



Behavioural and hormonal stress responses during chick rearing do not predict brood desertion by female in a small Arctic seabird



Katarzyna Wojczulanis-Jakubas^{a,*}, Dariusz Jakubas^a, Olivier Chastel^b

^a Department of Vertebrate Ecology and Zoology, University of Gdańsk, Wita Stwosza 59, 80-308 Gdańsk, Poland

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

ARTICLE INFO

Article history:

Received 5 December 2012

Revised 9 July 2013

Accepted 13 July 2013

Available online 21 July 2013

Keywords:

Alle alle

Biparental care

Corticosterone

Little auk

Prolactin

ABSTRACT

We examined behavioural and hormonal stress responses in a small seabird (little auk, *Alle alle*), which exhibits a transition from biparental to male-only care towards the end of the nesting period, in order to understand the mechanisms underlying this parental strategy. We hypothesized that the male staying with the chick should be less sensitive to stressors. As such the male might offer the offspring more efficient protection during the fledging period than the female. We tested this hypothesis by observing male and female behaviour in a neophobia test. We also measured the birds' baseline and stress-induced levels of corticosterone and prolactin using the standardized capture-and-restraint protocol. Both sexes respond rapidly to foreign objects, delaying the entry time to the nest with food, consuming the food load, and/or temporarily abandoning feeding. However, we did not find any differences between the sexes in the frequency of each behaviour or in the time of the first reaction to the experimental treatment. Level of both corticosterone and prolactin increased after the experimental treatment. However, we did not find sex differences in baseline and stress-induced hormone levels. The results indicate that the males are as much sensitive to the stress situation as the females. Thus, the pattern of male and female behavioural and hormonal responses to stress does not predict their behaviour at the final breeding stage.

© 2013 Elsevier Inc. All rights reserved.

Introduction

Parental investments are governed by a trade-off between the benefits and costs of resources allocated to current versus future reproductive performance (Clutton-Brock, 1991; Stearns, 1992). When exposed to stressors, such as inclement weather, food deprivation or predation risk, breeding adults face a dilemma: should they continue caring for their offspring or should they abandon it, thereby securing their own survival? Life-history theory predicts that resolving this dilemma depends on the relative importance of the two components in maximising fitness. If the value of the current brood is relatively high, birds will be expected to mitigate their stress response to ensure that the current reproductive event is not compromised ("brood value hypothesis" (Heidinger et al., 2006; Lendvai and Chastel, 2008; Lendvai et al., 2007)). Indeed, the stress response is attenuated when the chances of another breeding attempt are limited by environmental constraints (O'Reilly and Wingfield, 2001; Silverin and Goldsmith, 1997; but see Wingfield et al., 1995) or parental age (Heidinger et al., 2006; but see Angelier et al., 2007). Reducing response to a stressor also correlates with cumulating parental investments across the breeding period (Meddle et al., 2003), and in the sex that invests more in parental care (Holberton and Wingfield, 2003; O'Reilly and Wingfield, 2001; Wingfield et al., 1995). Altogether, coping with a stress situation

might be a strong selective trait influencing parental performance. Understanding the stress response may therefore provide rich insight into the evolution of parental strategies.

Endocrine mechanisms play a major role in stress response. Levels of glucocorticosteroid hormones such as corticosterone could be a reliable measurement of the response to stress in birds (e.g. Wingfield and Sapolsky, 2003): circulating corticosterone levels are elevated after a stressor has taken effect. A sudden and substantial increase in the corticosterone level shifts the birds into the "emergency life stage", which should secure their survival at a given moment (Wingfield et al., 1998). Prolactin can also change in response to a stressor (Angelier and Chastel, 2009; Angelier et al., 2009; Chastel et al., 2005). This is a hormone generally related to parental care, with elevated levels enhancing the expression of parental behaviour (incubation, brood guarding and provisioning; Buntin, 1996; Wang and Buntin, 1999). However, the concentration of circulating prolactin can decrease substantially in response to acute stress, and a prolonged decrease can trigger brood desertion (Angelier et al., 2009; Chastel and Lormée, 2002; Groscolas et al., 2008). For this reason, changes in the prolactin level might be informative when examining the willingness and/or ability of birds to maintain parental care in stressful circumstances (Angelier and Chastel, 2009).

In this study, we measured behavioural and hormonal responses in the little auk (*Alle alle*, order *Charadriiformes*) to understand the reasons underlying the transition from biparental to male-only care that is observed in this species. Although biparental care followed

* Corresponding author.

E-mail address: biokwj@univ.gda.pl (K. Wojczulanis-Jakubas).

by male-only care has been reported for a number of species in *Charadriiformes*, the reasons for such two-phase parental care seem to vary across the order, and so are poorly understood (Gaston and Jones, 1998; Székely et al., 2006). Moreover, most of the hypotheses explaining the transition from biparental to uniparental care so far proposed for *Charadriiformes* do not appear to be applicable to the little auk (Wojczulanis-Jakubas and Jakubas, 2012).

