Natural ‘poor start’ does not increase mortality over the lifetime

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Poor nutrition and other challenges during infancy can impose delayed costs, and it has been proposed that expression of costs during adulthood should involve increased mortality rather than reduced reproduction. Demonstrations of delayed costs come mostly from experimental manipulations of the diet and hormones of captive infants of short-lived species, and we know very little about how natural poor starts in life affect wild animals over their lifetimes. In the blue-footed booby, sibling conflict obliges younger brood members to grow up suffering aggressive subordination, food deprivation and elevated stress hormone, but surviving fledglings showed no deficit in reproduction over the first 5–10 years. A study of 7927 individuals from two-fledgling and singleton broods from 20 cohorts found no significant evidence of a higher rate of mortality nor a lower rate of recruitment in younger fledglings than in elder fledglings or singletons at any age over the 20 year lifespan. Development of boobies may be buffered against the three challenges of subordination. Experimental challenges to neonates that result in delayed costs have usually been more severe, more prolonged and more abruptly suspended, and it is unclear which natural situations they mimic.

Keywords: sibling conflict; growth; corticosterone; dominance; mortality; recruitment

1. INTRODUCTION

It is now widely accepted that when animals suffer quantitative or qualitative dietary restriction and other environmental challenges in their infancy (or before birth), they are likely to pay delayed costs during adulthood [1]. Mechanisms are not well understood, but in birds, fish and mammals experimental restriction of the neonatal diet or the compensatory growth that follows it can prejudice adult traits such as body size, metabolism, sexual maturation, secondary sexual characters, immunocompetence, competitive behaviour, age at recruitment and longevity [2,3]. Likewise, in nestling birds experimentally elevated circulating corticosterone (the stress hormone) can lead to adults with a diminished higher vocal centre in the brain [4], a deficit in problem-solving ability [5] or reduced exploratory behaviour and competitiveness [6]. Costs can be expressed over diverse timescales, they are often deferred (e.g. [7,8]), some are likely to be permanent (e.g. [9]), and they can involve accelerated ageing [10].

Nonetheless, experimental demonstration of delayed effects of ‘poor starts’ has usually involved captive members of short-lived species, and effects are typically measured only once or twice in the weeks or months after sexual maturity. Also, it is not known to what extent the timing, duration and magnitude of experimental dietary restrictions mimic natural dietary restrictions. Thus, while we are confident that food restriction and elevated corticosterone in infancy can produce deficits in the adult, little is known about how natural environmental challenges during infancy affect wild animals over their lifetimes. Importantly, there is experimental evidence from captive fish and birds that some challenges can be overcome, at least partially, through developmental plasticity. Female guppies (Poecilia reticulata) were able to cope with limited food (within natural values) during early development by modifying their investment in growth, reproduction and fat storage throughout adult life, to the extent of showing no deficit in total reproductive success over the first three reproductive events [11]. Although members of enlarged zebra finch (Taeniopygia guttata) broods were undersized throughout the nestling period (owing to presumed underfeeding) compared with birds from diminished broods, they matured faster (as revealed by tail feather development), and as adults showed enhanced singing and immune responses and no deficits in bill colour nor any measure of their first reproduction (laying date, clutch size and egg size) [12].

Different costs of early food deprivation may trade off against each other [13–16] and natural selection should often favour costs being expressed late in life [17]. Reproductive traits are thought to trade off against longevity (e.g. [18]), and when avian infants experience food restriction developmental programmes appear to prioritize reproduction over adult survival [13]. After deprivation as nestlings, male zebra finches attained normal adult tarsus length, bill size, secondary sexual traits, seriological traits and immunological traits, but their average post-fledging longevity declined by 24 per cent from 461 to 352 days (for a similar effect in females, see [19]). Increased adult mortality tends to follow dietary restriction during gestation and lactation in mammals [20], and is to be expected when a poor start is followed by compensatory growth because fast growth is associated with high adult mortality in birds, rodents, lizards and fish [21–23].
In wild vertebrates, comparisons of cohorts provide non-experimental evidence that poor early nutrition prejudices adult survival, although they do not allow us to discern which environmental variables play a causal role, when causal variables act, nor indeed whether survival effects are due to environmental variables or population responses to them. For example, weather in the natal year predicted adult survival rates of male and female red deer [24,25] and breeding longevity of red-billed choughs [26], but we cannot be sure that infant nutrition is responsible. Comparisons of individuals that grew up in more or less favourable local environments also provide non-experimental evidence for delayed effects of poor (and ‘silver spoon’) starts [17,27,28], although, again, interpretation of causation is complicated by multiple environmental variables, as well as variation in genetic and phenotypic quality of parents.

