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How fitness consequences of early-life conditions vary with age in a long-lived seabird: A Bayesian multivariate analysis of age-specific reproductive values

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Abstract

1. Evolutionary theory suggests that individuals can benefit from deferring the fitness cost of developing under poor conditions to later in life. Although empirical evidence for delayed fitness costs of poor developmental conditions is abundant, individuals that die prematurely have not often been incorporated when estimating fitness, such that age-specific fitness costs, and therefore the *relative importance* of delayed fitness costs are actually unknown.

2. We developed a Bayesian statistical framework to estimate age-specific reproductive values in relation to developmental conditions. We applied it to data obtained from a long-term longitudinal study of common terns *Sterna hirundo*, using sibling rank to describe variation in developmental conditions. Common terns have a maximum of three chicks, and later hatching chicks acquire less food, grow more slowly and have a lower fledging probability than their earlier hatched siblings.

3. We estimated fitness costs in adulthood to constitute *c*. 45% and 70% of the total fitness costs of hatching third and second, respectively, compared to hatching first. This was due to third-ranked hatchlings experiencing especially high pre-fledging mortality, while second-ranked hatchlings had lower reproductive success in adulthood. Both groups had slightly lower adult survival. There was, however, no evidence for sibling rank-specific rates of senescence.

4. We additionally found years with low fledgling production to be associated with particularly strong pre-fledging selection on sibling rank, and with increased adult survival to the next breeding season. This suggests that adults reduce parental allocation to reproduction in poor years, which disproportionately impacts low-ranked offspring.

5. Interpreting these results, we suggest that selection at the level of the individual offspring for delaying fitness costs is counteracted by selection for parental reduction in brood size when resources are limiting.

1 | INTRODUCTION

Although among-individual variation in life histories may partly be due to chance (Hartemink & Caswell, 2018; Snyder & Ellner, 2018; Tuljapurkar et al., 2020; van Daalen & Caswell, 2020), it may also result from variation in conditions during development (e.g. Cooper & Kruuk, 2018; Hamel et al., 2009; Hayward et al., 2013; Kruuk et al., 1999; Lummaa & Clutton-Brock, 2002; Metcalfe & Monaghan, 2001; Nussey et al., 2007; Reid et al., 2003; van de Pol et al., 2006). From an evolutionary perspective, reduced adult survival or reproduction in response to poor developmental conditions can be explained by individuals strategically allocating their limited resources to life-history traits that promote immediate survival (e.g. growth, competitive behaviour) at the expense of allocation to somatic maintenance or future reproductive success (Kirkwood, 1977; Kirkwood & Rose, 1991; Williams, 1966). Allocation strategies that thereby defer fitness costs from poor developmental conditions beyond first reproduction can be adaptive, because the strength of selection tends to decline with age after the onset of reproduction (Hamilton, 1966; Kirkwood, 1977; Medawar, 1952; Williams, 1957).

Studies estimating the effects of developmental conditions on late-life fitness have often only included individuals that made it to adulthood, and therefore have not been able to account for selection earlier in life. Poor natal conditions may, however, cause substantial non-random mortality during individual development. Exclusion of the, usually large, fraction of individuals that does not survive until fitness is measured (the 'invisible fraction'; Grafen, 1988) precludes conclusions regarding the effect an early-life environmental or phenotypic trait has on *total* fitness (Garratt et al., 2015; Goodrich & Roach, 2013; Mojica & Kelly, 2010). In contrast, estimating the late-life fitness consequences of variation in the natal environment, relative to the early-life fitness consequences, will provide a measure of the degree to which natural selection has deferred the costs of poor developmental conditions to adulthood and allows weighing the evolutionary relevance of both early- and late-life consequences.

Developmental conditions vary among individuals due to environmental variation in resource availability, but, in species with parental care, parents may mitigate, or exacerbate, such variation by increasing, or decreasing, parental allocation to reproduction in relation to resource availability (Descamps et al., 2016). If parents decrease postnatal investment in reproduction, an offspring's competitive rank relative to its siblings becomes an important component of the quality of its developmental conditions (Mock & Parker, 1997). Parents may benefit from promoting competitive asymmetries among their offspring from the start, because by forming stable hierarchies, or inducing rapid mortality of low-ranked offspring, resources wasted on sibling rivalry can be reduced (Caldwell Hahn, 1981; Lack, 1947; Mock & Ploger, 1987; Vedder et al., 2017, 2019).

Here, we develop a framework to estimate age-specific fitness consequences of developmental conditions, combining state-dependent life-history theory (Engen et al., 2012; McNamara & Houston, 1996; Taylor, 1990) with Bayesian multivariate modelling of fitness components. All relevant fitness components are assembled into posterior distributions for age and state-dependent reproductive values (RVs). Such RVs estimate the expected residual lifetime reproductive success (here in terms of number of fledglings) at a given age and state, integrating age- and state-specific strengths of viability and fertility selection (Fisher, 1930). We use this framework to quantify the effects of sibling rank on early- and late-life fitness components, using a large longitudinal dataset on common terns *Sterna hirundo*. Common terns are long-lived seabirds in which the dominance hierarchy among siblings (i.e. sibling rank) within a brood, and therefore their acquisition of food from the parents, is largely determined by their hatching order (Bollinger, 1994; Langham, 1972; Morris et al., 1991).

