because, with rare exceptions, fledglings of the focal population nest for the first time close to where they hatched, then nest close to their first nest site during the rest of their lives [28].

Methods

Study population and data collection. All demographic data were collected between 1989 and 2018 during lifelong annual monitoring of individual blue-footed boobies (*Sula nebouxii)* on Isla Isabel, Nayarit (21°53'N, 105°54'W), off the Pacific coast of Mexico [28,29].

Breeders were individually identified by bands fitted at fledging. Throughout each reproductive season (roughly February through July) all pairs in two study areas were monitored by recording their nest contents every 3-6 days through fledging (details in [29]). Nests in the study area and within 20 m of its borders, which correspond with natural borders of the colony, are too conspicuous on the beach and forest floor to escape detection by the team of two monitors [30]. This monitoring protocol allowed detection of nearly all recruitment and breeding of the focal fledglings through 2018.

For all analyses of breeders, samples included all members of the 18 birth cohorts (1989-2009) that recruited by age 6 years (the age by which 87% of fledglings recruit), thereby excluding individuals whose early nesting may have been missed. We analysed annual breeding success (number of 70-d old fledglings produced, regardless of brood size), fledgling viability (proportion of fledglings that recruited), adult lifespan (age at the last observed breeding), lifetime reproductive success (total recruits produced), and recruitment probability (whether an individual fledgling was resighted as a breeder; 1-0 variable), separately for females and males because pair mates are not statistically independent. Because fledglings are not sexed until they return to the colony as breeders, the analyses of fledgling recruitment probability and fledgling fitness were not separated by sex.

The sample for analysis of annual breeding success included all breeders from the 18 cohorts (2143 male and 1893 female boobies); the sample for analysis of fledgling viability included the fledglings produced by all breeders from those cohorts that fledged at least one chick at any age (1646 male and 1329 female breeders), and excluded fledglings born after 2013 because their recruitment could not be adequately scored (they were monitored for less than 6 years). The sample for analyses of adult lifespan and lifetime reproductive success included only the 1319 male and 1105 female breeders that died before 2013, allowing each of their fledglings at least 6 years to recruit during annual monitoring. Death was assumed when a breeder was absent during three consecutive breeding seasons; in the cohorts of 1989-1995, only 5-6% of breeders were ever resighted after three consecutive absences.

For males and females, respectively, ages of first reproduction (mean ± SD) were 4.14 ± 0.95 and 3.54 ± 0.98 years, and longevities were 8.05 ± 3.49 and 8.02 ± 3.99 years (range 1 to 22 years for both sexes). For analysing recruitment probability of fledglings, the sample included all 10604 individuals that were weighed and measured at age 70 days; for analysing lifetime reproductive success of fledglings, the sample comprised 10609 individuals. Self-selection for breeding in warm water conditions was tested in a sample of 4036 males and females by looking for increase in the proportional representation of individuals of above average quality, favourable ages (10-14 years) or born in (cool) La Niña years. An individual´s quality was the mean of all z-normal standardized annual breeding success values (fledglings produced) over its lifespan

For the recruitment probability analysis, the ratio between weight (grams) and ulna length (millimetres) at age 70 days was used as an indicator of body condition at fledging. This ratio accounts for the sexual size dimorphism of the boobies; at 79 days old, females weigh approximately 26% more than males, and their ulnas are 10% longer [31]. To remove year effects, individual body condition was calculated as the z-normal standardized annual body condition at fledging of the colony. Boobies weighed (mean ± SD) 1593.51 ± 256.2 grams at fledging with an ulna length of 205.57 ± 12.98 millimetres.

ENSO conditions during the reproductive season in which a focal breeder was born were expressed as the average of the 8 monthly (December to July) sea surface temperature anomalies (SSTA) at the closest oceanographic station, 55 km from the colony, obtained from the IRI Data Library http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.Reyn_SmithOIv2/.monthly/.ssta/ .La Niña years were characterized by the mean SSTA of at least -0.5°C using La Niña criteria of the NOAA, obtained from El Niño and La Niña Alert System https://www.climate.gov/news-features/understanding-climate/el-ni%C3%B1o-and-la-ni%C3%B1a-alert-system.The Southern Oscillation Index (SOI) was not used because SSTAs are more closely related to the breeding parameters and age at first reproduction of this population [15,26].

Statistical analysis. All analyses were performed in R statistical environment [32]. All variables were standardized prior to model fitting to minimize collinearity of linear and quadratic terms and to facilitate the interpretation of the relative strength of parameter estimates [33,34]. To further minimize multicollinearity among terms, the variance inflation factor (VIF) was calculated, and variables with VIF values higher than 2 were not included in the final analyses. Maximum VIF value of each model is reported in the supplementary material. Models were fitted with a Gaussian

error distribution and an identity link function. Variable standardization was carried out using the *rescale* function in the R package *arm* [35]. We used the *lmer* function in the package *lme4* [36] to build the LMMs; LMs were built using the built-in function *lm* in R. Model selection was carried out with *model.sel* function in the MuMIn package [37], *mod.avg* function was used to average models within a 95% confidence interval (CI) [38], and *confint* function to calculate the CI of each parameter.