We tested for effects of a natural poor start involving (i) poor initial growth followed by compensatory growth, (ii) high levels of circulating corticosterone and (iii) aggressive subordination on mortality rates across the entire post-fledging lifespan of a long-lived vertebrate, by comparing senior (first-hatched) and junior (second-hatched) chicks from two-chick broods of the blue-footed booby (Sula nebouxii). In two-chick broods, one chick (usually the junior one) is aggressively dominated by the other throughout infancy and, in consequence, receives less parentally provided food and grows more slowly and with elevated circulating corticosterone, although it catches up before fledging (references in §2a). Despite this three-pronged poor start, as far as we know, junior fledglings show no deficits in reproductive performance during at least the first 5–10 years of adulthood [29]. They may achieve this by trading off longevity against reproduction.

We therefore tested the hypothesis that the poor start of blue-footed booby subordinate chicks incurs a delayed survival cost, resulting in junior fledglings showing, during some part of post-fledging life, a greater rate of mortality than senior fledglings and singletons (from one-chick broods). We also tested for an alternative delayed cost: delayed recruitment into the breeding population as evidenced by a lower recruitment rate at some age.

This study represents a novel design for detecting delayed effects of a poor start. It is based on pairs of sibling fledglings that differ systematically in their early growth, circulating corticosterone and agonistic experience, but which are matched for environmental variables associated with year of birth (i.e. cohort), hatching date and natal nest site, and also for genetic and phenotypic quality of parents (but see [30]).

2. METHODS

(a) Study species

The blue-footed booby is a large-bodied socially monogamous Pelicaniform, with females larger and 32 per cent heavier than males. It nests on islands in the eastern Pacific Ocean [31]. At our study site on Isla Isabel, Mexico, 46.5 per cent of blue-footed booby broods comprise two chicks, 44.3 per cent comprise one chick and the remainder comprise three chicks. Both parents feed chicks sardines and anchovies for roughly three to four months, and chicks start flying at approximately three months of age. Adult boobies are not subject to predation, but on Isla Isabel eggs are depredated by Heermann’s gulls (Larus heermanni) and newly hatched chicks by milk snakes (Lampropeltis triangulum). The influence of El Niño Southern Oscillation (ENSO) at the study site is strong, affecting breeding participation, laying date, clutch size, hatching success, nestling growth rates, nest success, recruitment and adult survivorship [32,33].

