

# Age and the timing of breeding in a long-lived bird: a role for stress hormones?

Aurélie Goutte\*, Élodie Antoine, Henri Weimerskirch and Olivier Chastel

Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique, F-79360 Villiers en Bois, Deux-Sèvres, France

## Summary

1. Young birds often reproduce later in the season than older ones, with poorer breeding success, but the proximate mechanisms involved in such a pattern remain poorly studied, especially in long-lived species. One possible mechanism is the endocrine stress response which is accompanied by the release of corticosterone. Elevated corticosterone levels can trigger physiological and behavioural responses that may delay or even suppress reproduction.

2. We tested the hypothesis that the delayed timing of breeding of young birds may be related to a greater susceptibility to stress compared with older ones during the pre-laying period of the breeding season. For this purpose, known-age (7–44 years old) pre-laying snow petrels, *Pagodroma nivea*, were monitored for baseline and acute stress-induced corticosterone levels. We examined whether baseline and stress-induced corticosterone levels were related to age, and whether they could influence the decision to breed and egg-laying date.

3. Young snow petrels were more likely to skip the breeding season and to breed later than middle-aged birds. In addition, the oldest birds bred later than middle-aged ones, suggesting a possible senescence on laying dates. Baseline corticosterone levels were independent of age but young and very old birds were more sensitive to stress than middle-aged ones. However, there was no effect of stress-induced corticosterone levels on breeding decision and egg-laying date. Elevated baseline corticosterone levels during the pre-laying period were associated with a higher probability of skipping breeding in females and a delayed timing of egg-laying in both sexes.

4. These results suggest that the greater susceptibility of young breeders to stress was not the functional mechanism explaining their delayed timing of breeding. Baseline corticosterone levels, although independent of age, appear to be a more likely mediator of breeding decision and egg-laying date. In long-lived birds, the relationship between age and timing of breeding may be rather indirect, as other age-related factors such as breeding experience or foraging skills may have a deeper impact on baseline corticosterone than age *per se*.

**Key-words:** age, glucocorticoids, laying date, snow petrel (*Pagodroma nivea*), stress response

## Introduction

Breeding at the right time is a key factor for successful reproduction in fluctuating environments (Lack 1968; Perrins 1970; Nager & van Noordwijk 1995). The adjustment of breeding schedule allows a good overlap between offspring's energy requirements and local peak in food availability (*match–mismatch hypothesis*; Visser *et al.* 1998; Stenseth & Mysterud 2002; Durant *et al.* 2007). In bird species, although early breeders usually perform better than late breeders, the decision to start breeding greatly differs between individuals. Typically, young breeders reproduce

later in the season than older ones, and have lower reproductive success (Martin 1995; DeForest & Gaston 1996; Gonzalez-Solis *et al.* 2004; Ezard, Becker & Coulson 2007; McCleery *et al.* 2008; Blas, Sergio & Hiraldo 2009). This could be explained by (i) a progressive disappearance of late-breeders over age classes (*selection hypothesis*; Mauck, Huntington & Grubb 2004), (ii) an individual adjustment of life-history strategies: as it gets older, a bird would favour current breeding rather than survival (*restraint hypothesis*; Stearns 1992), (iii) an improvement of breeding skills with age owing to the accumulation of breeding experience (*constraint hypothesis*, Curio 1983) or (iv) a progressive incorporation of early breeders over age classes (*delayed-breeder hypothesis*; Forslund & Pärt 1995; Blas, Sergio & Hiraldo

\*Correspondence author. E-mail: goutte@cebc.cnrs.fr

2009). Ultimate factors explaining why young breeders reproduce later than older individuals have been discussed widely (Curio 1983; Forslund & Pärt 1995; Blas & Hiraldo 2010). However, the mechanisms underlying this age-specific timing of breeding are still poorly understood. In that respect, endocrine mechanisms deserve special attention as they mediate life-history strategies in relation to environmental conditions and to the physiological state of individuals (Wingfield *et al.* 1998; Ricklefs & Wikelski 2002).

Specifically, the endocrine stress response could play a key role in the age-specific timing of breeding. In vertebrates, stressful conditions such as harsh weather, scarce food availability or presence of predators, trigger an acute secretion of glucocorticoid hormones, that is, cortisol or corticosterone (Wingfield *et al.* 1998). In turn, this stress response allows individuals to cope with the stressors by suppressing reproductive functions (Wingfield & Sapolsky 2003; Landys, Ramenofsky & Wingfield 2006; Breuner, Patterson & Hahn 2008). Although the majority of such studies focused on the parental phase of the reproductive cycle (i.e. incubation and chick rearing in birds), very few studies have investigated relationships between glucocorticoids, known to interfere with the hypothalamic–pituitary–gonadal axis (Wingfield & Sapolsky 2003; Pérez-Rodríguez *et al.* 2006), and the timing of breeding (Salvante & Williams 2003; Schoech *et al.* 2009). These studies suggest a similar inhibiting role of corticosterone during the pre-laying period (i.e. before the onset of breeding). Elevated corticosterone levels were associated with delayed first clutch initiation during unfavourable years in Florida scrub jay (*Aphelocoma coerulescens*; Schoech *et al.* 2009). Furthermore, experimental administration of exogenous corticosterone in zebra finches (*Taeniopygia guttata*) greatly decreased the number of pairs initiating reproduction and delayed clutch initiation (Salvante & Williams 2003). Corticosterone appears therefore to be an excellent candidate adjusting the timing of breeding in response to environmental conditions (Schoech *et al.* 2009). Understanding the functional role of corticosterone implies to distinguish between (i) baseline corticosterone level, which is a marker of activities and energetic state (Kitaysky, Wingfield & Piatt 1999; Love *et al.* 2004; Landys, Ramenofsky & Wingfield 2006), and (ii) stress-induced corticosterone level, which mirrors the sensitivity to stress and less commitment to current reproduction (Lendvai, Giraudeau & Chastel 2007).

According to life-history theory, the stress response should be attenuated when the value of the current reproduction is high relative to the value of future breeding events (Wingfield & Sapolsky 2003). Recent experimental and comparative studies support this assumption (*brood value hypothesis*; Lendvai, Giraudeau & Chastel 2007; Lendvai & Chastel 2008; Bokony *et al.* 2009). Relating this to age-specific reproductive success, it has been predicted and observed that the stress response of old adults is attenuated, probably to ensure that reproduction is not inhibited (Heidinger, Nisbet & Ketterson 2006; Angelier *et al.* 2007a). During the pre-laying period, an attenuation of the stress response might therefore be the endocrine mechanism underlying early breeding in old birds.

Focusing on a long-lived species, the snow petrel (*Pagodroma nivea* Foster), we hypothesized that young birds are more sensitive to stress before the onset of reproduction than older ones. First, we tested whether young birds lay their egg later or whether they were more likely to skip the breeding season than older birds. Secondly, we tested whether baseline or stress-induced corticosterone levels varied with age. We predicted that young birds would exhibit higher baseline and/or stress-induced corticosterone levels than older birds during the pre-laying period. Thirdly, we predicted that individuals with high pre-laying baseline and/or stress-induced corticosterone levels would delay the onset of breeding or even halt their reproduction.