The little auk is a small (130–180 g), pelagic seabird, nesting colonially in rock crevices in the High Arctic. It is socially and genetically monogamous (Liffield et al., 2005; Wojczulanis-Jakubas et al., 2009a) with no plumage dimorphism, but males are slightly larger than females (Jakubas and Wojczulanis, 2007). Both parents incubate the single egg for four weeks, but males spend more time guarding the nest area during the mating and incubation period (Wojczulanis-Jakubas et al., 2009b; Wojczulanis-Jakubas and Jakubas, unpubl. data). During the chick rearing period males and females brood and feed the chick with similar frequency. Only a day or few before chick fledgling (chicks start to fledge from the 21st day of life), the female deserts the brood while the male continues the feeding and escorts the young during colony departure (Harding et al., 2004; Wojczulanis-Jakubas and Jakubas, 2012). It is believed that male's post-fledging care is continued at sea for the next few weeks (Stempniewicz, 1995).

It has been postulated that the remaining of the little auk male with the offspring could be related to his presumed aptitude for performing the final parental duty, i.e., escorting the young during its first flight to sea (Wojczulanis-Jakubas and Jakubas, 2012). The fledgling is the most fragile moment for the young little auks due to the high predation pressure at that time. The numbers of glaucous gulls *Larus hyperboreus* (the main predator) present in vicinity of the colony increase considerably when the fledglings depart the colony (Stempniewicz, 1995; Wojczulanis et al., 2005). To increase a chick's chance of surviving a gull attack, the escorting male performs a distracting manoeuvre (Stempniewicz, 1995). Similarly, at sea, parental presence seems to be crucial to the young bird's survival, as fledglings observed swimming alone at sea often fall victim to glaucous gulls (Jakubas and Wojczulanis-Jakubas, 2010; Stempniewicz, 1995). Being somewhat larger (Jakubas and Wojczulanis, 2007) and presumably also more aggressive, the little auk male could be more efficient than female in the chick protection against predator attack. Also, as the male spends more time in the colony than the female (Wojczulanis-Jakubas et al., 2009b; Wojczulanis-Jakubas K. and Jakubas D., unpubl. data), he inescapably experiences more risk during the whole breeding period. Accordingly, the male should be less risk-averse than female and hence he should be also less sensitive to stressors to ensure his greater commitment later in the chick rearing period. This hypothesis of one sex aptitude for performing a final parental duty has not been tested in any species, except for the Kentish plover (*Charadrius alexandrinus*), where hormonal stress response of the parents at hatching was used to predict their desertion at 2–24 day of the chick rearing period, with negative result (Kosztolányi et al., 2012).

Examining stress response in the little auks at the behavioural level, we measured the birds' propensity to take a risk using neophobia test. A novel object was supposed to induce a fear (Richard et al., 2008), thus simulate a stress situation. We expected that when a completely foreign, anxiety-inducing object was placed near the nest, the male (assumingly the less risk-averse sex) should be more determined than the female to enter the nest to feed the chick. As such, the male should be more predisposed to escort the young during the hazardous fledgling period. In order to understand the physiological mechanisms driving the birds' stress response, we measured baseline and stress-induced levels of corticosterone and prolactin using the standardized capture-and-restraint protocol (Wingfield, 1994). Given the slightly male-biased parental effort in the little auk parental care (related with nest guarding), we expected higher baseline levels of both corticosterone and prolactin in males than in females. For the same reasons, we assumed that brood value might be lower for females

than males. Thus, we expected that females would exhibit a stronger hormonal response to the capture-and-restraint protocol (Wingfield, 1994; i.e., higher and lower stress-induced corticosterone and prolactin levels, respectively) compared to the males.

We performed the study at the middle of chick rearing period, when the parental efforts are the highest, and sex differences in the parental investments (egg formation, nest guarding) are already exhibited (Harding et al., 2004; Wojczulanis-Jakubas and Jakubas, 2012). Thus, the stress response of the birds should be the highest considering the fitness-based parental economics.

