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Baseline and stress-induced prolactin and corticosterone concentrations in a species with female offspring desertion – The case of Whiskered Tern *Chlidonias hybrida*

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ABSTRACT

To understand the proximate mechanisms regulating brood desertion, we studied hormonal and behavioural stress responses during the chick-rearing period in adult Whiskered Terns (*Chlidonias hybrida*), a socially monogamous, semi-precocial species with prolonged post-fledging parental care. In contrast to males, almost all females of this species desert during the chick-rearing and post-fledging periods. Because of the expected link between corticosterone, prolactin and parental investment, we hypothesized that males and females should differ in circulating prolactin and corticosterone concentrations. Baseline hormone concentrations did not differ between males and females. In both sexes, prolactin and corticosterone concentrations decreased and increased in response to acute stress (30 min after capture), respectively. Baseline and stress-induced prolactin concentrations decreased significantly in both sexes with advancing brood age. As expected, males had significantly higher stress-induced prolactin concentrations than females. None of the nine males released after being held in captivity for 24 h deserted, whereas four (29%) of the 14 females kept in captivity for 24 h did so. Altogether, these results suggest that higher prolactin concentrations may be involved in the maintenance of parental care under stress. However, there was no statistically significant difference in stress-induced hormone levels between males, females that deserted and those that returned to the nest after prolonged stress (24 h). Our data indicate that males are probably more resistant to stress as regards the continuation of parental care. The pattern of male and female behavioural and hormonal responses to stress partially predicts their behaviour in terms of natural desertion.

1. Introduction

The cost of reproduction stipulates that investing in parental care is associated with survival costs (Williams, 1966) and that individuals should optimize their reproductive investment in order to maximize their fitness (Stearns, 1992). In this context, a conflict of interest can arise in bird species with biparental care if one parent tries to maximize its own fitness at the other's expense (Székely et al., 1996; Lessells, 2012). Natural brood desertion occurs when one parent abandons the offspring and burdens the other parent with the charge of raising the offspring until independence (Székely et al., 1996; Webb et al., 2010). Offspring desertion by a single parent occurs in many bird species, but particularly in Charadriiformes (Székely et al., 1996), where female desertion is usually more common. Brood desertion is a model system for understanding the conflict between parents as well as the trade-off between the costs and benefits of current versus future reproductive success (Lessells, 2012). To date, however, researchers have studied brood desertion mainly from ecological and evolutionary perspectives (e.g. Arnqvist and Rowe, 2005; Lessells, 2012; Székely et al., 1996; Pilastro et al., 2001), and the proximate mechanisms leading to brood desertion are not fully understood. Several studies have demonstrated the central role of specific hormonal pathways in triggering the abandonment of reproduction in response to body reserve depletions or harsh environmental conditions (e.g. Chastel and Lormée, 2002; Groscolas et al., 2008). However, the hormonal mechanisms that trigger natural brood desertion by males or females (not caused by stress or harsh conditions)

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as a strategy of sexual conflict in species with biparental care remain poorly understood.

