Effect of age, breeding experience and senescence on corticosterone and prolactin levels in a long-lived seabird: The wandering albatross

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Abstract

Although several studies have described age-specific pattern of breeding performance, physiological and endocrine mechanisms underlying the variation in reproductive success in relation to age are poorly understood. We described baseline levels of: (1) corticosterone, which can trigger nest desertion when secreted at high levels, and (2) prolactin, a hormone known to trigger parental behaviour in incubating known-aged (7–39 years old) wandering albatrosses (*Diomedea exulans*). In this long-lived species, reproductive performance increases with age and breeding experience before it stabilizes in middle-aged individuals and declines in senescent individuals. We found that breeding experience was a much better statistical predictor of hormone levels than age. Baseline corticosterone levels slightly increased with advancing experience and reached maximal levels about the sixth breeding attempt. Similarly, prolactin levels were positively correlated with breeding experience in males. No such relationship was found in females, but first-time breeding females had lower prolactin levels than experienced females. This parallel increases in hormonal levels with advancing experience could result from improvements of skills, development of an endocrine system adapted to energetic constraints of reproduction or may mirror a higher investment in reproduction. Corticosterone levels decreased in senescent birds, but such a decline was not observed for prolactin. Low corticosterone levels in senescent birds could be associated with a lower ability to secrete/sustain elevated corticosterone levels or with a decreased parental expenditure.
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1. Introduction

The influence of age on survival and reproductive performance is crucial in animal life history because it affects individual reproductive strategies (Stearns, 1992; Roff, 1992) and hence the dynamics of populations. Variation in these life-history traits with age is well documented for several long-lived animals. Regarding vertebrates, survival and reproductive performance generally increase with age (Clutton-Brock, 1988; Newton, 1989; Forslund and Pärt, 1995). However, for long-lived species, this increase is often followed by stabilization in survival and reproductive performance at middle age, then a decline in old age (Clutton-Brock, 1988; Weimerskirch,

1992; Forslund and Pärt, 1995; Kirkwood and Austad, 2000; Reid et al., 2003). This decline is called senescence that involves a loss of physiological functions and is accompanied by decreasing fertility and increased risks of mortality with advancing age (Kirkwood and Austad, 2000).

Although several studies have described age-specific pattern of breeding performance (Clutton-Brock, 1988; Pärt, 2001; Mauck et al., 2004), physiological mechanisms underlying the variation in reproductive expenditure in relation to age are poorly understood. Monitoring hormone levels can offer great insights into the understanding of mechanisms mediating age-specific patterns of life-history traits (Sinervo and Svensson, 1998; Ottinger et al., 2003), but to our knowledge only a few studies have focused on endocrine correlates of ageing in free-living birds (LH, progesterone, oestradiol and androgens; Hector et al., 1990; Nisbet et al., 1999). Moreover, none have simultaneously

described baseline levels of corticosterone and prolactin, the two hormones involved in reproductive behaviour, in relation to age and breeding experience.

In birds, plasma levels of corticosterone rapidly increase in response to stressful events and maintenance of elevated corticosterone levels during a prolonged period can ultimately trigger nest desertion by altering the allocation of available resources between body maintenance and reproductive processes (Silverin, 1986; Wingfield et al., 1998). However, this inhibitory response is generally activated at stress-induced levels, whereas baseline levels of corticosterone have different physiological and behavioural permissive effects (Romero, 2004). For instance, corticosterone plays a major role in the energy mobilization at baseline levels by activating gluconeogenesis (Sapolsky et al., 2000; Remage-Healey and Romero, 2001) and elevated baseline corticosterone levels during reproduction could therefore result from the high energetic demand of this life-history stage (Romero, 2002). Because depletion of body reserves results in increased baseline corticosterone levels (Cherel et al., 1988; Kitaysky et al., 1999; Love et al., 2005), baseline corticosterone levels can moreover be a witness of the stress imposed by sustained breeding activities. Focusing on corticosterone is thus relevant to studying the relationship between reproductive performance and age because this hormone plays a major role in breeding decision and reproductive expenditure (Wingfield et al., 1998).

Reproductive performance also depends on the ability of animals to provide parental care to their progeny (incubation care, guarding for protection 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 initiation and maintenance of avian parental behaviour (reviewed in Buntin, 1996) and prolactin enhances the expression of several parental behaviours such as feeding behaviour, nest attendance or defensive behaviour (Wang and Buntin, 1999). High prolactin levels also appear necessary to maintain parental care despite stressful or unfavourable conditions for parents (Lormée et al., 2000; Chastel et al., 2005). As a result, examining the relationship between prolactin and age is particularly interesting to assess the effect of age and breeding experience on parental care.

