

Effects of recruiting age on senescence, lifespan and lifetime reproductive success in a long-lived seabird

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Received: 4 August 2009 / Accepted: 10 January 2011 / Published online: 1 February 2011
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Abstract Theories of ageing predict that early reproduction should be associated with accelerated reproductive senescence and reduced longevity. Here, the influence of age of first reproduction on reproductive senescence and lifespan, and consequences for lifetime reproductive success (LRS), were examined using longitudinal reproductive records of male and female blue-footed boobies (*Sula nebouxi*) from two cohorts (1989 and 1991). The two sexes showed different relationships between age of first reproduction and rate of senescent decline: the earlier males recruited, the faster they experienced senescence in brood size and breeding success, whereas in females, recruiting age was unrelated to age-specific patterns of reproductive performance. Effects of recruiting age on lifespan, number of reproductive events and LRS were cohort- and/or sex-specific. Late-recruiting males of the 1989 cohort lived longer but performed as well over the lifetime as early recruits, suggesting the existence of a trade-off between early recruitment and long lifespan. In males of the 1991 cohort and females of both cohorts, recruiting age was apparently unrelated to lifespan, but early recruits reproduced more frequently and fledged more chicks over their lifetime than late recruits. Male boobies may be more likely than females to incur long-term costs of

early reproduction, such as early reproductive senescence and diminished lifespan, because they probably invest more heavily than females. In the 1991 cohort, which faced the severe environmental challenge of an El Niño event in the first year of life, life-history trade-offs of males may have been masked by effects of individual quality.

Keywords Cost of reproduction · Life-history · Southern Oscillation Index (SOI) · *Sula nebouxi* · Trade-off

Introduction

A trade-off between reproduction and survival is a major assumption of life-history theory (Stearns 1992). Iteroparous breeders should maximize their fitness by allocating energy and resources between current and future reproduction (Schaffer 1974; Partridge 1992), as demonstrated in diverse taxa (e.g., Partridge and Farquhar 1981; Gustafsson and Pärt 1990; Nussey et al. 2006). The benefits of early recruitment can include an increased number of reproductive events over the lifespan and shortening of generation time; the costs can include a reduction in survival or future reproduction (Blondel et al. 1992; Oli et al. 2002) and accelerated senescence. Therefore, the trade-offs together with selective processes on timing of recruitment should shape the life-history of organisms (Roff 2002).

Evolutionary theories of ageing are based on the idea that mutations whose effects are expressed at later ages will have a lower impact on fitness. Two non-mutually exclusive mechanisms have been proposed for the evolution of senescence: accumulation of mutations (Medawar 1952) and antagonistic pleiotropy (Williams 1957). According to the first, senescence occurs due to an accumulation of late-acting deleterious mutations because the strength of natural

Communicated by Christopher Johnson.

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selection declines with advancing age. According to the second, senescence can be promoted by selection favoring genes that improve early-life performance but have adverse effects in later life. In the phenotypic level, such genes could favor resource allocation to early reproduction over somatic maintenance, and consequently promote accelerated reproductive senescence in later life and reduced longevity (disposable soma; Kirkwood 1977; Kirkwood and Rose 1991).

Empirical exploration of effects of early reproduction on individual life-histories is limited. Early reproduction was associated with accelerated reproductive senescence of red deer (*Cervus elaphus*) and common guillemots (*Uria aalge*) (Nussey et al. 2006; Reed et al. 2008), and increased reproductive effort early in life was associated with accelerated senescence in fertility of collared flycatchers (*Ficedula albicollis*) (Gustafsson and Pärt 1990). The effects of recruiting age (age at first reproduction) on lifespan, senescence and lifetime reproductive success (LRS) have seldom been tested in a long-lived species, which requires measuring components of life-histories over entire individual lifespans (Viallefont et al. 1995). In two long-lived bird species, the western gull (*Larus occidentalis*) and the greater flamingo (*Phoenicopterus ruber roseus*), recruiting age of females was positively related to survival, suggesting a trade-off between early recruitment and lifespan, but fitness consequences of recruiting age were not measured (Pyle et al. 1997; Tavecchia et al. 2001).

Trade-offs are difficult to detect because individual differences in age-specific reproductive performance, lifespan and lifetime fitness can arise from individual strategic decisions regarding recruiting age, genetic variation in recruiting age and individual variation in environmental constraints. Where life-history data are available for marked individuals, trade-offs between early reproduction and senescence or lifespan can be difficult to detect when individual quality varies (Cam et al. 2002). Indeed, some studies of short-lived birds found that earlier recruits had higher LRS, and this association was interpreted as an effect of breeder quality (Newton 1985). Associations between breeder quality and life-history traits can mask trade-offs between early reproduction and senescence or lifespan, particularly when breeders adjust their early reproductive investment to current conditions or when breeder quality varies greatly with cohort or sex.

Life-history trade-offs and selection may also be affected by environmental conditions experienced by individuals. The environment experienced early in life can affect life-history traits by influencing individual condition at recruitment and reproduction (breeder quality; Moyes et al. 2009) and the cost of early reproduction (Sedinger et al. 1995; Lindström 1999; Descamps et al. 2008). In the

long-lived common guillemot, a harsh early-life environment was associated with accelerated senescent decline in breeding success (Reed et al. 2008). When different cohorts encounter different early environments they can face different trade-offs between recruiting age and senescence/lifespan and respond by recruiting at different ages. When the recruiting age of a cohort is closely related to individual condition, any trade-off between life-history traits is likely to be masked by effects of breeder condition.

Research on life-history trade-offs is often confined to a single sex, but life-history differences between the sexes are to be expected (Rice and Chippindale 2001) and the sexes may differ in selective advantages and as to how recruiting age trades off against lifespan and senescence, especially when the cost of early reproduction is greater for one sex. Firm evidence for sexual asymmetry in costs of reproduction is lacking in socially monogamous species (Tavecchia et al. 2001), but is available for polygamous species in which males and females differ greatly in the relative effort they put into mating versus parental care (e.g., Michener and Locklear 1990). A number of studies of socially monogamous species suggest that females invest more than males in egg laying and brood care (Monaghan et al. 1998) while males incur greater costs than females during competition for territories and mates (Bonduriansky et al. 2008), particularly when the operational sex ratio is male-biased (Ahnesjö et al. 2001). Different developmental trajectories could result in males and females being ready for reproduction at different ages.

In this study, we analyze longitudinal data on the blue-footed booby (*Sula nebouxii* Milne-Edwards), a long-lived tropical seabird. Blue-footed boobies are socially monogamous and both sexes contribute to care of eggs and chicks (Nelson 2005; Guerra and Drummond 1995). However, in the study population, competition for mates may be particularly severe among males since the operational sex ratio appears to be male biased despite absence of a bias in the sex ratio at recruitment (51% males in the period 1988–2004; Oro et al. 2010). Throughout the breeding cycle, both sexes spend a similar time caring for eggs and chicks but females, which are larger and heavier than males, provide a greater mass of food to chicks (Guerra and Drummond 1995). However, male boobies assume most of the costs of establishing a territory in the highly competitive colony environment (Nelson 2005). Boobies feed on epipelagic fish, and therefore their reproductive success and early development are closely tied to oceanographic conditions, particularly the El Niño Southern Oscillation (Anderson 1989; Nelson 2005). Survival rate of yearlings in the study population varies from 0.535 to 0.755 depending on sea surface temperature during the winter (Oro et al. 2010).