Methods

Study area and field methods

We conducted the study in the large little auk breeding colony on the Ariekammen slopes in Hornsund (SW Spitsbergen; 77° 00' N, 15° 33' E) in 2011. To examine the male and female behavioural response to a stress situation, we captured 5 females, 8 males and 15 pairs from 28 different nests and marked them with unique dyed signs on the breast feathers and a combination of coloured and metal leg-rings, just before hatching. We took a small blood sample for molecular sexing from each marked bird. We aimed with the timing of the subsequent observations at the moment when chicks are thermally independent and are frequently fed by both parents. Thus, when the chicks in the focal nests were on average 8 days old, we observed the marked parents for the first time in undisturbed, natural circumstances. On the next day, we performed the neophobia test. We observed the marked birds for a second time, having experimentally modified the immediate vicinity of their nest (up to 50 cm) by placing small, foreign objects (a 30 cm high bamboo cross with six 6 cm long strips of a plastic on the crossbar and a ca 5 × 5 cm sheet of blue plastic). We noted the time between the birds' arrival at the colony with a food load (the birds' appearance after an absence from the colony patch with full gular pouch) and entering the nest during the observation session in undisturbed conditions (hereafter natural latency). When the experimental objects were exposed, three different types of reaction occurred: a) delayed nest entry, b) temporary colony departure (for > 1 h), and c) consumption of the food load. In all these cases we noted the type of reaction and the time of its occurrence (hereafter latency after experimental treatment). We removed the experimental objects once we had established the first reaction of the focal bird. All the nests were situated in close proximity to each other within a small (200 m²) colony patch, which enabled two observers to track all the marked birds. We carried out both observations (in undisturbed and experimental conditions) from the same blind, situated in a distance of ca 10 m from the nearest nest. As the latency time to enter the nest was similar for all birds during the observation session in undisturbed conditions (mean = 7 min, SD = 6 min), and considerably shorter compared to the time of the first reaction occurrence (of any kind) in the experimental conditions (mean = 58 min; $t_{84} = -4.51$, $p < 0.001$), we assumed that the blind per se had not affected the birds' behaviour. All chicks from both experimental and control nests developed normally and fledged successfully (mean peak body mass: 130.0 g vs. 129.5 g; Student *t* test, $t_{55} = 0.25$, $p = 0.80$; fledging day: 27.7 vs. 27.8; Student *t* test, $t_{54} = -0.30$, $p = 0.76$). We monitored the experimental and control nests from hatching to fledging, checking the nests every two days for hatching and every three days to weigh chicks and to record fledging.

To establish the birds' hormonal stress responses, we used the standardized capture-and-restraint protocol (Wingfield, 1994), measuring baseline and stress-induced levels of corticosterone and prolactin in 34 breeders. We captured the birds (different from the ones subjected to the neophobia test) with noose-carpet deployed over the colony area. We considered only adults (≥ two years old), distinguished from subadults based on the appearance of the flight feathers and upper wing coverts (Stempniewicz, 2001), with gular pouches full of food,

indicating chick provisioning. Although we did not know the exact hatching time for each captured bird, strong synchrony of hatching (5 days) in the group of 32 monitored nests allowed us to assume a similar phase of breeding for all individuals, i.e. 13–18 day of chick rearing (according to the median date of hatching in the control nests). Immediately after capture, we collected an initial blood sample from the brachial vein in a 200 μL heparinized capillary. We timed the duration of the first sampling precisely (mean duration = 1.7 min). There was no correlation between the duration of the first sampling and the baseline concentration of either corticosterone or baseline prolactin (Pearson correlation coefficient, $p \geq 0.62$ for both hormones). We kept the birds in separate opaque cloth bags for 30 min before the second sampling to measure stress-induced corticosterone and prolactin levels. We sampled all the birds within a moderate time window of 9 h to avoid any potential effect of diurnal cycles on the hormone levels. Indeed, the baseline and stress-induced prolactin and corticosterone levels were not correlated with the time of day (in all cases $p > 0.05$). We ringed all birds to prevent double sampling of the same individual and released them unharmed after the whole procedure. In the field, the blood was kept cool (+4 °C) for 2–3 h until centrifugation for 10 min at 6000 rpm. The plasma and red cells were kept separately frozen (at –20 °C) and analysed within 4 months.

All fieldwork were done with the permission of the Norwegian Animal Research Committee and the Governor of Svalbard.

Hormone assay

We measured baseline and stress-induced concentrations of total (free and bound) corticosterone and prolactin by radioimmunoassay at the Centre d'Etudes Biologiques de Chizé, France. We measured total plasma corticosterone in samples after ethyl ether extraction using a commercial antiserum, raised in rabbits against corticosterone-3-(O-carboxymethyl) oxime bovine serum albumin conjugate (Biogenesis, UK). Cross-reaction was 9% with 1-desoxycorticosterone and less than 0.1% with other plasma steroids. We incubated duplicate aliquots (100 μL) of the extracts overnight at 4 °C with 8000 cpm of 3H-corticosterone (Amersham Pharmacia Biotech–France) and antiserum. We separated the free and bound fractions of corticosterone by adding dextran-coated charcoal. After centrifugation, we counted the bound fraction in a liquid scintillation counter. Minimal detectable corticosterone levels were 0.3 ng. We determined plasma levels of prolactin twice in each sample by a heterologous radio-immunoassay (RIA) as described in Cherel et al. (1994). The prolactin samples of the little auks produced a dose-dependent response curve that paralleled the one of standard chicken plasma (source: Dr. A.F. Parlow, UCLA Medical Center, Los Angeles). We ran all the samples in one assay for both hormones. To measure intra-assay variation, the same sample was included 4 times into the corticosterone and prolactin assays. The intra-assay variation for total corticosterone and prolactin levels was within the 5–12% range.