Albatrosses and petrels (order Procellariiformes) are a promising model to study the mechanism of ageing because they are long-lived seabirds with low annual fecundity (one egg per clutch with no replacement clutch; Lack, 1968; Warham, 1990). In these birds, the risk of increased mortality during a breeding attempt should also be reduced because of their high residual reproductive value (Stearns, 1992; Weimerskirch, 1999). Moreover, survival and breeding performance of these pelagic seabirds are easy to monitor because they are highly philopatric and often mate with the same individual throughout their life (Tickell, 1968; Warham, 1990).

The aim of this study is to examine the relationship between baseline corticosterone and prolactin levels in plasma in relation to age and breeding experience in the wandering albatrosses (*Diomedea exulans*). The breeding cycle of this large (up to 12 kg) seabird lasts a complete year and pairs that are successful in fledging a chick breed in alternate years, while those failing during incubation or during the early stages of chick-rearing breed again in the following year (Tickell, 1968). Sexual maturity is acquired on average at 8–9 years (Weimerskirch and Jouventin, 1987). Wandering albatrosses are long-lived birds (40+ years) that show a progressive increase in breeding success in relation to breeding experience between the first and fifth breeding attempts, which on average corresponds to 8–9 to 20 years of age (Weimerskirch, 1992). Thereafter, breeding success decreases after 6–7 breeding attempts, corresponding to birds aged over 20–25 years, suggesting senescence at older ages (Weimerskirch, 1992; Weimerskirch et al., 2005). Therefore, wandering albatrosses constitute an excellent study system to explore relationships between hormones and age-related breeding performances.

Elevated baseline levels of corticosterone are a witness of low foraging success (Kitaysky et al., 1999; Woodley et al., 2003; Angelier et al., submitted) and poor nutritional condition (Cherel et al., 1988; Kitaysky et al., 1999; Love et al., 2005) and could therefore be associated with low breeding capacities and low breeding success (Kitaysky et al., 1999). High levels of prolactin are associated with the maintenance of parental care (reviewed in Buntin, 1996), which plays a critical role in breeding success (Clutton-Brock, 1991). Therefore, we predict that (1) baseline corticosterone levels should be higher in young and older/senescent albatrosses than in middle-aged birds, whereas (2) baseline prolactin levels should be lower in young and older/senescent albatrosses compared to middle-aged birds.

2. Methods

2.1. Study area and birds

Fieldwork was carried out between 3 January and 13 February 1999, and 1 January and 25 February 2004 at Ile de la Possession, Crozet Archipelago, south-western Indian Ocean (46°S, 52°E). The ongoing mark-recapture programme of wandering albatrosses at Ile de la Possession has provided yearly information on the entire population of the island: approximately 400 breeding pairs each year for the last 40 years (Weimerskirch et al., 2005). Banding of chicks prior to fledging has been carried out since 1965. We were thus able to know the age and breeding experience (number of breeding attempts, i.e. 1 refers to the first breeding attempt) of each wandering albatross breeding on the island. However, banding of breeding birds of unknown age started in 1959. For these individuals banded as adults, we used an estimated age calculated from the year of banding and adding 6 years; the minimum age at first breeding (Weimerskirch et al., 1997). Hence, age and breeding experience of these birds are estimates. The sex of each bird was determined by body size and plumage characteristics (Weimerskirch et al., 1989).

2.2. Blood sampling and hormone assays

A total of 75 albatrosses were captured on the nest and bled during the early incubation period in both years (1999, $n = 22$; 2004, $n = 53$). Data were independent because birds sampled in 1999 were not sampled in 2004. One bird per nest was sampled in order to maintain independence of the

data. Immediately after capture, a blood sample (maximum: 1 ml) was collected from the tarsus vein with a 1-ml heparinized syringe and 25-gauge needle. Blood samples were centrifuged and plasma was decanted and stored at $-20\,°C$ until they were assayed. Plasma concentrations of prolactin were first determined by an heterologous radioimmunoassay (RIA) at the Centre d'Etudes Biologiques de Chizé (Cherel et al., 1994). Pooled plasma samples of albatrosses produced a dose–response curve that paralleled chicken prolactin standard curves ("AFP 4444B", source: Dr. Parlow, N.H.P.P. Harbor-UCLA Medical Center, Torrance, California, USA, Fig. 1). All samples were run in one assay and the intraassay variation was 4.2%. Time of day for blood sampling (males: $F_{1,38} = 0.375$, $P = 0.55$; females: $F_{1,35} < 0.01$, $P = 0.98$) did not influence prolactin levels. Plasma concentration of corticosterone was then determined with the remaining plasma ($n = 69$) by radioimmunoassay at the Centre d'Etudes Biologiques de Chizé as previously described (Lormée et al., 2003). At Ile de la Possession, Crozet Archipelago Island, wandering albatrosses are loosely colonial and typically nest in clusters of 1–8 nests. To reduce possible disturbance to nearby breeders during the blood sampling of an individual, only one bird was sampled within a cluster. As blood samples were collected within 3 min of capture, they were considered to reflect baseline levels of corticosterone (Wingfield et al., 1982; Kitaysky et al., 1999; Lormée et al., 2003). All samples were run in one assay and the intraassay variation was 6.3%. Time of day for blood sampling ($F_{1,68} = 1.52$, $P = 0.23$) did not influence corticosterone levels. Because body weight is known to influence corticosterone and prolactin levels (Cherel et al., 1988, 1994), a sub-sample of birds was weighed in 1999 to the nearest 50 g using a Salter spring balance (Salter Weightronix Ltd., West Bromwich, UK) to test for an effect of body weight on corticosterone levels ($n = 16$) and prolactin levels ($n = 22$).