We examined the reproduction and survival of two cohorts of male and female fledglings over 17 years of life, particularly how recruiting age trade-offs against reproductive senescence and lifespan. If recruiting age constrains other life-history traits, as predicted by the antagonistic pleiotropy theory of ageing (Kirkwood and Rose 1991), early recruits should experience faster senescent decline in reproductive performance and live shorter lives than late recruits. However, LRS should not be influenced by recruiting age unless strong effects of individual quality mask life-history trade-offs. We also studied sexual and environmental effects on the selection of early recruitment by examining the relationship between recruiting age and LRS.

Materials and methods

Study system and general field procedures

We studied the colony of blue-footed boobies on Isla Isabel, Nayarit (21°52'N, 105°54'W), off the Pacific coast of Mexico. Since 1989, the reproductive performance of all breeders in two study areas measuring 20,800 and 6,089 m² and roughly 400 m apart has been recorded. The majority of males and females recruit at age 2–6 years, and females recruit on average nearly half a year earlier than males (Osorio-Beristain and Drummond 1993; Drummond et al. 2003; Oro et al. 2010).

Every year, all nests with a clutch or brood in the study areas were marked with wooden stakes and fledglings were marked with steel rings. Brood sizes and chick survival were recorded during roughly 20 weeks by surveying all nests every few days from shortly after the start of hatching until each chick reached age 70 days, close to fledging, the last chicks doing so in July (Drummond et al. 2003). Exceptionally, in 1989, chick survival was surveyed until each chick fledged fully (completed plumage development; mean age = 86 days for males and 90.5 days for females; Drummond et al. 1991). Date of laying of the first egg in each clutch was recorded when it occurred during the survey period or estimated from the ulna and culmen lengths of the chick at first encounter. We analyzed brood size rather than clutch size because many clutches were not observed for the first time until days or weeks after laying (i.e., after possible egg loss). Each breeder's ring number was confirmed by independent readings on up to 3 days.

Sampling and environmental conditions

To examine effects of recruiting age on age-specific reproductive performance, lifespan, number of reproductive events during the lifetime and LRS, we analyzed all

breeding records up to age 17 years of all male and female fledglings from the 1989 and 1991 cohorts that recruited into the colony. No fledglings were ringed in 1990, and in 1992, few chicks fledged due to a severe El Niño event. Blue-footed boobies show long-term fidelity to their first breeding neighborhoods, and long-distance natal and breeding dispersal from the study colony seems rare (Kim et al. 2007b), so we were able to record complete life-histories of marked recruits to the breeding colony.

To examine the effects of recruiting age on annual breeding success, lifespan and LRS, we limited the sample to birds that recruited at ages 2–6 years. Among male and female recruits fledged in the 1989 and 1991 cohorts, 11.2% were recorded breeding for the first time at greater ages, between 7 and 16 years. Some of these extremely late recruits may have bred earlier but escaped sampling; first-time breeders often fail early in incubation due to inexperience and they escape sampling whenever they abandon their clutches before we can read their rings. The majority (73.8%) of these extremely late recruits were transients (birds that breed only once during the lifetime). Therefore, birds that recruited at >6 years were excluded from our analyses because they provide insufficient breeding records to examine longitudinal patterns of reproductive performance over the lifetime. Strictly, our conclusions apply only to birds that recruit in the first 6 years of life and may not apply to the poorest quality individuals. Systematic variation in probability of detecting marked animals can bias estimates of age-specific patterns (Boulinier et al. 1997). However, we have no data to evaluate whether recapture failure was related to age (see also Oro et al. 2010).

Environmental conditions experienced early in life by the two cohorts are indexed by the Southern Oscillation Index (SOI, Australian Bureau of Meteorology, <http://www.bom.gov.au/climate/current/soihtml1.shtml>) and the mean annual breeding success of the booby colony. During El Niño episodes in the Pacific Ocean, which are characterized by unusually warm surface temperatures, the SOI has a large negative value and upwelling of the cold, nutrient-rich waters that sustain large fish populations, and thence seabirds, is reduced. During La Niña episodes, which are characterized by cold surface temperatures in the Pacific, the SOI has a positive value. The two focal cohorts experienced different levels of environmental stress early in life. The 1991 cohort fledged in a year when breeding success of the colony was poor (Fig. 1) and in their first year these birds lived through the locally most severe El Niño episode of our 27-year population study (in 1992, few birds nested and nest success for the whole colony was zero; Drummond et al. 2003; Fig. 1). In contrast, the 1989 cohort fledged in a year of high colony breeding success late in a La Niña episode and did not experience a severe

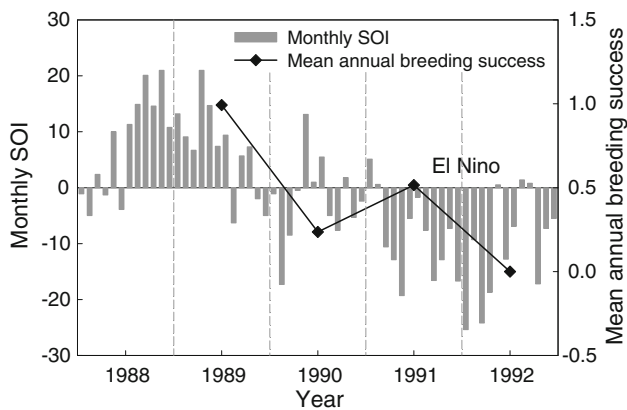


Fig. 1 Monthly Southern Oscillation Index (SOI) and mean annual breeding success (number of chicks fledged) in the Isla Isabel blue-footed booby (*Sula nebouxi*) colony between 1988 and 1992. SOI were obtained from the Bureau of Meteorology, Australia (<http://www.bom.gov.au/climate/current/soihtml1.shtml>)

El Niño episode until 3 years old. Only two individuals of the 1989 cohort recruited during the 1992 El Niño episode, although normally many individuals recruit at age 3 years (e.g., Drummond et al. 2003).