In broods of two, chicks hatch 4 days apart. Seniors begin pecking and biting their siblings on the cranium, nape, face and body at age 9–10 days, and sustain their daily attacking and vocal threatening until at least an age of three months, with no obvious interference by parents [34]. Aggression is most intense during the first weeks and peaks at 60 pecks or bites per 12 h day when the senior chick is 20–25 days old, by which time the junior chick is a ‘trained loser’ that submits to roughly 90 per cent of aggressions [35], rarely attacks and in experimental trials is unable to effectively challenge the dominance of a younger and smaller ‘trained winner’ [36,37]. Compared with dominants, subordinates receive fewer feeds and a lesser mass of fish from parents for at least the first 35 days of life: 17 per cent less fish during the first 7 days of life and an estimated 13 per cent less fish from 12 to 35 days of age [38,39]. By age 4 days, subordinates are significantly lighter than dominants, and they are smaller and lighter during roughly the first half of the nestling period (11% lighter at age 20 days in three cohorts [40]), but they largely catch up in size and mass by age 70–80 days [29,34], and at 70 days are only 3 per cent lighter (n = 2107 sibling pairs). This compensation is achieved in the second half of the nestling period, probably by accelerating rather than prolonging growth as juniors and seniors reach maximum body mass and complete their plumage development at similar ages [34]. Junior nestlings are more likely to die before fledging than seniors (40% versus 29% mortality; data from 24 seasons) because in families where senior nestlings are underfed they intensify their attacks until their siblings starve or exit the nest [41]. It is to ensure that this facultative siblicide falls on their siblings rather than themselves that senior chicks establish aggressive dominance and maintain it throughout the nestling period [42]. As a result of food deprivation, circulating corticosterone levels are 109 per cent higher in subordinate chicks than in dominant chicks at age 11–20 days, and possibly beyond that age [43]. Singletons are similar to seniors in corticosterone level and, initially at least, in growth [43], but of course they experience no sibling agonism. Analyses of large samples have hitherto failed to disclose delayed effects of subordination on any aspect of booby reproduction. Junior fledglings do not disperse further than seniors [44], and samples of junior recruits monitored over 5–10 years did not perform less well than seniors in relation to age, date, brood size and nest success at first reproduction, nor summed brood sizes and accumulated nest success [29,44].

(b) Population monitoring

Every year between 1988 and 2008, reproduction was monitored in two study areas (20 800 m$^2$ and 6089 m$^2$) by marking all nests (sites with clutch or brood) and inspecting each one every 3 or 6 days throughout the five-month season (details in [29]). Chicks were marked with plastic bands after hatching and steel bands at fledging (70 days), and all banded breeders were identified. Fledglings could not be sexed, but breeders were sexed by voice (females grunt, males whistle). Birds that nested outside the study area generally were not registered, but throughout at least the first 8

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years of life these boobies nest close to their natal sites [45] and the margins of our study areas are mostly areas where nesting is impossible or uncommon. In addition, nests within 20 m of the study areas were registered whenever one of the breeders was banded. Since seniors and juniors do not differ in their natal dispersal [44], loss of data through dispersal should not bias comparisons of them. Long-distance dispersal from Isla Isabel appears to be uncommon and carried out by first breeders rather than experienced breeders [45].

We analysed only fledglings that grew up in two-chick broods that suffered no nestling mortality and therefore experienced either a poor start or a privileged start throughout infancy. We also included singleton fledglings; in the event of seniors and juniors suffering in survival or recruitment, comparison with singletons could help determine whether it was seniors or juniors that were affected by early experience. We assumed that all seniors were dominant and all juniors were subordinate in the nestling period. However, dominance inversion occurs in an estimated 9.7 per cent of two-chick broods [34,35,40] and inverted broods probably tended to obscure estimated differences between adult mortality rates of dominants and subordinates. This effect should not be important in the context of our large samples.

(c) Capture–recapture modelling

In order to take the probability of recapture into account, we carried out capture–recapture multi-state modelling (CMR [46]) using M-SURGE software [47]. We built the capture–recapture histories of all 7927 fledglings of the 1988–2007 cohorts, 46 per cent of which were recaptured (i.e. were recaptured at least once as a breeder). Of fledglings, 36 per cent were singletons, 32 per cent seniors and 32 per cent juniors; of recruits, 35 per cent were singletons, 33 per cent seniors and 32 per cent juniors. Three types of parameter were estimated: local survival probabilities (S), transition probabilities between states (from non-breeder n to breeder b; i.e. recruitment, noted by $ \hat{g}^{nb} $ and recapture probabilities ($p$; details in [32]). Since the main hypothesis predicts differences in annual survival and recruitment among fledglings of different status (denoted in models by $g$), we started with an umbrella model $ \{S_n, \hat{g}^{nb}, p, \hat{c}_g\} $. Age and time (denoted in models by $a$ and $t$, respectively) were included as independent factors because they have been shown to shape survival, recruitment and recapture probabilities of boobies [32]. To avoid overparameterizing models, we did not include sex in our analysis; inclusion of three sexual categories (males, females and unrecruited/unsexed fledglings) would triplicate the 1304 parameters of the umbrella model (see §3). However, pooling the sexes should not cause any bias as hatch order and sex are not associated with this species, and the sex ratio is similar at hatching and fledging (56% versus 57% males), unrelated to brood size and, as far as we know, does not vary among years [48,49]. We began by testing for the influence of fledgling status in the more general model, first considering the parameter of least biological interest (recapture probability) and then concentrating on survival and recruitment.