2.3. Statistics

We used the information-theoretic approach to identify suitable models for predicting baseline levels of corticosterone and prolactin in breeding albatrosses (Burnham and Anderson, 2002). Candidate models were constructed with explanatory variables hypothesized to influence prolactin and corticosterone levels (e.g. age, breeding experience, year and date). Where inspection suggested that relationships between hormonal levels and age or breeding experience were nonlinear, squared terms (Age^2 and $Experience^2$) were included in models. Because age and breeding experience were strongly correlated in our study ($n = 75$, $r = 0.92$, $P < 0.001$), we did not include both variables in the same model to avoid multi-colinearity problems and we started our analysis from two general models (1—Year, Date, Breeding experience, Breeding experience^2 and interactions; 2—

Year, Date, Age, Age^2 and interactions). We used generalized linear models with normal errors and an identity link function to explain the effect of age, breeding experience, date of sampling and year of sampling on corticosterone and prolactin levels. Model fitting was performed by maximum likelihood with the PROC GENMOD procedure in SAS (SAS Institute, Inc., 1999). We used therefore maximum-likelihood techniques and Akaike's Information Criterion (AICc) statistics corrected for small sample size to compare the extent to which our data fitted each model (Burnham and Anderson, 2002). Because we used the same data set to test an effect of: (1) breeding experience and (2) age on hormonal levels, we can use AICc to compare the ability of models including age variable or breeding experience variable to describe data even if these models were not nested (Burnham and Anderson, 2002). We calculated the Akaike's Information Criterion corrected for small sample size using the formula $AICc = -2\log(\text{Likelihood}) + 2K + 2K(K+1)/(N-K-1)$, where N is the sample size and K the number of parameters estimated in each model. Values for difference in AICc values ($\Delta AICc$) were computed by subtracting the minimum AICc from all candidate model AICc. Differences between AICc values for different models can be used to determine which provides the most adequate description of the data based on the fewest model parameters. The model with the lowest AICc was considered the best-fit that describes the relationship. $\Delta AICc$ values >2 are a good indicator that the model with the lowest AICc is preferable, whereas $\Delta AICc$ values <2 indicate that models are fairly similar in their ability to describe the data (Burnham and Anderson, 2002). Previous studies showed that prolactin levels vary between sexes in the wandering albatross (Hector and Goldsmith, 1985), whereas corticosterone does not (Hector and Harvey, 1986). We verified these results with our data set by using generalized linear models. We used one model selection per sex to explain prolactin levels, whereas we pooled data from both sexes to analyse the effect of our explanatory variables on corticosterone levels. We included all combinations of parameters in our models because we had no a priori reason to exclude particular states of any parameter or combination of parameters. Moreover, we used the same method to assess the influence of the baseline levels of corticosterone on baseline levels of prolactin in each sex. We started therefore this last analysis from this general model (Year, Date, baseline levels of corticosterone and interactions). To make our tables easier to read, we represented only the five most parsimonious models and the model without any explanatory variable (the "Intercept model") in each table, and we ranked these models according to their AICc. Because body weight measurements were available only for a sub-sample of albatrosses, we could not incorporate the "body weight" variable in our model selection frameworks. We therefore tested for an effect of body weight on (1) corticosterone levels by using an ANCOVA and (2) prolactin levels by using one linear regression per sex because prolactin levels vary between sexes in albatrosses (Hector and Goldsmith, 1985).
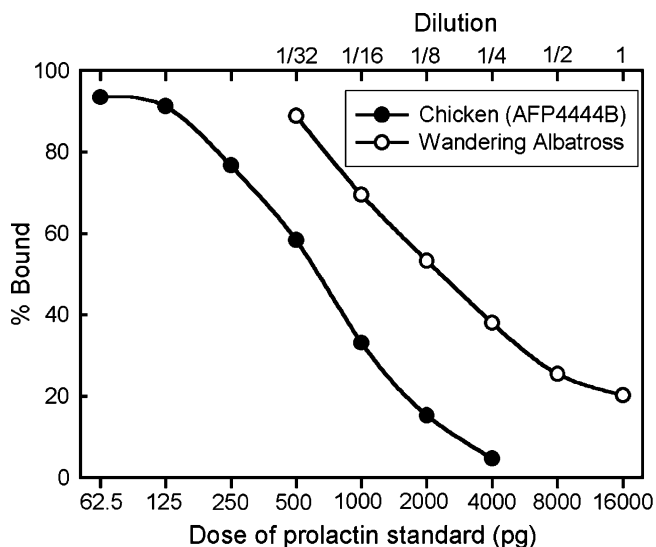
3. Results