To assess the effects of recruits' early-life conditions on their annual breeding success and offspring viability, we first constructed a base model (accounting for previously demonstrated effects in the species; *sensu* [39]) for each analysis; this contained the linear and quadratic expression of breeder age and laying date, with breeder identity as random effect. For annual breeding success, SSTA in each reproductive year was also included in base models. The linear expression of year of birth was included in every model, irrespective of its statistical significance (cf. [40]), to reflect the fact that the earlier an individual was born, the higher its longevity could be, biasing our dataset. From these base models, we constructed a series of competing models which included SSTA in the natal year (the early-life-condition variable), whether it was the individual's terminal reproductive event (1-0 variable), and the linear and quadratic expressions of age of first reproduction along with two-way interactions: SSTA in the natal year x age^2, age of first reproduction x age^2 and SSTA in the natal year x age of last reproduction. SSTA in the reproductive year was added to competing models for the analysis of offspring viability. Age of first reproduction was included to evaluate the indirect effects of early adversity, as this life history trait has been shown to vary with natal ENSO conditions [15] and is a major determinant of fitness [41]; its quadratic expression was added to detect an optimal onset of reproduction (e.g. [42]) The interactions were included to detect differences in senescence patterns due to natal conditions or age of first reproduction.

To test whether adult lifespan and lifetime reproductive success were influenced by early-life conditions, we used linear models (LMs). For both analyses, year of birth was also included in all competing models as a fixed variable. Variables included in the models were SSTA in the natal year and the linear and quadratic expression of age of first reproduction. For lifetime reproductive success adult lifespan was added to the competing models, along with its interaction with age of first reproduction.

To test whether fitness costs of adverse natal conditions are paid in the juvenile stage, we reran the lifetime reproductive success model including, along with all recruits, all fledglings that did not recruit, giving the latter a zero score for lifetime reproductive success. Age of first reproduction and

adult lifespan were not included because fledglings that fail to recruit cannot be assigned a value. Sex was not included because sexing occurs at recruitment.

To assess which fledglings managed to recruit under warm water conditions, and which breeders reproduce in these conditions (possible self-selection), we built LMMs. For both analyses, year of birth and SSTA in the natal year were included as fixed variables. For the recruitment analysis, body condition at fledging and chick rank (1st, 2nd or 3rd hatched) were included in the competing models, along with three two-way interactions: SSTA in the natal year x body condition, SSTA in the natal year x chick rank, and chick rank x body condition. Nest identity was added as a random effect because, in some cases, siblings were included in the analysis. Body condition and rank were included to test whether low values affect recruitment. The interactions tested whether poor natal environments exacerbate the cost of fledging with poor body condition or low rank, and evaluated whether body condition at fledging varies with rank.

To test for increased representation in warm water years of breeders of above average quality or peak reproductive ages(10-14 years, middle aged), or from cool water years (< -0.5 SSTA), as well as diminished representation of both young (1-9 years) and old (15-23 years) breeders, we built linear models including sex as a factor and using the linear expression of year of reproduction to account for progressive increase in the proportions of middle-aged and old birds among ringed birds with additional years of monitoring and ringing.

On the basis of AICc, ΔAICc, and AICc weights (*wi*) of the competing models, we selected the best supported model, or averaged a subset of the best-supported models with a cumulative Akaike weight of ~0.95. For each resulting model, we calculated the estimates (all reported effect sizes were standardized to two SDs) and 95% confidence intervals (CI). Model selection tables and summaries of best-supported and averaged models are provided in the supplementary material.

Results

Assessment of Recruits

Annual breeding success

For 2143 male breeders, natal warm water ENSO conditions affected annual breeding success over the lifespan but not in the expected direction. Males that experienced warm waters in their natal year annually produced slightly more fledglings than those born under more favourable conditions ($\beta = 0.009$ [95% Confidence Interval: 0.008 to 0.048]; Figure 1), with males fledged under a +0.8 $^{\circ}$C anomaly predicted to produce roughly 6% more fledglings than males fledged under a -0.8 $^{\circ}$C anomaly (the most extreme anomalies observed). For 1893 females, no effect of natal warm water ENSO conditions on annual breeding success was detected (Table S1; Figure 1). Consistent with previous reports [26,29], boobies of both sexes increased their annual breeding success with earliness of laying and current coolness of the sea, and showed senescence after a peak in reproductive success at, roughly, ages 10-14 years [43,44] (Table S2). Natal SSTA did not interact with age (Table S2), showing that warm natal waters had no effect on either the rate of increase in reproductive success during early adult years or the rate of decline during late adult years.