The goodness-of-fit (GOF) of the general multi-state Arnaason-Schwarz model was assessed using the U-CARE programme [50], following Oro et al. [32]. The age-structure in survival, recruitment and recapture probabilities was fitted by running a separate GOF test for each of the 20 cohorts and summing all the tests. Note that contingency tables did not necessarily contain structural zeros because only some individuals made the transition from one state to the other. A $ \hat{c} $ value of 1.14 was achieved and this value was applied to all models. Finally, we sought a consensual model [51]—that is, one more parsimonious (with fewer parameters explaining approximately the same variance) than the more general model, with its high number of potential combinations of factors (time, age and status)—for each of the parameters (survival, recruitment and recapture; see also [32]) and selected the best model using a second-order Akaike’s information criterion with correction for small samples (QAICc, see [52,53]).

3. RESULTS

The search for a consensual model (table 1) suggested that status did not influence survival, recruitment or recapture probabilities (umbrella model 18 compared with models 17, 16 and 15, respectively). Nevertheless, we explored alternative, biologically plausible models to probe further for effects of status on survival or recruitment probabilities, while allowing recapture probabilities to depend only on time and age (e.g. model 14). First, we included age as an independent variable because Oro et al. [32] showed that survival and recruitment were greater in years with good environmental conditions; juniors might survive and recruit less well than singletons and seniors in bad years only. With years categorized as either good or bad (denoted by 2 in models) on the basis of colony breeding success in the current year [33], the fit of both survival and recruitment models (e.g. model 7; table 1) improved greatly (more than when breeding success was included as a continuous variable). We then tested the main hypothesis of our study, namely whether fledgling status determined differential survival or recruitment, and more particularly whether juniors showed lower values than seniors and singletons. Model 7 was improved by retaining the effect of fledgling status on survival while discarding its effect on recruitment (model 5), and improved further by including the effect of status on recruitment but not including its effect on survival (model 2; table 1). However, eliminating the effect of status on recruitment (i.e. discarding status altogether and retaining only the effects of age and categorized years) yielded the best model (model 1) for explaining variations in the survival and recruitment of blue-footed boobies, so we rejected the null hypothesis of lower survival or recruitment for junior chicks. The effect of fledgling status on recruitment was negligible ($ \hat{x}_{10} = 37.55, p > 0.99 $).

We also tested whether variation in survival with age follows a differently shaped logarithmic relationship (denoted by lnA in the models) for each status category (for instance, a steeper senescent decline for junior fledglings than for singletons and senior fledglings). A clear relationship between age and survival emerged, but the differences between categories of fledglings looked small (figure 1). Indeed, all models incorporating an age trend in survival (e.g. models 8, 19 and 20; table 1) performed badly, as did quadratic and other relationships between survival and age (results not shown).

Finally, we tested for a cohort-dependent effect of fledgling status on survival and recruitment (denoted by 2c in the models). Possibly only in cohorts that grew up in bad natal years do junior fledglings show inferior survival and recruitment compared with singletons and seniors.

