

# Age, experience and reproductive performance in a long-lived bird: a hormonal perspective

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**Abstract** The ultimate factors influencing age-specific reproductive performance in birds have been widely discussed, and several hypotheses have been suggested to explain why young/inexperienced breeders have lower reproductive success than older individuals. In comparison, proximate factors and, particularly, hormonal mechanisms influencing age-related reproductive performance have received lesser attention. In this paper, we examined how baseline levels of corticosterone and prolactin, two hormones involved in reproduction, changed with age and experience in a long-lived bird, the Black-browed albatross (*Thalassarche melanophris*) during the brooding stage. Corticosterone levels were not linked to age, whereas prolactin levels increased until individuals reached 15 years of age. First-time breeders had higher corticosterone levels and lower prolactin levels than experienced ones. Corticosterone levels were not correlated with breeding experience among experienced birds, whereas prolactin levels slightly increased with advancing experience. Among experienced breeders, there was no effect of individual quality on corticosterone and prolactin levels. Baseline corticosterone and prolactin levels were respectively, positively and negatively correlated to time spent fasting/brooding on the nest. Moreover, the probability of successfully fledging a chick was negatively related to corticosterone levels, but not to prolactin levels. Elevated corticosterone levels in first time breeders may serve as evidence for depleted body reserves resulting from lower foraging/brooding capabilities and therefore support

the constraint hypothesis. Low prolactin levels in young/inexperienced birds may be interpreted either as evidence for their lower breeding capacities (constraint hypothesis) or for their limited breeding investment (restraint hypothesis). Finally, we report, for the first time, the hormonal changes associated with the onset of senescence. The very old and most experienced birds, which had the lowest probability of successfully fledging a young, displayed elevated corticosterone levels and low prolactin levels, possibly indicating a degradation of breeding skills and/or a disruption of the endocrine system in senescent birds.

**Keywords** Reproduction · Age · Senescence · Hormones · Corticosterone · Prolactin · Black-browed albatross

## Introduction

Survival and reproductive performances generally increase with age in long-lived species, before stabilizing at mid-age and declining in old individuals as an expression of senescence (Clutton-Brock 1988; Newton 1989; Forslund and Pärt 1995). The ultimate factors influencing age-specific reproductive performance have been widely discussed by theoreticians (Williams 1966; Curio 1983; Clutton-Brock 1984, 1988; Stearns 1992; Roff 1992; Weimerskirch 1992; Forslund and Pärt 1995) and empirical ecologists (Clutton-Brock 1988; Newton 1989; Cam and Monnat 2000; Robertson and Rendell 2001; Saino et al. 2002; Cichoń 2003; Mauck et al. 2004) and three main hypotheses have been suggested to explain this pattern of performance (review in Forslund and Pärt 1995): (1) the constraint hypothesis suggests that young individuals are less reproductively efficient due to a lack of reproductive experience and an imperfect maturation of

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reproductive skills (Curio 1983); (2) the restraint hypothesis suggests that breeding investment increases with age as the residual reproductive value declines (mortality increases and fecundity decreases) and breeding events become more valuable (Curio 1983); and (3) the selection hypothesis suggests a progressive disappearance of low quality phenotypes, resulting in an increase of reproductive performance with age (Curio 1983; Forslund and Pärt 1995).

Proximate factors influencing age-related reproductive performance have received much less attention and only a few studies have described the endocrine correlates of ageing in free-living birds (LH, progesterone, oestradiol and androgens, Hector et al. 1990; Nisbet et al. 1999; corticosterone, Baker and O'Reilly 2000; melatonin and corticosterone, Tarlow et al. 2003). However, physiological and hormonal mechanisms are tightly linked to reproductive performance so that understanding the influence of age on these mechanisms will allow us to better appreciate the age-specific patterns of reproductive performance.

The hormone corticosterone deserves specific attention because of its potential role in mediating breeding decisions (Sinervo and Svensson 1998, Wingfield and Sapolsky 2003). High corticosterone levels can be indicative of the stress imposed by sustained breeding activities (resulting in depleted body reserves, Cherel et al. 1988) or by environmental stressors (review in Wingfield et al. 1998) and can ultimately trigger nest desertion (Silverin 1986; Love et al. 2004) by altering the allocation of available resources between body maintenance and reproductive processes (Silverin 1986). There is, however, growing evidence that moderately elevated baseline corticosterone levels (below those inducing desertion) may be inherent and necessary for successful reproduction (Moore and Jessop 2003; Love et al. 2004) because of their stimulatory effect on the foraging activities of reproducing animals (Astheimer et al. 1992; Challet et al. 1995). As a result, we can make two predictions regarding this hormone:

- 1) Young/inexperienced breeders display low corticosterone levels; this could be interpreted either as lower breeding activities reflected by low corticosterone secretion ("the restraint hypothesis", Curio 1983) or by the inability of young/inexperienced breeders to secrete corticosterone to sustain parental activities ("the constraint hypothesis", Curio 1983).
- 2) Young/inexperienced breeders display high corticosterone levels; in this case, higher corticosterone levels in young/inexperienced birds may signal poor body condition, lower foraging efficiency, poor breeding capacities and a greater susceptibility to environmental stressors ("the constraint hypothesis", Curio 1983).

Reproductive performance also depends on the ability of animals to provide parental care to their progeny (incuba-

tion, guarding against predators, intensive brooding for thermoregulation, etc., reviewed in Clutton-Brock 1991). In this context, the hormone prolactin is of particular interest. This hormone is involved in the expression of avian parental behaviour (incubation, brooding, provisioning, defensive behaviour) and is stimulated by visual and tactile stimuli of eggs and chicks (Buntin 1996). Elevated prolactin levels also appear necessary to maintain parental care despite stressful or unfavourable conditions (Lormée et al. 1999; Chastel et al. 2005).