Statistical analyses

Laying dates were expressed as proportional rank among all breeding pairs in our study areas in each year (0 the earliest breeder, 1 the latest breeder), as timing of the breeding season (Julian date) varied across years and the distribution differed from normal (Kim et al. 2007a). Mean brood size (number of chicks that hatched) and breeding success (number of chicks that survived until age 70 days) of all breeding pairs in the study areas varied among years between 1991 and 2008 (ANOVA: brood size: $F_{17,18,200} = 237.16$, $P < 0.001$; breeding success: $F_{17,18,200} = 318.21$, $P < 0.001$). Therefore, brood size and breeding success of individuals in any season were standardized within years by the z-transformation (mean = 0, SD = 1) prior to analysis, using the annual population-wide mean and SD performance of all observed breeding pairs (not solely known-age breeders). Lifespan of recruits was their age at the last observed breeding record up to 2006 and 2008 for the 1989 and 1991 cohorts, respectively (maximum age 17 years). LRS was the total number of chicks fledged during each recruit's lifetime up to age 17 years. Although at least 5% of birds from the 1989 and 1991 cohorts were still alive at age 17 years, these measures provide approximate lifespan and LRS of most individuals. Lifespan calculated as age at the last observed reproduction is possibly inaccurate in those birds that survived until age 17 years, but a better estimate of lifespan is unlikely to diminish the pattern observed in our

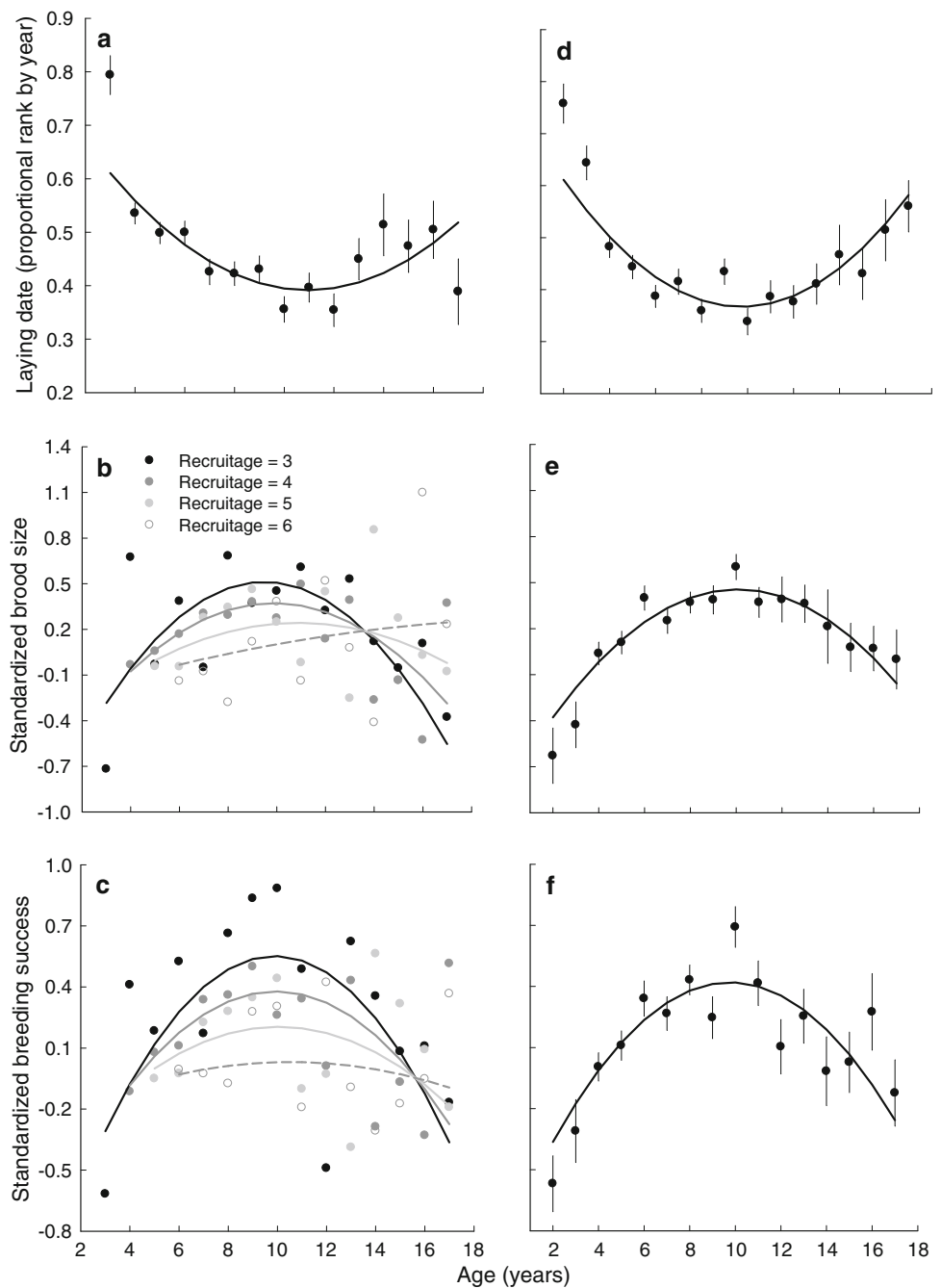
results because the positive correlation between recruiting age and lifespan may be underestimated in our analysis (see “Results”).

To examine effects of cohort and sex on recruiting age, we used a Generalized Linear Model (GLM) with a Poisson error distribution and a log link function.

We used linear mixed effect models (LMEs) for male and female breeders to examine effects of recruiting age, lifespan and current age on components of breeding performance such as laying date, brood size and breeding success. Individual identity (ring number) was included as a random effect in LMEs since most birds bred repeatedly. By analyzing males and females separately in the individual-based models, we avoided replication of data points from paired birds. Since not all birds in the study area were ringed, we could not include identities of breeding partners in the models. The duration of pair bonds is short (on average 1.7 years, unpublished data) and ages of mated breeders were not correlated ($r = 0.08$, $P = 0.07$, 537 pairs in 2007, unpublished data) in the study population. Therefore, the degree of non-independence due to correlation of female and male identity across the duration of the pair bond and assortative mating by age was minor.

Cross-sectional studies may wrongly estimate the abilities of young breeders by including low-quality, poorly performing individuals that die young or individuals that invest heavily in reproduction and survive few breeding seasons (Reid et al. 2003; Velando et al. 2006a; Kim et al. 2007a; Nussey et al. 2008); and conditions during year of birth may affect reproduction throughout the lifetime. Therefore, we initially included lifespan (age at the last observed breeding event) and cohort in LMEs (van de Pol and Verhulst 2006; van de Pol and Wright 2009). A quadratic term for current age was included in LMEs because reproductive performance declines at advanced ages in our study species (e.g., after age 10–11 years; Velando et al. 2006a). However, a quadratic age effect may be driven by improvement early in life even when performance merely levels off rather than declining. Therefore, we additionally fitted piecewise regression models to estimate a threshold where senescent decline starts and slopes before and after the threshold. Piecewise linear regression allows multiple linear models to be fit to the data for different ranges of independent variable, and a threshold is the value where the slope of the linear function changes. The value of the unknown threshold and slopes were estimated by interactive Marquardt method that optimizes the residual sum of squares regressing the residuals onto the partial derivatives of the model with respect to the parameters until the estimates converge (SAS Institute 1999). Whenever the interaction between recruiting age and age was significant in a LME, a piecewise regression model was fitted to subsamples of each recruiting age (see Fig. 2).