2 | MATERIALS AND METHODS

2.1 | Species and study population

We analysed data obtained from a long-term study of free-living common terns in a monospecific breeding colony located in the Banter See at Wilhelmshaven on the German North Sea coast (53°30′40″N, 08°06′20″E). Common terns are migratory seabirds that arrive at the breeding colony in early spring (Becker & Ludwigs, 2004). They are socially and genetically monogamous, typically have a clutch of two to three eggs per breeding attempt, and generally do not have more than one successful breeding attempt per year, such that the annual number of fledglings per pair varies between 0 and 3 (Becker & Ludwigs, 2004). Eggs typically hatch in the order of laying (Nisbet & Cohen, 1975), with the second and third hatchlings, on average, hatching 0.7 and 2.0 days after the first hatchling respectively (Vedder et al., 2019). Chicks compete over food brought in by the parent. Because hatching order determines the competitive rank within the brood, this causes later hatching offspring to acquire less food, to grow more slowly and to have a lower fledging probability than their earlier hatched siblings (Bollinger, 1994; Langham, 1972; Morris et al., 1991; Vedder et al., 2017). Males fledge *c.* 5% heavier than females, but this disparity develops only shortly prior to fledging (Becker & Wink, 2003). Offspring sex does not vary systematically with hatching order (Benito et al., 2013), nor does average fledging probability differ between the sexes (Vedder et al., 2016). After fledging, common terns return to the natal colony from the age of two, after which they settle as breeders in the natal colony, or emigrate elsewhere, in later years (Becker & Ludwigs, 2004). There is no effect of hatching order on body mass in adulthood (S. Bouwhuis, unpublished results). Within individuals, annual fledgling production increases into old

age, before levelling off (Zhang et al., 2015a), while adult annual survival probability declines with age (Zhang, Rebke, et al., 2015). There is no detectable sex difference in age-specific fitness (RV) among adults (Zhang, Rebke, et al., 2015).

The Banter See colony site consists of six artificially constructed rectangular concrete islands, each measuring 10.7 m × 4.6 m and surrounded by 60 cm high walls. Since 1992, all nests have been checked three times a week throughout each breeding season (May–August). At these checks, all newly hatched chicks were ringed and their age was estimated in days (always between 0 and 2 days old), based on a combination of size, developmental stage, dryness of down feathers and the retraction of the yolk sac. In a minority of cases where multiple chicks of the same brood were estimated to be of the same age, they were still assigned a separate hatching order based on these criteria.

All chicks receive a small subcutaneously implanted transponder (TROVAN ID 100; TROVAN) shortly before fledging. The walls of the islands used for breeding have 44 regularly spaced resting platforms, which are equipped with antennae that automatically read transponder codes from a distance of ≤11 cm (Becker & Wendeln, 1997). In addition, antennae are placed around each nest for at least 24 hr during incubation. Because both sexes incubate, this allows an annual detection probability of 1.0 for all breeders, and an estimated detection probability of 0.81 for non-breeders (Szostek & Becker, 2012). Between 1992 and 2014, the annual number of breeding pairs averaged 320 and ranged between 90 and 570. Chick mortality prior to fledging varied considerably among years (12%–75%), which was mostly caused by variation in food availability (Dänhardt & Becker, 2011; Vedder et al., 2019), as the colony is protected against ground predators and aerial predation is rare.

2.2 | Data and definitions

The 'brood size at hatching' varied between 1 and 3, and was defined as the total number of hatchlings. We use the term 'sibling rank' to describe an individual's hatching order, which, in the case of common terns, accurately reflects the dominance rank within a brood (Bollinger, 1994; Langham, 1972; Morris et al., 1991). The rank of 1, 2 and 3 refer to the first, second and third hatching chick, respectively, and we write of 1 as being the highest rank.

A chick was assumed to have fledged successfully if it disappeared from the colony site after it reached an age and physical state that would allow successful fledging. Fledging success was assessed for all hatchlings of known hatching order between 1992 and 2014 ($n = 14,748$). Recruitment of fledglings as breeders in the natal colony was assessed until 2015 for all chicks that fledged prior to 2011 ($n = 3,909$), based on whether they were identified incubating a clutch. This is reliable, as 93% of breeders recruit within 5 years of fledging ($n = 963$). The age at first breeding (AFB) ranged from 2 to 15 years, but since only 4% of birds had an AFB > 7, we pooled these birds. The annual survival of established breeders was assessed up to 2013, with individuals assumed to have died after the year of last observation (as breeder or non-breeder), or for individuals recorded

in 2013 if they were not recorded in 2014 and 2015 ($n = 4,591$ bird–year combinations). The reliability of this assumption is high as well, as 96% of individuals do not evade detection in the colony for more than 1 year after first breeding (Bouwhuis et al., 2015; Zhang et al., 2015b). Although we cannot distinguish between death and permanent emigration, it is safe to assume that emigration is rare, as breeders are known to be colony-faithful (Becker & Ludwigs, 2004) and local annual survival estimates are very high (see Section 3). Annual fledgling production of established recruits was determined for all years an individual was recorded in the colony, up to 2013, with 0 fledglings assigned to years of skipped breeding.