Molecular sexing

We extracted DNA for sexing from the frozen blood cells using a Blood Mini kit (A&A Biotechnology, Gdynia, Poland). We performed CHD gene-based analyses with the primer pair F2550 and R2718, according to Griffiths et al. (1998), using a 50 °C annealing temperature for the PCR reaction. The sex differences in the PCR products were clearly visible in UV-light when we separated the fragments on 2% agarose gel stained in ethidium bromide.

Statistical analyses

Since there was no correlation between the natural latency (undisturbed: ($r = 0.07$, $t_{15} = 0.26$, $p = 0.80$) as well as latency after experimental treatment of pair members from focal nests ($r = 0.08$,

$t_{15} = 0.29$, $p = 0.78$), we treated the partners independently, and used t tests for independent variables to test the sex differences in the natural latency. We compared the frequency of occurrence of each reaction type [a) an increase in the latency, b) colony departure for a period of >1 h, and c) consumption of delivered food load] between the sexes using χ^2 tests, and Fisher's exact test when the sample size for a given category was <10. To examine the influence of the experimental treatment on the latency after experimental treatment we performed two-way repeated-measures ANOVA, with sex and type of reaction included as fixed factors. We also used two-way repeated-measures ANOVA to determine whether the standardized capture-and-restraint protocol elevated corticosterone and prolactin levels, with sex included in the analysis (fixed factor). We performed a separate analysis for each hormone. We used Pearson correlation to analyse the relationship between corticosterone and prolactin concentrations. We performed all analyses in STATISTICA 9.0 (StatSoft Inc. 2010).

Results

Behavioural stress response

Males and females spent a similar amount of time before entering the nest in undisturbed conditions (Student t test for independent variables, $t_{41} = -1.39$, $p = 0.17$; Fig. 1). The frequency of each reaction after experimental treatment was similar in the two sexes (increase in the latency, χ^2 test, $\chi^2 = 0.09$, $p = 0.77$; colony departure for a period of >1 h, χ^2 test, $\chi^2 = 0.01$, $p = 0.93$; consumption of delivered food load, Fisher's exact test, $p = 0.44$). The latency after experimental treatment was significantly longer compared to the natural conditions (two-way repeated measures ANOVA, $F_{1,37} = 11.57$, $p = 0.002$). However, neither the sex ($F_{1,37} = 0.03$, $p = 0.87$) nor the type of reaction ($F_{2,37} = 0.60$, $p = 0.55$) affected the latency after experimental treatment. Also, the interaction of the latency \times sex ($F_{1,37} = 0.12$, $p = 0.73$), and the latency \times type of reaction ($F_{2,37} = 0.32$, $p = 0.73$) were not significant.

Hormonal stress response

No sex differences were found either in the baseline levels of corticosterone (Student t test, $t_{32} = -1.31$, $p = 0.20$) and prolactin ($t_{28} = 0.78$, $p = 0.44$) or in the levels following treatment with the standardized stress protocol (corticosterone: $t_{27} = -1.18$, $p = 0.24$, prolactin: $t_{27} = 1.61$, $p = 0.12$; Fig. 2). Levels of both hormones increased significantly in response to the stress protocol (two-way repeated ANOVA, corticosterone: $F_{1,32} = 377.16$, $p < 0.001$; prolactin: $F_{1,24} = 8.27$, $p = 0.008$; Fig. 2). No sex-specific responses were recorded for either corticosterone (two-way repeated ANOVA, $F_{1,32} = 2.09$, $p = 0.16$) or prolactin ($F_{1,24} = 1.60$, $p = 0.22$; Fig. 2). Also, interaction hormone concentration \times sex was insignificant both for corticosterone

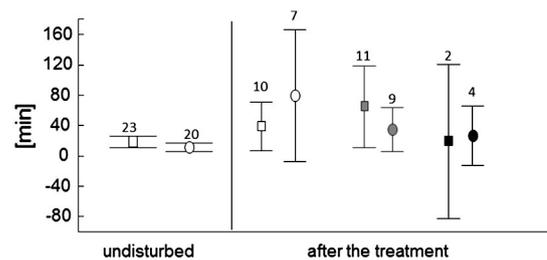


Fig. 1. Time before entering the nest with a food load by little auk males (squares) and females (circles) in undisturbed conditions, and the time prior to the first reaction [delayed nest entry (white shapes), colony departure (grey) or food load consumption (black)] after the experiment with foreign objects (means and 95% confidence intervals). The numbers above the bars denote the relevant numbers of birds.