Circulating hormones are thought to be primary physiological mediators of life-history trade-offs (Ricklefs and Wikelski, 2002; Angelier et al., 2016b; Taff and Vitousek, 2016). In the context of parental behaviour, two hormones deserve specific attention. Firstly, corticosterone – the primary avian glucocorticoid – is known to be involved in the decision to abandon reproduction in response to stress (Wingfield, 2004; Wingfield and Sapolsky, 2003). In response to environmental perturbations or depletion of body reserves, corticosterone secretion is increased. Elevated corticosterone levels then trigger an emergency life-history stage that aims to promote immediate survival at the expense of other fitness-related components, such as reproduction (Wingfield et al., 1998). For example, experimentally elevated concentrations of corticosterone are associated with a reduction of parental care (e.g. Angelier et al., 2009; Almasi et al., 2013) and with nest desertion (e.g. Silverin, 1986; Cherel et al., 1988; Groscolas et al., 2008; Spée et al., 2011). Secondly, prolactin is a hormone generally involved in parental behaviour, i.e. incubation, brooding and food provisioning (Vleck and Vleck, 2002; Angelier and Chastel, 2009), and several studies have reported that reduced circulating prolactin concentrations can be associated with reduced parental care (Angelier et al., 2009; Thierry et al., 2013; Smiley and Adkins-Regan, 2016) and even brood desertion (e.g. Groscolas et al., 2008; Angelier et al., 2007, Angelier et al., 2016b). Interestingly, it has also been shown that prolactin concentrations decrease in response to a wide variety of stressors (reviewed in Angelier and Chastel, 2009), and for this reason, changes in the prolactin stress response level may be informative as a signal of parental investment (Angelier et al., 2016a). Because both hormones are involved in parental care and are functionally connected (Angelier et al., 2013), simultaneously studying the corticosterone and prolactin stress responses appears relevant to a better understanding of the proximate causes of brood desertion (Angelier et al., 2016b; Wojczulanis-Jakubas et al., 2013).

It is proposed that the prolactin and corticosterone stress response can be used to test hypotheses related to life-history theory and, specifically, to parental and reproductive investment in birds (reviewed in Chastel et al., 2005; Angelier and Chastel, 2009). It is assumed that the change in hormone concentrations in response to a standardized stressor is a surrogate measure of parental investment. Some studies showed that birds attenuate their hormones response to acute or prolonged stress to ensure that reproduction is not inhibited when the fitness value of current the reproductive event is high (Lendvai et al., 2007; Bókony et al. 2009; Angelier and Chastel, 2009). Elevated prolactin level could permit the maintenance of parental care and maximizing current parental effort during stressful situations (Chastel et al. 2005). Therefore some authors suggest that in species with natural offspring desertion, brood abandonment can be predicted by the prolactin stress response (Kosztolányi et al., 2012; Wojczulanis-Jakubas et al., 2013). Therefore it is suggested that individuals that desert their broods would have a stronger prolactin stress response (i.e., lower stress-induced prolactin concentrations) compared with individuals that do not desert.

In this study, we measured baseline hormone concentrations (immediately after capture), followed by measurements after acute stress (30 min after capture) and prolonged stress (24 h after capture) in male and female Whiskered Terns (*Chlidonias hybrida*, Charadriiformes) in order to investigate the proximate mechanisms underlying the transition from biparental to male-only care. Whiskered Tern is especially relevant for understanding the role of corticosterone and prolactin in mediating parental care and brood desertion because natural brood desertion is frequently observed in this species. During the chick-rearing and post-fledging periods, almost all females desert their offspring, whereas males maintain and even intensify paternal care to compensate for the lack of maternal care (Ledwoń and Neubauer, 2017).

To test the role of corticosterone and prolactin in mediating parental care and brood desertion, we compared baseline and stress-induced prolactin and corticosterone concentrations between the sexes during the chick-rearing period. Nest desertions occur only during the chick-rearing and post-fledging periods. In addition, males deliver about 25% more food to the chicks than females and, in contrast to females, they hardly ever abandon their broods (Ledwoń and Neubauer, 2017). Because of these sexual and stage-related differences in parental care, we expected differences in prolactin and corticosterone concentrations between males and females if these two hormones are indeed involved in parental decisions (Wingfield and Sapolsky, 2003; Angelier and Chastel, 2009). Specifically, we predicted that females should have lower baseline and stress-induced prolactin concentrations and higher baseline and stress-induced corticosterone concentrations than males during the chick-rearing period because they are more likely to desert the brood than males (Ledwoń and Neubauer, 2017). Assuming that the decrease in prolactin in response to a stressor is a surrogate measure of parental investment (Angelier and Chastel, 2009), we predicted that females that deserted their chicks after prolonged stress would have lower stress-induced prolactin concentrations compared with non-deserting females and with males.

