


Age-related parental care in a long-lived bird: implications for offspring development

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Abstract

In long-lived species, behaviour is expected to vary across the lifespan, first improving with maturation and experience and then declining with senescence, but measurement is rare, particularly during old age. Measuring nest defence intensity in 255 known-age blue-footed boobies (*Sula nebouxi*) of 19 age classes confirmed the inverted-U pattern: intensity of nest defence increased in young males and females until roughly 11–12 years and declined progressively afterwards. We discuss the processes that may generate this distinctive pattern. Regardless of the underlying processes, this study establishes the existence of age-related variation in parental care in a long-lived species. Natural variation in natal conditions has recently been shown to have long-term impacts on development, so this study raises the question whether age-related changes in parental care generate systematic variation in offspring phenotypes.

Significance statement

In theory, age-related change in parental care can result in differences among offspring produced at different ages. However, parental behaviour has never been measured over the whole

age-span of any long-lived species because of the difficulty of sampling very old animals in the field. We measured intensity of nest defence over the age-span and confirmed that blue-footed boobies exhibit an age-related quadratic pattern in this parental behaviour: defence intensity increases in early life and declines progressively afterwards. Our results imply that similar-shaped patterns may exist in other components of parental care, such as feeding and social interaction, potentially affecting the long-term development of offspring.

Keywords Age-related · Nest defence · Parental age · Parental care · Life history · Ageing

Introduction

According to life history theory, trade-offs between growth, somatic maintenance and reproduction will occur throughout an individual's life, affecting its fitness. Longitudinal studies of diverse taxa have shown that reproductive success, physiological function and survival tend to vary across the lifespan in a distinctive inverted-U pattern (Forslund and Pärt 1995; Ericsson et al. 2001; Berman et al. 2009). This suggests that fitness components first increase with age and experience (Forslund and Pärt 1995), probably due to maturation and learning (Robertson and Rendell 2001), then decline progressively with senescence (Jones et al. 2008; McNamara et al. 2009; Beamonte-Barrientos et al. 2010). In addition, long-lived species are expected to maximise lifetime fitness by strategically adjusting their reproductive effort and related behaviours across their lifetime (Stearns 2000). However, there is division of opinion over whether members of long-lived species maximise lifetime fitness by increasing (Clutton-Brock 1984) or reducing (McNamara et al. 2009) reproductive effort toward the end of the lifespan.

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Behavioural traits should be sensitive indicators of both capability and willingness to invest but, to our knowledge, behaviour itself has never been measured over the whole age-span of any long-lived species because of the difficulty of sampling very old animals in the field. We investigated possible change across the lifespan in parental behaviour, potentially of great interest because it could have temporary or long-term effects on offspring development. A promising behaviour for doing this is the defence of progeny. In birds and mammals, avoiding hazards to the nest can be a major reproductive challenge because it involves elevated risk and, indeed, the intensity of nest defence is highly variable. It can increase with clutch age (Greig-Smith 1980), and it can be higher in males than females (Brunton 1990). Age-related increase in intensity of nest defence has been inferred in the California gull (*Larus californicus*; Pugesek 1983) and the great skua (*Catharacta skua*; Hamer and Furness 1991), but uncertainty over sampling of age classes and sexing of individuals leaves doubt over the shape of the relationship, particularly during old age.

To test for an inverted-U pattern in nest defence, we measured it over the age-span in a marked population of a long-lived marine bird where most individuals' sexes and exact ages are known. In blue-footed boobies (*Sula nebouxi*), breeding traits such as hatching success, brood size and fledging have success peak at parental ages of 9–11 years and then decline (Drummond and Rodríguez 2015). There is also evidence that young and middle-aged adults strategically adjust their reproductive investment to their age, condition and natal environmental conditions (Velando et al. 2006; Ancona et al. 2011). Mean life expectancy is 10.01 ± 0.17 (\pm SE) and 9.55 ± 0.26 years for males and females, respectively, and the maximum recorded age is 25 years (HD, unpublished data).

Methods

Study species

The blue-footed booby lays one to three eggs on the ground and cares for the eggs during roughly 40–48 days and the chicks during 3–4 months. Throughout this time, the parents singly and jointly defend their nest and territory against conspecific and heterospecific intruders. In the study population, they regularly defend against Heermann's gulls (*Larus heermanni*), Mexican spiny-tailed iguanas (*Ctenosaura pectinata*), feral cats (*Felis silvestris catus*, extinct since 1995; CONANP 2005), milksnakes (*Lampropeltis triangulum nelsoni*) and humans, using menaces, yes head-shakes, wing flails and, occasionally, violent pecks and jabbing or seizing and tossing (Nelson 1978; Sánchez-Macouzet and Drummond 2011). However, fearful boobies sometimes back

away from a human or flee, leaving their nest temporarily exposed (HD, personal observations).