3.1. Effect of body weight, sex, year and date of sampling on hormonal levels

There was no significant relationship between body weight and plasma corticosterone or prolactin levels within both sexes (corticosterone, ANCOVA, $F_{2,13} = 0.02$, $P = 0.89$; prolactin, linear regressions, male: $F_{1,13} = 2.329$, $P = 0.15$, female: $F_{1,5} = 0.657$, $P = 0.45$). Baseline corticosterone levels did not vary between sexes because the model including "Sex" as a variable had a larger AICc than the "Intercept model" ($\Delta AICc = 2.10$). For prolactin, the model including "Sex" as a variable had a much smaller AICc than the "Intercept" model ($\Delta AICc = 19.37$), with prolactin levels being significantly higher in females than in males (Figs. 2a and b). The information-theoretic approach
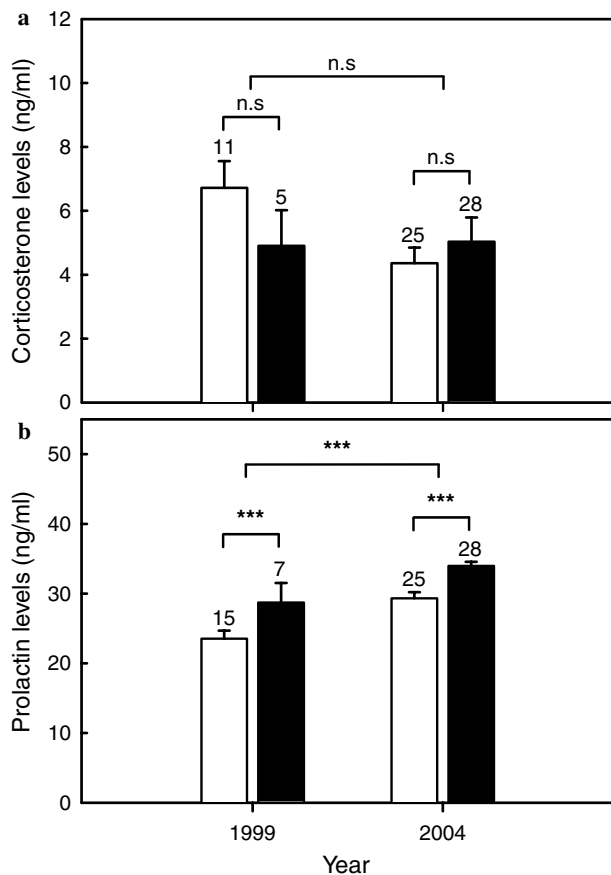

Fig. 1. Dose–response curve for prolactin in poultry chickens and wandering albatrosses. Prolactin standard is expressed in pg per tube.

Fig. 2. Baseline corticosterone (a) and prolactin (b) levels (ng ml^{-1}) of male (white bars) and female (black bars) breeding wandering albatrosses in 1999 and 2004. Data are expressed as means ± SE. Numbers above bars denote sample sizes. Asterisks indicate significant differences between groups; n.s. indicates no significant differences between groups.

identified two models with similar AICc as the best approximating models to explain baseline levels of corticosterone (Table 1, Models 1 and 2, ΔAICc = 0.74). Both models included "Date" as a variable and the second model included "Year" as a variable. Estimates of parameters of these models demonstrated that baseline levels of cortico-

sterone decreased with date of sampling (Table 1, estimates of parameters) and were slightly higher in 1999 than in 2004, ($n = 69$, $\chi^2 = 1.68$, $P = 0.19$). Similarly, two models with similar AICc were identified as the best approximating models to explain baseline prolactin levels in both sexes (Table 2a, Models 1 and 2, ΔAICc = 1.83; Table 2b, Models 1 and 2, ΔAICc = 1.05). Both included "Year" as a variable and the second model included "Date" as a variable. Estimates of parameters demonstrated that baseline levels of prolactin were higher in 2004 than in 1999 (Tables 2a and 2b, estimates of parameters) but did not vary significantly with the date of sampling (males, $n = 39$, $\chi^2 = 0.70$, $P = 0.40$; females, $n = 36$, $\chi^2 = 1.32$, $P = 0.25$).