2.3 | Statistical analyses of fitness components

Fledging and recruitment probability were analysed with logistic binomial models. To account for non-independence (i.e. correlations) among individuals born in the same nest and among nests in the same year, corresponding normal 'random effect' deviates were added at the linear predictor scale. As categorical predictor variables, we used 'sibling rank' and 'brood size at hatching', as well as their interaction. By including 'brood size at hatching' as a predictor variable, we filtered out any sibling rank effects that are not due to sibling rank per se, but instead may result from the fact that third hatchlings can only occur in broods of three.

Age at first breeding was analysed with an ordinal regression model, including only the categorical predictor variable of 'sibling rank'. Adult annual fecundity (ordinal) and survival (logistic binomial) were analysed with multivariate models, with a joint multivariate distribution of among-year effects and allowing for a within-individual correlation between fecundity and survival. We used 'sibling rank' as a categorical predictor variable, while smoothing splines (Wood, 2017) of age were used as a continuous predictor. We additionally tested for interactions between sibling rank and age, by fitting rank-specific smoothers with respect to age, to account for the possibility that birds of different sibling rank differed in their rate of decline with age (i.e. senescence).

We fitted Bayesian Markov chain Monte Carlo models with brms 2.10.0 (Bürkner, 2017), using the sampler provided by RStan version 2.19.2 (Stan Development Team, 2019) with R version 3.6.2 (R Development Team, 2019) in RStudio 1.2.1114 (RStudio Team, 2019). Full details about statistical models are provided in the Supporting Information.

2.4 | Estimating age-specific natural selection

As a common fitness currency, we used each individual's state-dependent RV, which can be regarded as its relative expected contribution to the future gene pool (Taylor, 1990). We discriminated between age (denoted a) and non-age (denoted x; e.g. sibling rank) state variables. RVs were normalized such that the average RV of fledglings equalled 1; as a consequence, the RV of a random hatchling was just its probability of fledging, while the RV of a random adult ($a \geq 2$) equalled 1/2

times its expected lifetime production of fledglings, where the factor $1/2$ was the genetic contribution (or relatedness) of an adult to its offspring. Defined recursively, and assuming a stationary population, the expected RV of an individual with age a and state x can be written as

$$V_{a,x} \overset{\text{def}}{=} \frac{1}{2}F_{a,x} + S_{a,x}V_{a+1,x}. \tag{1}$$

Here the fecundity term $F_{a,x}$ is the expected number of fledglings, multiplied by their average RV of 1, $S_{a,x}$ is the probability of survival from one age class to the next and $V_{a+1,x}$ is the expected RV of a survivor. Note that this definition assumes that x is invariant with respect to age; for our purpose this was justified because we only used sibling rank and AFB as non-age state variables.

We used recursion (1) in two ways: first, we solved it for each combination of age a and state x to estimate population-level posterior distributions of $V_{a,x}$ in terms of the posterior distributions of fecundity and survival, which in turn were generated by the statistical models for these fitness components (see above and Supporting Information). The solution to (1) is the remaining lifetime reproductive success at age a and in state x:

$$V_{a,x} = \frac{1}{2}F_{a,x} + \frac{1}{2}\sum_{i=1}^{a_{max}}\prod_{j=a}^{i} S_{j,x}F_{i+1,x}. \tag{2}$$

We used a maximum age of $a_{max} = 25$, which is achieved by less than 1% of adult birds. In our dataset, the oldest bird is 20 years, so we extrapolated age-specific fecundity and survival beyond 20 years of age by using the estimated smoothers. Posterior densities of $V_{a,x}$ were derived from the posterior densities of age-specific fecundity and survival.

Second, we used (1) to compute for each individual i of a given age a and state x its individual RV, $v_{i,a,x}$, by combining individual realizations of fecundity $F_{i,a,x} = 0, \ldots, 3$ and survival $S_{i,a,x} = 0, 1$ with population-level state-dependent RVs:

$$v_{i,a,x} \overset{\text{def}}{=} \frac{1}{2}F_{i,a,x} + S_{i,a,x}V_{a+1,x}. \tag{3}$$

Multiplying individual fecundity and survival with population-level RVs, rather than individual RVs, is accurate when selection (after fledging) is weak (Engen et al., 2012). These individual RVs were used to analyse selection (see Engen et al., 2012 for a similar approach). Specifically, for each individual we calculated its age-specific relative reproductive value (RRV).

$$\tilde{v}_{i,a,x} = \frac{v_{i,a,x}}{V_a}. \tag{4}$$

Here V_a represents the average RV of all individuals of age a in the dataset. The resulting RRVs determined the age-specific *selection differentials* with respect to state variable x:

$$\Delta w_{a,x} = \text{cov}_i\left(\%\tilde{v}_{i,a,x}, x\right). \tag{5}$$

The covariance was taken over all individuals i of age a. Note that the right-hand side of (5) has no denominator (more precisely, a

denominator equal to 1), because the average relative RV equals 1. Next, an age-specific *selection gradient* with respect to x was the least squares regression coefficient of RRV versus x:

$$\beta_{a,x} = \frac{\text{cov}_i\left(\tilde{v}_{i,a,x}, x\right)}{\text{var}_i(x)} = \frac{\Delta w_{a,x}}{\text{var}_i(x)}. \tag{6}$$

The *total* selection gradient over all age classes a was a weighted sum of the age-specific selection gradients:

$$\beta_x = \sum_a U_a V_a \beta_{a,x}. \tag{7}$$

The weights are the so-called class RVs $U_a V_a$ (Engen et al., 2012; Taylor, 1990), where U_a is the relative frequency of age class a, such that $\sum U_a = 1$, and V_a, as before, represents the average RV of all individuals of age class a. We estimated the age class frequencies $U_{a \geq 2}$ directly from the overall empirically observed age distribution. To obtain a corresponding number of nestlings U_0, we multiplied the total number of nests in the dataset with the population-average number of hatchlings per nest.