2. Methods

2.1. Study species

Whiskered Tern is a small (80–100 g) water bird species, nesting colonially on aquatic plants (Cramp, 1985; Mužinić and Delić, 1997; Gochfeld et al., 2020). It is a socially monogamous species, with a low level of extra-pair paternity (Minias et al., 2013; unpublished results). Its plumage is not sexually dimorphic, but males are larger than females (Ledwoń, 2011). In this species, both mates make a large investment in parental care: males feed females before clutch completion, females lay a three-egg clutch that represents about one-third of their body mass, and both parents incubate the eggs and brood the chicks to an equal extent (Spina, 1982; Paillisson et al., 2007; Ledwoń, 2010). Females contribute significantly less than males to provisioning the chicks (Ledwoń and Neubauer, 2017). During the chick-rearing period, half of the females desert, while the other half does so during the post-fledging period. Desertion starts when chicks are thermally emancipated, i.e. 5 days old. Deserted males continue to provide care for at least 1–2 months. Termination of parental care by females has no effect on fledging success.

2.2. Fieldwork

We carried out the fieldwork in 2016 and 2017, in breeding colonies on carp pond complexes in the northern part of the Upper Vistula Valley, southern Poland (for a detailed description of the study area, see Ledwoń et al., 2013, 2014; Gwiazda and Ledwoń, 2015). Birds were trapped in 2016 and 2017 in one colony (Za Stodołami pond, 50°01′20.1″N 19°24′00.5″E) in the Przeręb carp pond complex to determine baseline and stress-induced hormone concentrations (30 min after capture). To study the hormone concentrations after prolonged stress – in birds held in captivity for 24 h after being captured – the birds were trapped only in 2017, in two colonies: in the Bugaj carp pond complex (Wierzbowiec Stary pond, 49°58′15.2″N 19°25′06.8″E) and in the Spytkowice complex (Róża pond, 50°00′36.3″N 19°29′29.2″E). We usually entered the colony twice a week to inspect nests and to trap the birds. Monitoring of all nests started during the early stages of incubation (up to about the 10th day after egg laying). We erected plastic mesh fences around the monitored nests with eggs to prevent the chicks from escaping until they had fledged (for a detailed description of the enclosure, see Ledwoń et al., 2015; 2016). In addition, the majority of enclosures were lined with plastic foil to prevent the chicks from injuring themselves. The exact hatching date was deduced on the basis of nest visits: from the presence of freshly hatched chicks, readily identified as they were still wet after having just emerged from the egg; by the presence of the hatching star on the egg, which indicates that the chick will emerge from the egg within 24 h; and on the basis of chick wing length (Paillisson et al., 2008; Banach et al., 2021).

2.3. Baseline and acute stress

In 2016 and 2017, we caught the birds at the nests using roof traps (for a detailed description of the trapping method, see Ledwoń et al., 2015; 2016). In all nests both parents were present during trapping. The birds for the study of baseline and stress-induced hormone concentrations (30 min after capture) were caught during chick-rearing periods (between the day of hatching, thereafter named day 0, and the 7th day of life). We measured the exact time between the capture (initiation of stress) to the moment when the blood was sampled, and all the samples were taken within three minutes of the capture. There was no significant correlation between the time that passed between capture and the first sampling, and the baseline concentrations of either corticosterone or prolactin. After capture, about 250 µL of blood was collected from the brachial vein, and the bird was then placed in a cloth bag. To establish the birds' hormonal stress responses, we used the standardized capture-and-restraint protocol given in Wingfield (1994). We kept the birds in separate opaque cloth bags for 30 min before the second sampling to measure stress-induced hormone concentrations. We sampled all the birds between 08:00 and 15:00 hrs, i.e. within a moderate time window of 8 h so as to avoid any potential effect of diurnal cycles on the hormone concentrations.