Fig. 2 Means (\pm SE) laying date (proportional rank by year), brood size and breeding success (standardized by year) according to current age in male and female blue-footed boobies from the 1989 and 1991 cohorts. *Fitted lines* are derived relationships in LME models (see Table 1): **a** male laying date, **b** male brood size, **c** male breeding success, **d** female laying date, **e** female brood size, **f** female breeding success



To examine effects of recruiting age, cohort and sex on lifespan up to maximum age 17 years, number of reproductive events over the lifetime and LRS, we used GLMs with a quasi-Poisson error distribution and a log link function rather than Poisson errors to account for overdispersion (recommended by Crawley 2007). Here, recruiting age was standardized by cohort and sex prior to the analyses to avoid colinearity between independent variables.

Initially, all explanatory variables and two- and three-way interactions of interest were fitted in a maximal model,

then non-significant interactions and main terms were dropped sequentially to simplify the model. To compare the simplified minimal adequate model with the model including a non-significant term or with the model excluding a significant term, we used likelihood ratio tests for LMEs and *F* tests for GLMs (Crawley 2007). We present the simplified minimal adequate models with estimates and SEs of each parameter. All LMEs and GLMs were fitted using R (v. 2.7.2; R Development Core Team 2008) and piecewise regression models were fitted using PROC NLIN procedure in SAS (SAS Institute 1999).

Results

Age of recruitment

A total of 645 chicks fledged and were ringed in 1989; a total of 429 chicks survived until age 70 days and were ringed in 1991. Of the marked fledglings, 57.0% of the 1989 cohort and 32.2% of the 1991 cohort recruited to the colony. A total of 208 males and 181 females recruited to the study area, showing similar recruiting success for fledglings of the two sexes (Chi-square test: $\chi^2_1 = 1.12$, $P = 0.29$) on the basis of the observed fledgling sex ratio of the 1989 cohort (326 males and 246 females; Torres and Drummond 1999). Among fledglings of the 1991 cohort, 69 males and 69 females recruited.

Among birds of the 1989 cohort, 0, 2, 115, 57 and 13 males and 10, 0, 101, 40 and 12 females recruited when 2, 3, 4, 5 and 6 years old, respectively. Among birds of the 1991 cohort, 16, 22, 14 and 7 males and 36, 17, 5 and 1 females recruited when 3, 4, 5 and 6 years old, respectively. Birds of the 1989 cohort recruited at older ages (on average half a year older) than those from the 1991 cohort

(GLM: deviance₁ = 5.35, $P = 0.02$). Recruiting age was independent of sex and cohort \times sex (sex: deviance₁ = 2.45, $P = 0.12$; cohort \times sex: Deviance₁ = 1.79, $P = 0.18$).

Age-specific annual reproductive performance

A total of 246 males and 222 females nested up to maximum ages of 17 years, performing 1,477 and 1,409 breeding events, respectively. Both males and females produced progressively earlier clutches and progressively greater brood sizes and breeding success up to age 8–11 years; beyond that age, they laid progressively later, with declining brood sizes and breeding success up to age 17 years, as shown by significant quadratic effects of age and piecewise regressions (Tables 1 and 2; Fig. 2). Cohort, cohort \times age, cohort \times age², recruitment \times cohort \times age and recruitment \times cohort \times age², and also lifespan, were nonsignificant in all LMEs, so these terms were excluded from the minimal adequate models of both sexes (Table 1).

The recruitment \times age interaction was significant for brood size of males and the recruitment \times age² interaction

Table 1 Summary of minimal adequate LMEs with breeder identity as a random effect examining the effects of recruiting age (recruitment) and breeding age (up to age 17 years) on laying date (proportional rank by year), brood size and breeding success (standardized by year)

Fixed effects	Males			Females		
	Estimate \pm SE	χ^2_1	P	Estimate \pm SE	χ^2_1	P
Laying date						
Intercept	0.807 \pm 0.049			0.754 \pm 0.044		
Age	-0.076 \pm 0.011	23.10	<0.001	-0.079 \pm 0.010	2.85	0.092
Age ²	0.003 \pm 0.001	33.95	<0.001	0.004 \pm 0.001	57.64	<0.001
Brood size						
Intercept	-2.076 \pm 0.972			-0.842 \pm 0.151		
Recruitment	0.295 \pm 0.235	3.55	0.060	NS		
Age	0.665 \pm 0.214	5.95	0.015	0.258 \pm 0.035	7.88	0.005
Age ²	-0.037 \pm 0.011	30.62	<0.001	-0.013 \pm 0.002	45.95	<0.001
Recruitment \times age	-0.102 \pm 0.051	4.06	0.044	NS		
Recruitment \times age ²	0.006 \pm 0.003	5.55	0.018	NS		
Breeding success						
Intercept	-2.141 \pm 1.001			-0.819 \pm 0.156		
Recruitment	0.307 \pm 0.242	8.00	0.005	NS		
Age	0.654 \pm 0.220	4.41	0.036	0.253 \pm 0.037	46.83	<0.001
Age ²	-0.033 \pm 0.011	33.92	<0.001	-0.013 \pm 0.002	43.85	<0.001
Recruitment \times age	-0.098 \pm 0.052	3.56	0.059	NS		
Recruitment \times age ²	0.005 \pm 0.003	3.82	0.051	NS		

Full model: recruitment + age + age² + cohort + lifespan + recruitment \times cohort + recruitment \times age + recruitment \times age² + cohort \times age + cohort \times age² + recruitment \times cohort \times age + recruitment \times cohort \times age²

NS $P > 0.05$ and term dropped from model

was significant for brood size of males and marginally significant for breeding success of males (Table 1; Fig. 2), suggesting different senescence patterns among different recruiting age classes. In additional piecewise regression models fitted separately to males that recruited at ages 3, 4 and 5 years, the lifetime peak in brood size appeared at ages 9, 11 and 8 years, respectively, but the model with a threshold did not converge in males that recruited at age 6 years (Table 2). The peak in breeding success for males that recruited at ages 3, 4, 5 and 6 appeared at ages 9, 8, and 10 years, respectively (Table 2). After the pick, male brood size and breeding success decreased with age, but the decline was faster in early recruits (Table 2).

Lifespan, number of reproductions and lifetime reproductive success

The interaction between recruiting age, cohort and sex (recruitment × cohort × sex) was significant for number of reproductions and marginally significant for LRS, while only a two-way interaction, recruitment × cohort, was significant for lifespan (Table 3). Lifespan (age at last reproduction) was positively correlated with recruiting age in males from the 1989 cohort but not in males from the 1991 cohort (Fig. 3a). However, the interaction between recruiting age and cohort was less evident in females (Fig. 3a). Recruiting age was unrelated to either total number of reproductive events over the lifetime or LRS in males from the 1989 cohort, but was negatively correlated

to both traits in males from the 1991 cohort and females of both cohorts (Fig. 3b, c). Thus, in the (environmentally favored) 1989 cohort, males that recruited later apparently lived longer but with no reproductive pay-off; whereas in the (environmentally disfavored) 1991 cohort, late male recruits reproduced less often and less successfully overall over a lifetime that was not prolonged by delaying reproduction. In females from both the 1989 and 1991 cohorts, early recruits reproduced more often and more successfully over a lifetime.