Figure 1. A male booby´s annual breeding success (fledglings produced) increased slightly with the Sea Surface Temperature Anomaly in its natal year. Female annual breeding success was unaffected by natal conditions. Points represent 2143 male and 1893 female breeders observed over their lifespans. Solid line represents model predictions, with 95% confidence intervals in blue; for females, grey line shows a statistically unsupported relationship.

Fledgling viability

For 1646 male and 1329 female breeders, natal warm water conditions did not affect the viability of the fledglings they produced at any age over their lifespan (Table S3), although other variables were influential. Fledglings produced by both sexes in warm water years were less likely to recruit (Males: $\beta = -0.194$ [95% CI: -0.222 to -0.166]; Females: $\beta = -0.195$ [95% CI: -0.231 to -0.159]) and, at all ages, earliness of laying increased the viability of fledgings produced (Males: $\beta = -0.128$ [95% CI: -0.156 to -0.101]; Females: $\beta = -0.112$ [95% CI: -0.146 to -0.077]). Consistent with a previous study of this population based on just two cohorts [45], a breeder's age had a quadratic effect on the probability its offspring would recruit (Table S4), with peaks at roughly 10 years in male breeders and 11 years in female breeders.

Lifespan

The lifespan of recruits was unaffected by natal warm water conditions (Table S5), but increased with late recruitment in both sexes (Males: 0.139 [95% CI: 0.090 to 0.0.189]; Females: 0.213 [95% CI: 0.160 to 0.266]), although this effect might arise simply because late recruits cannot die early.

Lifetime reproductive success

Natal warm water conditions did not affect lifetime reproductive success measured as total recruits produced (Figure 2a; Table S7), although in both sexes age of recruitment and adult lifespan were influential. Boobies that first reproduced at younger ages produced more recruits over their lifetime than those that started later in life (Males: β = -0.086 [95% CI: -0.126 to -0.046]; Females: β = -0.062 [95% CI: -0.119 to -0.013]). Greater adult lifespan, itself associated with delayed age of first reproduction, also increased lifetime production of recruits in both sexes (Males: β = 0.715 [95% CI: 0.670 to 0.761]; Females: β = 0.619 [95% CI: 0.561 to 0.677]).

Figure 2. a) Lifetime production of recruits of 1319 male and 1105 female breeders was not affected by natal warm water conditions. Grey lines show the statistically unsupported tendency for lifetime reproductive success to increase in both sexes with warm natal waters. b) Lifetime reproductive success of 10609 male and female fledglings belonging to 18 birth cohorts decreased slightly with the warmth of their natal waters.

Lifetime Reproductive Success of Fledglings

In the sample of (unsexed) fledglings, those from warm water years were considerably less likely to recruit, particularly 2nd and 3rd chicks (Table S12; Figure. 3a). Body condition was key: in all cohorts, poor condition reduced the probability of recruiting (β = 0.07 [95% CI: 0.05 to 0.08]; Figure. 3b). Consequently, cohorts of fledglings that experienced warm water natal conditions produced fewer recruits over their lifespan (β = -0.04 [95% CI: -0.06 to -0.03]; Figure. 2b), although the difference was much smaller than their poor recruitment would suggest: boobies fledged under a +0.8 °C anomaly were predicted to produce roughly 7% fewer recruits than boobies fledged under a -0.8°C anomaly (the most extreme anomalies observed over the 30-year study).

Figure 3. The probability of recruiting for 10604 unsexed fledglings a) decreased with the warmth of natal waters, especially for second and third chicks, and in every year, b) was higher for boobies that fledged with good body condition.

Self-selection for Warm-water Breeding

In warm water years neither boobies of above average quality nor boobies born in cool (la Niña) years increased their proportional representation among breeders (n = 4036; Tables S13-S14) but, contrary to expectation, middle-aged boobies substantially diminished theirs (β = -0.317 [95% CI: -0.470 to -0.164]) and the proportions of both young (1-9 years) and old (>14 years) boobies among breeders increased (Young: β = 0.193 [95% CI: 0.068 to 0.318]; Old: β = 0.175 [95% CI: 0.020 to 0.331]) .