The *standardized* age-specific selection gradients are useful to compare selection gradients across age classes, and they are

$$\tilde{\beta}_{a,x} \overset{\text{def}}{=} \frac{U_a V_a \beta_{a,x}}{\beta_x}. \tag{8}$$

Note that, summed over all age classes, they add up to 1.

Posterior distributions for all measures of selection (5)–(8) can be derived 'for free' using the posterior distributions of the population-level state-dependent RVs.

3 | RESULTS

3.1 | Fitness components and reproductive value

Fledging probability was strongly associated with sibling rank; later hatched chicks were less likely to survive than earlier hatched chicks, both in broods of three and two chicks (Figure 1a). Fledging probability was also associated with brood size; for a given rank, chicks from larger broods survived better than chicks from smaller broods (Figure 1a). A model with an interaction between hatching order and brood size slightly outperformed a model with additive effects, reflecting a stronger effect of brood size on survival of second-hatched than of first-hatched chicks (Table S1). There was considerable variation in fledging probability among years, and a positive correlation among siblings from the same nest (Table S1). The magnitude of among-year variation in nestling survival varied with both brood size and sibling rank; among-year variation was greatest among the lowest ranking chicks (Table S1).

In contrast to fledging probability, recruitment probability was not associated with sibling rank and brood size (Figure 1b; Table S2). Recruitment probability did vary among nests and years, but not as strongly as the probability of fledging (Table S2).

Likewise, the AFB did not vary among birds of different sibling ranks (Table S3).

Annual adult survival among recruits varied among years and declined roughly linearly with age from *c.* 90% among 2-year olds to *c.* 80% among ≥14-year olds (Figure 2a; Table S4). The rate of decline was independent of sibling rank, but, across all age classes, first-hatched chicks survived slightly better than their lower ranked siblings (Figure 2a; Table S4).

The mean annual number of fledglings produced by recruits increased strongly with age, from *c.* 0.2 fledglings for 2-year olds to

c. 0.9 fledglings for 9-year olds, after which it levelled off (Figure 2b; Table S4). There was no interaction between sibling rank and age, but adults ranked second tended to produce fewer fledglings across all age classes (Figure 2b; Table S4).

At the individual level, after controlling for age and rank, survival and fecundity were positively correlated (Table S4), suggesting that individuals vary in 'quality'. The best model, however, also supported a negative correlation between survival and fecundity among years: adult survival was higher following years with low fledgling production (Figure 3; Table S4).
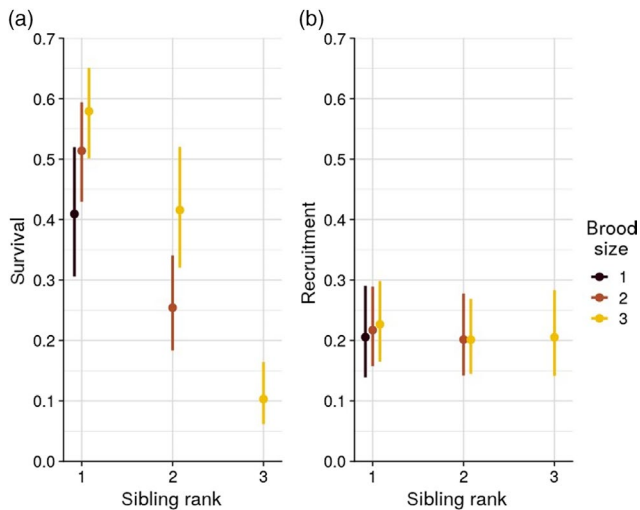

FIGURE 1 Survival and recruitment probabilities (mean and 95% CI) in relation to sibling rank and brood size. (a) Survival from hatching to fledging; (b) post-fledging recruitment. Also see Tables S1 and S2
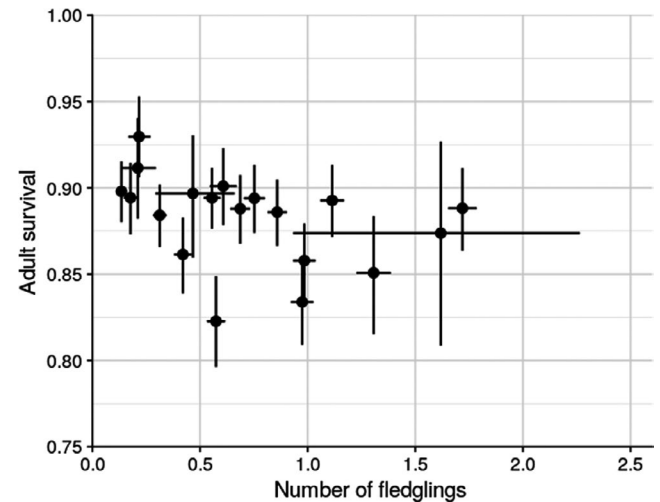