## Materials and methods

### STUDY SITE AND SPECIES

The study was carried out on Ile des Pétrels, Pointe Géologie Archipelago, Terre Adélie (66°40'S, 140°01'E), Antarctica. Snow petrels (250–500 g; Fig. 1) are very long-lived birds with low annual fecundity and high adult life expectancy (Chastel, Weimerskirch & Jouventin 1993; Jenouvrier, Barbraud & Weimerskirch 2005). Like all Procellariiform species, breeding pairs lay only one egg per season, with no replacement clutch in case of failure (Chastel, Weimerskirch & Jouventin 1993; Barbraud & Weimerskirch 2001). The age at first breeding is 10 years on average and birds breed annually, although a significant proportion of birds skip the breeding season (Chastel, Weimerskirch & Jouventin 1993). Nest and mate fidelity is high (Bried, Pontier & Jouventin 2003). Males and females provide roughly similar amounts of parental care (incubation of the egg and care for the chick). Birds arrive on the breeding ground in early November. The courtship and mating period typically lasts about 2 weeks. Then, individuals of both sexes forage at sea to accumulate resources and females build up reserves for the egg (pre-laying exodus). The laying period ranges from late November to mid-December. Within one breeding season, egg-laying dates differ between individuals over a period of 2 weeks (Barbraud, Lormée & LeNeve 2000).

The ongoing mark-recapture programme of the snow petrels population began in 1963 (see Chastel, Weimerskirch & Jouventin 1993; Barbraud & Weimerskirch 2001 for detailed methodology). Every



**Fig. 1.** A pair of courting snow petrels during the pre-laying period, in Terre Adélie, Antarctica. Photo by Aurélie Goutte.

chick of the monitored colonies has been banded prior to fledging every year since 1963. Thus, a part of the current population is of known age.

#### BLOOD SAMPLING, BODY CONDITION AND PHENOLOGY

Adult male and female snow petrels were handled during the 2007 pre-laying period (6–19 November, that is,  $26.93 \pm 0.76$  days before egg-laying). A total of 55 known-age adults (7–40 years old) and 11 unknown-age adults (but they were ringed as adults and they were at least 11 years old) were caught at their nest, in 65 different nests. In one nest, both partners of the pair were of known age and we randomly selected one bird of this pair. A blood sample from the alar vein was taken immediately ( $157.5 \pm 5.8$  s) after capture using a 1-mL heparinized syringe and a 25-gauge needle. For nine of them, bleeding time exceeded the time required for baseline corticosterone levels (Romero & Reed 2005), so these nine values were not used for the analysis. Birds were then placed into cloth bags, and subsequent blood samples were collected 30 min later, according to the standardized capture/restraint stress protocol (Wingfield *et al.* 1994). Skull length (head + bill) and tarsus length were measured using a calliper to the nearest 0.5 mm, wing length to the nearest 1 mm and weight to the nearest 2 g using a spring balance. As univariate metrics may be inadequate to estimate overall body size in birds, we used the first component (PC1) of a principal component analysis as an index of size. As male and female snow petrels differ greatly in size (Barbraud & Jouventin 1998), males ( $N = 38$ ) and females ( $N = 28$ ) were analysed separately. The first component accounted for 76 and 72% of the total variance in male and female measurements, respectively, and was highly positively correlated with all variables ( $r > 0.83$  for both sexes). PC1 scores increased with the size of the birds. Standardized body condition was then calculated for males and females separately from a least-squares linear regression of body mass against body size (PC1). Petrels were then marked with spots of dye on the forehead to distinguish them from their partner and were released at their nest. Then, we checked the 65 nests every 2 days to monitor the presence or absence of the marked birds, breeding decision (i.e. decision to lay an egg or to skip the breeding season) and the egg-laying date. The time between sampling and egg-laying did not differ between the sexes ( $F_{1,52} = 1.078$ ,  $P = 0.304$ ) and was not related to age ( $F_{1,44} = 0.377$ ,  $P = 0.542$ ).

In addition, we prospectively for other known-age birds during the incubating period to increase the sample size. A total of 109 known-age adults (6–44 years old) were indeed monitored for breeding decision, and 96 eggs were followed every day until hatching to assess hatching success and hatching date. As blood sampling and bird handling might disturb the breeding phenology, we compared breeding decision and hatching date of manipulated birds with the sample of non-manipulated birds nesting in the long-term study plots (see Chastel, Weimerskirch & Jouventin 1993), where birds were seldom handled ( $N = 221$  for the breeding decision and  $N = 142$  for the hatching date). Timing of hatching for handled birds was similar to non-handled ones ( $N = 142$ ; Wilcoxon's  $w = 2665.5$ ,  $P = 0.721$ ). The proportion of breeders tended to be slightly reduced by handling (handled birds:  $83.33 \pm 4.62\%$ ; non-handled birds:  $90.95 \pm 1.93\%$ ;  $N = 221$ ,  $\chi^2 = 3.072$ ,  $P = 0.080$ ).

#### MOLECULAR SEXING AND HORMONE ASSAY

Blood samples were centrifuged and plasma was decanted and stored at  $-20$  °C until assayed. Red cells were also kept frozen for molecular

sexing at the Centre d'Etudes Biologiques de Chizé (CEBC). Sex was determined by polymerase chain reaction (PCR) amplification of a part of two highly conserved genes (CHD) present on the sex chromosomes (Fridolfsson & Ellegren 1999), as detailed in Weimerskirch, Lallemand & Martin (2005). Plasma concentrations of total baseline and stress-induced corticosterone were determined by radioimmunoassay at the CEBC, as described by Lormée *et al.* (2003). Only one assay was performed and the intra-assay coefficient of variation was 5.6% ( $N = 4$  duplicates).

#### STATISTICAL ANALYSES

All analyses were performed using R 2.8.0 (<http://r-project.org/>). We used generalized linear model (GLM) with binomial error distribution and a logit link function to explain breeding decision, and GLM with normal errors and an identity link function to explain egg-laying date and hormone levels. Dependent continuous variables were previously tested for normality with a Shapiro–Wilk test and were log-transformed when necessary. An information-theoretic approach was used to select the best models (Burnham & Anderson 2002). Model selection criteria included the corrected version of Akaike's information criterion (AICc) for small sample sizes and the difference in AICc between each candidate model and the model with the lowest AICc value ( $\Delta$ AICc; Burnham & Anderson 2002). AICc weight can be used as a measure of the relative probability of a model for being the best model with a given data set among other potential models. Selected models were then checked for assumptions, that is, constancy of variance and residual normality. Parameters' estimates  $\pm$  SE were given for models with the highest AICc weight and by removing interactions with covariables (Quinn & Keough 2002).

#### Age, breeding decision and timing of breeding

As female body size is known to account for a great part of the variation in the egg-laying date of snow petrels (Barbraud, Lormée & LeNeve 2000), we included body size in our analysis. Therefore, we tested whether breeding decision and egg-laying date were influenced by standardized body condition, body size, sex and the interaction body condition  $\times$  sex and body size  $\times$  sex in pre-laying snow petrels ( $N = 66$ ). To test for an effect of age, we used known-age snow petrels handled during the pre-laying period and the 54 known-age birds handled after the egg-laying period. As hatching date was monitored for each nest and was highly correlated to egg-laying date (estimate =  $0.770 \pm 0.077$ ,  $F_{1,36} = 99.30$ ,  $P < 0.001$ ), we used hatching date instead of egg-laying date in this model. We tested whether breeding decision and hatching date were influenced by 'sex', 'age', 'age<sup>2</sup>' and the interaction 'sex (age + age<sup>2</sup>)'. Within breeding pairs, the age of the male was positively correlated with that of the female ( $F_{1,23} = 6.522$ ,  $P = 0.018$ ).