In this booby, young-with-old parental pairings produce the most viable (likely to recruit) fledglings [30], so we hypothesized that overrepresentation of young and old breeders in warm years could increase the proportion of young + old pairings and hence the average quality of fledglings. We tested this by calculating the proportional representation of all six possible pairings of young, middle aged and old boobies in every year between 1993 and 2017 (Table S16). Our LMs included the linear expression of year of reproduction to account for progressive increase in the proportions of middle-aged and old birds among ringed birds with additional years of monitoring and ringing; they did not include sex because greater viability of offspring of young-old pairs is independent of which sex is the older pair mate [30,46]. These analyses showed that warm water is indeed associated with an increase in the proportion of young + old pairings and a decrease in the proportion of young + middle-aged pairings (Young + old: β = 0.280 [95% CI: 0.072 to 0.487]; Young + Middle-aged: β = -0.340 [95% CI: -0.614 to -0.067]; Figure. 4)

Figure 4. In warm water years the proportion of young-old pairs increased, and the proportion of young-middle aged pairs decreased.

Discussion

Even the most extreme warm water conditions experienced by recruits of the 18 cohorts in their natal year did not subsequently prejudice their annual breeding success or the viability of their fledglings at any age over the recruits' lifespan, nor reduce adult lifespan or the total number of recruits produced over that span. Furthermore, warm natal waters elicit neither change in the rate of increase in breeding success in young adulthood nor a change in the rate of decline in old age (senescence). These results confirm that male and female recruits are capable of comprehensively resisting the developmental penalties of a harsh natal environment, although it remains to be shown that the viable offspring of recruits from warm water cohorts pay no reproductive costs (an intergenerational effect [14]). To our knowledge, this is the first study to report comprehensive avoidance over the entire adult age span of a long-lived animal of deficits due to natural environmental stresses experienced during early development. Similarly comprehensive avoidance has been reported in short-lived species and animals facing anthropogenic natal adversity, although in some of those cases breeding success of one of the two sexes is prejudiced (reviewed in [3]). In the blue-footed booby both sexes are similarly resistant.

Similar resistance to developmental impacts was found when we analysed cohorts of fledglings instead of recruits, thereby including the juvenile stage in the analysis of fitness. Despite failure to recruit being substantially more common after birth in a warm water year (especially in 2nd and 3rd chicks), the lifetime reproductive success of warm water fledglings was not greatly affected; fledglings from the warm-water extreme were predicted to produce only 7% fewer recruits than those from the cool-water extreme. This implies that recruits from warm water fledgling cohorts are of high enough quality to largely compensate for the zero reproductive success of cohort members that fail to recruit. This quality effect could be what enabled warm natal water male recruits to achieve roughly 6% higher annual breeding success than cool water males over the lifespan. There was no corresponding increase in the lifetime reproductive success of these males, presumably because boobies that experience warm natal waters space their breeding events more widely [15], at least in their young adulthood. Warm natal water females showed no such increase in annual breeding success, but females are nearly one third heavier than males and more susceptible to food deprivation [47,48].

The extraordinary equivalence of recruits (and near equivalence of fledglings) that developed in the most stressful environments and those that developed in the most benign environments could, in principle, be explained by the most reproductively competent boobies self-selecting for breeding in warm water years, and transmitting their own high quality to their offspring, genetically or

phenotypically. Self-selection there was, but surprisingly not by boobies of either proven high quality or a silver spoon (cool water) birth, but rather by the age categories with the lowest annual breeding success: the young and old (see also [49–52]). And self-selection for breeding by young and old boobies in warm water years was associated with increased representation of young + old pairs, whose fledglings are known to have the highest likelihood of recruiting [30]. Overrepresentation of young + old pairs could account for fledglings from warm years almost matching the lifetime reproductive success of those from cool years, despite experiencing slow growth, late fledging [26] and diminished recruitment (Fig. 3a, [53]); and for recruits from warm water years actually matching the lifetime reproductive success of recruits from cool water years. It also offers the most credible explanation for male recruits' counterintuitive increase in annual breeding success with natal water temperature: high average quality of offspring due to overrepresentation of young + old pairs in warm years may boost not only their recruitment but also their reproduction. The mechanism by which young + old pairs produce the most viable offspring is unknown, but might involve complexly age-related parental investment, or superior genetic quality due to greater heterozygosity or a combination of good genes and less germ-line DNA damage in offspring of dissimilar-aged parents (discussed in [30,54]).

Increased hatching failure and nestling mortality in warm water years (Ancona et al. 2011) could also increase the average quality of fledglings and recruits from warm water cohorts either by filtering out poor quality individuals [23] or possibly by boosting the food ingestion and growth of surviving brood members. In blue-footed booby broods 4-day hatch intervals result in age-based dominance hierarchies and aggressive elimination of subordinates during periods of food shortage [55,56]. However, it is unknown whether nestling quality influences mortality and whether fledglings from reduced broods outperform those from broods that fledge intact [55].