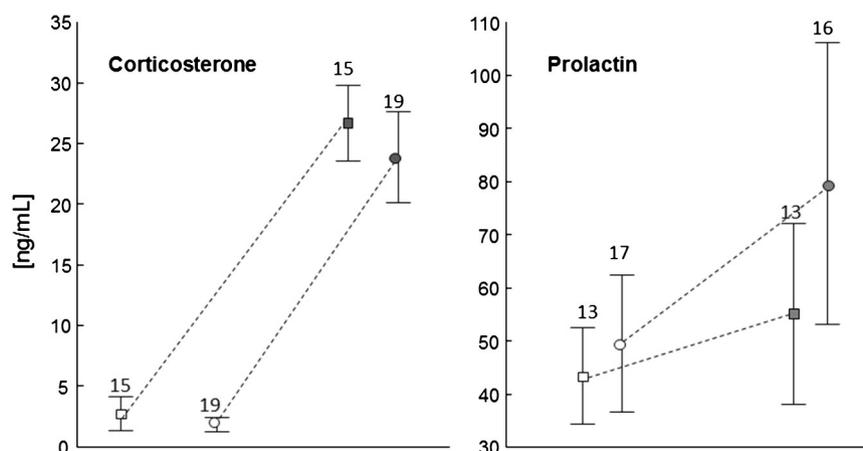


Fig. 2. Baseline levels of corticosterone and prolactin (white shapes) and levels following the standardized stress protocol (grey shapes) in breeding little auk males (squares) and females (circle) (means and 95% confidence intervals). The numbers above the bars denote the relevant numbers of birds.

(two-way repeated ANOVA, $F_{1,32} = 0.67$, $p = 0.42$) and prolactin ($F_{1,24} = 2.76$, $p = 0.11$). Baseline corticosterone and prolactin levels were not correlated with each other (males: $r_{13} = 0.05$, $p = 0.87$; females: $r_{17} = -0.13$, $p = 0.61$). Similarly, no significant relationship between the two hormones was found after the stress protocol treatment (males: $r_{13} = 0.04$, $p = 0.49$; females: $r_{16} = 0.01$, $p = 0.65$).

Discussion

We did not find any sex differences in response to stress situations, in respect either of the birds' behaviour or their baseline and stress-induced corticosterone and prolactin levels. Our results do not support the hypothesis that the little auk male is less risk-averse than the female, and as such is predisposed for the final parental duties. They are also in contrast with the model of male-biased aggression towards a predator observed in the razorbill (*Alca torda*) and Brünnich's guillemot (*Uria lomvia*), alcids with similar pattern of transition from biparental to paternal-only care (Paredes and Insley, 2010). The interspecific differences could be related to the birds' size. Both the razorbill and Brünnich's guillemot are twice as large as the little auk, so the difference in body size between these birds and their potential predators [gulls, the Arctic fox (*Vulpes lagopus*)] confers a greater advantage of the bigger auk species. Indeed, the little auk takes off whenever a predator appears (Wojczulanis et al., 2005), whereas the other two auk species were observed to actively protect themselves and their offspring (Paredes and Insley, 2010). This suggests that the transition from biparental to uniparental care in closely-related species might be a combination of convergent and divergent evolutionary paths of parental behaviour.

The similarity of the stress response in the little auk male and female suggests that brood value is also comparable for the two sexes. This further suggests similar current and/or prospective reproductive efforts of the male and female. This seems reasonable, given very similar parental duties, with only sex differences in the nest guarding and time budget (Harding et al., 2004; Welcker et al., 2009; Wojczulanis-Jakubas et al., 2009b). Thus, if the stress response and so brood value and reproductive prospects were similar for the two sexes, consequently the male and female should have similar aptitude for escorting the young during the hazardous fledging period. However, this is obviously not the case in the little auk. The reasons for which the male stays with the chick while the female departs, apparently require a further investigation.

The lack of differences between the sexes in the response to stress does not entirely invalidate the hypothesis about the

little auk male's special anti-predatory role. It is still possible that the male is predisposed to care for his offspring during the fledging and post-fledging periods through parent-offspring recognition. During fledging, the young and parent are in constant vocal contact, which presumably serves to guide the inexperienced young to the sea (Stempniewicz, 1995; K. Wojczulanis-Jakubas and D. Jakubas, pers. obs). Individual voice recognition could help the young bird and its parent to find each other, when the two become separated, for instance, as a result of a gull attack. Parent-offspring recognition has been tested in the razorbill, the result showing male-biased chick recognition (Insley et al., 2003). However, similar breeding biology traits may be driven by different mechanisms. Thus, parent-offspring vocal recognition in the little auk undoubtedly deserves separate study.