FIGURE 3 Model predicted annual adult survival to the next breeding season in relation to annual number of fledglings produced (means and 95% CI). For statistical analysis, see Table S4
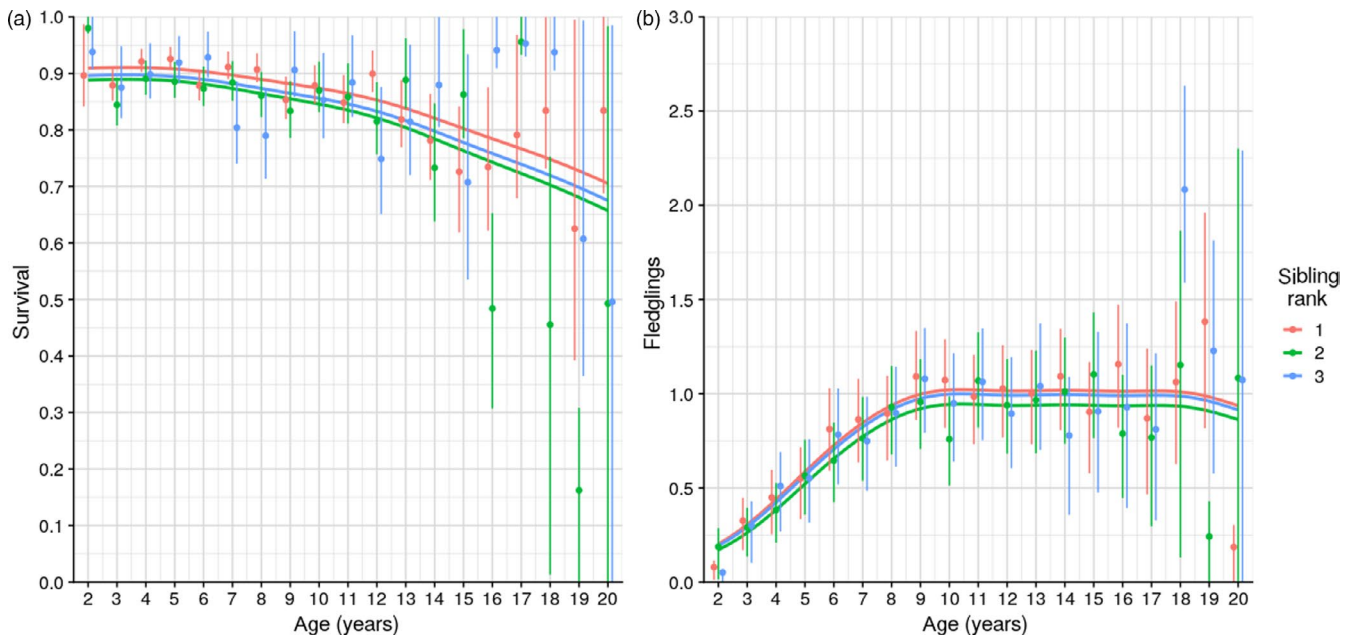

FIGURE 2 Age and sibling rank-specific annual (a) survival and (b) fecundity (number of fledglings) of recruits. Circles and error bars represent posterior means and 95% CI. The curves are predicted mean values derived from statistical models with age as a continuous predictor (see Table S4)

Posterior distributions for absolute and relative age- and rank-specific RVs were derived from posterior distributions of individual fitness components and are summarized in Figure 4. Absolute RVs peaked at around 5 years of age, and gradually declined thereafter. Among hatchlings (age = 0), absolute RVs strictly increased with rank: the first-hatched outperformed the second- and third-hatched,

and the second-hatched outperformed the third-hatched (Figure 4a). Differences in absolute RVs were smaller in adulthood, but first-hatched chicks continued to perform best (Figure 4a). RRVs varied especially strongly among hatchlings, by a factor of at least 3 between first- and third-ranked chicks. Variation among ranks was considerably smaller in adulthood (Figure 4b), but second-ranked chicks performed worst.
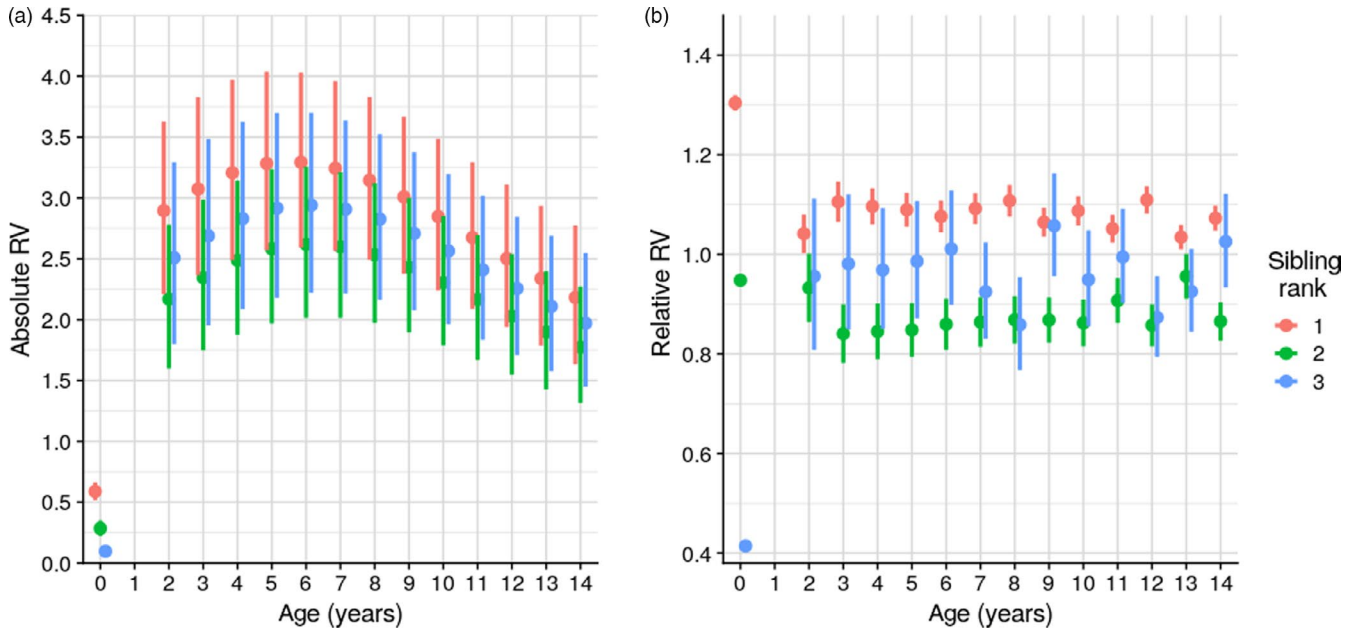