#### Age and stress hormones

Because standardized body condition was negatively related to sampling date (see 'Results'), we first tested whether baseline and stress-induced corticosterone levels were influenced by body condition, sex and the interaction 'sex  $\times$  body condition' by using linear regressions. Then we analysed whether baseline and stress-induced corticosterone levels were influenced by the sampling date (hereafter 'date'), 'sex', 'age', 'age<sup>2</sup>' and the interaction 'sex (age + age<sup>2</sup>)'.

Moreover, we ran the analysis again adding the 'time before egg-laying' variable (i.e. the time between sampling and egg-laying date)

to take into account a potential hormonal change with advancing time. 'Time before egg-laying' and 'sampling time' were tested separately as they were significantly negatively linked ( $F_{1,52} = 39.580$ ,  $P < 0.001$ ).

### Stress hormones, breeding decision and timing of breeding

We tested the influence of pre-laying baseline (or stress-induced) corticosterone on breeding decision and egg-laying date. As baseline and stress-induced corticosterone levels differed between sexes (see 'Results'; Table 1), we could not include the 'sex' and 'baseline (or stress-induced) corticosterone levels' variables simultaneously in a model. Thus, we standardized baseline (or stress-induced) corticosterone levels for each sex by subtracting for each sex the mean baseline (or stress-induced) corticosterone levels from each observed value, and dividing by the SD. Because sex and standardized corticosterone levels were no longer associated, we started our analyses from the general model including the 'date', 'sex', 'baseline (or stress-induced) corticosterone levels' variables and the 'sex  $\times$  baseline (or stress-induced) corticosterone levels' interaction. To test for an effect on breeding decision and on egg-laying date, we considered all monitored nests prospected during the pre-laying period and then only eggs which hatched successfully.

## Results

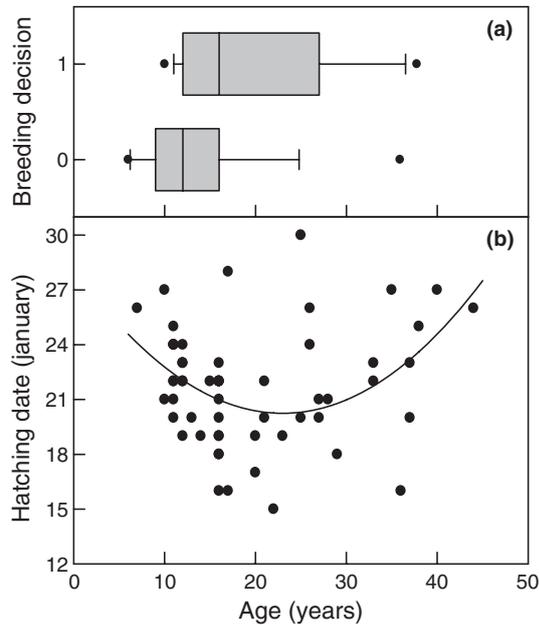
Pre-laying body condition was not related to age (estimate =  $0.009 \pm 0.014$ ,  $F_{1,53} = 0.427$ ,  $P = 0.516$ ). Pre-laying body condition decreased with the date of sampling (estimate =  $-0.111 \pm 0.029$ ,  $F_{1,64} = 14.961$ ,  $P < 0.001$ ), but was not affected by the time between sampling and egg-laying date (estimate =  $0.047 \pm 0.028$ ,  $F_{1,52} = 2.779$ ,  $P = 0.102$ ).

### AGE, BREEDING DECISION AND TIMING OF BREEDING

Breeding decision and egg-laying date were not influenced by pre-laying body condition or body size (for all tests:  $P > 0.16$ ). Breeding decision was influenced by the breeder's age ( $N = 109$ ,  $\chi^2 = 8.586$ ,  $P < 0.001$ ): birds that skipped breeding were mainly younger ( $< 13$  years old; Fig. 2a). There was a significant effect of age on hatching date, in a quadratic way: young (less than 13 years old) and very old (more than 30 years old) birds bred later than the 13–30-year-old birds (Fig. 2b;  $N = 60$ ; age: estimate =  $-0.484 \pm 0.209$ ,  $\chi^2 = 4.976$ ,  $P = 0.026$ ; age<sup>2</sup>: estimate =  $0.010 \pm 0.004$ ,

**Table 1.** Model selection using corrected version of Akaike's information criterion (AICc) to explain (a) baseline corticosterone levels ( $N = 47$ ) and (b) stress-induced corticosterone levels ( $N = 53$ ).  $K$  refers to the number of parameters. Candidate models and models without any explanatory variable (the 'intercept model') are ranked according to their AICc. The second part of the table includes the parameter estimates for the selected model: (a) 'Date; Sex' and (b) 'Date; Sex; Age; Age<sup>2</sup>'

| No.        | Model  | AICc             | $\Delta$ AICc     | AICc weight | $K$       |
|------------|--|------------------|-------------------|-------------|-----------|
| <b>(a)</b> |  |                  |                   |             |           |
| 1.         | Date; Sex  | 120.58           | 0                 | 37.6%       | 4         |
| 2.         | Date   | 121.73           | 1.15              | 21.1%       | 3         |
| 3.         | Date; Sex; Age   | 122.93           | 2.35              | 11.6%       | 5         |
| 4.         | Date; Sex; Age; Sex $\times$ Age                                 | 123.64           | 3.07              | 8.1%        | 6         |
| 5.         | Date; Age  | 124.01           | 3.43              | 6.8%        | 4         |
| 6.         | Intercept  | 124.36           | 3.78              | 5.7%        | 2         |
| 7.         | Date; Sex; Age; Age <sup>2</sup> ; Sex (Age + Age <sup>2</sup> ) | 125.23           | 4.65              | 3.7%        | 8         |
| 8.         | Date; Sex; Age; Age <sup>2</sup>                                 | 125.41           | 4.84              | 3.4%        | 6         |
| 9.         | Date; Age; Age <sup>2</sup>                                      | 126.38           | 5.80              | 2.1%        | 5         |
|            | Selected model   | Parameters       | Estimate $\pm$ SE | Chi-squared | $P$       |
|            | Date; Sex  | Intercept        | $1.44 \pm 0.48$   | 9.11        | 0.003     |
|            |  | Date             | $0.08 \pm 0.04$   | 4.87        | 0.027     |
|            |  | Sex              | $0.44 \pm 0.24$   | 3.35        | 0.067     |
| <b>(b)</b> |  |                  |                   |             |           |
| 1.         | Date; Sex; Age; Age <sup>2</sup>                                 | 480.42           | 0                 | 63.2%       | 6         |
| 2.         | Date; Age; Age <sup>2</sup>                                      | 484.21           | 3.80              | 9.5%        | 5         |
| 3.         | Date; Sex  | 484.38           | 3.96              | 8.7%        | 4         |
| 4.         | Date; Sex; Age   | 485.12           | 4.71              | 6.0%        | 5         |
| 5.         | Date; Sex; Age; Age <sup>2</sup> ; Sex (Age + Age <sup>2</sup> ) | 485.22           | 4.80              | 5.7%        | 8         |
| 6.         | Date   | 486.23           | 5.81              | 3.5%        | 3         |
| 7.         | Date; Sex; Age; Sex $\times$ Age                                 | 487.45           | 7.03              | 1.9%        | 6         |
| 8.         | Date; Age  | 487.88           | 7.46              | 1.5%        | 4         |
| 9.         | Intercept  | 502.98           | 22.56             | 0%          | 2         |
|            | Selected model   | Parameters       | Estimate $\pm$ SE | Chi-squared | $P$       |
|            | Date; Sex; Age; Age <sup>2</sup>                                 | Intercept        | $75.17 \pm 26.58$ | 8.04        | 0.005     |
|            |  | Date             | $3.51 \pm 0.94$   | 13.87       | $< 0.001$ |
|            |  | Sex              | $14.37 \pm 5.87$  | 5.99        | 0.014     |
|            |  | Age              | $-5.76 \pm 2.06$  | 7.83        | 0.005     |
|            |  | Age <sup>2</sup> | $0.12 \pm 0.04$   | 6.94        | 0.008     |