Life history adjustments by recruits born in warm water years also help explain their equivalence. Their ability to produce as many fledglings in the first 10 years of life as those born in cool years has been attributed to the observation that they bring forward their age of first reproduction and breed less frequently [15]. We found that early recruitment generally increases lifetime reproductive success, and suspect that warm water cohorts manage to obtain this benefit while avoiding increase in mortality at any adult age [53] and sidestepping the possible longevity cost (Table S5) of reproductive investment early in life by skipping some breeding seasons. Boobies may make facultative life history adjustment to natal conditions or higher quality individuals may tend to recruit early and skip years. Females of the reintroduced Mauritius kestrel (*Falco punctatus*)

mitigate fitness penalties of an anthropogenically modified natal environment by making similar life-history adjustments [16], although it is unclear whether their lifespan is affected.

In conclusion, contrary to the widespread expectation that extenuating natal environments impose profound and often permanent deficits during adulthood [25,57] this study demonstrates that adult blue-footed boobies which experienced the stressful conditions of the planet´s most dramatic climate oscillation in their natal year are fully equivalent to adults that experienced the most benign conditions. The evidence suggests that this is achieved by an increase in offspring quality in El Niño years due to increased representation of young + old breeding pairs, possible filtering out of poor-quality nestlings and juveniles, and life history adjustments. In addition, we suggest that exposure of this species to El Niño-like events since at least the mid-Holocene [58] has probably honed the evolution of developmental resilience.

Ethics. Permission to conduct this research was granted by SEMARNAT (permits 517, 574, 5664, 10470, SGPA/DGVS/01323, SGPA/DGVS/3152, SGPA/DGVS/1543, SGPA/DGVS/0491, SGPA/DGVS/1547, SGPA/DGVS/10832, SGPA/DGVS/01916, SGPA/DG VS/00733, SGPA/DGVS/00357, SGPA/DGVS/00505, SGPA/DGVS/00091); protocols followed the ASAB/ABS Guidelines for the Use of Animals in Research and complied with Mexican legal requirements for animal conservation and welfare.

Data accessibility. The datasets supporting this article have been uploaded as part of the supplementary material.

Authors' contributions. S.O, C.R. and H.D. C.R. and H.D. collected the data designed the study. S.O. analysed the data. S.O., C.R and H.D. wrote the manuscript. All the authors contributed to revisions of earlier drafts of the manuscripts. All the authors contributed critically to the drafts and gave their final approval for publication.

Competing interest. We declare we have no competing interests.