2.4. Prolonged stress

In 2017, some adults were caught and kept in captivity for 24 h to study the effect of prolonged stress on hormone concentrations and brood desertion. The original aim of this study had been to provoke the desertion of one of the mates (the trapped one) in order to obtain nests with uniparental care (for a detailed description of this experiment, bird handling methods and a description of the trapping procedure, see Ledwoń et al., 2019). Therefore, this part of the experiment was conducted when the first desertions were observed – the chicks were older, had developed thermoregulation and no longer required intense brooding (4–9 days after hatching). We were unable to obtain baseline concentrations and stress-induced hormone concentrations 30 min after capture for these birds: catching the parents when chicks are older is difficult because the adults are reluctant to enter the trap. The birds were always trapped in the morning. They were released 24 h after being trapped (~08:00 hrs CET the next day) at a distance of 7 km from the breeding colony. The removed parent was kept in a cardboard box (21 cm × 30 cm × 25 cm) in a shed that was sheltered from wind and rain. Blood samples were taken immediately before release. Behavioural observations of the focal nests were carried out to determine whether the birds returned to the nest after release and to estimate breeding success (for a detailed description of the methods, see Ledwoń et al., 2019). Observations usually started when the removed birds were released and were continued every 2–4 days in the morning for an average of 190 min per nest. Birds not observed on the first day after release were never seen again on the nest, despite repeated observations; it can be safely assumed that they deserted immediately after having been removed.

2.5. Blood samples and hormonal analyses

In the field, the blood samples were kept cool for a few hours until centrifugation for 10 min at 6000 rpm. The plasma and red cells were kept separately frozen (at − 20 °C) and analysed within 6 months. The adults were molecularly sexed according to Ledwoń (2011) and Goławski et al. (2016), and the results were validated by morphometric measurements. Each individual trapped was ringed, measured and weighed. Baseline and stress-induced concentrations of corticosterone and prolactin were measured by radioimmunoassay at the Centre d'Etudes Biologiques de Chizé (France). Corticosterone assay was carried out as previously described (Lormée et al. 2003; Angelier et al. 2006). Briefly, plasma corticosterone was measured in samples (50 µL) after ethyl ether extraction by radioimmunoassay using a commercial antiserum. Duplicate aliquots of the extracts were incubated overnight at 4 °C with 8000 cpm of ^{3}H-Corticosterone and antiserum. The bound and free corticosterone were separated by adding dextran-coated charcoal. After centrifugation, the bound fraction was counted in a liquid scintillation counter.

Table 1
Sample size of baseline, stress-induced hormone concentrations 30 min and 24 h after capture in male and female Whiskered Terns.

	Baseline		Stress-induced (30 min after capture)		Stress-induced (24 h after capture)	
	Female	Male	Female	Male	Female	Male
Prolactin						
2016	8	7	9	6	0	0
2017	18	13	19	14	15	10
Sum	26	20	28	20	15	10
Corticosterone						
2016	7	7	7	6	0	0
2017	18	13	18	13	16	9
Sum	25	20	25	19	16	9

Prolactin radioimmunoassay was carried out by a double-antibody method as previously described (Cherel et al. 1994). Highly purified chicken prolactin preparation was labelled with Na^{125}I. All reactants were diluted with barbital-bovine serum albumin buffer. A sample of diluted antiserum containing normal rabbit serum and the labelled prolactin were added to 25 µL of whole plasma or standard, and the solution was incubated for at 40 °C. A sample of a sheep anti-rabbit gamma-globulin serum was then added to each tube. After a second incubation period, the tubes were centrifuged, the supernatants were discarded, and the precipitated bound labelled prolactin complexes were measured on an automatic gamma counter. The plasma samples were measured in duplicate and levels are given relative to the chicken prolactin standard. The pooled plasma samples from the Whiskered Terns produced a dose–response curve that paralleled chicken prolactin standard curves, therefore validating our prolactin assay for Whiskered Terns. Minimal detectable corticosterone and prolactin levels were 0.28 ng mL^{-1} and 0.45 ng mL^{-1}, respectively. All the samples were run in one assay for prolactin (intra-assay variation: 8.58%). All samples were run in 2 assays for corticosterone (inter-assay variation: 8.78%; intra-assay variation: 9.19%).