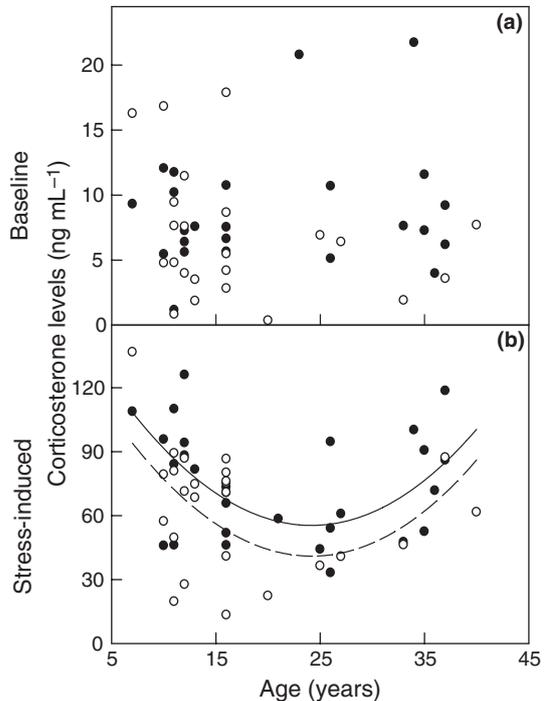
**Fig. 2.** (a) Breeding decision (0 = non-breeder; 1 = breeder) in relation to age in snow petrels (The median, 10th, 25th, 75th and 90th percentiles are plotted as horizontal boxes with error bars) and (b) hatching date in relation to age in snow petrels. The probability of breeding increased with age, whereas young and very old birds bred later than middle-aged ones.

$\chi^2 = 6.190$ ,  $P = 0.013$ ). As mentioned, the use of hatching date was more powerful (larger sample size) than the use of egg-laying date ( $N = 33$ ). However, this did not affect the detected trend (egg-laying date =  $-0.375 \times \text{age} + 0.009 \times \text{age}^2$  vs. hatching date =  $-0.484 \times \text{age} + 0.010 \times \text{age}^2$ ).

#### AGE, BODY CONDITION AND STRESS HORMONE LEVELS

Baseline corticosterone levels were not associated with pre-laying body condition (estimate =  $-0.042 \pm 0.631$ ,  $F_{1,55} = 0.006$ ,  $P = 0.940$ ) even when considering an interaction with sex (estimate =  $0.105 \pm 0.290$ ,  $F_{1,53} = 0.124$ ,  $P = 0.726$ ). However, baseline corticosterone levels were higher in males than in females ( $8.255 \pm 0.758$  and  $6.620 \pm 0.972$  ng mL<sup>-1</sup>, respectively), increased with the date of sampling (Table 1a), but were not influenced by age (Table 1a and Fig. 3a).

During the pre-laying period, males and females responded to the stress of capture by increasing their corticosterone levels significantly ( $P < 0.001$  for paired Student's *t*-tests). Stress-induced corticosterone levels were independent of baseline corticosterone levels (estimate =  $0.003 \pm 0.004$ ,  $F_{1,54} = 1.115$ ,  $P = 0.296$ ). Stress-induced corticosterone levels were negatively correlated to body condition (estimate =  $-13.690 \pm 3.139$ ,  $F_{1,62} = 19.022$ ,  $P < 0.001$ ). Moreover, stress-induced corticosterone levels were higher in males than in females ( $77.937 \pm 4.213$  and  $67.860 \pm 5.657$  ng mL<sup>-1</sup>, respectively), increased with the date of sampling and were correlated to age in a quadratic



**Fig. 3.** (a) Baseline and (b) stress-induced corticosterone levels during the pre-laying period in relation to age in males ( $N = 29$ , closed circles with solid best-fit line), and females ( $N = 25$ , open circles with dashed best-fit line) snow petrels.

way (Table 1b): young and very old birds were more sensitive to stress than middle-aged ones (Fig. 3b).

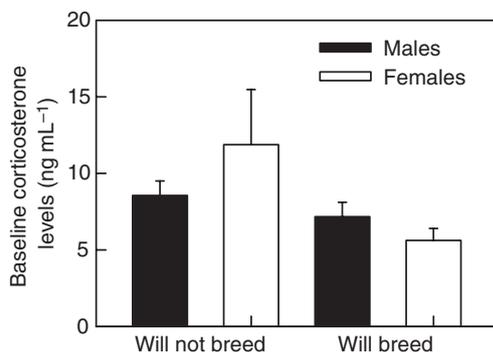
After running the analysis with the 'time before egg-laying' variable instead of the 'sampling date' variable, stress hormone levels were not associated with the time before egg-laying ( $P > 0.17$  for baseline and stress-induced corticosterone levels).

#### STRESS HORMONES, BREEDING DECISION AND TIMING OF BREEDING

Elevated baseline corticosterone levels during the pre-laying period were associated with a higher probability of skipping breeding in females (Table 2a and Fig. 4). Breeding decision was not influenced by stress-induced corticosterone levels (Table 2b). When considering all laid eggs (i.e. eggs that hatched successfully and eggs that failed to hatch), egg-laying dates were neither influenced by the standardized baseline corticosterone levels (estimate =  $0.123 \pm 0.111$ ,  $F_{1,43} = 1.236$ ,  $P = 0.272$ ), nor by the standardized stress-induced corticosterone levels (estimate =  $0.206 \pm 0.529$ ,  $F_{1,50} = 0.027$ ,  $P = 0.869$ ), even when considering an interaction effect 'sex  $\times$  standardized corticosterone levels' (baseline: estimate =  $-1.037 \pm 1.148$ ,  $F_{1,41} = 0.817$ ,  $P = 0.371$ ; stress-induced: estimate =  $0.461 \pm 1.079$ ,  $F_{1,48} = 0.183$ ,  $P = 0.671$ ). However, hatching success was negatively correlated with standardized baseline corticosterone levels (estimate =  $-0.924 \pm 0.423$ ,  $N = 40$ ,  $\chi^2 = 9.037$ ,  $P = 0.003$ ): snow petrels with elevated standardized baseline corticoste-