General methods

On Isla Isabel, Mexico (21° 52' N, 105° 54' W), between 6 and 16 March 2014, after the start of hatching, we recorded how 112 males 3–20 years old ($\bar{X} = 9.08$) and 143 females 3–25 years old ($\bar{X} = 8.65$) defended against human intruders. In nesting areas with few courting pairs at 7.00–13.00 and 15.00–18.00 hours, two observers haphazardly sampled boobies ringed at fledging that were caring singly (at that moment) for progeny at 255 nests (240 with eggs, 15 with chicks). No neighbours within a 10-m radius of any focal nest were tested; local nest densities within this radius ranged from 0 to 41 nests ($\bar{X} = 13.09$).

After identifying each subject's sex (females grunt, males whistle; Nelson 1978), both observers slowly and silently walked in single file toward the nest, approximately 50 cm apart. The rear observer stopped 6 m from the nest and recorded the subject's behaviour. The leading observer continued approaching, looking the subject in the eyes, then stopped 50 cm from the nest and waited for 5 s. If the subject fled, exposing its nest, both observers immediately withdrew 10 m from the nest until the subject's return; eggs were covered with leaves to conceal them from gulls. All fleeing boobies returned to their nests within a minute and no clutch or brood was lost nor abandoned as a result of the tests.

On the basis of each subject's response to the approach, the intensity of its defence was assigned to one of seven categories (in ascending order): (1) fled when the observer was > 5 m from the nest or (2) < 5 m from it, (3) uncovered its clutch but remained within 1 m of the nest, (4) remained on the nest without making vocal threats, (5) remained on the nest and started making vocal threats when the observer was 0.75–3.4 m distant or (6) 3.5–6 m distant or (7) remained on the nest and pecked toward the observer. The seven categories were assigned 0–6 points, respectively; each subject was allocated to the highest category it performed. Data were recorded blindly; identities/ages of subjects were not known at the time of testing or assigning response categories.

Statistical analyses

To analyse the relationship between nest defence and parental age, we built a linear mixed model (LMM), including six additional predictors that might influence defence, using an information-theoretic approach (Burnham and Anderson 2002). All variables were standardized prior to model fitting to minimize linear and quadratic terms'

collinearity and to facilitate the interpretation of the relative strength of parameter estimates (Grueber et al. 2011; Cade 2015). Fixed effects comprised the linear and quadratic expressions of the focal bird's age, sex, nest content (clutch/brood), brood size, local nest density (number of nests in a 10-m radius), linear and quadratic expressions of time of day and date of the test. Nest content and brood size were included to control for their possible effects on investment in defence; local nest density was included to account for neighbours' possible influence on the subjects' responses to an intrusion, and time of day was included to control for possible circadian changes in behaviour.

We fitted the models with a Gaussian error distribution and an identity link function, including nest identity as a random effect because both members of the pair were studied in 37 cases. Rather than fitting models for all possible combinations of predictors, we generated 19 hypothesis-based candidate models (plus a null model), ranked from "best" to "worst" using Akaike's information criterion corrected for small samples (AIC_c). We then computed Akaike weights to estimate the relative support in the data for each of the fitted models (Burnham and Anderson 2002). Based on these Akaike weights, we averaged the fits of a subset of the best-fitting models which, together, had a cumulative Akaike weight (w_i) of ~ 0.95 (Table 1). This multi-model averaging approach accounts for model selection uncertainty and reduces model selection bias by considering the relative support for each competing model, thus providing more robust parameter estimates than those obtained from any single-model approach (Burnham and Anderson 2002). Additionally, we repeated the analysis after deleting an extremely old bird (25 years) from the sample to test whether it influenced the regression coefficients of age and age² (Supplementary material, S1).

All analyses were performed in R statistical environment (v3.3.3) (R Development Core Team 2017). We used *lmer* function in *lme4* package (Bates et al. 2016) to construct our model. To standardize all model variables we used *rescale* function in package *arm* (Gelman et al. 2016). We used the *mod.avg* function to average models within a 95% confidence interval (CI) (Burnham et al. 2011) in MuMIn package (Bartón 2016) and *confint* function to calculate the CI of each parameter.