3.2. Effect of age and breeding experience on hormonal levels

Age and breeding experience distribution were similarly distributed in 1999 and 2004 (Age, 1999, mean = 18.50, min = 7, max = 33, 2004, mean = 22.19, min = 7, max = 38; breeding experience, 1999, mean = 5.59, min = 1, max = 13, 2004, mean = 6.68, min = 1, max = 15). Both models identified as the best approximating models to explain variations in baseline corticosterone levels included "Experience" and "Experience^2" as variables, demonstrating a strong effect of breeding experience on baseline levels of corticosterone (Table 1, Models 1 and 2). Baseline levels of corticosterone increased therefore with breeding experience to reach a maximum at the sixth breeding attempt, and then decreased with the increasing breeding experience (Fig. 3, Table 1, estimates of parameters). There was however no effect of age on baseline levels of corticosterone because models including "Age" or "Age^2" variables had much larger AICc than the "Intercept model".

Both models identified as the best approximating models for baseline levels of prolactin in males included "Experience" as a variable, demonstrating a strong influence of breeding experience on baseline levels of prolactin in males (Table 2a, Models 1 and 2, ΔAICc = 1.83). Consequently, there was a positive linear relationship between breeding experience and baseline levels of prolactin in

Table 1
Model selection using Akaike's Information Criterion (AICc) to explain baseline corticosterone levels measured at the nest ($n = 69$)

No.	Model	K	Log likelihood	AICc	ΔAICc
1	Experience; Experience^2; Date	4	−168.16	344.95	0
2	Year; Experience; Experience^2; Date	5	−167.37	345.69	0.74
3	Year; Experience; Experience^2; Date; Date × Year	6	−167.20	347.75	2.80
4	Year; Experience; Experience × Year; Experience^2; Experience^2 × Year; Date	7	−166.20	348.24	3.29
5	Date	2	−172.74	349.66	4.71
6	Intercept	1	−178.96	359.98	15.03
	Selected model	Parameter	Estimate ± SE	Chi-square	p
	Experience; Experience^2; Date	Intercept	4.61 ± 1.28	12.93	<0.001
	Experience; Experience^2; Date	Experience	1.03 ± 0.37	7.73	0.005
	Experience; Experience^2; Date	Experience^2	−0.08 ± 0.03	9.32	0.002
	Experience; Experience^2; Date	Date	−0.08 ± 0.02	12.67	<0.001

General linear models with normal distribution and identity link were used to test for variable effect. K refers to the number of parameters. The five most parsimonious models and the model without any explanatory variable (the "Intercept model") are represented and are ranked according to their AICc. The second part of the table includes the parameter estimates for the selected model.

Table 2a
Model selection using Akaike's Information Criterion (AICc) to explain baseline prolactin levels in males ($n = 39$)

No.	Model	K	Log likelihood	AICc	ΔAICc
1	Year; Experience	3	−107.88	222.45	0
2	Year; Date; Experience	4	−107.55	224.28	1.83
3	Year; Experience; Experience × Year	4	−107.91	225.00	2.55
4	Year	2	−110.55	225.43	2.98
5	Year; Date; Date × Year; Experience	5	−107.27	226.36	3.91
6	Intercept	1	−119.41	240.93	18.48
	Selected model	Parameter	Estimate ± SE	Chi-square	p
	Year; Experience	Intercept	26.29 ± 1.54	291.98	<0.001
	Year; Experience	Year (1999)	−6.47 ± 1.33	23.48	<0.001
	Year; Experience	Year (2004)	—	—	—
	Year; Experience	Experience	0.45 ± 0.20	5.34	0.021

Generalized linear models with normal distribution and identity link were used to test for variable effect. *K* refers to the number of parameters. The five most parsimonious models and the model without any explanatory variable (the "Intercept model") are represented and are ranked according to their AICc. The second part of the table includes the parameter estimates for the selected model.

Table 2b
Model selection using Akaike's Information Criterion (AICc) to explain baseline prolactin levels in females ($n = 36$)

No.	Model	K	Log likelihood	AICc	ΔAICc
1	Year	2	−101.78	207.92	0
2	Year; Date	3	−101.11	208.97	1.05
3	Year; Experience	3	−101.59	209.93	2.01
4	Year; Age	3	−101.81	210.37	2.45
5	Year; Date; Date × Year	4	−101.11	211.51	3.59
6	Intercept	1	−106.98	216.08	8.16
	Selected model	Parameter	Estimate ± SE	Chi-Square	p
	Year	Intercept	33.97 ± 0.79	1828.58	<0.001
	Year	Year (1999)	−5.70 ± 1.69	11.45	<0.001
	Year	Year (2004)	—	—	—