**Table 2.** Model selection using corrected version of Akaike's information criterion (AICc) to explain breeding decision (0 = non-breeder; 1 = breeder) in relation to (a) standardized baseline corticosterone levels (Bas. CORT,  $N = 57$ ) and standardized stress-induced corticosterone levels (Max. CORT,  $N = 64$ ) during the pre-laying period.  $K$  refers to the number of parameters. Candidate models and models without any explanatory variable (the 'intercept model') are ranked according to their AICc. The second part of the table (a) gives the estimates of parameter (absolute baseline corticosterone levels) for males ( $N = 32$ ) and females ( $N = 25$ )

| No.                                    | Model                                    | AICc           | $\Delta$ AICc     | AICc weight | $K$     |
|--|--|----------------|-------------------|-------------|---------|
| (a)                                    |  |                |                   |             |         |
| 1.                                     | Bas. CORT; Sex; Bas. CORT $\times$ Sex   | 57.62          | 0                 | 39.6%       | 4       |
| 2.                                     | Intercept                                | 57.92          | 0.30              | 34.0%       | 1       |
| 3.                                     | Bas. CORT                                | 59.14          | 1.52              | 18.5%       | 2       |
| 4.                                     | Bas. CORT; Sex                           | 60.82          | 3.20              | 8.0%        | 3       |
| Selected model                         |  | Parameters     | Estimate $\pm$ SE | Chi-squared | $P$     |
| Bas. CORT; Sex; Bas. CORT $\times$ Sex |  | <i>Males</i>   |                   |             |         |
|  |  | Intercept      | 0.55 $\pm$ 1.02   | 17.301      | < 0.001 |
|  |  | Bas. CORT      | 0.09 $\pm$ 0.12   | 0.542       | 0.461   |
|  |  | <i>Females</i> |                   |             |         |
|  |  | Intercept      | 3.83 $\pm$ 1.36   | 89.867      | < 0.001 |
|  |  | Bas. CORT      | -0.26 $\pm$ 0.12  | 7.315       | 0.007   |
| (b)                                    |  |                |                   |             |         |
| 1.                                     | T Intercept                              | 61.47          | 0                 | 50.6%       | 1       |
| 2.                                     | T Max. CORT                              | 62.46          | 0.98              | 31.0%       | 2       |
| 3.                                     | T Max. CORT; Sex                         | 64.16          | 2.68              | 13.2%       | 3       |
| 4.                                     | T Max. CORT; Sex; Max. CORT $\times$ Sex | 66.04          | 4.56              | 5.2%        | 4       |



**Fig. 4.** Standardized baseline pre-laying corticosterone levels ( $\text{ng mL}^{-1}$ , mean and SE) of snow petrels in relation to breeding decision (will skip or will breed). Black-filled bars denote males and white-filled bars denote females.

rone levels during the pre-laying period were more likely to lose their egg. When only considering eggs that hatched successfully, there was a positive and significant correlation between standardized baseline corticosterone and egg-laying date (Table 3a and Fig. 5a). Pre-laying stress-induced corticosterone levels were not associated with the egg-laying date of hatched eggs (Table 3b and Fig. 5b).

## Discussion

As found in other avian species (Forslund & Pärt 1995; Gonzalez-Solis *et al.* 2004; Ezard, Becker & Coulson 2007; McCleery *et al.* 2008), young snow petrels (less than 13 years old) bred later than middle-aged birds (from 13 to 30 years). Moreover, young snow petrels were more likely to skip a breeding attempt than old ones. In addition, the oldest birds

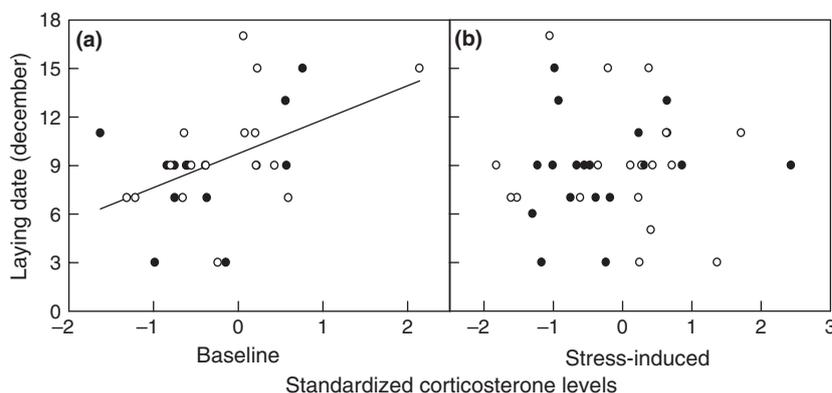
(> 30 years old) bred later than middle-aged ones, suggesting a possible effect of older age on the timing of breeding, a pattern only reported to date in the common tern (*Sterna hirundo*; Ezard, Becker & Coulson 2007) and the mute swan (*Cygnus olor*; McCleery *et al.* 2008). In parallel, young birds and very old birds were more sensitive to stress than middle-aged ones during the pre-laying period. However, there was no link between stress-induced corticosterone levels and egg-laying date. However, elevated baseline corticosterone levels were associated with a higher probability to skip breeding in females and a delayed timing of egg-laying in both sexes.

## AGE AND STRESS HORMONES

During the pre-laying period, snow petrels exhibited a 10-fold increase in corticosterone levels related to capture and handling. This magnitude was similar during incubation and was lower during chick rearing in petrel species (Adams *et al.* 2005; Angelier *et al.* 2007a, 2009). Adults in poor body condition were more sensitive to stress than those in good body condition as shown in many other species (Wingfield *et al.* 1998; Angelier *et al.* 2009). Furthermore, baseline and stress-induced corticosterone levels increased with sampling date, whereas body condition decreased with sampling date, but not with the time before egg-laying. During the pre-laying period, early-arrived petrels were indeed in better condition than late-arrived ones (Chastel, Weimerskirch & Jouventin 1995). Birds in poor condition and showing elevated corticosterone levels may then be of lower quality (e.g. low foraging skills) and may not be able to arrive early in the season. Males exhibited slightly higher baseline and stress-induced corticosterone levels than females, possibly in response to different pre-laying energetic constraints and activities (Wingfield *et al.*

**Table 3.** Model selection using corrected version of Akaike's information criterion (AICc) to explain laying date of hatched egg in relation to (a) standardized baseline corticosterone levels (Bas. CORT,  $N = 30$ ) and standardized stress-induced corticosterone levels (Max. CORT,  $N = 37$ ) during the pre-laying period.  $K$  refers to the number of parameters. Candidate models and models without any explanatory variable (the 'intercept model') are ranked according to their AICc. The second part of the table (a) includes the parameter estimates for the selected model 'Bas. CORT'

| No.        | Model                                  | AICc       | $\Delta$ AICc     | AICc weight | $K$     |
|------------|--|------------|-------------------|-------------|---------|
| <b>(a)</b> |  |            |                   |             |         |
| 1.         | Bas. CORT                              | 156.41     | 0                 | 66.8%       | 3       |
| 2.         | Bas. CORT; Sex                         | 158.62     | 2.21              | 22.2%       | 4       |
| 3.         | Bas. CORT; Sex; Bas. CORT $\times$ Sex | 161.26     | 4.85              | 5.9%        | 5       |
| 4.         | Intercept                              | 161.56     | 5.15              | 5.1%        | 2       |
|            | Selected model                         | Parameters | Estimate $\pm$ SE | Chi-squared | $P$     |
|            | Bas. CORT                              | Intercept  | 9.74 $\pm$ 0.58   | 277.020     | < 0.001 |
|            |  | Bas. CORT  | 2.10 $\pm$ 0.75   | 7.618       | 0.006   |
| <b>(b)</b> |  |            |                   |             |         |
| 1.         | Intercept                              | 198.60     | 0                 | 63.3%       | 2       |
| 2.         | Max. CORT                              | 200.59     | 1.99              | 23.4%       | 3       |
| 3.         | Max. CORT; Sex                         | 202.47     | 3.87              | 9.1%        | 4       |
| 4.         | Max. CORT; Sex; Max. CORT $\times$ Sex | 204.05     | 5.45              | 4.1%        | 5       |



**Fig. 5.** Relationship between the egg-laying date (December) and standardized pre-laying baseline (a) and stress-induced (b) corticosterone levels of breeders. Closed circles denote males and open circles denote females.