Discussion

Effects of recruiting age on reproductive senescence

Our analyses of long-lived individuals of two cohorts that experienced different environmental conditions in early life show that, after reaching their reproductive peak at age 8–11 years, both male and female blue-footed boobies experience reproductive senescence; and that senescence involves delayed egg laying, diminishing brood sizes (a function of clutch size and hatching success) and declining annual breeding success. Similarly, initial increase in annual breeding success followed by senescent decline was shown when the sample was limited to males that survived to at least age 13 years (Velando et al. 2006a) and females that survived to at least age 16 years (Beamonte-Barrientos et al. 2010). Males presumably influence laying date, clutch

Table 2 Effects of age on laying date, brood size and breeding success of male and female blue-footed boobies from the 1989 and 1991 cohorts

Model	Estimate ± SE (95% CI)				P
	Intercept	Slope ₁	Threshold	Slope ₂	
Males					
Laying date	0.662 ± 0.036	-0.029 ± 0.005 (-0.040, -0.019)	10.00 ± 0.61	0.017 ± 0.006 (0.005, 0.029)	<0.001
Brood size	-0.472 ± 0.140	0.098 ± 0.023 (0.053, 0.143)	8.75 ± 0.65	-0.049 ± 0.017 (-0.082, -0.016)	<0.001
Recruitment = 3	-0.786 ± 0.332	0.159 ± 0.056 (0.049, 0.270)	9.35 ± 1.33	-0.116 ± 0.065 (-0.244, 0.012)	0.008
Recruitment = 4	-0.251 ± 0.126	0.065 ± 0.018 (0.029, 0.101)	10.72 ± 0.75	-0.113 ± 0.038 (-0.189, -0.038)	<0.001
Recruitment = 5	-0.840 ± 0.529	0.151 ± 0.089 (-0.024, 0.327)	7.90 ± 1.14	-0.041 ± 0.026 (-0.091, 0.009)	0.028
Recruitment = 6 ^a	-0.500 ± 0.322	0.058 ± 0.031 (-0.003, 0.119)	-	-	0.062
Breeding success	-0.576 ± 0.144	0.116 ± 0.024 (0.070, 0.162)	8.51 ± 0.54	-0.060 ± 0.017 (-0.094, -0.026)	<0.001
Recruitment = 3	-0.974 ± 0.405	0.217 ± 0.074 (0.070, 0.364)	8.52 ± 1.15	-0.114 ± 0.057 (-0.227, -0.002)	0.003
Recruitment = 4	-0.661 ± 0.224	0.139 ± 0.041 (0.058, 0.219)	7.84 ± 0.71	-0.052 ± 0.020 (-0.092, -0.013)	<0.001
Recruitment = 5	-0.736 ± 0.528	0.132 ± 0.089 (-0.044, 0.307)	7.91 ± 1.21	-0.050 ± 0.026 (-0.100, 0.000)	0.056
Recruitment = 6	-0.389 ± 0.932	0.057 ± 0.127 (-0.196, 0.309)	9.96 ± 5.13	-0.027 ± 0.061 (-0.149, 0.094)	0.902
Females					
Laying date	0.587 ± 0.033	-0.025 ± 0.005 (-0.035, -0.015)	9.93 ± 0.55	0.027 ± 0.006 (0.015, 0.039)	<0.001
Brood size	-0.367 ± 0.113	0.094 ± 0.018 (0.060, 0.129)	9.84 ± 0.56	-0.083 ± 0.021 (-0.124, -0.042)	<0.001
Breeding success	-0.508 ± 0.135	0.122 ± 0.023 (0.077, 0.166)	8.31 ± 0.54	-0.061 ± 0.018 (-0.095, -0.026)	<0.001

Parameter estimates (*slope*₁ slope before the threshold, *slope*₂ slope after the threshold) from the best fit piecewise regression models

^a A convergence problem occurred when fitting a piecewise regression model with a threshold

Table 3 Summary of minimal adequate GLMs with a quasi-Poisson error distribution and a log link examining the effect of recruiting age, cohort and sex on lifespan (age at last breeding), number of reproductive events during lifetime and lifetime reproductive success

(=total number of chicks fledged during lifetime) of male and female blue-footed boobies from the 1989 and 1991 cohorts (males: $n = 246$; females: $n = 222$)

	Estimate \pm SE	Deviance ₁	<i>P</i>
Lifespan			
Intercept	2.337 \pm 0.021		
Recruitment	0.048 \pm 0.021	2.15	0.242
Cohort	0.053 \pm 0.041	2.75	0.185
Recruitment \times cohort	-0.108 \pm 0.042	10.72	0.009
Number of reproductions			
Intercept	1.787 \pm 0.042		
Recruitment	0.018 \pm 0.042	23.89	<0.001
Cohort	-0.016 \pm 0.088	2.41	0.272
Sex	0.023 \pm 0.062	2.08	0.308
Recruitment \times cohort	-0.299 \pm 0.091	11.13	0.018
Recruitment \times sex	-0.153 \pm 0.060	5.28	0.104
Cohort \times sex	0.121 \pm 0.122	0.76	0.537
Recruitment \times cohort \times sex	0.299 \pm 0.127	10.93	0.019
Lifetime reproductive success			
Intercept	1.527 \pm 0.059		
Recruitment	-0.005 \pm 0.059	25.52	0.003
Cohort	0.067 \pm 0.119	6.78	0.130
Sex	0.103 \pm 0.084	7.37	0.114
Recruitment \times cohort	-0.317 \pm 0.123	9.31	0.076
Recruitment \times sex	-0.123 \pm 0.082	1.17	0.529
Cohort \times sex	0.054 \pm 0.163	0.00	0.993
Recruitment \times cohort \times sex	0.327 \pm 0.170	10.86	0.055

Full model: recruitment + cohort + sex + recruitment \times cohort + recruitment \times sex + cohort \times sex + recruitment \times cohort \times sex

size and brood size through the timing and quality of the territories and mates they obtain, by investing in territory and incubation, and by inducing investment by their mates (Reid et al. 2002; Velando et al. 2006b). Age-specific reproductive performance was not related to lifespan, suggesting that progressive improvement of young adults was real and not due to poor quality breeders dying young.

There was a marked sexual difference (but no cohort effect) in the relationship between recruiting age and rate (and onset) of senescent decline. The earlier males recruited, the faster they experienced senescence in brood size and breeding success, suggesting a trade-off between recruiting age and reproductive senescence as predicted by the antagonistic pleiotropy theory of ageing. In contrast, recruiting age of females was unrelated to age-specific patterns of reproductive performance. These are the first observations on birds suggesting that beginning reproduction early in life results in accelerated reproductive senescence, and interestingly, this pattern was evident only in males. Senescence is expected to be influenced by reproductive effort (Beckman and Ames 1998), and

acceleration of senescence could result from increased energy expenditure on reproduction at early ages (Kirkwood and Rose 1991; Partridge 1992; Metcalfe and Monaghan 2001; Reed et al. 2008).