Results

We used the six best-fitting models (Table 1) for the model averaging procedure. Age and age² were the predictors of nest defence intensity with the highest relative support in the data (both of 1), and the only terms whose regression coefficients were statistically different from zero ($\beta = 0.87$ and 95% confidence interval (CI) = 0.42 to 1.32 and

$\beta = -1.37$, CI = 2.01 to -0.73 , respectively; Table 2; Fig. 1). There was low relative support for the linear and quadratic expressions of time of day, nest content, date of test, local nest density and brood size (Table 2). After excluding the 25-year-old bird, only the regression coefficient of the quadratic relationship between parental age and nest defence intensity remained statistically different from zero; its relative support was diminished and the pattern of increase followed by decline in defence with age was more symmetrical (Supplementary material, S2, S3, S4, S5). To test whether the decline in defence in old age was supported by the data, we re-applied the model selection procedure to the sample of boobies older than 11 years (the age at which reproductive variables peak; Beamonte-Barrientos et al. 2010; Drummond and Rodríguez 2015), including the factors retained in the averaged model except the quadratic expression of age. This analysis confirmed the linear decrease in nest defence intensity between ages 12 and 25 years ($\beta = -0.57$, CI = -1.39 to -0.03 ; Supplementary material, S6, S7, S8).

Discussion

The intensity with which blue-footed boobies of Isla Isabel defended their nests against human intruders varied with parental age, increasing up to roughly age 11–12 years and declining thereafter. This quadratic relationship between parental age and nest defence was independent of sex, nest content, brood size, local nest density, time of day and test date. After the removal of a 25-year-old bird from the sample, the U-pattern remained, but the decline with old age was less well supported; widening of the confidence interval at old ages admits the possibility that nest defence plateaus in late life, as observed in other species (Angelier et al. 2007; Berman et al. 2009), rather than declining. Nonetheless, the combined analyses of the complete data set and the subset for ages 12–25 years supported a pattern of increase in early life and decline in old age, and the confidence intervals showed that late-life decline is unlikely to be absent and may be steep. To our knowledge, this is the first study to report directly observed parental behaviour of known-age individuals across the entire natural age-span of a long-lived species in the wild.

The increase in intensity of nest defence through roughly age 11–12 years is most readily explained by maturation and learning (Robertson and Rendell 2001): older birds with more experience in pairing, territory acquisition, foraging and breeding (including nest defence) may simply be more able to prudently mount a strong defence. Similarly, progressive reduction in nest defence intensity in old age is most readily explained by senescent decline in those same capabilities.

Table 1 Models investigating variation in nest defence intensity ranked according to their relative support in the data, from best to worst

Model	Fixed effects	df	logLik	AIC _c	ΔAIC _c	w _i
1	<i>Age + Age²</i>	5	- 448.22	906.68	0.00	0.34
2	<i>Age + Age² + Time of day + Time of day²</i>	7	- 446.66	907.77	1.09	0.19
3	<i>Age + Age² + Nest content</i>	6	- 447.77	907.88	1.20	0.19
4	<i>Age + Age² + Date</i>	6	- 448.08	908.50	1.82	0.14
5	<i>Age + Age² + Local nest density</i>	6	- 448.76	909.86	3.19	0.07
6	<i>Age + Age² + Brood size</i>	6	- 448.89	910.12	3.45	0.06
7	Null	3	- 456.84	919.77	13.09	0.00
8	Time of day + Time of day ²	5	- 455.24	920.72	14.05	0.00
9	Global model	12	- 447.73	920.75	14.07	0.00
10	Nest content	4	- 456.50	921.16	14.48	0.00
11	Age	4	- 456.62	921.40	14.72	0.00
12	Date	4	- 456.64	921.45	14.77	0.00
13	Age + Nest content	5	- 456.14	922.52	15.84	0.00
14	Age + Time of day + Time of day ²	6	- 455.16	922.66	15.98	0.00
15	Local nest density	4	- 457.53	923.23	16.55	0.00
16	Brood size	4	- 457.57	923.31	16.63	0.00
17	Sex	4	- 457.57	923.31	16.63	0.00
18	Age + Date	5	- 456.57	923.38	16.70	0.00
19	Age + Local nest density	5	- 457.29	924.81	18.14	0.00
20	Age + Brood size	5	- 457.34	924.92	18.24	0.00

Best-fitting models with a cumulative Akaike weight (w_i) of ~ 0.95 are in italics. Sample size of 255 birds. Fixed terms effects for each model in electronic supplementary material (S1)

logLik log likelihood, *AIC_c* Akaike Information Criterion adjusted for small sample sizes, *ΔAIC_c* difference in *AIC_c* scores between current model and the most parsimonious model, *Age* focal bird's age, *Age²* squared focal bird's age, *Nest content* brood or clutch, *Date* test date, *Local nest density* number of nests within a 10-m radius of the focal bird's nest, *Time of day* time of day when the focal bird was tested, *Time of day²* squared time of day, *Brood size* number of eggs or chicks, *Sex* focal bird's sex, *Global model* all terms included

However, this species' age-related curves of responsiveness to human intruders (an inverted-U; this study) and to experimentally standardised conspecific intruders (no effect across ages 5–13 years; Sánchez-Macouzet and Drummond 2011) differ, implying that strategy is also involved.