1998; Landys, Ramenofsky & Wingfield 2006) such as fasting and strong intrasexual competition (Barbraud & Chastel 1999).

Contrary to our prediction, pre-laying baseline corticosterone levels were not correlated with age, as reported in other long-lived birds (Angelier *et al.* 2006; Heidinger, Nisbet & Ketterson 2006; Angelier *et al.* 2007a,b). This may suggest that baseline corticosterone is more likely to be influenced daily by short-term stressful events (Landys, Ramenofsky & Wingfield 2006) and be independent of age. However, breeding experience (i.e. number of previous breeding attempts) greatly differs between snow petrels of the same age, because they frequently skip a breeding attempt and the age when first breeding is greatly variable between individuals (Chastel, Weimerskirch & Jouventin 1993). In long-lived birds, breeding experience explains better the variation of baseline corticosterone than age *per se* (Angelier *et al.* 2006, 2007b). This suggests that baseline corticosterone levels are not only influenced by short-term factors but can also be influenced by longer-term factors such as breeding experience.

According to our prediction, young pre-laying birds were more sensitive to stress than middle-aged ones. This has also been observed during incubation in another long-lived bird

(Heidinger, Nisbet & Ketterson 2006) and is commonly interpreted as a mechanism for low commitment into current reproduction (Heidinger, Nisbet & Ketterson 2006; Angelier *et al.* 2007a). Young birds should favour future reproductive opportunities, likely through high pre-laying stress-induced corticosterone levels. Stress resistance may have arisen from a habituation process to handling with age. However, known-age snow petrels have been seldom handled prior to this study and a similar study found no effect of recapture history on stress hormone levels (Heidinger, Nisbet & Ketterson 2006). The lower stress response in middle-aged snow petrels compared with younger ones may originate from a decrease in adrenal capacity as suggested by a recent study of known-age common terns (Heidinger, Ketterson & Nisbet 2008).

Interestingly, we found that the oldest birds (> 30 years) showed a stronger response to stress than the 13–30-year-old birds. To our knowledge, this is the first report of a magnified stress response at an older age in a free-living organism. The stronger stress response in the oldest birds may therefore originate from a possible physiological senescence of the hypothalamo-pituitary-adrenal (HPA) system, as observed in elderly humans and rats (Sapolsky,

Krey & McEwen 1986a,b; Wilkinson, Peskind & Raskind 1997; Sapolsky 1999; Otte *et al.* 2005).

An alternative hypothesis could be a progressive disappearance of adults excessively sensitive to stress over time. This would imply that the magnitude of the stress response is fixed early in the reproductive life of an individual. However, as shown experimentally in the house sparrow (*Passer domesticus*; Lendvai, Giraudeau & Chastel 2007), the same individual can modulate its hormonal stress response flexibly according to the value of the reproductive event. Furthermore, this 'selection hypothesis' would not explain the magnified stress response found in the oldest birds.

#### AGE, STRESS HORMONES AND TIMING OF BREEDING

As found in Florida scrub jay and zebra finches (Salvante & Williams 2003; Schoech *et al.* 2009), elevated pre-laying baseline corticosterone levels were associated with the decision to skip breeding in female snow petrels, and with a postponed egg-laying date in both sexes. Baseline corticosterone seems therefore to fine-tune the timing of breeding with regard of stress occurring during pre-laying, suggesting energetic constraints.

Male stress hormone levels were important for the timing of breeding, although it is thought that females mainly drive the egg-laying date (Caro *et al.* 2009). This suggests that baseline corticosterone levels of one partner may reflect the global state of the breeding pair (e.g. quality of the nest, male's ability to defend the nest), or an assortative mating according to stress levels. However, male corticosterone levels were not as decisive as in females for breeding decision. This highlights a potential sex difference in the response to environmental cues related to seasonal events (Ball & Ketterson 2008; Blas & Hiraldo 2010).

How could baseline corticosterone orchestrate breeding decision and timing of breeding? In domesticated animals, cortisol suppresses luteinizing hormone (LH, a pituitary hormone involved in the onset of breeding) secretion by inhibiting pituitary response to gonadotropin-releasing hormone (GnRH; Breen & Karsch 2004). Moreover, corticosterone potentially acts via the gonadotropin-inhibiting hormone (GnIH), a recently discovered peptide, that downregulates the hypothalamic–pituitary–gonadal axis (Bentley *et al.* 2006; Ubuka *et al.* 2006; Calisi, Rizzo & Bentley 2008; Greives *et al.* 2008; Kirby *et al.* 2009). Thereby, in snow petrels, stress hormones might activate the GnIH system and postpone the timing of breeding or even cancel the breeding attempt.

However, the positive correlation between baseline corticosterone levels and egg-laying date was only observed in snow petrels that incubated their egg successfully. Failed clutches belonged to parents with high baseline corticosterone levels during the pre-laying period. We did not observe any disappearance of egg owing to predation and all case of failure were because of nest desertion. In snow petrels, incubation requires petrels to fast on the nest. Birds bearing elevated baseline corticosterone levels may then be of lower quality

(e.g. low foraging skills; Angelier *et al.* 2007c) and may not be able to cope with the energetic constraints of incubation. In conclusion, higher baseline corticosterone levels in snow petrels during the pre-laying period were correlated to a higher probability (i) to skip the breeding attempt, (ii) to loose the egg or (iii) to start breeding later in the season.

Our aim was to test whether the often observed age-specific timing of breeding could be related to higher stress sensitivity in young breeders compared with older ones. Contrary to our prediction and in spite of a strong age-specific stress response during the pre-laying period, the sensitivity to stress was not the functional mechanism involved in age-specific timing of breeding pattern observed in snow petrels. Our sample size was sufficient to rule out any hidden effect. Stress-induced levels of corticosterone are not as flexible and reactive to daily environmental cues than baseline corticosterone (Kitaysky, Piatt & Wingfield 2007). Thus, stress-induced corticosterone levels might be inappropriate to rule the adjustment of timing of breeding or the decision to breed.

However, baseline corticosterone levels, which predicted breeding decision and timing of breeding, were independent of age. How can the age-specific differences in timing of breeding be explained? The link between age and timing of breeding could possibly be indirect and originate from other age-related parameters (see Blas & Hiraldo 2010). In snow petrels, timing of breeding is better explained by previous breeding experience than age *per se* (unpublished data). We suggested that baseline corticosterone levels would be higher in inexperienced birds as found in other long-lived birds (Angelier *et al.* 2006, 2007b), and in turn would explain the functional mechanism of late breeding in young birds. Regarding the very old snow petrels, their late breeding could be the consequence of reduced foraging skills (Catry *et al.* 2006) and/or the possible death of their previous mate. Newly formed pairs breed later than long-term partners (snow petrels, unpublished data) and may exhibit higher baseline corticosterone levels, as shown in black-legged kittiwakes (Angelier *et al.* 2007d). Thus age-related factors, like previous breeding experience, foraging ability or change of mates may influence the timing of breeding rather than age *per se*. In turn, these age-related factors could influence the baseline corticosterone levels of pre-laying birds.

#### Acknowledgements

This research project no. 109 was performed at Dumont d'Urville Station and was supported by the French Polar Institute (IPEV). A. Goutte was supported by a BDI grant from CNRS/Région Poitou-Charentes. This article benefited greatly from the comments of three anonymous reviewers and of one associate editor. The authors thank A. Jacquet for her precious assistance on the field. They also acknowledge M. Authier, C. Barbraud, K. Delord and A. Lescroël for helpful comments on the manuscript; S. Dano, A. Lacroix and C. Trouvé for their technical assistance for the assays and molecular sexing; and D. Besson for help in managing the long-term data base.