The relationship between baseline levels of prolactin and age/breeding experience has rarely been examined. Two studies, for which the age of the birds was unknown, showed that levels of prolactin were lower in first-time breeders than in experienced birds (Deviche et al. 2000; Prévault et al. 2005). We can therefore predict that plasma levels of prolactin should be lower in young/inexperienced breeders. Such a likely pattern can, however, be interpreted either as evidence for a lower investment in reproduction ("the restraint hypothesis", Curio 1983) or for lower capacities of young/inexperienced breeders to produce proper amount of prolactin and exhibit appropriate parental behaviour ("the constraint hypothesis", Curio 1983).

In this paper, we examine how age and breeding experience influence reproductive performance in a long-lived bird, the black-browed albatross (*Thalassarche melanophris*), from a hormonal perspective. First, using a long-term longitudinal survey of individual breeding success, we examine if young, inexperienced birds have lower reproductive success than older, more experienced breeders (Forslund and Pärt 1995). Second, we examine the relationships between age, breeding experience and baseline corticosterone and prolactin. Lastly, as individuals may vary in their intrinsic quality (Clutton-Brock 1988) and may show signs of senescence (Finch 1990; Holmes and Austad 1995; Ricklefs 1998), we also report, for the first time, the hormonal correlates of individual quality and senescence.

## Materials and methods

### Age, experience and breeding performances

Black-browed albatrosses (3–4 kg) are long-lived birds with a high survival probability (Weimerskirch et al. 1987) and a low fecundity (one egg per year). Sexual maturity is acquired on average at 11 years of age and the breeding cycle lasts 205 days (Weimerskirch et al. 1986, 1987). Birds breed annually although a small proportion of birds skip breeding each year (Prince et al. 1994).

The long-term banding study has been conducted at Cañon des Sourcils Noirs, Kerguelen islands, south-western Indian Ocean (50°S, 70°E). At this site, an ongoing mark-recapture

programme has provided yearly information on approximately 200 pairs breeding each year for the last 25 years. Bands of breeding birds were checked after egg laying (late October) and their nests were marked with a plastic tag in order that they could be monitored during hatching and fledging stages (early January, late March, respectively). All the chicks at this site have been banded before fledging every year since 1980. Banding of breeding birds of unknown age started in 1976 and has been done each year when unbanded breeding birds were found in the colony. As a result of this effort, we have data on the age and the breeding experience (number of breeding attempts) of each bird banded as a chick. For individuals banded as breeding birds, we used an estimated age calculated from the year of banding and adding 11 years, the average age of the first reproductive attempt (Weimerskirch, unpublished data). Thus, age and breeding experience were probably underestimated for birds captured as adults.

#### Hormonal and behavioural data

Our specific field study was carried out from 3 to 11 January 2004 during the brooding period when chicks were 5–10 days old. Adult birds were captured by hand off the nest just after their mate relieved them from their brooding duties. Only one bird was captured per nest and thus our data on males and females are independent with respect to nest. For 63 adults, we collected blood samples from the tarsus vein with a 1-ml heparinised syringe and a 25-gauge needle. The handling time was minimal (5 min maximum) and all birds were released near their nests after the procedure. No bird abandoned its nest after capture and bleeding.

Before capturing birds, we measured the duration of brooding shifts of 20 of the 63 birds sampled. Birds were marked with picric acid on the chest without handling the bird. Marked birds were then observed from dawn (5:00 a.m.) to dusk (9:00 p.m.) to quantify the time spent brooding (fasting).

Twenty-three of the sampled albatrosses had been banded as chicks and we knew their age and breeding experience with certainty. Forty birds had been banded as adults and 18 of these were at least 24 years old and were attempting at least their thirteenth breeding effort. The relative quality of the sampled birds was estimated from their past reproductive performance as the average breeding success over at least 3 years before 2004 (Weimerskirch et al. 2005). Estimates of relative quality were not available for first-time breeders. At the end of the breeding cycle, each nest was checked to determine the breeding success of the 63 birds sampled, except four nests at which the tags were lost.

#### Molecular sexing and hormone assays

Blood samples were centrifuged, the plasma was decanted, and then both blood and plasma were stored at  $-20^{\circ}\text{C}$  before

analysis. All laboratory analyses were performed at the Centre d'Etudes Biologiques de Chizé (CEBC). DNA was extracted from the red blood cells and then sex of the individuals was determined through polymerase chain reaction (PCR) amplification of the CHD gene following the standard procedures (Fridolfsson and Ellegren 1999). Plasma concentrations of corticosterone were determined ( $n=63$ ) following the methods described in (Lormée et al. 2003). As blood samples had been collected within 3 min of capture, the corticosterone levels were considered to reflect baseline levels (Wingfield et al. 1982; Kitaysky et al. 1999; Romero and Reed 2005). Concentrations of prolactin were determined with the remaining plasma ( $n=55$ ) by a heterologous radioimmunoassay (RIA) as detailed in Cherel et al. (1994). The pooled plasma samples produced a dose–response curve that was similar to those of the chicken prolactin standard curves (“AFP 4444B”, source: Dr. Parlow, N.H.P.P. Harbor-UCLA Medical Center, Torrance, California, USA).