Birds of both sexes responded strongly to the foreign objects placed in the vicinity of their nests, delaying nest entry or causing a temporarily hiatus in feeding. This means the objects induced predicted effect of the birds' anxiety, so the whole experiment indeed measured the birds' response to a stress situation. Also, the five-fold increase in the concentration of circulating glucocorticosteroid in response to the capture-and-restraint treatment was presumably high enough to enable the birds to make a temporary escape from the stress situation. These birds' responses to the stress are in agreement with the hypothesis that in a long-lived species, such as the little auk (K. Wojczulanis-Jakubas and D. Jakubas, unpubl. data), individuals should secure their own survival above that of their offspring (Drent and Daan, 1980; Stearns, 1992). On the other hand, this may seem to contradict the brood value hypothesis. As a result of the long-lasting and energetically demanding breeding period (Konarzewski et al., 1993), the value of a little auk brood is expected to be high. Hence, one would imagine that adults, having invested so much time and energy in rearing their single chick, would be reluctant to abandon it. However, as little auk chicks are relatively safe from predators in their nest chambers (Wojczulanis et al., 2005), they do not appear to benefit much from the adult staying in the nest during a risk situation, whereas the adult escaping at a given moment ensures not only its own survival but also future parental care for the current offspring.

The pattern of corticosterone stress responses in adult little auks is consistent with the one widely reported for many bird species (e.g. Bókony et al., 2009; Wingfield, 1994). The response pattern to prolactin stress was unexpected, however. We hypothesized that the prolactin level should decrease in response to stress but we found the opposite pattern. Three, not necessarily mutually exclusive hypotheses, can be put forward to explain the elevated level of prolactin in response to stress. First, this might be a specific

adaptation to continue parental care, despite spending a long time away from the stimulus of the nest (Vleck, 1998). Breeding little auks exploiting distant food resources (Jakubas et al., 2012) spend much time at sea, sometimes being absent from the colony for more than 24 h (Welcker et al., 2009; Wojczulanis-Jakubas et al., 2010). Second, an elevated prolactin level could be a hormonal tactic permitting the maintenance of parental care and maximising current parental effort during stressful situations (Chastel et al., 2005). Since little auks forage mainly on Arctic zooplankters, which abundance may vary considerably in their foraging areas (e.g. Jakubas et al., 2011), when the conditions are unfavourable, a temporary secretion of corticosterone can trigger an increase in foraging efforts (Kitaysky et al., 2001). Thus, the hormonal mechanism preventing the drop in prolactin may facilitate a flexible time-budget that has been interpreted as a buffer against environmental variability (Jakubas et al., 2011). Finally, an elevated level of prolactin may prevent nest abandonment by the little auks, despite their being under constant pressure of predation from the glaucous gulls present in the breeding colony (Wojczulanis et al., 2005).

Moreover, we cannot rule out the possibility that the prolactin response may depend on the stage of the breeding period, i.e., the baseline level of prolactin. A decrease in the prolactin level in response to stress was reported during incubation and mid chick rearing in the Manx shearwater (*Puffinus puffinus*) when the baseline prolactin level was the highest, whereas an opposite pattern was the case when the baseline level of the hormone was lower, at the late chick rearing period (Riou et al., 2010). A preliminary study of the changes in the prolactin level in the little auk throughout the breeding season shows a lower level of the hormone in the chick rearing than in the incubation period (Wojczulanis-Jakubas et al., in prep). Thus, during incubation, when its concentration is much higher, the stress response could typically decrease the level of prolactin concentration as it would be still high enough to provide parental care without disturbance. In contrast, during the chick rearing period, when the initial concentration of prolactin is relatively low, the prolactin stress response might increase as the hormone level cannot drop beyond a certain threshold if parental care is to be maintained.

One could question explaining the phenomena of female's chick desertion occurring at the end of chick rearing period by the birds stress response at the mid chick rearing period. However, the timing could affect the magnitude of the stress response but not the pattern for the two sexes. A varied but not sex-specific pattern of changes in hormonal stress response throughout the breeding season has been reported in the Manx shearwater (Riou et al., 2010). If there was no sex differences in the stress response and so brood value at the middle of chick rearing period in the little auk, when the offspring demands are the highest and eventual sex differences in the parental investments already exhibited (Harding et al., 2004; Wojczulanis-Jakubas et al., 2009a,b), this should be also the case 1–2 weeks later, during the chick fledgling.

Acknowledgments

Thanks go to Peter Senn for improvements in English usage. The study was supported by a grant from the Polish Ministry of Science and Higher Education (Iuventus Plus 0470/P01/2010/70) and grant from the University of Gdansk (538-L120-0814-12). At the CEBC, we thank C. Parenteau and C. Trouvé for their excellent technical assistance in hormone assays.

References

Angelier, F., Chastel, O., 2009. Stress, prolactin and parental investment in birds: a review. *Gen. Comp. Endocrinol.* 163, 142–148.