FIGURE 4 Age-dependent absolute (a) and relative (b) sibling rank-specific reproductive values (RVs). Points and error bars indicate posterior means and 95% CI. Absolute RVs are population-level estimates based on models with age as a continuous predictor, while relative RVs are based on models with age as a discrete predictor. The considerably smaller error bars for relative RVs are due to the positive posterior correlation between age- and rank-specific RV and average age-specific RV
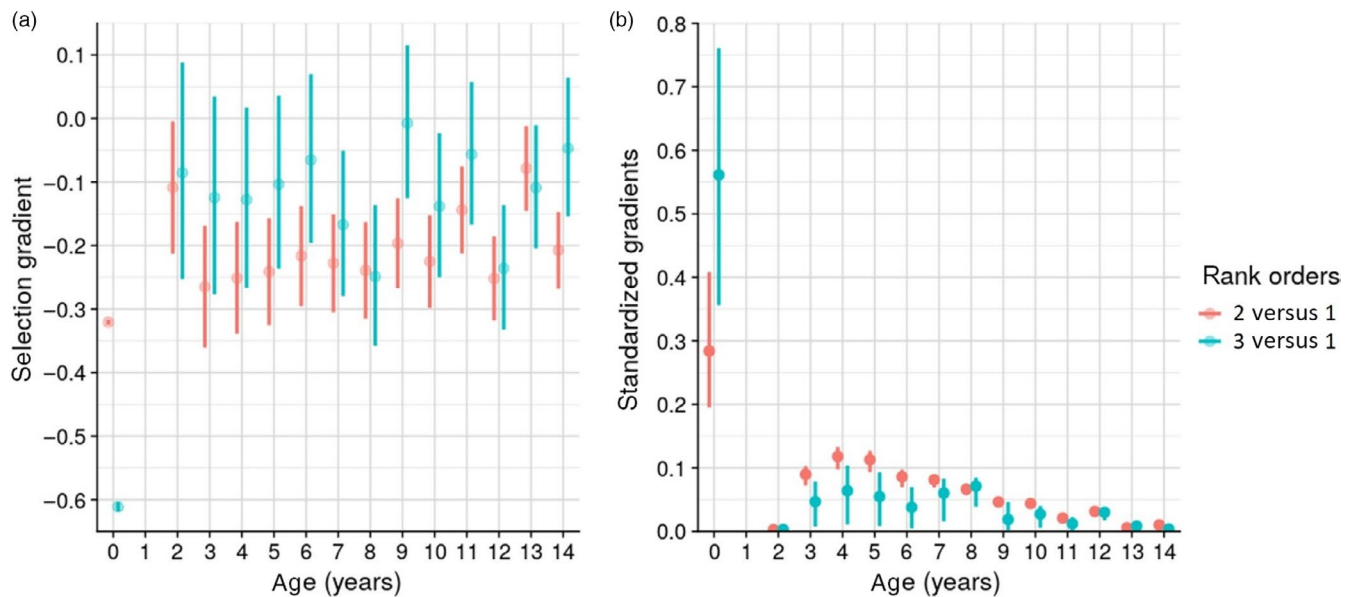
FIGURE 5 Absolute (a) and standardized (b) age-specific selection gradients of individuals of second and third rank, compared to those of first rank. Circles and error bars indicate posterior means and 95% CI. Negative values in (a) correspond to selection against the lower rank. Values in (b) indicate the proportional contribution of each age class to the total selection against the rank. Note that differences in performance between individuals of different hatching order after age 13 have a negligible effect on total fitness, due to too few individuals reaching this age