The concentrations of both hormones were determined in one assay. The intra-assay variation was 4.5% for corticosterone and 5.1% for prolactin. The minimal detectable corticosterone and prolactin levels were 0.4 and 5 ng/ml, respectively, and no samples fell below these limits. The date and time of day for blood sampling did not influence the levels of either hormone (date: corticosterone:  $F_{1,61}=2.55$ ,  $p=0.116$ , prolactin:  $F_{1,53}=1.21$ ,  $p=0.277$ ; time of day: corticosterone:  $F_{1,61}=1.04$ ,  $p=0.312$ , prolactin:  $F_{1,53}<0.01$ ,  $p=0.999$ ).

#### Statistical analyses

All analyses were performed with SAS statistical software (SAS Institute, v 8.02). We used a step-down approach (backward elimination) starting from the most global model (Lebreton et al. 1992). Likelihood ratio statistics (Sydeman et al. 1991) and likelihood ratio tests (LRT) were used to select the most parsimonious model (Burnham and Anderson 2002). This approach has been widely used in recent studies (Pyle et al. 2001; Reid et al. 2003; McDonough 2005; Duriez et al. 2005). We used generalised linear models (GLM) with a normal/binomial error distribution and an identity/logit link function to test our biological assumptions (Myers and Montgomery 1997).

#### *Age- and experience-specific reproductive performance*

We tested whether age (age variable) and breeding experience (experience variable) predicted breeding performance among birds whose age and experience were known ( $n=358$  birds,  $n=1324$  observations) by using data from the long-term survey. Because previous inspection in black-browed albatrosses suggested that relationships between age or breeding experience and breeding success were non-

linear, squared terms (age<sup>2</sup> or experience<sup>2</sup>) were included in the initial model designed to explain the probability of successfully fledging a young as a function of age or breeding experience (Reid et al. 2003). A significant quadratic regression does not prove that a dependent variable declines significantly after the peak, so we additionally tested whether fledging success and age/breeding experience were correlated beyond the estimated peak in fledging success (Reid et al. 2003).

Mean fledging success in this population varied among years and so we included a year effect into the models. Mean fledging success of each year was included as a covariate in the GLM (year variable). This approach has been widely used (Robertson and Rendell 2001; Laaksonen et al. 2002; Reid et al. 2003). We did not use age and breeding experience in our initial model because both variables were correlated. We therefore used two step-down approaches starting with two models designed to explain the probability of successfully fledging a young (1: age, age<sup>2</sup> and year variables, 2: experience, experience<sup>2</sup> and year variables). Most black-browed albatrosses bred many times during their life and our fledging success data were not independent. We therefore used generalised linear mixed models (GLMM) by including bird identity as a random factor in our models. Because these analyses suggested that fledging success could be linked to a lack of breeding experience (see “Results” section), we tested if fledging success varied between first-time breeders and experienced birds by using a categorical variable (experience variable: first-time breeders vs experienced breeders). We then tested whether fledging success varied with advancing breeding experience among experienced birds (from 2 to 11 breeding attempts). Furthermore, to test whether differences in breeding performance between inexperienced and experienced birds resulted from a low survival of poor breeders (“the selection hypothesis”, Forslund and Pärt 1995), we compared the probability of successfully fledging offspring during the first breeding attempt for birds breeding only once in their lives vs birds breeding at least twice ( $n=250$ ).

Because the banding of chicks only began in 1980, we had not enough very old and experienced known age to test an effect of senescence. To test whether a decline in fledging success occurred as a function of age, we focused on a second data set that included birds ringed as breeders between 1976 and 1986 (Crespin et al. 2006) and which subsequently bred at least 15 times ( $n=28$  birds). We used GLMM to compare the fledging success of these birds between their first monitored breeding attempts (second to seventh breeding attempts, estimated age from 11 to 23 years) and their last monitored breeding attempts (thirteenth to fifteenth breeding attempts, estimated age at least 24 years). Moreover, we examined whether overall fledging success varied through the study period (1980–

2004) to test whether age-specific reproductive performances were a consequence of variation in overall fledging success through the study period.

#### *Age- and experience-specific patterns of corticosterone and prolactin levels*

We tested whether age and breeding experience explained a significant proportion of the variation in baseline corticosterone and prolactin levels. Because breeding performance varied continuously with age (see “Results” section), we first examined whether hormone levels varied with age (from 5 to 21 years old; Table 1). Fledging success varied mainly between first-time breeders and experienced breeders (see “Results” section), and therefore we also examined whether hormone levels differed between experienced birds (from 2 to 10 breeding attempts) and first-time breeders (Table 1). We also examined (Table 1) the following: (1) whether hormone levels varied with advancing experience among experienced birds (from 2 to 10 breeding attempts); (2) whether hormone levels varied between experienced breeders (from 2 to 10 breeding attempts) and the most experienced/very old breeders (at least 13 breeding attempts and 24 years old); (3) whether prolactin levels were associated with corticosterone levels; (4) whether hormone levels were influenced by our quality index among experienced birds; (5) whether baseline corticosterone and prolactin levels were influenced by the time spent fasting on the nest and by breeding experience; and (6) whether the probability of successfully fledging a young was associated to hormone levels.