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Table 1. Modelling the influence of fledgling status (\(g\)) on survival (\(S\)), recruitment (\(\psi\)) and recapture (\(p\)) probabilities of the blue-footed booby on Isla Isabel during 1988–2008. The umbrella model \(S_{\kappa g}, \psi_{\kappa g}, p_{\kappa g}\) (model 18) was the starting point to find a consensual model (model 15; see 3). Abbreviations: np, number of estimable parameters; dev, relative deviance of each model; QAICc, Akaike Information Criterion corrected for \(c\); \(\Delta_i\), QAICc difference between current model and umbrella model; \(w_i\), current model weight for each group of models for survival, recruitment and recapture parameters. The asterisk represents an interaction tested between predictor terms; 2t shows when years are categorized as ‘good’ or ‘bad’, using the actual breeding success of the colony as a proxy for environmental quality; 2c indicates the test of a cohort-dependent effect of fledgling status on survival and recruitment; lnA shows when a log trend in survival and recruitment was tested.

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However, in neither bad-year cohorts nor good-year cohorts were there differences among status categories in survival or recruitment (models 10 and 3, respectively). Accordingly, we finally selected model 1 (table 1), which shows that survival and recruitment varied with time and age but not with status category (figure 1).

Inspection of particular ages in figure 1 confirms that seniors and juniors were consistently similar in both survival and recruitment. At 15 of 20 ages, mean annual survival estimates for seniors were slightly higher than for juniors, hinting at a possible difference; but confidence intervals for both survival and recruitment estimates overlapped at most ages among the three types of chicks, showing lack of significant differences. The only significant differences were isolated cases of singletons performing less well than seniors and juniors (figure 1).

4. DISCUSSION

Analysis of 7927 fledglings from 20 cohorts over a 21-year period embracing the full range of ENSO-related environmental variation failed to reveal any effects of status in the natal brood on post-fledging survival or recruitment over a long lifespan. There was no evidence that the three challenges faced by most surviving subordinate blue-footed booby chicks during the nestling period (food deprivation, elevated corticosterone and aggressive subordination) prejudice their survival or recruitment after fledging, or that such effects appear in bad years or in birds that grew up in bad years. Previous analysis of cohorts 1989, 1991, 1993, 1994 and 1995 that used a generalized linear model and did not take the probability

![Figure 1. Variation in (a) survival and (b) recruitment with age, averaging over all 20 years of the study (1989–2008); estimates were from models \(S_{\kappa g}, \psi_{\kappa g}, p_{\kappa g}\) and \(S_{\kappa}, \psi_{\kappa}, p_{\kappa}\) (models 6 and 12, respectively, table 1); white squares show the survival of singletons, black circles that of senior fledglings and white circles that of junior fledglings. Bars show 95% confidence intervals.](http://rspb.royalsocietypublishing.org/Downloaded from http://rspb.royalsocietypublishing.org/) on June 29, 2017

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of recapture into account [29] showed that recruitment during the years up to 1999 was more common in seniors than juniors in two cohorts, although in other cohorts there were non-significant differences in the other direction and overall recruitment of seniors and juniors did not differ. We conclude, therefore, that while in particular cohorts seniors and juniors may differ in probability of recruitment by a specified age (even when allowed up to 10 years to recruit), there is no general tendency for either status category to outperform the other in either good years or bad years, nor indeed overall. Similarity of both junior and senior fledglings to singletons in mortality and recruitment rates over the lifetime implies that the survival of neither category is harmed or benefited by dominance subordination during infancy, or it implies that both are affected similarly over the lifetime. A three-pronged poor start appears not to prejudice either reproduction in the first 10 years of life [29] or the post-fledging longevity of this large-bodied, late-recruiting, long-lived bird.

A similar design detected reduced survival and delayed recruitment in junior kittiwake (Rissa tridactyla) fledglings [30], and these effects were attributed to rank (dominance status). However, the results are difficult to interpret in a poor start context because the junior kittiwake’s start has not been well characterized and because seniors were combined with singletons, a quite different category in terms of brood size, agonistic experience, and possibly quality of parents.