FIGURE 6 Annual pre-fledging selection gradient (posterior means and 95% CI) of hatchlings of second and third rank, compared to those of first rank, in relation to the mean probability of survival to fledging, for each year during 1992–2014. Note that in years with lower overall chick survival, selection against lower ranked chicks was stronger
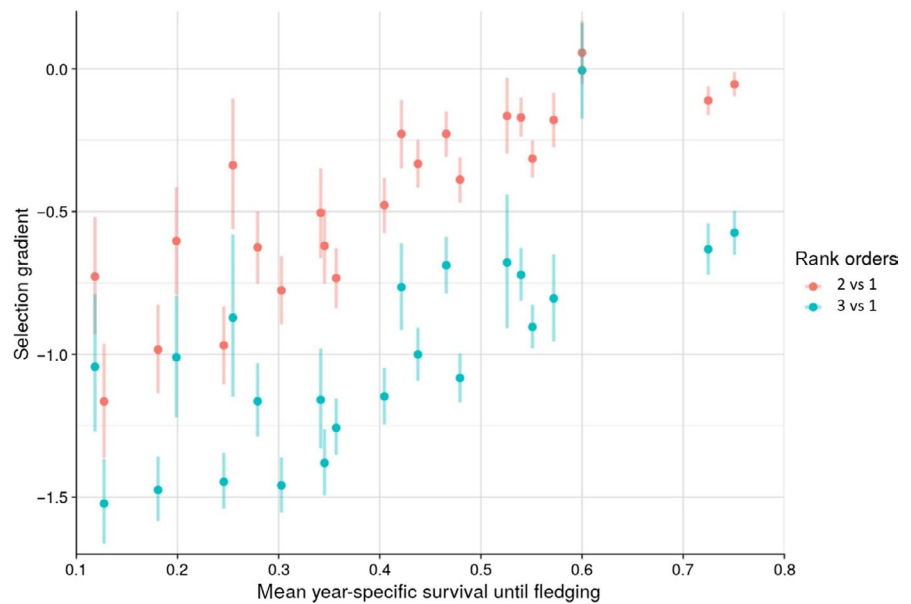
3.2 | Selection partitioned over age

Posterior distributions for age-specific selection gradients with respect to sibling rank (2 and 3 vs. 1) are summarized in Figure 5. Overall, selection gradients were negative, with the lowest overall fitness for individuals of rank 3, and individuals of rank 2 having an intermediate overall fitness (age = 0 in Figure 5a). Selection during the nestling phase was stronger than during adulthood, although for most adult age classes the 95% credible intervals did not overlap with zero, indicating that fitness costs of lower rank persisted into adulthood (Figure 5a). When corrected for the relative frequencies and RVs of birds of the different age classes (Figure 5b), individuals of ranks 2 and 3 incurred approximately 30% and 55% of their total fitness costs prior to fledging (age = 0) respectively (Figure 5b). For both ranks, the remaining fitness costs were mostly spread out across the ages of 3–8 years (Figure 5b).

The strength of selection with respect to sibling rank in the nestling period varied considerably among years, with the magnitude of selection gradients increasing systematically with the annual average nestling mortality (Figure 6; Table S1), indicating that lower ranked chicks were especially prone to die prior to fledging, relative to their higher ranked siblings, in years with low overall fledging success.

4 | DISCUSSION

We found substantial fitness costs associated with sibling rank, with individuals of rank 1 having the highest overall fitness, individuals of rank 3 the lowest and individuals of rank 2 having an intermediate overall fitness. However, in individuals of rank 3, *c.* 45% of the overall fitness costs was incurred during adulthood (i.e. reduced adult survival and reproduction), while the other 55% was the result of a reduced fledging probability. In contrast, individuals of rank 2 incurred *c.* 70% of their overall fitness costs in adulthood, and only 30% as a

result of mortality prior to fledging. Since we are not aware of any other study that explicitly quantified these contributions, it is difficult to evaluate to which extent this pattern is typical among species.

Two other long-term studies on sibling rank effects in adulthood suggest the post-recruitment fitness costs to be relatively small: little or no effect of sibling rank was found on post-recruitment demographic parameters in the black-legged kittiwake *Rissa tridactyla* (Cam et al., 2003), and there was little evidence for an effect of sibling rank on adult reproductive success in the blue-footed booby *Sula nebouxii* (Drummond & Rodriguez, 2013). Our study, however, demonstrates that although differences in annual reproductive success and/or survival in adulthood can appear small (Figure 2), they can sum up to a considerable proportion of the overall fitness costs. In our case, this effect may be particularly pronounced due to annual reproductive success of individuals increasing into old age. This mitigates the decline in RV with age (Figure 4), thereby increasing the relative contribution of late-life performance to total fitness. In long-lived mammals, senescence in RV is generally a lot stronger than in birds (Bouwhuis et al., 2012; Bouwhuis & Vedder, 2017). This should cause among-individual variation in late-life performance to contribute to a smaller fraction of the total fitness costs of a poor start. However, inferring generality on how fitness costs of poor developmental conditions—that are by definition unavoidable—are allocated across age, or life stages, must await more studies to quantitatively partition these fitness costs.