## Results

### Age, breeding experience and reproductive performance

Fledging success increased with age/breeding experience (Fig. 1a,b) with significant effects of age and age<sup>2</sup> or experience and experience<sup>2</sup> on fledging success (GLMM: age,  $F_{1,963}=18.52$ ,  $p<0.001$ , age<sup>2</sup>,  $F_{1,963}=11.49$ ,  $p=0.007$ ; GLMM: experience,  $F_{1,963}=17.17$ ,  $p<0.001$ , experience<sup>2</sup>,  $F_{1,963}=6.99$ ,  $p=0.009$ ). Age/breeding experience and fledging success were not, however, correlated after the estimated peak in fledging success (estimated peak: age, 17 years old; experience, eight breeding attempts; GLMM: age,  $F_{1,135}=0.53$ ,  $p=0.466$ ; experience,  $F_{1,58}=0.31$ ,  $p=0.578$ ), demonstrating that fledging success did not significantly decline with advancing age/breeding experience (Fig. 1a,b). Fledging success was mainly influenced by the lack of breeding experience because first-time breeders had a lower probability of successfully fledging a young than experienced breeders (mean±SE, first-time breeders: 0.522±



**Table 1** Biological assumptions tested and associated generalised linear models

| Biological assumption                                      | Dependent variable | Independent variable                               | <i>n</i> |
|--|--------------------|--|----------|
| Effect of age on hormone levels                            | Corticosterone     | Sex, age, age <sup>2</sup> and interactions        | 23       |
|  | Prolactin          | Sex, age, age <sup>2</sup> and interactions        | 22       |
| Effect of breeding experience on hormone levels            | Corticosterone     | Sex, experience1 and interaction                   | 23       |
|  | Prolactin          | Sex, experience1 and interaction                   | 22       |
| Effect of aging on hormone levels                          | Corticosterone     | Sex, experience 2 and interaction                  | 36       |
|  | Prolactin          | Sex, experience 2 and interaction                  | 31       |
| Effect of corticosterone levels on prolactin levels        | Prolactin          | Sex, corticosterone and interaction                | 55       |
| Effect of individual quality on hormone levels             | Corticosterone     | Sex, experience 2, quality and interactions        | 31       |
|  | Prolactin          | Sex, experience 2, quality and interactions        | 26       |
| Effect of time spent fasting on the nest on hormone levels | Corticosterone     | Sex, experience 3, fasting                         | 20       |
|  | Prolactin          | Sex, experience 3, fasting                         | 16       |
| Effect of hormone levels on fledging success               | Fledging success   | Sex, corticosterone (or prolactin) and interaction | 59 (52)  |

Model selection was performed by a step down approach (Lebreton et al. 1992) starting from the global model including all the independent variables (*n* denotes sample size). Baseline corticosterone or prolactin levels were indicated by ‘corticosterone’ or ‘prolactin’ variables. The ‘experience 1’, ‘experience 2’ and ‘experience 3’ factors are comparing, respectively, first-time breeders and experienced breeders (from 2 to 10 breeding attempts); experienced breeders and oldest/most experienced breeders (at least 24 years old and 13 breeding attempts); first-time breeders, experienced birds and oldest/most experienced birds. The ‘quality’ variable is an index of individual quality. The ‘fasting’ variable means the time spent fasting on the nest before blood sample.

0.027, experienced breeders:  $0.702 \pm 0.015$ ; GLMM,  $F_{1,964} = 49.91$ ,  $p < 0.001$ , Fig. 1b) and fledging success did not vary between the second and the eleventh breeding attempts (GLMM,  $F_{1,736} = 2.55$ ,  $p = 0.111$ ). There was no difference in the probability of successful breeding during the first breeding attempt between birds that reproduced only once during their life and birds that reproduced at least twice (GLM,  $F_{1,248} < 0.01$ ,  $p = 0.995$ ).

We detected a decline in the fledging success of the oldest and most experienced albatrosses that were ringed as adults. They had a lower fledging success between their thirteenth and fifteenth monitored breeding attempts than they had between their second and seventh (mean  $\pm$  SE, second to seventh breeding attempts:  $0.857 \pm 0.030$ , thirteenth to fifteenth breeding attempts:  $0.537 \pm 0.055$ ; GLMM,  $F_{1,221} = 6.74$ ,  $p = 0.010$ , Fig. 1a,b). Overall fledging success of the population did not vary significantly through the study period (1980–2004:  $F_{1,23} = 0.82$ ,  $p = 0.777$ ).

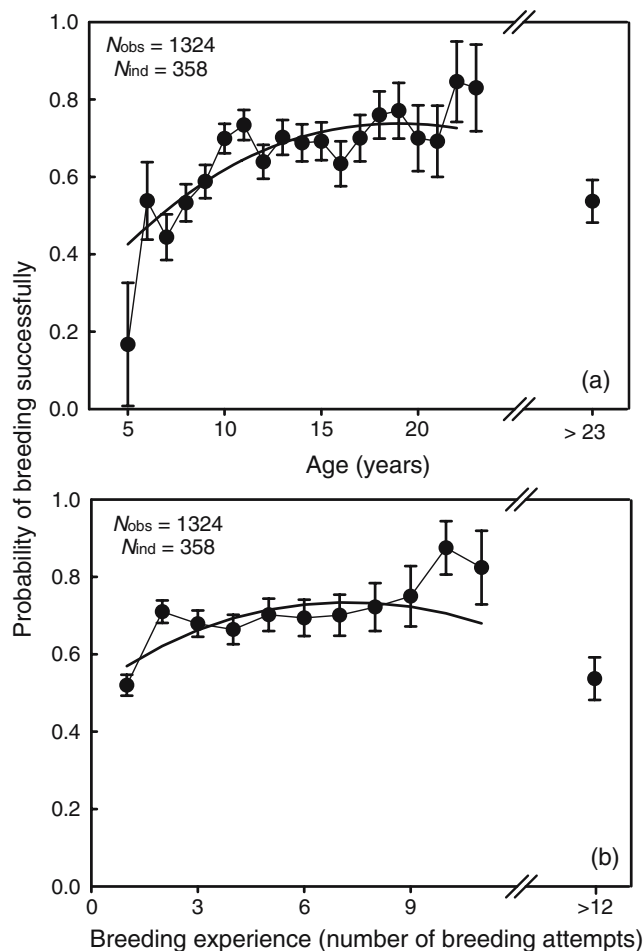
#### Age, breeding experience and hormone levels