#### References

- Adams, N.J., Cockrem, J.F., Taylor, G.A., Candy, E.J. & Bridges, J. (2005) Corticosterone responses of grey-faced petrels (*Pterodroma macroptera*

- gouldii*) are higher during incubation than during other breeding stages. *Physiological and Biochemical Zoology*, **78**, 69–77.
- Angelier, F., Shaffer, S.A., Weimerskirch, H. & Chastel, O. (2006) Effect of age, breeding experience and senescence on corticosterone and prolactin levels in a long-lived seabird: the wandering albatross. *General and Comparative Endocrinology*, **149**, 1–9.
- Angelier, F., Moe, B., Weimerskirch, H. & Chastel, O. (2007a) Age-specific reproductive success in a long-lived bird: do older parents resist stress better? *Journal of Animal Ecology*, **76**, 1181–1191.
- Angelier, F., Weimerskirch, H., Dano, S. & Chastel, O. (2007b) Age, experience and reproductive performance in a long-lived bird: a hormonal perspective. *Behavioral Ecology and Sociobiology*, **61**, 611–621.
- Angelier, F., Shaffer, S.A., Weimerskirch, H., Trouvé, C. & Chastel, O. (2007c) Corticosterone and foraging behavior in a pelagic seabird. *Physiological and Biochemical Zoology*, **80**, 283–292.
- Angelier, F., Moe, B., Clement-Chastel, C., Bech, C. & Chastel, O. (2007d) Corticosterone levels in relation to change of mate in black-legged kittiwake. *The Condor*, **109**, 668–674.
- Angelier, F., Moe, B., Blanc, S. & Chastel, O. (2009) What factors drive prolactin and corticosterone responses to stress in a long-lived bird species (Snow Petrel *Pagodroma nivea*)? *Physiological and Biochemical Zoology*, **82**, 590–602.
- Ball, G.F. & Ketterson, E.D. (2008) Sex differences in the response to environmental cues regulating seasonal reproduction in birds. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **363**, 231–246.
- Barbraud, C. & Chastel, O. (1999) Early body condition and hatching success in the snow petrel *Pagodroma nivea*. *Polar Biology*, **21**, 1–4.
- Barbraud, C. & Jouventin, P. (1998) What causes body size variation in the Snow Petrel *Pagodroma nivea*? *Journal of Avian Biology*, **29**, 161–171.
- Barbraud, C., Lormée, H. & LeNeve, A. (2000) Body size and determinants of laying date variation in the Snow Petrel *Pagodroma nivea*. *Journal of Avian Biology*, **31**, 295–302.
- Barbraud, C. & Weimerskirch, H. (2001) Contrasting effects of the extent of sea-ice on the breeding performance of an Antarctic top predator, the Snow Petrel *Pagodroma nivea*. *Journal of Avian Biology*, **32**, 297–302.
- Bentley, G.E., Perfito, N., Moore, I.T., Ukena, K., Tsutsui, K. & Wingfield, J.C. (2006) Gonadotropin-inhibitory hormone in birds: possible modes of action. *Acta Zoologica Sinica*, **52**, 178–182.
- Blas, J. & Hiraldo, F. (2010) Proximate and ultimate factors explaining floating behavior in long-lived birds. *Hormones and Behavior*, **57**, 169–176.
- Blas, J., Sergio, F. & Hiraldo, F. (2009) Age-related improvement in reproductive performance in a long-lived raptor: a cross-sectional and longitudinal study. *Ecography*, **32**, 647–657.
- Bokony, V., Lendvai, A.Z., Liker, A., Angelier, F., Wingfield, J.C. & Chastel, O. (2009) Stress response and the value of reproduction: are birds prudent parents? *American Naturalist*, **173**, 589–598.
- Breen, K.M. & Karsch, F.J. (2004) Does cortisol inhibit pulsatile luteinizing hormone secretion at the hypothalamic or pituitary level? *Endocrinology*, **145**, 692–698.
- Breuner, C.W., Patterson, S.H. & Hahn, T.P. (2008) In search of relationships between the acute adrenocortical response and fitness. *General and Comparative Endocrinology*, **157**, 288–295.
- Bried, J., Pontier, D. & Jouventin, P. (2003) Mate fidelity in monogamous birds: a re-examination of the Procellariiformes. *Animal Behaviour*, **65**, 235–246.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference*. Springer-Verlag, New York.
- Calisi, R.M., Rizzo, N.O. & Bentley, G.E. (2008) Seasonal differences in hypothalamic EGR-1 and GnIH expression following capture-handling stress in house sparrows (*Passer domesticus*). *General and Comparative Endocrinology*, **157**, 283–287.
- Caro, S.P., Charmantier, A., Lambrechts, M.M., Blondel, J., Balthazart, J. & Williams, T.D. (2009) Local adaptation of timing of reproduction: females are in the driver's seat. *Functional Ecology*, **23**, 172–179.
- Catry, P., Phillips, R., Phalan, B. & Croxall, J.P. (2006) Senescence effects in an extremely long-lived bird: the grey-headed albatross *Thalassarche chrysoloma*. *Proceedings of the Royal Society B*, **273**, 1625–1630.
- Chastel, O., Weimerskirch, H. & Jouventin, P. (1993) High annual variability in reproductive success and survival of an antarctic seabird, the Snow Petrel *Pagodroma-nivea* – a 27-year study. *Oecologia*, **94**, 278–285.
- Chastel, O., Weimerskirch, H. & Jouventin, P. (1995) Influence of body condition on reproductive decision and reproductive success in the Blue Petrel. *Auk*, **112**, 964–972.
- Curio, E. (1983) Why do young birds reproduce less well. *Ibis*, **125**, 400–404.
- DeForest, L.N. & Gaston, A.J. (1996) The effect of age on timing of breeding and reproductive success in the thick-billed Murre. *Ecology*, **77**, 1501–1511.
- Durant, J.M., Hjermmann, D.O., Ottersen, G. & Stenseth, N.C. (2007) Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*, **33**, 271–283.
- Ezard, T.H.G., Becker, P.H. & Coulson, T. (2007) Correlations between age, phenotype, and individual contribution to population growth in common terns. *Ecology*, **88**, 2496–2504.
- Forslund, P. & Pärt, T. (1995) Age and reproduction in birds – hypotheses and tests. *Trends in Ecology & Evolution*, **10**, 374–378.
- Fridolfsson, A.K. & Ellegren, H. (1999) A simple and universal method for molecular sexing of non-ratite birds. *Journal of Avian Biology*, **30**, 116–121.
- Gonzalez-Solis, J., Becker, P.H., Jover, L. & Ruiz, X. (2004) Individual changes underlie age-specific pattern of laying date and egg-size in female common terns (*Sterna hirundo*). *Journal of Ornithology*, **145**, 129–136.
- Greives, T.J., Kriegsfeld, L.J., Bentley, G.E., Tsutsui, K. & Demas, G.E. (2008) Recent advances in reproductive neuroendocrinology: a role for RFamide peptides in seasonal reproduction? *Proceedings of the Royal Society of London B-Biological Sciences*, **275**, 1943–1951.
- Heidinger, B.J., Ketterson, E.D. & Nisbet, I. (2008) Changes in adrenal capacity contribute to a decline in the stress response with age in a long-lived seabird. *General and Comparative Endocrinology*, **156**, 564–568.
- Heidinger, B.J., Nisbet, I.C.T. & Ketterson, E.D. (2006) Older parents are less responsive to a stressor in a long-lived seabird: a mechanism for increased reproductive performance with age? *Proceedings of the Royal Society B-Biological Sciences*, **273**, 2227–2231.
- Jenouvrier, S., Barbraud, C. & Weimerskirch, H. (2005) Long-term contrasted responses to climate of two antarctic seabird species. *Ecology*, **86**, 2889–2903.
- Kirby, E.D., Geraghty, A.C., Ubuka, T., Bentley, G.E. & Kaufer, D. (2009) Stress increases putative gonadotropin inhibitory hormone and decreases luteinizing hormone in male rats. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 11324–11329.
- Kitaysky, A.S., Piatt, J.F. & Wingfield, J.C. (2007) Stress hormones link food availability and population processes in seabirds. *Marine Ecology-Progress Series*, **352**, 245–258.
- Kitaysky, A.S., Wingfield, J.C. & Piatt, J.F. (1999) Dynamics of food availability, body condition and physiological stress response in breeding black-legged Kittiwakes. *Functional Ecology*, **13**, 577–584.
- Lack, D. (1968) *Ecological Adaptations for Breeding in Birds*. Methuen, London.
- Landys, M.M., Ramenofsky, M. & Wingfield, J.C. (2006) Actions of glucocorticoids at a seasonal baseline as compared to stress-related levels in the regulation of periodic life processes. *General and Comparative Endocrinology*, **148**, 132–149.
- Lendvai, A.Z. & Chastel, O. (2008) Experimental mate-removal increases the stress response of female house sparrows: the effects of offspring value? *Hormones and Behavior*, **53**, 395–401.
- Lendvai, A.Z., Giraudeau, M. & Chastel, O. (2007) Reproduction and modulation of the stress response: an experimental test in the house sparrow. *Proceedings of the Royal Society B-Biological Sciences*, **274**, 391–397.
- Lormée, H., Jouventin, P., Trouve, C. & Chastel, O. (2003) Sex-specific patterns in baseline corticosterone and body condition changes in breeding red-footed Boobies *Sula sula*. *Ibis*, **145**, 212–219.
- Love, O.P., Breuner, C.W., Vézina, F. & Williams, T.D. (2004) Mediation of a corticosterone-induced reproductive conflict. *Hormones and Behavior*, **46**, 59–65.
- Martin, K. (1995) Patterns and mechanisms for age-dependent reproduction and survival in birds. *American Zoologist*, **35**, 340–348.
- Mauck, R.A., Huntington, C.E. & Grubb, T.C. (2004) Age-specific reproductive success: evidence for the selection hypothesis. *Evolution*, **58**, 880–885.
- McCleery, R.H., Perrins, C.M., Sheldon, B.C. & Charmantier, A. (2008) Age-specific reproduction in a long-lived species: the combined effects of senescence and individual quality. *Proceedings of the Royal Society B-Biological Sciences*, **275**, 963–970.
- Nager, R.G. & van Noordwijk, A.J. (1995) Proximate and ultimate aspects of phenotypic plasticity in timing of great tit breeding in a heterogeneous environment. *American Naturalist*, **146**, 454–474.
- Otte, C., Hart, S., Neylan, T.C., Marmar, C.R., Yaffe, K. & Mohr, D.C. (2005) A meta-analysis of cortisol response to challenge in human aging: importance of gender. *Psychoneuroendocrinology*, **30**, 80–91.
- Pérez-Rodríguez, L., Blas, J., Vinuela, J., Marchant, T.A. & Bortolotti, G.R. (2006) Condition and androgen levels: are condition-dependent and testos-