2.6. Data analysis

We measured baseline and stress-induced (30 min after capture) hormone concentrations during the chick-rearing period in both 2016 and 2017 (Table 1). Baseline and stress-induced prolactin concentrations were obtained from 44 birds, while baseline and stress-induced corticosterone concentrations were measured in 41 birds. Hormone concentrations after 24 h of captivity were measured (only in 2017) in an attempt to understand the consequence of prolonged stress on hormone concentrations.

We used linear models to assess the importance of various factors on hormone concentrations. In first analysis (ordinary GLM), we compared baseline hormone concentrations, as well as these concentrations after acute stress (30 min after capture) and after prolonged stress (24 h after capture). The predefined factors in the global model included duration of stress (three concentrations: baseline, 30 min and 24 h), sex (male or female), body condition (estimated as residuals of body mass regressed on total head length) and interactions of these effects. We limit this analysis to only the days of overlap between groups, therefore this analysis included only nests from 2017 and only adults which were

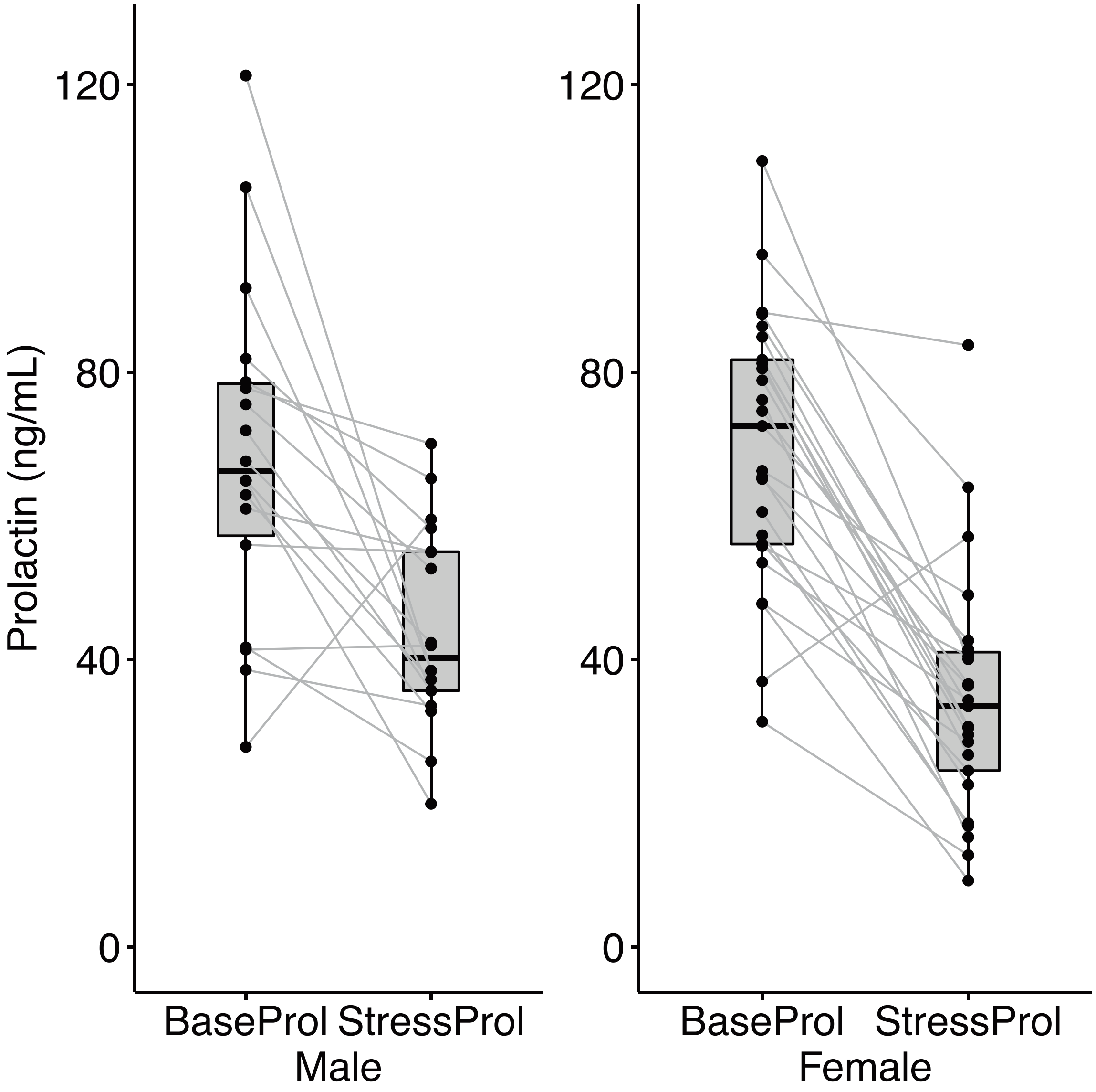

Fig. 1. Individual baseline and stress-induced (30 min after capture) prolactin concentrations and boxplots of hormone levels in Whiskered Tern during the chick-rearing period. Boxes – 25%–75% interquartile range; central line – median; dots – original measurements of individual birds.

trapped between the 5th and 7th days of chick life. In the model, we excluded the number of chicks, age of brood, date of laying and colony to avoid overfitting the dataset and because the variation in these factors was small (there were 2 or 3 chicks; all the eggs were laid during 3 weeks; chick age was 5–7 days; birds which were held in captivity were trapped in a different colony from birds in other groups). Furthermore, initial data exploration indicated no significant relationship between these factors and hormone concentrations.

In two separate analyses, we investigated whether the baseline and stress-induced (30 min after capture) level of hormones were correlated with chick age and other predefined factors. The factors in the global model (ordinary GLM) included the sex of the parent bird; year factor (two levels); brood age (referred to the day of trapping since hatching) measured in days (range 0–7; the hatching day of the oldest chick, coded as day 0); body condition; and sex-year, sex-brood age and sex-body condition interactions. For the reasons given above, we excluded brood size and laying date from the analysis.