Baseline corticosterone levels were similar between the sexes (ANOVA,  $F_{1,61} = 0.04$ ,  $p = 0.83$ ), whereas baseline prolactin levels were higher in females than in males (ANOVA,  $F_{1,53} = 8.18$ ,  $p = 0.006$ ). Baseline corticosterone levels were not linked to age (GLM, age:  $F_{1,20} = 2.11$ ,  $p = 0.147$ , age<sup>2</sup>:  $F_{1,20} = 1.53$ ,  $p = 0.216$ , Fig. 2), whereas prolactin levels increased with age up to 15 years (GLM, age:  $F_{1,18} = 7.98$ ,  $p = 0.005$ , age<sup>2</sup>:  $F_{1,18} = 5.59$ ,  $p = 0.018$ ,  $r^2 = 0.470$ , Fig. 2). First-time breeders had higher corticosterone levels and lower prolactin levels than experienced ones (GLM, corticosterone:  $F_{1,21} = 13.26$ ,  $p < 0.001$ ; prolactin:  $F_{1,19} = 10.20$ ,  $p = 0.001$ , Fig. 3a,b). Corticosterone levels were not correlat-

ed with breeding experience among experienced birds (from 2 to 10 breeding attempts, GLM,  $F_{1,16} = 1.46$ ,  $p = 0.227$ ), whereas prolactin levels slightly increased with advancing experience (GLM,  $F_{1,14} = 5.10$ ,  $p = 0.04$ ). The oldest and most experienced (at least 24 years old and 13 breeding attempts) birds had higher corticosterone levels and lower prolactin levels than less experienced (from 2 to 10 breeding attempts) birds (GLM, corticosterone:  $F_{1,34} = 6.17$ ,  $p = 0.013$ ; prolactin:  $F_{1,28} = 4.07$ ,  $p = 0.044$ , Fig. 3a,b). Baseline prolactin levels were negatively associated with baseline corticosterone levels (GLM, sex:  $F_{1,52} = 8.05$ ,  $p = 0.005$ ; corticosterone:  $F_{1,52} = 5.27$ ,  $p = 0.022$ ,  $r^2 = 0.214$ ). Finally, there was no effect of individual quality on corticosterone (GLM, sex:  $F_{1,22} = 9.61$ ,  $p = 0.005$ , experience 2:  $F_{1,22} = 7.02$ ,  $p = 0.015$ , quality  $F_{1,22} = 2.70$ ,  $p = 0.114$ ) and prolactin levels (GLM, sex:  $F_{1,26} = 1.79$ ,  $p = 0.191$ , experience 2:  $F_{1,26} = 3.64$ ,  $p = 0.040$ , quality  $F_{1,26} = 0.38$ ,  $p = 0.541$ ).

#### Hormones and reproductive behaviour

Hormone levels were strongly influenced by the time spent fasting on the nest. Baseline corticosterone and prolactin levels were positively and negatively correlated, respectively, to time spent fasting on the nest. Experienced albatrosses had lower corticosterone levels and higher prolactin levels than first-time breeders, and than most experienced albatrosses (GLM, corticosterone: time spent fasting,  $F_{1,16} = 12.6$ ,  $p = 0.0004$ , experience3,  $F_{2,16} = 18.02$ ,  $p = 0.0001$ ,  $r^2 = 0.784$ , Fig. 4a; prolactin: time spent fasting,  $F_{1,11} = 8.14$ ,  $p = 0.0043$ , experience3,  $F_{2,11} = 7.96$ ,  $p = 0.0187$ ,  $r^2 = 0.720$ ; Fig. 4b). Although first-time breeders spent slightly more time fasting on the nest than experienced ones (ANOVA,  $F_{1,11} = 3.73$ ,  $p = 0.0534$ ), time spent fasting



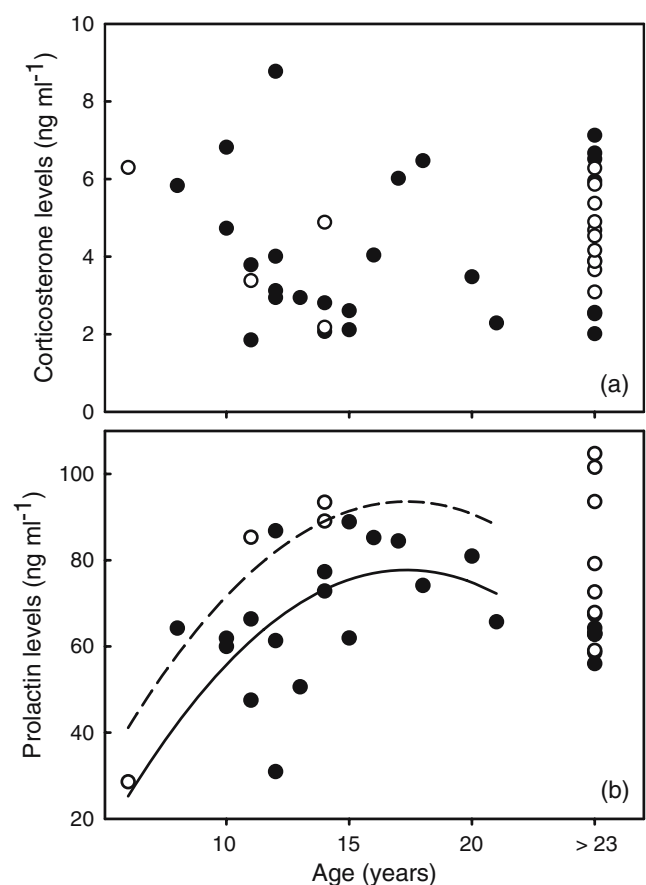
**Fig. 1** Relationships between (a) age or (b) breeding experience and the probability of successfully fledging a young (mean $\pm$ SE) among black-browed albatrosses. This probability varied significantly with individual age and individual age<sup>2</sup> (age,  $F_{1,963}=18.52$ ,  $p<0.001$ , age<sup>2</sup>,  $F_{1,963}=11.49$ ,  $p=0.007$ ). First-time breeders reproduced less well than experienced breeders ( $F_{1,964}=49.91$ ,  $p<0.001$ ). Probability of successfully fledging a young declined in oldest and most-experienced birds, i.e. at least 24 years old and 13 breeding attempts ( $F_{1,221}=6.74$ ,  $p=0.010$ ). Nobs and Nind refer to the total number of observations and individuals