General linear models with normal distribution and identity link were used to test for variable effect. *K* refers to the number of parameters. The five most parsimonious models and the model without any explanatory variable (the "Intercept model") are represented and are ranked according to their AICc. The second part of the table includes the parameter estimates for the selected model.
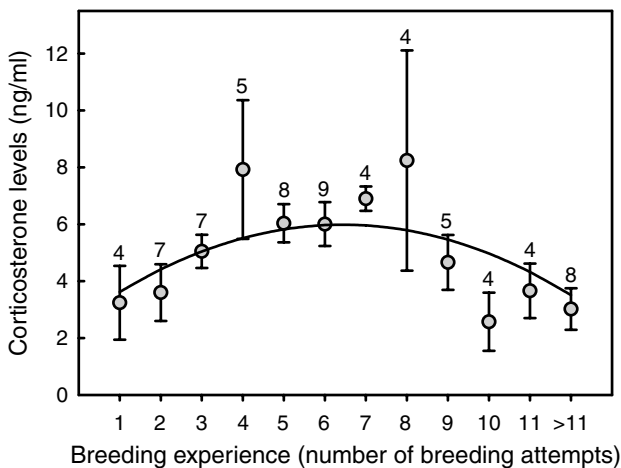

Fig. 3. Baseline corticosterone (ng ml^{-1}) levels and breeding experience in wandering albatrosses ($n = 69$). Statistical analyses treated each hormone measurements as single observations. Data are expressed as means ± SE. Numbers above bars denote sample sizes. Solid line represents the relationship described by the best model (lowest AICc) selected to explain baseline corticosterone levels (Table 1, Model 1). Male and female data were pooled.

males (Fig. 4a, Table 2a, estimates of parameters). The information-theoretic approach identified two models with similar AICc as the best approximating models for baseline levels of prolactin in females, but none of these models included "Experience" as a variable (Table 2b, Models 1 and 2, ΔAICc = 1.05). Plasma levels of prolactin were therefore not explained by breeding experience in females (Fig. 4b). Prolactin levels were, however, lower in inexperienced females than in experienced individuals (Kruskall–Wallis test, $n = 36$, $P = 0.023$, Fig. 4b). Plasma levels of prolactin were not explained by age in males and females. In both sexes, models including "Age" as a variable were not selected as the best approximating models for baseline levels of prolactin. Furthermore, the baseline levels of prolactin were not explained by baseline levels of corticosterone in both sexes. The information-theoretic approach identified models without baseline levels of corticosterone as the best approximating models for baseline levels of prolactin.

4. Discussion

4.1. Difference in hormonal levels between years, dates and sex

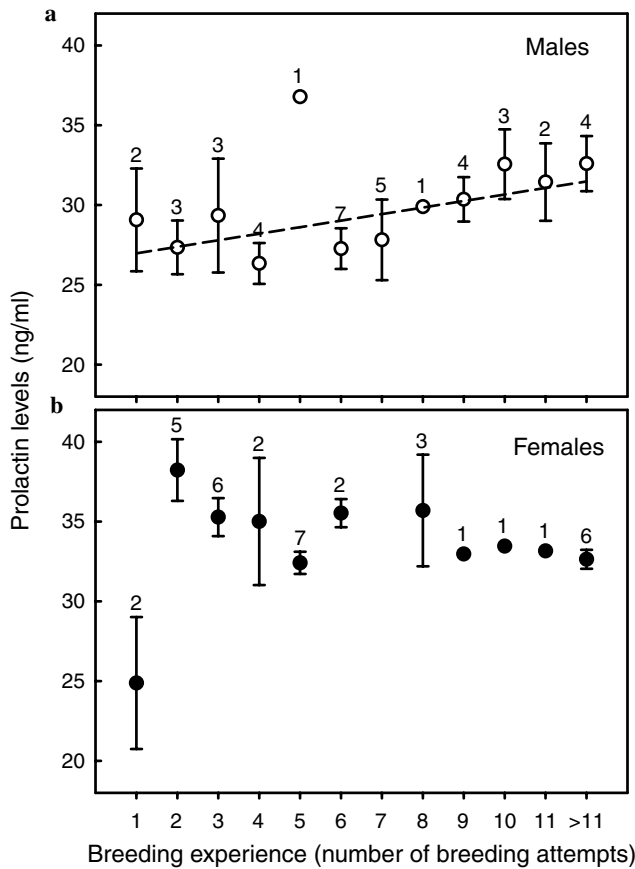In our study, we found no relationships between body weight and hormones levels. Wandering albatrosses have a

Fig. 4. Baseline prolactin levels ($ng\,ml^{-1}$) and breeding experience in male and female wandering albatrosses ($n = 75$). Statistical analyses treated each hormone measurements as single observations. Data were corrected for a year effect and are expressed as means ± SE. Numbers above bars denote sample size.