Negative effects of recruiting age on rate of senescence in males but not females could arise because male blue-footed boobies incur a higher cost of breeding than females, particularly at early ages. Females deliver a greater mass of food to the brood than males, but since this difference is apparently related to their larger body size rather than longer foraging stints (Anderson and Ricklefs 1992; Guerra and Drummond 1995), it does not necessarily imply greater investment (Evans 1990) in chick provisioning by females. Costs of egg production may be relatively low, since most clutches are of one or two eggs and represent only 3.5–6.9% of female body mass (Castillo-Alvarez and Chavez-Peón 1983; but see Monaghan et al. 1998). Male blue-footed boobies, on the other hand, invest more heavily than females in establishing territories and competing for mates (Nelson 2005). Furthermore, experimental analysis of changes in body mass in relation to parental effort suggests that whereas

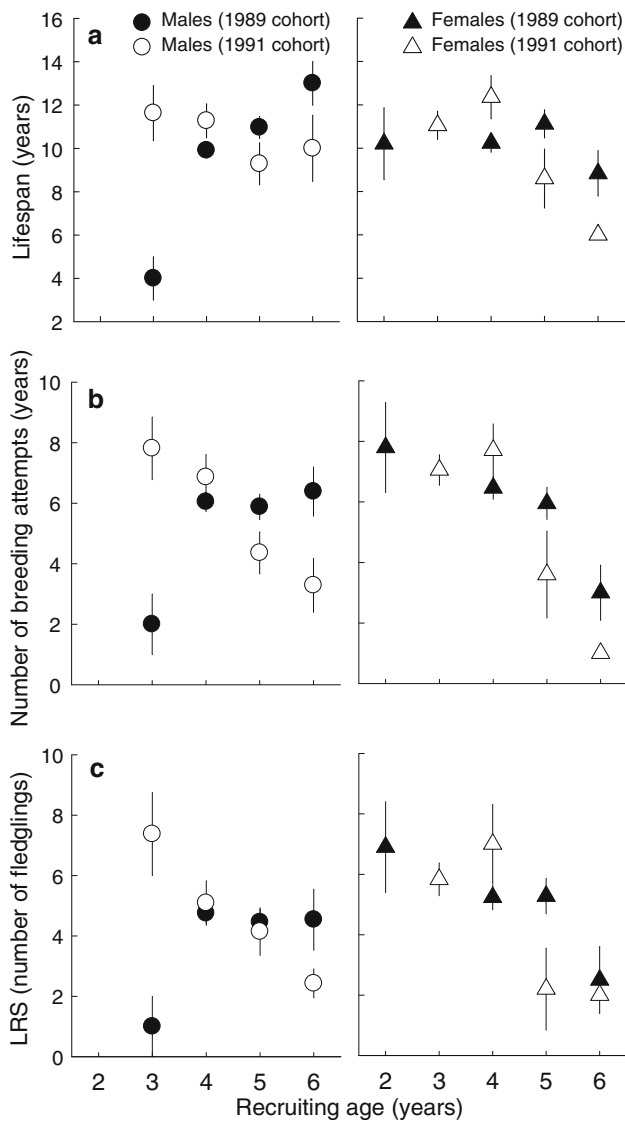


Fig. 3 Means \pm SE **a** lifespan (age at the last breeding), **b** number of breeding attempts over up to 17 years of lifetime and **c** lifetime reproductive success (LRS) (= total number of chicks fledged until age 17 years) according to the recruiting age in male and female breeders from the 1989 and 1991 cohort

female blue-footed boobies are flexible and sometimes allocate resources preferentially to self-maintenance, males work at their physiological maximum (Velando and Alonso-Alvarez 2003). Energetic costs of reproduction are greater for first-time breeders than for experienced breeders (Hadley et al. 2007), particularly in species such as the blue-footed booby whose site- and mate-fidelity are likely to reduce costs of settlement and pairing after the first breeding experience (Kim et al. 2007a). The more heavily investing sex (here, males) may be especially likely to incur long-term costs such as early reproductive senescence and diminished lifespan when it reproduces first at a young age.

Cohort- and sex-specific effects of recruiting age on life-history traits and LRS

Males of the 1989 cohort showed different relationships between recruiting age and other life-history traits (lifespan, number of reproduction and LRS) from males of the 1991 cohort and females of the two cohorts. Late-recruiting males of the 1989 cohort lived longer and generally performed as well over their lifetime as early recruits, suggesting the existence of a trade-off between early recruitment and long lifespan. However, in males of the 1991 cohort and females, earlier recruits reproduced more times and fledged more chicks over their lifetime. The negative associations between recruiting age and number of reproductions and LRS could be explained by variation in individual quality: high-quality individuals may recruit earlier (Forslund and Pärt 1995) and reproduce more frequently and successfully over their lifetime. Trade-offs and costs of early reproduction may exist only under particular environmental conditions, manifesting a genotype (individual quality) by environment interaction (van Noordwijk and de Jong 1986; Reznick et al. 2000). The superior performance of the presumed best-quality breeders was largely due to reproducing more frequently. High quality could be due to superior genes or more favorable circumstances during development (Lindström 1999). Our comparison of only two cohorts is probably insufficient to draw a general conclusion regarding specific cohort effects on life-history trade-offs. However, our results suggest that life-history trade-offs vary with individual quality and environmental conditions.

The two cohorts experienced the same fluctuations of El Niño Southern Oscillation (ENSO) over the lifespan, but at quite different ages. Birds of the 1991 cohort experienced the stress of an exceptionally strong El Niño episode throughout the first 2 years of life, and possibly even during prenatal development, since female investment in egg mass and composition varies between years with contrasting breeding conditions (Dentressangle et al. 2008). Birds of the 1989 cohort did not confront that episode until they were 2 years old. Body condition at fledging and during early life affect survival and recruitment of young birds (Reed et al. 2003), as demonstrated by fledglings of the 1989 cohort being nearly twice as likely to recruit as those of the 1991 cohort. In males of the 1991 cohort, the expected trade-off between recruiting age and lifespan may have been overridden by a positive association between the two traits in conditions where breeder quality is paramount. This would suggest that individual quality is paramount when conditions in infancy are sufficiently harsh to permanently prejudice the general performance of lower quality individuals, setting back their recruitment and annual reproductive success (i.e., a genotype by environment interaction). However, other age-

specific environmental conditions over the lifetime could also have resulted in the association between recruiting age and other life-history traits being different in males of the two cohorts.