on the nest was similar between experienced and the oldest/most experienced breeders (ANOVA,  $F_{1,16}=1.025$ ,  $p=0.326$ ). Moreover, the probability of successfully fledging a chick was negatively related to baseline corticosterone levels during brooding (GLM,  $F_{1,57}=7.72$ ,  $p=0.007$ , Fig. 5), but not to baseline prolactin levels (GLM, sex:  $F_{1,48}=2.17$ ,  $p=0.147$ ; prolactin:  $F_{1,48}=0.01$ ,  $p=0.937$ ; prolactin  $\times$  sex:  $F_{1,48}=2.24$ ,  $p=0.141$ ).

## Discussion

### Early reproductive performance and hormone levels

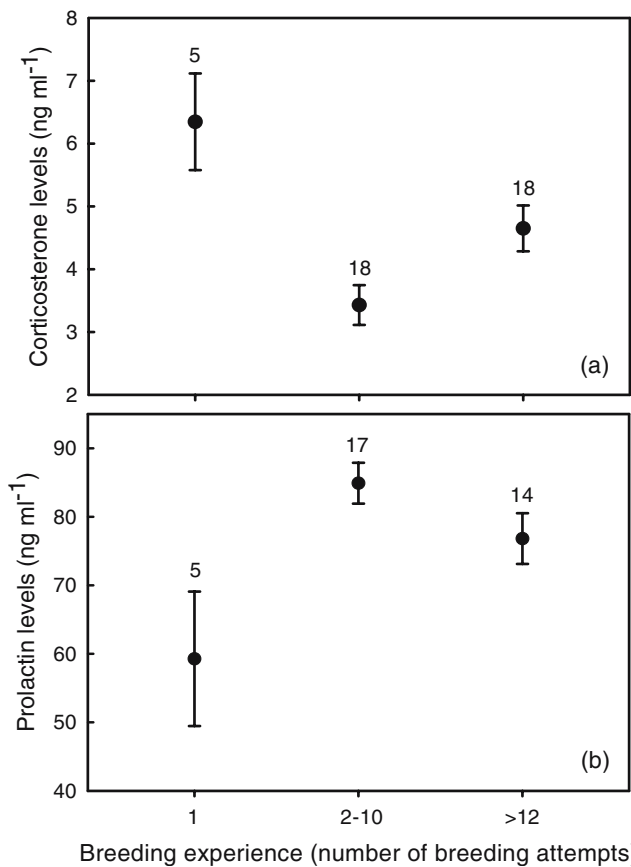
In our study, reproductive success of black-browed albatrosses improved with age and breeding experience as has been



**Fig. 2** Relationship between baseline corticosterone (a) or prolactin (b) levels and age among breeding black-browed albatrosses. Corticosterone levels did not vary with age between 5 and 21 years of age ( $n=23$ ), whereas prolactin levels did ( $n=22$ , solid line males, dashed line females). Filled symbols denote males and open ones denote females

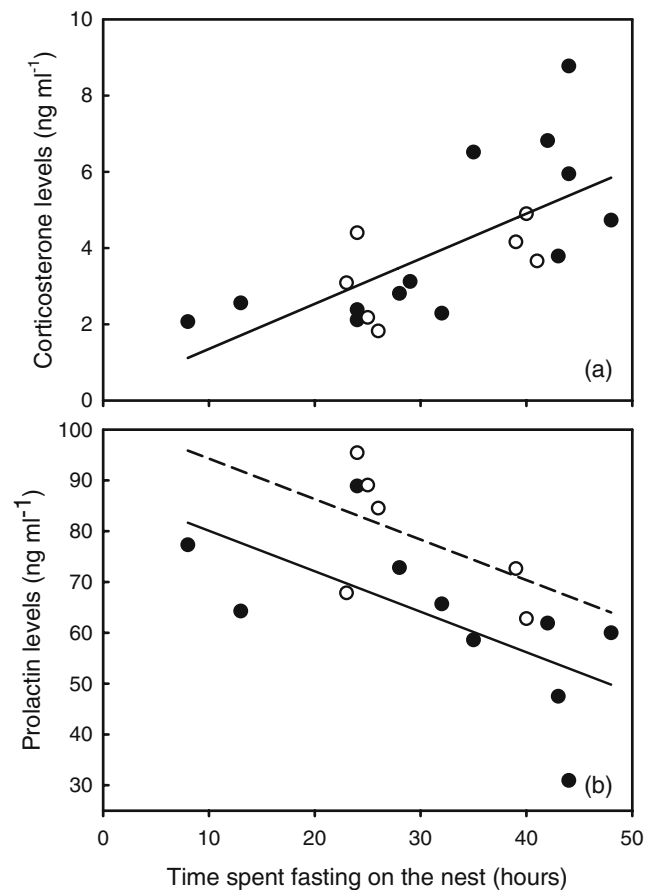
found in several other species (Clutton-Brock 1988; Newton 1989; Weimerskirch 1992; Forslund and Pärt 1995; Newton and Rothery 1997; Cam and Monnat 2000; Robertson and Rendell 2001; Saino et al. 2002; Reid et al. 2003; Mauck et al. 2004). First-time breeders did not reproduce, as well as other individuals, whereas breeding success did not vary with breeding experience among experienced birds. This suggests that the lack of breeding experience is probably the main cause of breeding failure in young albatrosses rather than age per se. Similarly, Cichoń (2003) experimentally demonstrated that breeding experience in collared flycatchers (*Ficedula albicollis*) is much more important than age in the ability of birds to rear chicks. Moreover, since albatrosses breeding at least twice in their lifetime reproduced as well during their first breeding attempt as birds breeding only once, improvement in breeding success as a function of advancing breeding experience probably does not result from a higher mortality of lower quality birds (“the selection hypothesis”, Forslund and Pärt 1995).