Sampling of ages was cross-sectional, so the observed increase and decrease in nest defence could alternatively be

explained by differential survival of individuals that differed in defensiveness (and possibly in other reproductive traits; Forslund and Pärt 1995; McCleery et al. 2008) or even by differences among birth cohorts. It is difficult to construct a plausible hypothesis based on such effects that can account for the whole inverted-U pattern, but the decline in old age could in theory arise from high mortality among more aggressive

Table 2 Summary of the averaged model explaining the relationship between age and nest defence intensity

	Estimate*	Unconditional SE	95% CI	Relative support
Intercept	–	–	–	–
Age	0.87	0.22	0.42 to 1.32	1.00
Age ²	- 1.37	0.32	- 2.01 to - 0.73	1.00
Hour	0.10	0.25	- 0.00 to 1.09	0.20
Hour ²	- 0.17	0.45	- 2.15 to 0.37	0.20
Nest content	0.07	0.22	- 0.35 to 1.11	0.19
Date	- 0.33	0.10	- 0.59 to 0.10	0.14
Local nest density	0.00	0.05	- 0.22 to 0.48	0.07
Brood size	0.00	0.04	- 0.26 to 0.44	0.06

Age and age² have the highest relative support, suggesting that they are more informative than the other parameters. Estimated variance of the random factor nest identity was 0.29

*Effect sizes have been standardized on two SDs

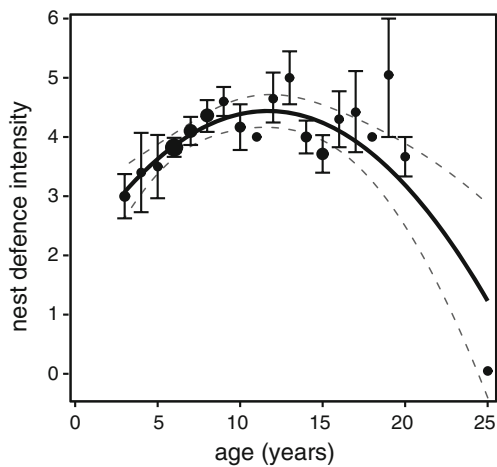


Fig. 1 Nest defence intensity according to parental age. Black dots denote mean nest defence of sampled age classes with standard errors. Solid line represents model prediction with 95% confidence intervals (in dashed lines). Dot size is related to number of birds per age class. Sample sizes, from left to right, are 17, 10, 8, 63, 39, 31, 5, 12, 1, 6, 5, 13, 21, 10, 7, 1, 2, 3 and 1

individuals. Strategic modification of resource allocation with age could partially account for the inverted U-shaped curve and also for the high variation in nest defence in old blue-footed boobies, which sometimes increase investment in their last reproductive event (Torres et al. 2011). Complete accounting for the shape of the whole inverted-U pattern may well require consideration not only of maturation, learning and senescence but also of differential survival of varied phenotypes and strategic adjustments of resource allocation.

Discovery of this booby's age-related U-shaped pattern of defence implies that similar-shaped patterns may exist in other components of parental care such as incubation, nestling provisioning and social interactions, with potentially important consequences for offspring characteristics and parental fitness. Similarly, other animal species may show age-related linear or quadratic patterns in components of parental care, resulting in differences in offspring produced at different ages. Avian and mammalian offspring raised in poor ecological conditions in nature have shown a panoply of effects on their adult survival, reproduction and ageing, including adoption of alternative life histories (Nussey et al. 2007; Drummond and Ancona 2015; Douhard et al. 2016) and, in principle, age-related variation in parental care could generate similar developmental effects. Effects of parental age over the age-span on offspring growth and viability have recently been uncovered (Torres et al. 2011; Drummond and Rodríguez 2015; Preston et al. 2015), but to our knowledge, the possibility of age-related change in parental care itself affecting the characteristics of offspring has not been directly tested in any species.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national and/or institutional guidelines for the care and use of animals were followed. The Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT) provided the permit for this study (SGPA/DGVS/10856/13).

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Data availability

All data generated or analysed during this study are included in this published article and its supplementary information files.