Our results showed that LRS was not related to the age at recruitment in males of the 1989 cohort. Variation within the 1989 cohort in the recruiting ages of males could be due to variation in particular conditions encountered or variation in individual potential. That is, individuals may have been similar in potential but channelled into different life-history strategies by fortuitous events (such as local availability of territories and potential mates) that affected their recruiting ages and consequently their subsequent patterns of senescence and longevity. Alternatively, individuals may have differed in potential, some being suited to early recruitment and others to late recruitment, with each individual tending to recruit at the particular age that maximized its LRS. Individual differences in potential and strategy could arise from different genotypes or adaptive phenotypic plasticity (Charmantier et al. 2006; Fordyce 2006). Conditions encountered during the embryonic, nestling or post-fledging stages could calibrate each bird's trade-offs differently, such that LRS of some individuals is maximized by recruiting early despite suffering an early death, while that of others is maximized by recruiting late and living long (Alonso-Alvarez et al. 2006).

Conclusions

Our results document differences in how age of recruitment relates to lifespan and reproductive performance across the lifespan in males and females of two cohorts. Early female recruits of both cohorts showed higher reproductive success. Thus, selection possibly favors early start of reproduction in females. Early female recruits are probably high-quality breeders since they lived longer and reproduced more offspring. In contrast, males showed a more complex (cohort-specific) pattern. In males, early recruitment was positively related to LRS in the 1991 cohort, but not in the 1989 cohort, suggesting cohort-specific selection for recruiting age. Interestingly, trade-off between early reproduction and late performance was detected only when age of recruitment was unrelated to fitness, suggesting that the apparent trade-off was not masked by individual quality. Environmental- and sex-dependent selection may explain how genetic variation in recruiting age (as demonstrated in the blue-footed booby; Kim et al. 2011) is maintained (Kruuk et al. 2008). Given the strong influence of ENSO on populations of marine birds in the tropical Pacific Ocean, including the blue-footed booby (Ancona S, Sánchez-Colon S, Rodríguez MC and Drummond H, unpublished data), it is at least plausible that differences

between the two cohorts shown here were largely due to the different oceanographic conditions they faced during the first 1 or 2 years of life. Future studies should explore the role of ENSO on the maintenance of genetic variability in life-history traits in tropic animal populations by analyzing several cohorts.

Acknowledgments We thank P. Monaghan and N. Metcalfe for very helpful comments on an earlier manuscript, J. Stamps for references and discussion, and C. Rodríguez, J. L. Osorno and numerous volunteers and students for dedicated work in the field and on the database. Annual fieldwork on Isla Isabel depended on the generous support of many fishermen, the Mexican Secretaría del Medioambiente y Recursos Naturales and the Mexican navy. Finance was provided by the Mexican Consejo Nacional de Ciencia y Tecnología (4722-N9407, C01-47599, D112-903581, PCCNCNA-031528), the Universidad Nacional Autónoma de México (IN211491), the National Geographic Society (3065-85, 4535-91), and the Conservation and Research Foundation. S.-Y. Kim was supported by a postdoctoral fellowship of the UNAM and by the Spanish Ministerio de Ciencia y Tecnología (CGL2006-10357-C02-01/BOS) and the Xunta de Galicia (Isidro Parga Pondal fellowship). The field procedures we performed did not involve any licensed procedures and complied with the current laws of Mexico.

References

- Ahnesjö I, Kvarnemo C, Merilaita S (2001) Using potential reproductive rates to predict mating competition among individuals qualified to mate. *Behav Ecol* 12:397–401
- Alonso-Alvarez C, Bertrand S, Devevey G, Prost J, Favre B, Chastel O, Sorci G (2006) An experimental manipulation of life-history trajectories and resistance to oxidative stress. *Evolution* 60:1913–1924
- Anderson DJ (1989) Differential responses of boobies and other seabirds in the Galápagos to the 1986–87 El Niño Southern Oscillation event. *Mar Ecol Prog Ser* 52:209–216
- Anderson DJ, Ricklefs RE (1992) Brood size and food provisioning in masked and blue-footed boobies (*Sula* spp.). *Ecology* 73:1363–1374
- Beamonte-Barrientos R, Velando A, Drummond H, Torres R (2010) Senescence of maternal effects: aging influences egg quality and rearing capacities of a long-lived bird. *Am Nat* 175:469–480
- Beckman KB, Ames BN (1998) The free radical theory of aging matures. *Physiol Rev* 78:547–581
- Blondel J, Pradel R, Lebreton J-D (1992) Low fecundity insular blue tits do not survive better as adults than high fecundity mainland ones. *J Anim Ecol* 61:205–213
- Bonduriansky R, Maklakov A, Zajitschek F, Brooks R (2008) Sexual selection, sexual conflict and the evolution of ageing and life span. *Funct Ecol* 22:443–453
- Boulinier T, Sorci G, Clobert J, Danchin E (1997) An experimental study of the costs of reproduction in the kittiwake *Rissa tridactyla*: comment. *Ecology* 78:1284–1287
- Cam E, Link WA, Cooch EG, Monnat J-Y, Danchin E (2002) Individual covariation in life-history traits: seeing the trees despite the forest. *Am Nat* 159:96–105
- Castillo-Alvarez A, Chavez-Peón A (1983) Ecología reproductiva e influencia del comportamiento en el control del número de crías en el bobo de patas azules, *Sula nebouxi*, en la Isla Isabel, Nay. BSc Thesis, Universidad Nacional Autónoma de México, México
- Charmantier A, Perrins C, McCleery RH, Sheldon BC (2006) Quantitative genetics of age at reproduction in wild swans:

- support for antagonistic pleiotropy models of senescence. *Proc Natl Acad Sci USA* 103:6587–6592
- Crawley MJ (2007) *The R book*. Wiley, Chichester
- Dentressangle F, Boeck L, Torres R (2008) Maternal investment in eggs is affected by male feet colour and breeding conditions in the blue-footed booby, *Sula nebouxi*. *Behav Ecol Sociobiol* 62:1899–1908
- Descamps S, Boutin S, Berteaux D, Gaillard J-M (2008) Age-specific variation in survival, reproductive success and offspring quality in red squirrels: evidence of senescence. *Oikos* 117:1406–1416
- Drummond H, Osorno JL, García C, Torres R, Merchant H (1991) Sexual dimorphism and sibling competition: implications for avian sex ratios. *Am Nat* 138:623–641
- Drummond H, Torres R, Krishnan VV (2003) Buffered development: resilience after aggressive subordination in infancy. *Am Nat* 161:794–807
- Evans RM (1990) The relationship between parental input and investment. *Anim Behav* 39:797–798
- Fordyce JA (2006) The evolutionary consequences of ecological interactions mediated through phenotypic plasticity. *J Exp Biol* 209:2377–2383
- Forslund P, Pärt T (1995) Age and reproduction in birds—hypotheses and tests. *Trends Ecol Evol* 10:374–378
- Guerra M, Drummond H (1995) Reversed sexual size dimorphism and parental care: minimal division of labour in the blue-footed booby. *Behaviour* 132:479–496
- Gustafsson L, Pärt T (1990) Acceleration of senescence in the collared flycatcher *Ficedula albicollis* by reproductive costs. *Nature* 347:279–281
- Hadley GL, Rotella JJ, Garrott RA (2007) Evaluation of reproductive costs for weddell seals in Erebus Bay, Antarctica. *J Anim Ecol* 76:448–458
- Kim S-Y, Torres R, Rodríguez C, Drummond H (2007a) Effects of breeding success, mate fidelity and senescence on breeding dispersal of male and female blue-footed boobies. *J Anim Ecol* 76:471–479
- Kim S-Y, Torres R, Domínguez CA, Drummond H (2007b) Lifetime philopatry in the blue-footed booby: a longitudinal study. *Behav Ecol* 18:1132–1138
- Kim S-Y, Drummond H, Torres R, Velando A (2011) Evolvability of an avian life-history trait declines with father's age. *J Evol Biol* 24:295–302
- Kirkwood TBL (1977) Evolution of ageing. *Nature* 270:301–304
- Kirkwood TBL, Rose MR (1991) Evolution of senescence—late survival sacrificed for reproduction. *Philos Trans R Soc Lond B* 332:15–24
- Kruuk LEB, Slate J, Wilson AJ (2008) New answers for old questions: the evolutionary quantitative genetics of wild animal populations. *Annu Rev Ecol Syst* 39:525–548
- Lindström J (1999) Early development and fitness in birds and mammals. *Trends Ecol Evol* 14:343–348
- Medawar PB (1952) An unsolved problem of biology. Lewis, London
- Metcalfe NB, Monaghan P (2001) Compensation for a bad start: grow now, pay later? *Trends Ecol Evol* 16:254–260
- Michener GR, Locklear L (1990) Differential costs of reproductive effort for male and female Richardson's ground squirrels. *Ecology* 71:855–868
- Monaghan P, Nager RG, Houston DC (1998) The price of eggs: increased investment in egg production reduces the offspring rearing capacity of parents. *Proc R Soc Lond B* 265:1731–1735
- Moyes K, Morgan BJT, Morris A, Morris SJ, Clutton-Brock TH, Coulson T (2009) Exploring individual quality in a wild population of red deer. *J Anim Ecol* 78:406–413
- Nelson JB (2005) *Pelicans Cormorants and their relatives*. Oxford University Press, Oxford
- Newton I (1985) Lifetime reproductive output of female sparrow-hawks. *J Anim Ecol* 54:241–253
- Nussey DH, Kruuk LEB, Donald A, Fowlie M, Clutton-Brock TH (2006) The rate of senescence in maternal performance increases with early-life fecundity in red deer. *Ecol Lett* 9:1342–1350
- Nussey DH, Coulson T, Festa-Bianchet M, Gaillard J-M (2008) Measuring senescence in wild animal populations: towards a longitudinal approach. *Funct Ecol* 22:393–406
- Oli MK, Hepp GR, Kennamer RA (2002) Fitness consequences of delayed maturity in female wood ducks. *Evol Ecol Res* 4:563–576
- Oro D, Torres R, Rodríguez C, Drummond H (2010) Climatic influence on demographic parameters of a tropical seabird varies with age and sex. *Ecology* 91:1205–1214
- Osorio-Beristain M, Drummond H (1993) Natal dispersal and deferred breeding in the blue-footed booby. *Auk* 110:234–239
- Partridge L (1992) Lifetime reproductive success and life-history evolution. In: Newton I (ed) *Lifetime reproduction in birds*. Academic, London, pp 421–440
- Partridge L, Farquhar M (1981) Sexual activity reduces lifespan of male fruitflies. *Nature* 294:580–582
- Pyle P, Nur N, Sydeman WJ, Emslie SD (1997) Cost of reproduction and the evolution of deferred breeding in the western gull. *Behav Ecol* 8:140–147
- R Development Core Team (2008) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna. ISBN 3-900051-07-0. <http://www.R-project.org>
- Reed ET, Gauthier G, Pradel R, Lebreton J-D (2003) Age and environmental conditions affect recruitment in greater snow geese. *Ecology* 84:219–230
- Reed ET, Kruuk LEB, Wanless S, Frederiksen M, Cunningham EJA, Harris MP (2008) Reproductive senescence in a long-lived seabird: rates of decline in late-life performance are associated with varying costs of early reproduction. *Am Nat* 171:E89–E101
- Reid JM, Monaghan P, Ruxton GD (2002) Males matter: the occurrence and consequences of male incubation in starlings (*Sturnus vulgaris*). *Behav Ecol Sociobiol* 51:255–261
- Reid JM, Bignal EM, Bignal S, McCracken DI, Monaghan P (2003) Age-specific reproductive performance in red-billed choughs *Pyrrhocorax pyrrhocorax*: patterns and processes in a natural population. *J Anim Ecol* 72:765–776
- Reznick D, Nunney L, Tessier A (2000) Big houses, big cars, superfleas and the costs of reproduction. *Trends Ecol Evol* 15:421–425
- Rice WR, Chippindale AK (2001) Intersexual ontogenetic conflict. *J Evol Biol* 14:685–693
- Roff DA (2002) *Life history evolution*. Sinauer, Sunderland
- SAS Institute (1999) *SAS/STAT, version 8*. SAS Institute, Cary
- Schaffer WM (1974) Selection for optimal life histories: the effects of age structure. *Ecology* 55:291–303
- Sedinger JS, Flint PL, Lindberg MS (1995) Environmental influence on life-history traits: growth, survival, and fecundity in black brant (*Branta bernicla*). *Ecology* 76:2404–2414
- Stearns SC (1992) *The evolution of life histories*. Oxford University Press, Oxford
- Tavecchia G, Pradel R, Boy V, Johnson AR, Cézilly F (2001) Sex- and age-related variation in survival and cost of first reproduction in greater flamingos. *Ecology* 82:165–174
- Torres R, Drummond H (1999) Variably male-biased sex ratio in a marine bird with females larger than males. *Oecologia* 118:16–22
- van de Pol M, Verhulst S (2006) Age-dependent traits: a new statistical model to separate within- and between-individual effects. *Am Nat* 167:764–771
- van de Pol M, Wright J (2009) A simple method for distinguishing within versus between-subject effects using mixed models. *Anim Behav* 77:753–758

- van Noordwijk AJ, de Jong G (1986) Acquisition and allocation of resources: their influences on variation in life history tactics. *Am Nat* 128:137–142
- Velando A, Alonso-Alvarez C (2003) Differential body condition regulation by males and females in response to experimental manipulations of brood size and parental effort in the blue-footed booby. *J Anim Ecol* 72:846–856
- Velando A, Drummond H, Torres R (2006a) Senescent birds redouble reproductive effort when ill: confirmation of the terminal investment hypothesis. *Proc R Soc Lond B* 273:1443–1448
- Velando A, Beamonte-Barrientos R, Torres R (2006b) Pigment-based skin colour in the blue-footed booby: an honest signal of current condition used by females to adjust reproductive investment. *Oecologia* 149:535–542
- Viallefont A, Cooch EG, Cooke F (1995) Estimation of trade-offs with capture-recapture models: a case study on the lesser snow goose. *J Appl Stat* 22:847–861
- Williams GC (1957) Pleiotropy, natural selection and the evolution of senescence. *Evolution* 11:398–411