Baseline hormone levels, which significantly differed between first time breeders and experienced birds (from 2 to



**Fig. 3** Relationship between breeding experience (number of breeding attempts) and baseline corticosterone (a) or prolactin (b) levels (mean $\pm$ SE). Corticosterone and prolactin levels varied between first-time breeders, experienced (from 2 to 10 breeding attempts) and most experienced (at least 13 breeding attempts). Prolactin levels were corrected for a sex effect (prolactin levels were higher in females). Numbers above bars denote sample size

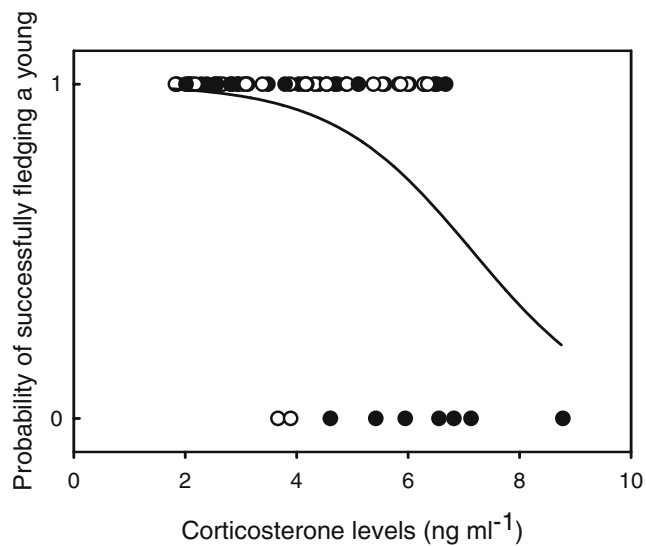
10 breeding attempts), were significantly more affected by experience than they were by age. Hormone levels (at least corticosterone) did not vary with advancing experience among experienced birds. Furthermore, the lack of relationship between individual quality and hormone levels lends support for an influence of breeding experience on hormonal patterns. Baseline corticosterone levels were nearly twice as elevated in first-time breeders in comparison to experienced breeders. Corticosterone is well known to increase in response to environmental stressors (Wingfield et al. 1998). Elevated baseline corticosterone are known to mirror poor food availability (Kitaysky et al. 1999) and, at the individual level, poor foraging success is associated with elevated corticosterone levels in the wandering albatross, *Diomedea exulans* (Angelier et al., submitted). First-time breeding black-browed albatrosses may be poor foragers (Desrochers 1992; Ratcliffe and Furness 1999; Rutz et al. 2006), or may be dominated by more experienced birds in foraging areas (Burger 1988). Although we did not measure the body



**Fig. 4** Relationships between the time spent fasting on the nest and baseline corticosterone (a) or prolactin (b) levels among breeding black-browed albatrosses (corticosterone:  $n=20$ , prolactin:  $n=16$ ). Corticosterone levels increased with time spent fasting on the nest (solid line) whereas prolactin levels decreased (solid line males, dashed line females). Filled symbols denote males and open ones denote females

condition of the birds, we found a negative relationship between baseline corticosterone levels and time spent fasting on the nest during the brooding period. In birds, poor body condition imposed by fasting is generally associated with elevated corticosterone levels (Cherel et al. 1988; Marra and Holberton 1998; Kitaysky et al. 1999; Lynn et al. 2003; Love et al. 2005) and the duration of brooding is therefore a good index of the influence of body condition on hormone levels. In seabirds, the brooding period often appears constrained (Shaffer et al. 2003) as adults face a trade-off between the needs of the chick to be fed regularly and brooded, and that of the adult to spend enough time at sea to restore its body reserves and find food for the chick (Tveraa et al. 1998a,b). Therefore, the elevated corticosterone levels found in first-time breeders probably reflect their lower ability to conduct proper brooding/fasting routines.