Our analysis could underestimate effects of this booby’s poor start if differential mortality of junior chicks in the nestling period (40% versus 29% in seniors) falls selectively on individuals of poor quality, thereby raising the average quality of junior fledglings in relation to senior fledglings. However, to the extent that quality of siblings is correlated, this effect may be counterbalanced to some degree by the automatic deletion from our sample of the correlated, this effect may be counterbalanced to some degree by the automatic deletion from our sample of the correlated with other vertebrate neonates not only in being natural but also in being generally more moderate in severity, shorter in relative duration, less abruptly suspended and encountered in a complex natural environment offering no mortality after poor start H. Drummond et al.

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chicks that cohabited with an elder broodmate throughout the nestling period (unpublished data on 24 cohorts). Absence of impacts on mortality and recruitment could also mean that boobies keep these three challenges and their impacts within adaptive bounds by adjustments (facultative or otherwise) to diverse aspects of their reproduction such as clutch and brood sizes, progeny sex ratios, nutrient and hormone composition of eggs, parental feeding rates, length of nestling period, and sibling submissiveness and aggressiveness. For example, parents could extend the duration or amount of parental feeding whenever the cost of extra feeding is exceeded by the future benefit obtained through reduced adult mortality of offspring; and senior nestlings’ willingness to attack their siblings and deprive them of food could be constrained by the indirect fitness costs they will pay if their siblings’ adult survival is reduced. Parents and siblings should limit damage to subordinate chicks, including delayed costs, to the extent that limitation enhances their own inclusive fitness [54–56].

Compared with the three developmental challenges faced by subordinate blue-footed boobies in the first half of their nestling period, experimental treatments that have generated delayed costs in neonate animals have generally been stronger and more sustained, some of them considerably so. Most studies of food restrictions applied to birds, fishes and mammals do not report the body mass deficits induced, but some provide graphs from which mean maximum deficits can be estimated. In birds, food restriction was usually applied from a few days after hatching until the end of the nestling period and all estimated body mass deficits exceed the average 11 per cent deficit experienced by booby subordinates: 23.0 per cent [57], 21.2 per cent [19], greater than 21.0 per cent [13], 13.4 per cent [58], 12.9 per cent [8]. In juvenile fish, experimental deprivation during several weeks (up to four months) induced estimated mean body mass deficits of 18.2 to 24.7 per cent [7], 17.0 per cent [16] and 6.8 to 17.0 per cent [23]. The study of a mammal that limited food available to lactating mothers induced estimated mean body mass deficits in their offspring of 42.6 per cent at age 25 days and 54.0 per cent at age 50 days [59]. Further, experimenters have generally switched subjects abruptly from restricted feeding to abundant or ad libitum feeding, possibly propitiating the accelerated compensatory growth that is most likely to generate delayed costs during adulthood [58]. In contrast, subordinate booby nestlings probably catch up with their siblings in size by gradually increasing ingestion as they progressively escape from sibling control. Finally, the strength of experimental hormone treatments has varied. The mean level of circulating corticosterone applied to nestlings in two doses a day for 12 days by Spencer & Verhulst [6] was roughly 50 times higher than baseline values, but the more sustained increases of up to 80.8 per cent and 138.5 per cent applied by Kitaysky et al. [5] using implants were reportedly close to natural values, and, indeed, to the mean natural increase of 109 per cent experienced by subordinate boobies [43].

The challenges experienced by blue-footed booby junior chicks differed from challenges experimentally posed to other vertebrate neonates not only in being natural but also in being generally more moderate in severity, shorter in relative duration, less abruptly suspended and encountered in a complex natural environment offering
greater scope for evasive and mitigatory responses by both parents and progeny. Experimental treatments that have successfully induced delayed costs have not been explicitly designed to mimic natural challenges, and many tests have used a domesticated strain of zebra finch, some of whose responses to experimental deprivation differ from those of wild-caught zebra finches. For example, brood enlargement and associated underfeeding of chicks resulted in greater mortality (24% versus 4.9%) between 12 and 90 days in domesticated zebra finches but not in wild-caught zebra finches [12]. Surely the biggest questions hanging over the poor start literature concern which species and precisely which challenges actually.

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