4.2. Parallel increase in hormonal levels over the first six breeding attempts

We showed for the first time that breeding experience was a much better statistical predictor of corticosterone and prolactin levels than age per se in wandering albatrosses. Similarly, Cichoń (2003) has experimentally demonstrated a larger contribution of previous breeding experience than age on breeding performances. In our study, baseline corticosterone and prolactin levels exhibited a concomitant increase over the first six breeding attempts, which shows a striking parallel with the improvement in breeding performance (Weimerskirch, 1992; Weimerskirch et al., 2005).

Corticosterone can be seen either as a stimulator of breeding activities (Love et al., 2004) and/or as witness of the stress imposed by sustained breeding activities (reviewed in Wingfield et al., 1998). Thus, the corticosterone patterns we found: (1) might be explained either by a direct influence of previous breeding experience on the ability to secrete corticosterone or (2) might be elevated in response to the extra parental expenditure that might be expended by experienced successful birds.

Because elevated baseline corticosterone levels are traditionally associated with a poor body condition (Kitaysky et al., 1999; Cherel et al., 1988; Love et al., 2005), a lower ability to extract resources from the environment (Woodley et al., 2003; Angelier et al., submitted) and a lower breeding success (Kitaysky et al., 1999), we predicted that inexperienced albatrosses would bear elevated corticosterone levels. The pattern we found was however the reverse. It could however be explained according to several recent studies, which found that plasma corticosterone levels could be moderately elevated during reproductive event without inducing breeding abandonment (Koch et al., 2002; Romero, 2002; Moore and Jessop, 2003; Love et al., 2004). Although these moderately elevated corticosterone levels might only result from the stress of an increased foraging expenditure necessary to breed successfully, several experimental studies have shown that small elevations of corticosterone levels trigger foraging activity (Astheimer et al., 1992; Kitaysky et al., 2001; Breuner and Hahn, 2003) and could therefore permit to meet the energetic demands of reproduction (Love et al., 2004). Recent findings suggest even that small elevations in corticosterone are an inherent component of successful reproduction because they may facilitate parental behaviour by increasing parental provisioning (Love et al., 2004; Koch et al., 2004; Carlson et al., 2006).

This increase in baseline corticosterone with advancing experience is paralleled by the concomitant increase in prolactin levels in males. Although prolactin levels did not vary with breeding experience among experienced females, inexperienced birds had the lowest prolactin levels. To our knowledge, this relationship between breeding experience and prolactin levels has only been examined in two species of monkeys: urinary prolactin levels increased with experience in captive cottontop tamarins (*Saguinus oedipus*, Ziegler et al., 1996), but not in captive common marmoset fathers (*Callithrix jacchus*, Schradin and Anzenberger, 2004).

wide safety margin of energy reserves and are able to buffer the costs of fasting for several weeks without neglecting their egg (Weimerskirch, 1995, 1999) and without significant changes in corticosterone and prolactin levels (Hector and Goldsmith, 1985; Hector and Harvey, 1986). Corticosterone levels were identical between males and females (Hector and Harvey, 1986; this study), illustrating a similar shared breeding expenditure between sexes in wandering albatrosses (Weimerskirch, 1995). Prolactin levels were higher in females than in males (Hector and Goldsmith, 1985; this study), a pattern commonly observed in several bird species but still not well understood (Ball, 1991; Vleck, 1998; Lormée et al., 2000) because males and females provide roughly similar amounts of parental care in the great majority of seabirds (Lack, 1968). We also found that baseline levels of corticosterone and prolactin, respectively, varied with date and year of sampling. This could result either from differences in energetic needs (Love et al., 2004; Chastel et al., 2005) or from differences in environmental conditions/stressors through the study period (Delahanty et al., 1997; Wingfield et al., 1998; Kitaysky et al., 1999; Pravosudov et al., 2001; Wingfield and Kitaysky, 2002; Chastel et al., 2005).

Prolactin can be seen either as a stimulator of parental behaviour or as a result of parental activity (reviewed in Buntin, 1996). Thus, the prolactin patterns we found might be explained either (1) by a direct influence of previous breeding experience on the ability to secrete prolactin or (2) by the intrinsic quality of birds with higher prolactin which may be more successful breeders and therefore breed more often. In most bird species, stimuli from nest, egg or chick are necessary to maintain elevated prolactin secretion rates and prolactin levels decrease dramatically within few hours when these stimuli are removed (El Halawani et al., 1980; Hall, 1987; Book, 1991; Wang and Buntin, 1999). However, pelagic seabirds such as albatrosses and penguins undergo very long absences from the nest when foraging (weeks or even months; Jouventin and Weimerskirch, 1990) and have probably evolved an endogenously scheduled prolactin secretion poorly influenced by stimuli from nest, egg or chick (Hector and Goldsmith, 1985; Garcia et al., 1996; Vleck, 1998; Lormée et al., 1999; Vleck et al., 2000). Moreover, in the wandering albatrosses, successful breeders will systematically undergo a sabbatical year (Tickell, 1968) entirely spent at sea (Weimerskirch and Wilson, 2000), whereas failed breeders will breed again in the following year (Tickell, 1968). All these features strongly suggest a direct influence of previous breeding experience on the ability to secrete prolactin in the wandering albatross. Because elevated prolactin levels are an essential component of reproduction (reviewed in Buntin, 1996), the lower breeding success of inexperienced albatrosses (Weimerskirch, 1992) could result from a lower ability to secrete prolactin.