A possible lower foraging ability in first-time breeding albatrosses results in increased corticosterone levels, which may decrease parental attendance (Kitaysky et al. 2001)



**Fig. 5** Relationship between fledging success and baseline corticosterone levels among breeding black-browed albatrosses ( $n=59$ ). The probability of successfully fledging the young was negatively influenced by corticosterone levels (solid line). Filled symbols denote males and open ones denote females

during the brooding period and increase the probability of loss of the chick. Because most of breeding failures occurred among first-time breeders that also had the highest corticosterone levels, we cannot confirm that breeding failure results from elevated corticosterone levels rather than from an intrinsic effect of breeding experience. Experimental studies in other species have, however, demonstrated that elevated corticosterone levels suppress reproductive behaviour (Wingfield and Sapolsky 2003), and decrease parental effort and trigger nest desertion (Silverin 1986, 1998). The corticosterone pattern we found suggests a greater susceptibility of first-time breeders to constraints imposed by breeding activities and favours a reproductive inferiority of first-time breeders (“the constraint hypothesis”, Curio 1983) rather than a lower investment in reproduction (“the restraint hypothesis”, Curio 1983). Baseline corticosterone levels were negatively correlated with the probability of successfully fledging the young in black-browed albatrosses, suggesting therefore that baseline corticosterone levels could be a reliable predictor of fledging success (Kitaysky et al. 1999). Because our data set was limited to one year of sampling, we cannot confirm that corticosterone levels would always be a reliable predictor of fledging success.

We found that baseline prolactin levels were lower in young and first-time breeders. A similar influence of breeding experience on prolactin levels has been found in the dark-eyed junco (*Junco hyemalis*, Deviche et al. 2000) and in the European blackbird (*Turdus merula*, Pr eault et al. 2005). In birds, prolactin can be negatively affected by depletion of body reserves (Cherel et al. 1994) and

environmental stressors (Chastel et al. 2005). In black-browed albatrosses, time spent fasting on the nest negatively influenced baseline prolactin levels, suggesting that first-time breeders may be less able to cope with the constraints imposed by the brooding period (Tveraa et al. 1998a,b; Shaffer et al. 2003). In most bird species, stimuli from either the nest, egg or chick are necessary to maintain elevated prolactin secretion rates (El Halawani et al. 1980; Hall 1987; Book 1991; Wang and Buntin 1999). However, pelagic seabirds such as albatrosses often undergo very long absences (up to 1 month) from the nest when foraging (Jouventin and Weimerskirch 1990) and have probably evolved an endogenously scheduled prolactin secretion that is relatively independent from stimuli originating from the nest, egg or chick (Hector and Goldsmith 1985). Therefore, the low levels we found in young/inexperienced birds could also arise as a result of their lower functional ability to secrete prolactin (“the constraint hypothesis”, Curio 1983).

Corticosterone levels were identical between males and females (Hector and Harvey 1986, this study), illustrating a similar shared breeding expenditure between sexes in this species (Weimerskirch et al. 1997). Baseline prolactin levels were higher in females than in males, a pattern commonly observed in several bird species but still not well understood (Ball 1991; Vleck 1998; Lorm e et al. 2000).

#### Senescence and hormone levels

We found that breeding success declined in the most experienced and very old birds. Although fledging success varied among years, this decline could not be an artefact of generally low fledging success during the most recent years for several reasons. First, we included a ‘year effect’ in the GLM to avoid a confounding effect of year of observation on breeding performance pattern (Robertson and Rendell 2001; Laaksonen et al. 2002; Reid et al. 2003). Moreover, the breeding success is on average high and shows little variation at Kerguelen (Pinaud and Weimerskirch 2002) and overall fledging success of the population did not show any general trend through the study period. The terminal investment hypothesis (Clutton-Brock 1984) predicts that breeding individuals should enhance their reproductive effort with advancing age to maximise fitness and compensate for a decreasing residual reproductive value. The decline we observed in the breeding success of very old and experienced albatrosses suggests the onset of senescence (Finch 1990; Holmes and Austad 1995; Ricklefs 1998).

The decline in breeding success among oldest and most experienced birds was associated with an increase in corticosterone levels and a decrease in prolactin levels. These hormonal changes may reflect a degradation of the foraging skills of the oldest individuals. A degradation of



foraging skills and a decrease in access to resources could result in inefficient brooding routine, low nutritional status and therefore elevated corticosterone and low prolactin levels. However, we found no difference in the time spent fasting on the nest between experienced/middle-aged and oldest/most experienced birds, suggesting that another factor likely explains elevated corticosterone levels in oldest/most experienced birds. For example, aging could disrupt the endocrine system, inducing a higher sensitivity of the hypothalamo–pituitary–adrenal (HPA) axis to stressful events in very old and most experienced birds and triggering the secretion of glucocorticosteroids. Several studies have supported this hypothesis and have shown that changes in the HPA axis occurred in old rats (Sapolsky et al. 1986) and old human males (Van Cauter et al. 1996; Wilkinson et al. 1997; Boscaro et al. 1998; Bergendahl et al. 2000). In humans and monkeys, there is much evidence for an attenuation of the glucocorticoid negative feedback with ageing (Wilkinson et al. 1997; Boscaro et al. 1998; Gust et al. 2000) which might explain the more elevated corticosterone levels found in oldest and most experienced black-browed albatrosses. Similarly, aging or the cumulative costs of previous breeding attempts (Gustafsson and Pärt 1990) could induce a reduction in prolactin levels and/or a lower ability to secrete prolactin, which negatively affects parental abilities (Buntin 1996; Wang and Buntin 1999; Duckworth et al. 2003).

We have reported, for the first time, an age/experience-specific pattern of both baseline corticosterone and prolactin levels in relation to reproductive performance. To our knowledge, this study is also the first to describe corticosterone and prolactin levels in senescent breeders. At the moment, very few data exists on the effect of age and breeding experience on baseline hormone levels (Angelier et al. 2006) and our results underline the need to describe age-specific baseline hormonal patterns in other species with various life-history strategies. Moreover, because corticosterone and prolactin responses to stressful conditions can reflect parents' breeding investment (Wingfield and Kitaysky 2002; Chastel et al. 2005), it would also be especially relevant to study how young or senescent parents modulate their hormonal responses to stressful events (Wingfield and Sapolsky 2003).

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