- terone-mediated traits two sides of the same coin? *Animal Behaviour*, **72**, 97–103.
- Perrins, C.M. (1970) Timing of birds breeding seasons. *Ibis*, **112**, 242–255.
- Quinn, G.P. & Keough, M.J. (2002) *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Melbourne.
- Ricklefs, R.E. & Wikelski, M. (2002) The physiology/life-history nexus. *Trends in Ecology and Evolution*, **17**, 462–468.
- Romero, L.M. & Reed, J.M. (2005) Collecting baseline corticosterone samples in the field: is under 3 min good enough? *Comparative Biochemistry and Physiology A-Molecular & Integrative Physiology*, **140**, 73–79.
- Salvante, K.G. & Williams, T.D. (2003) Effects of corticosterone on the proportion of breeding females, reproductive output and yolk precursor levels. *General and Comparative Endocrinology*, **130**, 205–214.
- Sapolsky, R.M. (1999) Glucocorticoids, stress, and their adverse neurological effects: relevance to aging. *Experimental Gerontology*, **34**, 721–732.
- Sapolsky, R.M., Krey, L.C. & McEwen, B.S. (1986a) The adrenocortical axis in the aged rat: impaired sensitivity to both fast and delayed feedback inhibition. *Neurobiology of Aging*, **7**, 331–335.
- Sapolsky, R.M., Krey, L.C. & McEwen, B.S. (1986b) The neuroendocrinology of stress and aging – the glucocorticoid cascade hypothesis. *Endocrine Reviews*, **7**, 284–301.
- Schoech, S.J., Rensel, M.A., Bridge, E.S., Boughton, R.K. & Wilcoxon, T.E. (2009) Environment, glucocorticoids, and the timing of reproduction. *General and Comparative Endocrinology*, **163**, 201–207.
- Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, New York.
- Stenseth, N.C. & Mysterud, A. (2002) Climate, changing phenology, and other life history and traits: nonlinearity and match-mismatch to the environment. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 13379–13381.
- Ubuka, T., Ukena, K., Sharp, P.J., Bentley, G.E. & Tsutsui, K. (2006) Gonadotropin-inhibitory hormone inhibits gonadal development and maintenance by decreasing gonadotropin synthesis and release. *Endocrinology*, **147**, 1187–1194.
- Visser, M.E., van Noordwijk, A.J., Tinbergen, J.M. & Lessells, C.M. (1998) Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society of London Series B-Biological Sciences*, **265**, 1867–1870.
- Weimerskirch, H., Lallemand, J. & Martin, J. (2005) Population sex ratio variation in a monogamous long-lived bird, the wandering albatross. *Journal of Animal Ecology*, **74**, 285–291.
- Wilkinson, C.W., Peskind, E.R. & Raskind, M.A. (1997) Decreased hypothalamic–pituitary–adrenal axis sensitivity to cortisol feedback inhibition in human aging. *Neuroendocrinology*, **65**, 79–90.
- Wingfield, J.C. & Sapolsky, R.M. (2003) Reproduction and resistance to stress: when and how. *Journal of Neuroendocrinology*, **15**, 711–724.
- Wingfield, J.C., DeWitte, P., Sharbaugh, S., Astheimer, L.B., Holberton, R., Suydam, R. & Hunt, K. (1994) Seasonal-changes of the adrenocortical responses to stress in redpolls, *Acanthis-flammea*, in Alaska. *Journal of Experimental Zoology*, **270**, 372–380.
- Wingfield, J.C., Maney, D.L., Breuner, C.W., Jacobs, J.D., Lynn, S., Ramenofsky, M. & Richardson, R.D. (1998) Ecological bases of hormone–behavior interactions: the “emergency life history stage”. *American Zoologist*, **38**, 191–206.

Received 9 October 2009; accepted 4 March 2010

Handling Editor: Juan Soler