- Angelier, F., Moe, B., Weimerskirch, H., Chastel, O., 2007. Age-specific reproductive success in a long-lived bird: do older parents resist stress better? *J. Anim. Ecol.* 76, 1181–1191.
- 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*)? *Physiol. Biochem. Zool.* 82, 590–602.
- Bókony, 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? *Am. Nat.* 173, 589–598.
- Buntin, J.D., 1996. Neural and hormonal control of parental behaviour in birds. In: Rosenblatt, J.S., Snowdon, C.T. (Eds.), *Advances in the Study of Behavior*. Academic Press, New York, pp. 161–213.
- Chastel, O., Lormée, H., 2002. Patterns of prolactin secretion in relation to incubation failure in a tropical seabird, the red footed booby. *Condor* 104, 873–876.
- Chastel, O., Lacroix, A., Weimerskirch, H., Gabrielsen, G.W., 2005. Modulation of prolactin but not corticosterone responses to stress in relation to parental effort in a long-lived bird. *Horm. Behav.* 47, 459–466.
- Cherel, Y., Mauger, R., Lacroix, A., Gilles, J., 1994. Seasonal and fasting related changes in circulatory gonadal steroids and prolactin in king penguins, *Aptenodytes patagonicus*. *Physiol. Biochem. Zool.* 67, 1154–1173.
- Clutton-Brock, T.H., 1991. *The Evolution of Parental Care*. Princeton University Press, Princeton.
- Drent, R.H., Daan, S., 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68, 225–252.
- Gaston, A.J., Jones, I.L., 1998. *The Auks*. Oxford University Press, Oxford.
- Griffiths, R., Double, M.C., Orr, K., Dawson, R.J.G., 1998. A DNA test to sex most birds. *Mol. Ecol.* 7, 1071–1075.
- Groscolas, R., Lacroix, A., Robin, J.P., 2008. Spontaneous egg or chick abandonment in energy-depleted king penguins: a role for corticosterone and prolactin? *Horm. Behav.* 53, 51–60.
- Harding, A.M.A., Pelt, T.V., Lifjeld, J.T., Mehlum, F., 2004. Sex differences in little auk *Alle alle* parental care: transition from biparental to parental-only care. *Ibis* 146, 642–651.
- 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? *Proc. R. Soc. Lond. B* 273, 2227–2231.
- Holberton, R.L., Wingfield, J.C., 2003. Modulating the corticosterone stress response: a mechanism for balancing individual risk and reproductive success in arctic-breeding sparrows? *Auk* 120, 1140–1150.
- Insley, S.J., Paredes, R., Jones, I., 2003. Sex differences in razorbill (*Alca torda*) parent-offspring recognition. *J. Exp. Biol.* 206, 25–31.
- Jakubas, D., Wojczulanis, K., 2007. Predicting the sex of dovekeys by discriminant analysis. *Waterbirds* 30, 92–96.
- Jakubas, D., Wojczulanis-Jakubas, K., 2010. Glaucous gull predation on dovekeys: three new hunting methods. *Arctic* 63, 468–470.
- Jakubas, D., Gluchowska, M., Wojczulanis-Jakubas, K., Karnovsky, N.J., Keslinka, L., Kidawa, D., Walkusz, W., Boehnke, R., Cisek, M., Kwaśniewski, S., Stempniewicz, L., 2011. Foraging effort does not influence body condition and stress level in little auks. *Mar. Ecol. Prog. Ser.* 432, 277–290.
- Jakubas, D., Iliszko, L., Wojczulanis-Jakubas, K., Stempniewicz, L., 2012. Foraging by little auks in the distant marginal sea ice zone during the chick-rearing period. *Polar Biol.* 35, 73–81.
- Kitaysky, A.S., Wingfield, J.C., Piatt, J.F., 2001. Corticosterone facilitates begging and affects resource allocation in the black-legged kittiwake. *Behav. Ecol.* 12, 619–625.
- Konarzewski, M., Taylor, J.R.E., Gabrielsen, G.W., 1993. Chick energy requirements and adult energy expenditures of Dovekeys (*Alle alle*). *Auk* 110, 343–353.
- Kosztolányi, A., Küpper, C., Chastel, O., Parenteau, C., Yilmaz, K.T., Miklósi, A., Székely, T., Lendvai, A.Z., 2012. Prolactin stress response does not predict brood desertion in a polyandrous shorebird. *Horm. Behav.* 61, 734–740.
- Lendvai, Á.Z., Chastel, O., 2008. Experimental mate-removal increases the stress response of female house sparrows: the effects of offspring value? *Horm. Behav.* 53, 395–401.
- Lendvai, Á.Z., Giraudeau, M., Chastel, O., 2007. Reproduction and modulation of the stress response: an experimental test in the House sparrow. *Proc. R. Soc. Lond. B* 274, 391–397.
- Lifjeld, J.T., Harding, A.M.A., Mehlum, F., Øigarden, T., 2005. No evidence of extra-pair paternity in the little auk *Alle alle*. *J. Avian Biol.* 36, 484–487.
- Meddle, S.L., Owen-Ashley, N.T., Richardson, M.I., Wingfield, J.C., 2003. Modulation of the hypothalamic-pituitary-adrenal axis of an arctic-breeding polygynandrous songbird, the Smith's longspur, *Calcarius pictus*. *Proc. R. Soc. Lond. B* 270, 1849–1856.
- O'Reilly, K.M., Wingfield, J.C., 2001. Ecological factors underlying the adrenocortical response to capture stress in arctic-breeding birds. *Gen. Comp. Endocrinol.* 124, 1–11.
- Paredes, R., Insley, J.I., 2010. Sex-biased aggression and male-only care at sea in Brünnich's guillemots *Uria lomvia* and razorbills *Alca torda*. *Ibis* 152, 48–62.
- Richard, S., Wacrenier-Cer, N., Hazard, D., Saint-Dizier, H., Arnould, C., Faure, J.M., 2008. Behavioural and endocrine fear responses in Japanese quail upon presentation of a novel object in the home cage. *Behav. Process.* 77, 313–319.
- Riou, S., Chastel, O., Lacroix, A., Hamer, K.C., 2010. Stress and parental care: prolactin responses to acute stress throughout the breeding cycle in a long-lived bird. *Gen. Comp. Endocrinol.* 168, 8–13.
- Silverin, B., Goldsmith, A., 1997. Natural and photoperiodically induced changes in plasma prolactin levels in male great tits. *Gen. Comp. Endocrinol.* 105, 145–154.
- Stearns, S.C., 1992. *The Evolution of Life History*. Academic Press, London.
- Stempniewicz, L., 1995. Predator–prey interactions between glaucous gull *Larus hyperboreus* and little auk *Alle alle* in Spitsbergen. *Acta Ornithol.* 29, 155–170.
- Stempniewicz, L., 2001. *Alle alle* little Auk. BWP update. *J. Birds West. Palearct.* 3, 175–201.
- Székely, T., Thomas, G.H., Cuthill, I.C., 2006. Sexual conflict, ecology, and breeding systems in shorebirds. *Bioscience* 56, 801–808.