In another separate analysis, we investigated whether predefined factors influenced stress-induced hormone concentrations (24 h after capture). The factors in the global model (ordinary GLM) included body condition, sex and the sex-body condition interaction. We excluded the number of chicks, age of brood, laying date and colony to avoid overfitting the dataset and because the variation in these factors was small (there were 2 or 3 chicks; chick age was 4–9 days; all the eggs were laid during 3 weeks; there were only two colonies). Moreover, initial data investigation showed no significant relationship between these factors and hormone concentrations.

Since the sample size was small (Table 1), we applied nonparametric bootstrapping (Davison and Hinkley 1997) to our data to estimate variances and compare mean stress-induced hormone concentrations between males, females that did and did not desert after the removal experiment (24 h in captivity). This approach has no requirements in respect to normality of empirical distributions (in our case, observed prolactin distribution did not conform with normal one) and sample sizes.

Collinearity was not a problem: correlation coefficients between the covariates were < 0.5 in all cases. The global model and all the simpler, nested models, missing one or more terms, were fitted in the MuMIn library (Bartoń, 2015) in R 3.4.3 (R Core Team, 2018). Since the model weights were balanced (Supplementary Material), model averaging and model-averaged prediction were applied, taking the models with ΔAICc ≤ 2 in the AICcmodavg library into consideration (Mazerolle, 2015).

Table 2
Descriptive statistics of baseline and stress-induced prolactin and corticosterone concentrations in Whiskered Tern during the chick-rearing period. For detailed description of sampling see Methods.

Hormone concentrations	Females			Males		
	n	Mean (ng/ml)	SE	n	Mean (ng/ml)	SE
Prolactin						
Baseline	26	70.06	3.62	20	75.17	7.77
30 min after capture	28	34.20	3.04	20	45.34	3.52
24 h after capture	15	31.58	4.78	10	32.06	6.59
Corticosterone						
Baseline	25	16.76	1.62	20	17.01	1.92
30 min after capture	25	57.23	2.33	19	63.74	3.80
24 h after capture	16	53.01	4.95	9	41.68	4.89

3. Results

The prolactin level in 41 out of 44 birds (93%) decreased after the standardized capture-and-restraint protocol (Fig. 1, Table 2). The level of corticosterone increased after stress in all 41 birds (Fig. 2, Table 2).