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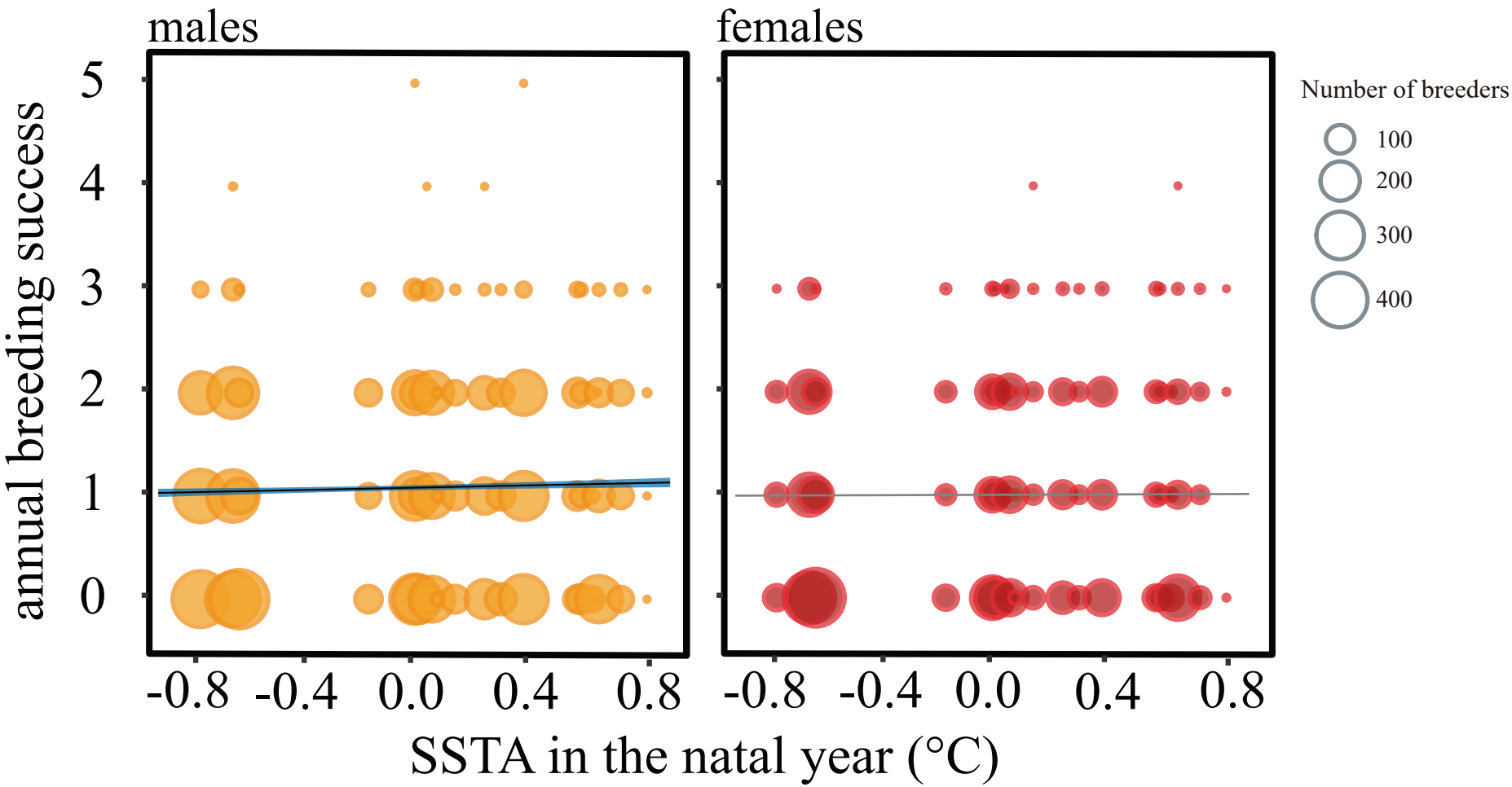
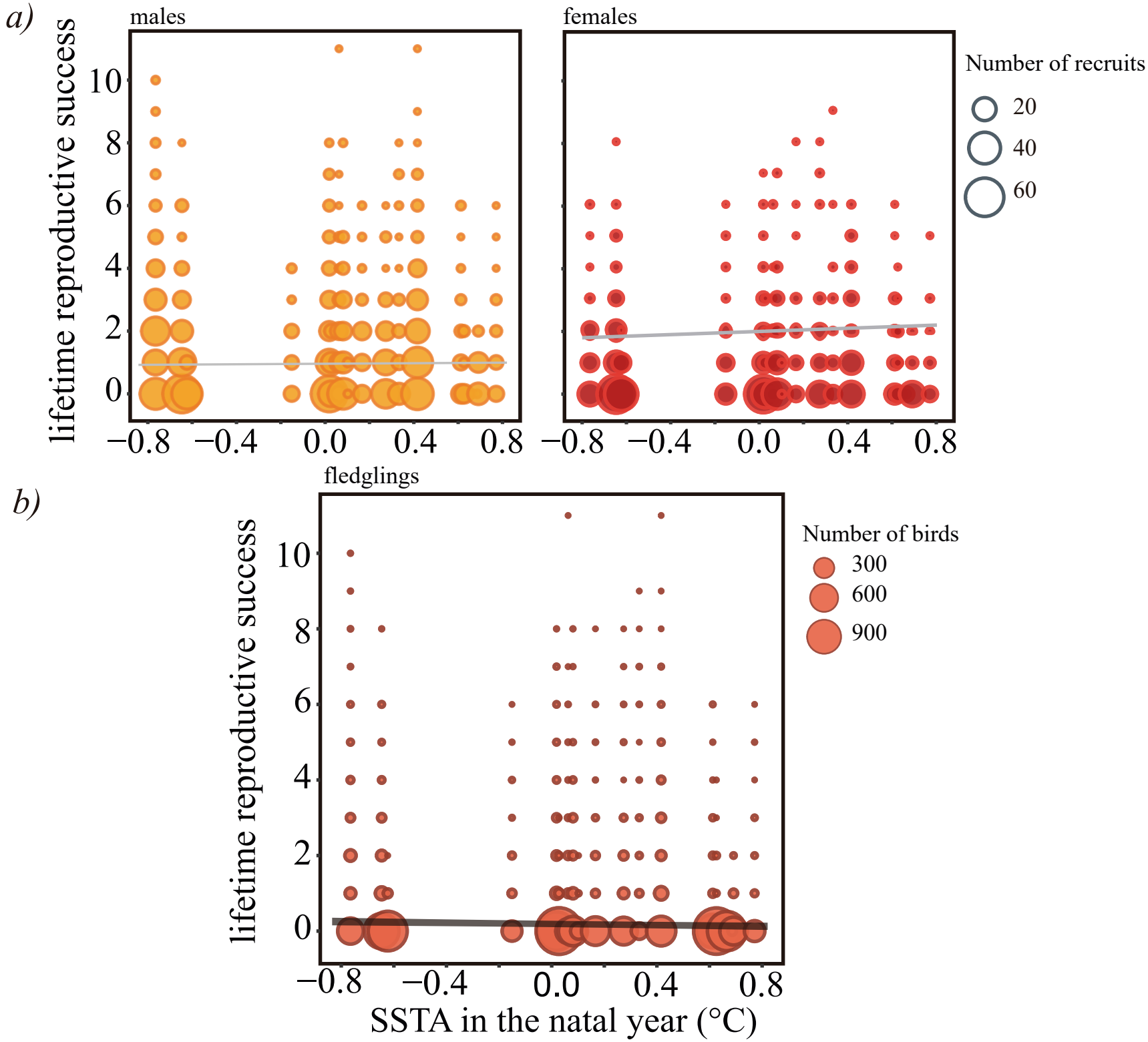
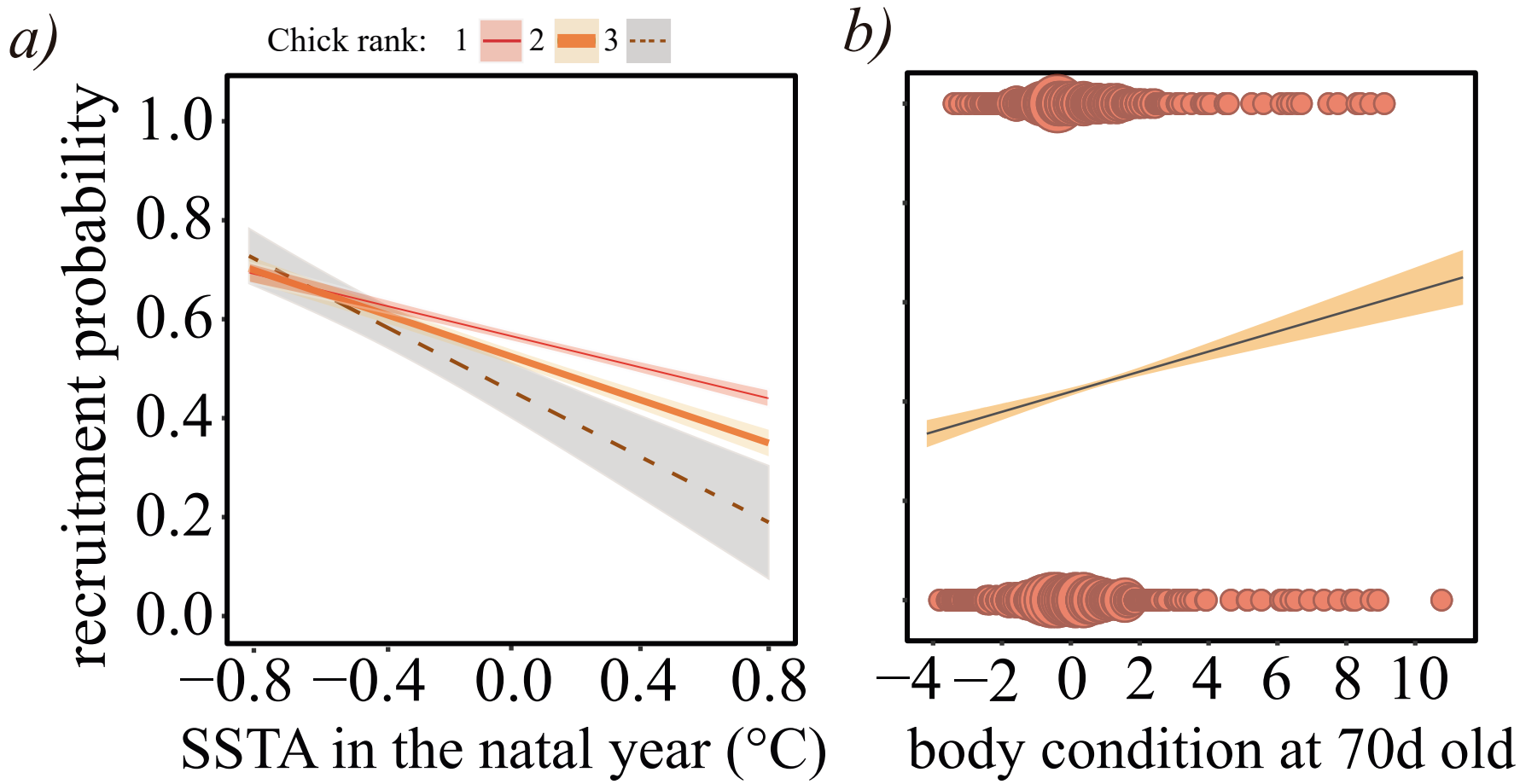
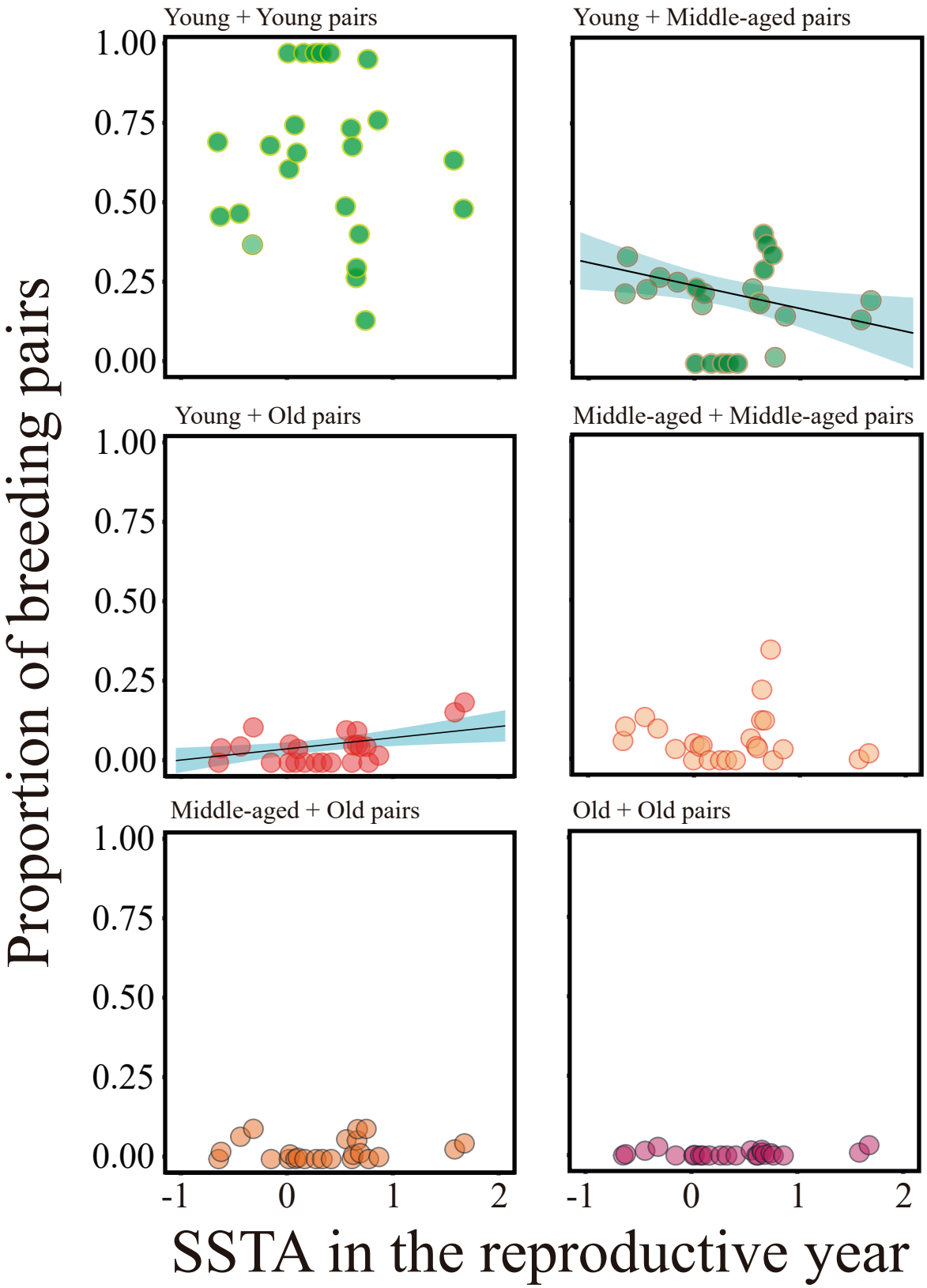

males
females
annual breeding success
5
4
3
2
1
0
-0.8
-0.4
0.0
0.4
0.8
SSTA in the natal year (°C)
Number of breeders
100
200
300
400


a)
males
females
lifetime reproductive success
Number of recruits
20
40
60
fledglings
b)
lifetime reproductive success
Number of birds
300
600
900
SSTA in the natal year (°C)


a)
Chick rank: 1 2 3
recruitment probability
1.0
0.8
0.6
0.4
0.2
0.0
−0.8 −0.4 0.0 0.4 0.8
SSTA in the natal year (°C)
b)
−4 −2 0 2 4 6 8 10
body condition at 70d old


Young + Young pairs
Young + Middle-aged pairs
Young + Old pairs
Middle-aged + Middle-aged pairs
Middle-aged + Old pairs
Old + Old pairs
1.00
0.75
0.50
0.25
0.00
-1
0
1
2
Proportion of breeding pairs
SSTA in the reproductive year