The increase in baseline hormonal levels with advancing experience observed in wandering albatrosses would suggest an increase in parental investment over the first six breeding attempts (Forslund and Pärt, 1995; the "restraint" hypothesis, Curio, 1983). According to this hypothesis, hormonal secretion would then be down-regulated in less experienced albatrosses resulting in low hormonal levels which in turn may limit breeding expenditure (Love et al., 2004; Koch et al., 2004) or stressful breeding activities would then be limited in less experienced birds resulting therefore in low corticosterone levels (Wingfield et al., 1998). Alternatively, the increase in baseline hormonal levels with advancing experience may result from the development of an endocrine system adapted to energetic constraints of reproduction which results in the inability of inexperienced birds to secrete a large amount of hormones or from the lack of experience to sustain stressful breeding activities in less experienced birds resulting then in limited stressful breeding activities and in low corticosterone levels (Forslund and Pärt, 1995; the "constraint" hypothesis, Curio, 1983).

To test these hypotheses, we need to explore the causes of these hormonal changes occurring with advancing experience. The "constraint hypothesis" (Curio, 1983) would be validated if inexperienced birds are unable to secrete a large quantity of hormones. Alternatively, the "restraint hypothesis" (Curio, 1983) would be validated if inexperienced birds are physiologically able to secrete a large quantity of hor-

mones, but down-regulate this secretion either by endocrine mechanisms (i.e. regulation of corticosterone secretion by the hypothalamic–pituitary–adrenal axis) or by limiting their stressful breeding activities. For example, the ability to secrete corticosterone could be investigated by focusing on physiological changes occurring in the hypothalamic–pituitary–adrenal axis with advancing experience. Changes in adrenal's sensitivity to ACTH (which control adrenal corticosterone release) with advancing experience could be tested by injecting inexperienced and experienced birds with ACTH (Ait-Chaoui et al., 1995; Wilson and Holberton, 2001). Similarly, testing whether increases in corticosterone secretion with advancing experience results from a higher pituitary's sensitivity to releasing factors controlling ACTH secretion could be evaluated by injecting these releasing factors to known-experienced birds (Romero et al., 1998).

4.3. Hormonal levels among senescent birds

In our study, we found that corticosterone levels decreased in senescent breeders which shows a striking parallel with the decrease in breeding performance (Weimerskirch, 1992; Weimerskirch et al., 2005). The decrease in corticosterone levels we found among senescent albatrosses might be explained either (1) by a direct influence of the accumulating reproductive costs of previous breeding attempts on the ability to secrete corticosterone (physiological senescence) or (2) by a decreased parental expenditure in senescent birds. The decrease in baseline corticosterone levels that we found among senescent birds resembles the pattern found by Goya et al. (1989) in senescent female rats. This decrease could therefore result from physiological changes in the hypothalamic–pituitary–adrenal axis among senescent birds. For example, this decrease could occur from changes in adrenal's sensitivity to ACTH. Similarly, an alteration of the pituitary's sensitivity to releasing factors controlling ACTH secretion (i.e. corticotropin-releasing factor, arginine vasotocin and mesotocin) could result in this decrease in corticosterone levels (Romero et al., 1998). The possible decline in adrenal's or pituitary's sensitivity in senescent birds might be tested by injecting known-experienced birds with ACTH or releasing factors controlling ACTH secretion (Ait-Chaoui et al., 1995; Brudieux et al., 1995).

In our study, we did not observe the same decline in prolactin levels. Although we cannot exclude that senescence may be accompanied by a deficit in prolactin ability to stimulate parental care, the lack of a decline in prolactin levels among senescent birds may suggest that their low breeding success does not result from poor quality care during incubation.

5. Conclusion

We showed for the first time that baseline corticosterone and prolactin levels varied with breeding experience in a long-lived species, the wandering albatross. Currently, no

data exist on the effects of age, experience and senescence on avian prolactin and corticosterone secretion. Our results underline the need to describe baseline hormone levels and age in more bird species in relation to different life-styles and life-history traits. There is also a need to identify the physiological mechanisms involved in such experience-related hormonal patterns. Future studies should also focus on corticosterone and prolactin responses to acute stress in relation to age and breeding experience because these hormonal responses have been considered as adaptive because they may trigger behavioural and physiological responses which promote fitness of individuals during stressful periods (Wingfield et al., 1998; Chastel et al., 2005).

Acknowledgments

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