Importantly, our study illustrates that selection on parental behaviour that promotes resources to be directed to the most profitable offspring as early as possible should not be ignored when predicting the optimal age-specific expression of fitness costs of a poor start in life. In species for which the cost of producing a zygote is relatively small and resource availability varies unpredictably, parents should benefit from the initial production of an optimistic number of offspring that can be reduced rapidly when resources become limiting (Hamilton, 1966; Kozlowski & Stearns, 1989; Temme & Charnov, 1987). Rapid reduction of offspring numbers

can be achieved through a range of parental tactics, including selective abortion of embryos and enforcement of competitive asymmetries among offspring (Kozlowski & Stearns, 1989; Lack, 1947; Mock & Parker, 1997). Competitive asymmetries appear to be more commonly promoted by parents in relatively large, long-lived species (Muller & Groothuis, 2013; Slagsvold et al., 1984), for which the initial cost of producing an excess of offspring may be small (Williams, 1966). This is also the case in common terns, as the strong negative correlation between the annual fledging probability and the annual strength of pre-fledging selection on sibling rank (Figure 6) confirms that the conditions for raising offspring vary considerably among years, and that the birds reduce allocation to the lowest ranked offspring when conditions for reproduction are poor. This results in rapid mortality of the lowest ranked offspring, which is exacerbated in years with a poor food supply (Vedder et al., 2017, 2019). Selection on parental behaviour that promotes resources to be directed to the most profitable offspring as early as possible will thus conflict with selection on individual offspring to defer the fitness costs of resource limitation during development as long as possible. Ultimately, the balance between these conflicting selective forces should determine the relative contribution of late-life fitness costs to the total fitness costs of developing in a poor environment.

Our multivariate analysis of adult fecundity and survival revealed that years with high fledgling production were additionally characterized by low subsequent adult survival. This suggests that common tern parents adjust their relative allocation to reproduction in response to annual resource availability. Increasing the relative allocation to reproduction under favourable conditions is predicted for long-lived species in a stochastic environment (Erikstad et al., 1998) and fits with the observation that, in our system, years with high fledging success are characterized by high food availability (Dänhardt & Becker, 2011; Vedder et al., 2019). The presence of a positive correlation between total resource availability and the share of resources that is allocated to reproduction should indeed allow detection of a trade-off in species with long life span and low annual fecundity (Descamps et al., 2016), and the strong negative correlation between annual fledging success and selection against low sibling rank that we found (Figure 6) confirms that the hierarchy among siblings facilitates such reduced parental allocation to reproduction in poor years.

Despite third hatchlings experiencing the poorest developmental conditions, as suggested by their lowest fledgling probability (Figure 1) and them generally acquiring the least food from their parents (Bollinger, 1994; Langham, 1972; Morris et al., 1991), second hatchlings experienced larger fitness costs in adulthood (Figures 2 and 4). Perhaps second- and third-hatched chicks within a brood are 'set' for different tactics. The initial disadvantage of second-hatched chicks is smaller than that of third-hatched chicks (Vedder et al., 2019), such that for them it may pay to allocate resources to growth and competition, at the expense of allocation to late-life performance (Figure S1), while additional allocation to growth and competition may not be enough to overcome the disadvantage for third-hatched chicks (Figure S1). If this is the case, increased competitiveness of third-hatched chicks would only waste resources

that could otherwise be utilized by siblings or parents, without increasing a third-hatched chick's fledging probability. In that sense, third-hatched chicks may be more strongly parentally primed for an efficient brood reduction than second-hatched chicks, causing their trade-off between early- and late-life performance to be more balanced to late-life performance (Figure S2). This idea is consistent with the observation that, in common terns, the third egg is generally smaller than the first two (Bollinger, 1994; Garcia et al., 2011). Moreover, concentrations of maternally derived androgens (testosterone, dihydrotestosterone, androstenedione) in the yolk of common tern eggs were found to be highest in the second egg (French et al., 2001). Such variable maternal hormone deposition to the developing embryo has been suggested to mediate early- versus late-life trade-offs, with higher levels of androgens promoting growth and competition at the expense of survival during adulthood (Eising, 2004; Groothuis et al., 2005). More empirical support would, however, be needed to confirm that higher androgen levels during development are causally responsible for the late-life disadvantage of second-hatched chicks that we observed.

As is practically unavoidable in any study on a wild non-isolated population, we were unable to quantify the fitness effects of sibling rank among emigrants. We therefore cannot exclude the possibility that our fitness estimates are biased if a correlation between rank and emigration were to exist. Our data, however, are not suggestive of such a correlation, since the probability of a fledgling to settle as a breeder in the natal colony was independent of sibling rank (Figure 1b). Moreover, additional analyses showed that sibling rank does not predict the probability of locally hatched individuals that were known to have survived their early years—by being recorded as a non-breeding adult by the automatic registration system in the colony—to not settle as a breeder in the natal colony (Figure S2; Table S6). Although this does not exclude the possibility that emigrants differ from local birds in the effects of sibling rank on adult fitness components, without evidence for such an interaction we consider this scenario not very likely. We also do not consider it very likely for adults to permanently emigrate from the colony after years of high fledgling production, such that our conclusions on adult survival in relation to annual productivity would be biased.

Overall, we hope that our modelling approach will inspire more researchers to estimate the complete fitness costs of poor developmental conditions and to partition these costs to the relevant life-history stages. This would facilitate formal comparison among populations and species and provide us with a better understanding of the evolution of age-specific fitness costs in relation to resource limitation during development, as well as the trade-off between early- and late-life performance that is thought key to the evolution of ageing.

AUTHORS' CONTRIBUTIONS

O.V., I.P. and S.B. designed the study; S.B. collated the data; I.P. and O.V. analysed the data; O.V. and I.P. wrote the manuscript with contributions from S.B.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.2rbnzs7mx (Vedder et al., 2021).

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