- Vleck, C.M., 1998. Hormonal control of incubation/brooding behavior: lessons from wild birds. *Proc. WPSA 10th European Poultry Conference, Israel*, pp. 163–169.
- Wang, Q., Buntin, J.D., 1999. The roles of stimuli from young, previous breeding experience, and prolactin in regulating parental behavior in ring doves (*Streptopelia risoria*). *Horm. Behav.* 35, 241–253.
- Welcker, J., Steen, H., Harding, A.M.A., Gabrielsen, G.W., 2009. Sex-specific provisioning behaviour in a monomorphic seabird with a bimodal foraging strategy. *Ibis* 151, 502–513.
- Wingfield, J.C., 1994. Modulation of the adrenocortical response in birds. In: Davey, K.G., Peter, R.E., Tobe, S.S. (Eds.), *Perspectives in Comparative Endocrinology*. National Research Council of Canada, Ottawa, pp. 520–528.
- Wingfield, J.C., Sapolsky, R.M., 2003. Reproduction and resistance to stress: when and how. *J. Neuroendocrinol.* 15, 711–724.
- Wingfield, J.C., O'Reilly, K.M., Astheimer, L.B., 1995. Modulation of the adrenocortical responses to acute stress in arctic birds: a possible ecological basis. *Am. Zool.* 35, 285–294.
- 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". *Am. Zool.* 38, 191–206.
- Wojczulanis, K., Jakubas, D., Stempniewicz, L., 2005. Changes in the glaucous gull predatory pressure on little auks in southern Spitsbergen. *Waterbirds* 28, 430–435.
- Wojczulanis-Jakubas, K., Jakubas, D., 2012. When and why does my mother leave me? The question of desertion of the dovekie chick. *Auk* 129, 1–6.
- Wojczulanis-Jakubas, K., Jakubas, D., Øigarden, T., Lifjeld, J.T., 2009a. Extra-pair copulations are frequent but unsuccessful in a highly colonial seabird, the little auk, *Alle alle*. *Anim. Behav.* 77, 433–438.
- Wojczulanis-Jakubas, K., Jakubas, D., Stempniewicz, L., 2009b. Sex-specific parental care by incubating little auks (*Alle alle*). *Ornis Fennica* 86, 140–148.
- Wojczulanis-Jakubas, K., Jakubas, D., Karnovsky, N.J., Walkusz, W., 2010. Foraging strategy of little auks under divergent conditions on feeding grounds. *Polar Res.* 29, 22–29.