The baseline level of prolactin between the 5th and 7th days of chick life in 2017 was significantly higher in both sexes in comparison with both stress-induced concentrations (30 min and 24 h after capture); these latter two concentrations did not differ (Fig. 3, Table 3 and Table A1). The corticosterone level increased significantly in both sexes 30 min after capture, and decreased 24 h after capture but was still higher than the baseline level (Fig. 4, Table 4 and Table A2). All three concentrations differed among each other.

The baseline prolactin level decreased similarly in both sexes and both years in relation to chick age (Fig. 5, Table 5 and Table A3). The stress-induced (30 min after capture) prolactin level decreased in relation to chick age in both sexes, but the concentrations of this hormone were higher in males than in females (Fig. 6, Table 6 and Table A4). The prolactin level after 24 h of stress was not influenced by any of the factors examined (Table A5).

There was a similar decrease in baseline corticosterone level in relation to body condition in both sexes (Fig. 7, Table 7 and Table A6). Variation in stress-induced corticosterone level (30 min after capture) was not associated with any of the factors analysed (Table 8 and Table A7). Stress-induced corticosterone concentrations after 24 h in

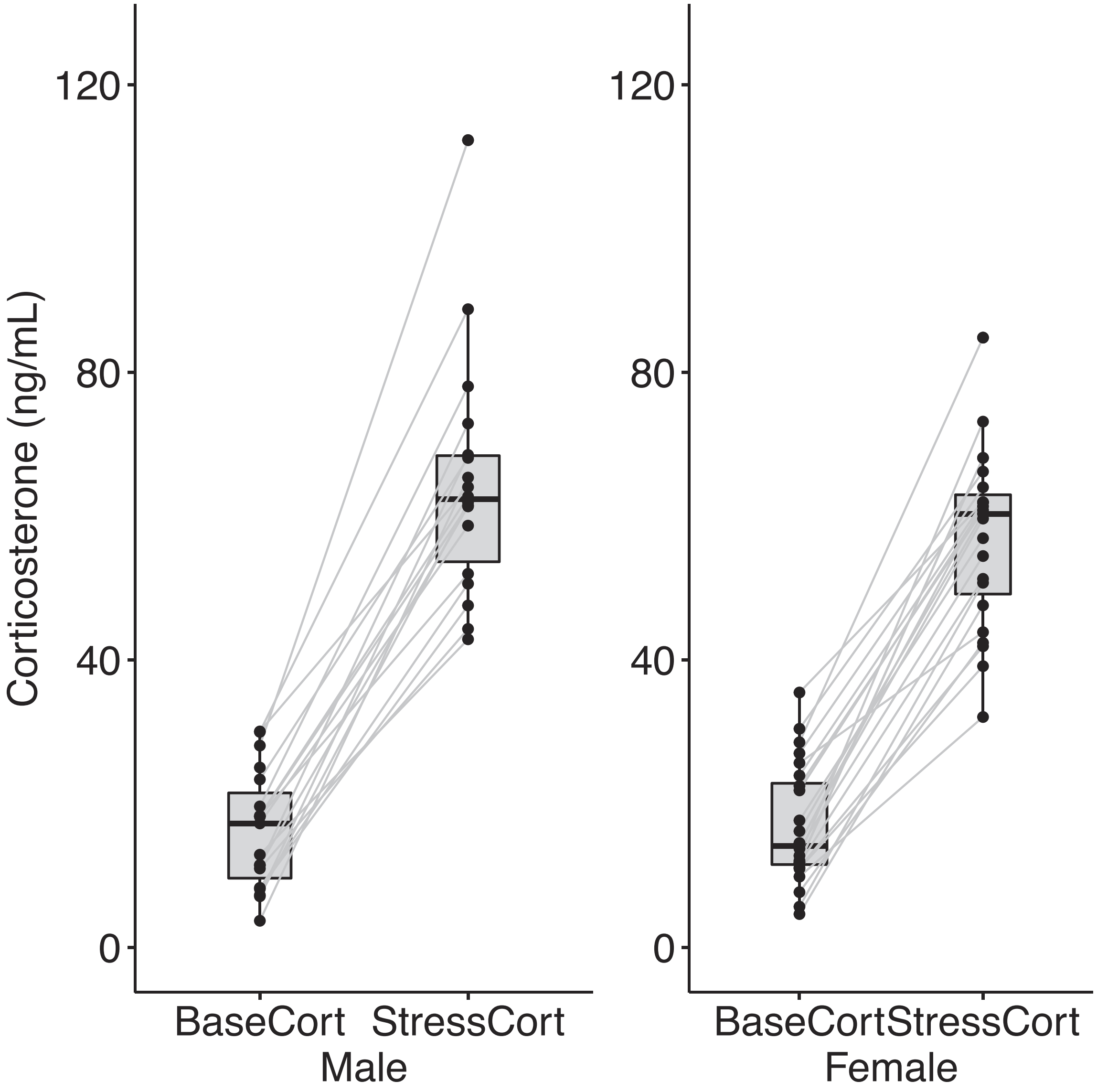

Fig. 2. Individual baseline and stress-induced (30 min after capture) corticosterone concentrations and boxplots of hormone levels in Whiskered Tern during the chick-rearing period. Boxes – 25%–75% interquartile range; central line – median; dots – original measurements of individual birds.

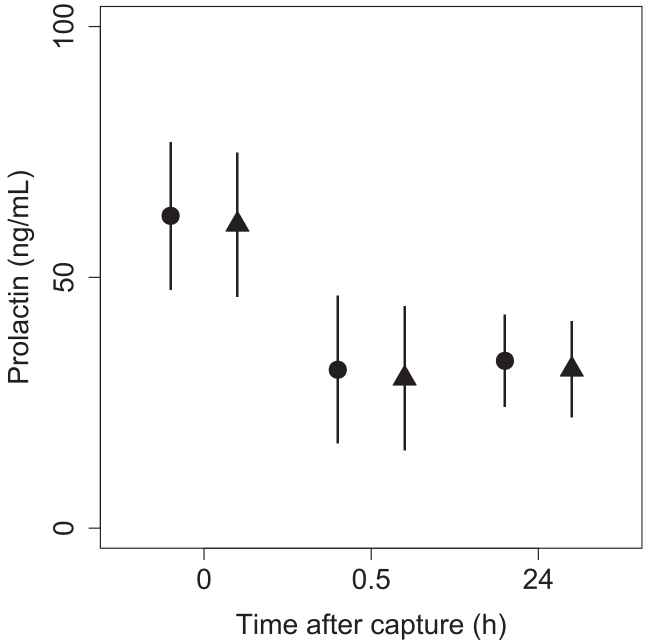

Fig. 3. Relationship between prolactin concentration and stress duration (0 – baseline, 0.5 h after capture, 24 h after capture) in adult Whiskered Terns in 2017. Symbols show model-averaged means, whiskers – 95% confidence intervals. Circles – females, triangles – males.

Table 3

Model-averaged coefficients and unconditional standard errors from generalized linear models used to explain variation in the prolactin concentration in 2017 in relation to the duration of stress (three levels: no stress – baseline concentration, 30 min and 24 h after capture), body condition, sex and their interactions.

Parameter	Estimate	SE	z	*p*
Intercept	62.265	7.698	8.088	**<0.001**
Stress: 30 min	−30.683	10.264	2.989	**<0.001**
Stress: 24 h	−28.898	8.450	3.420	**<0.001**
Sex: male	−1.732	4.491	0.386	0.700

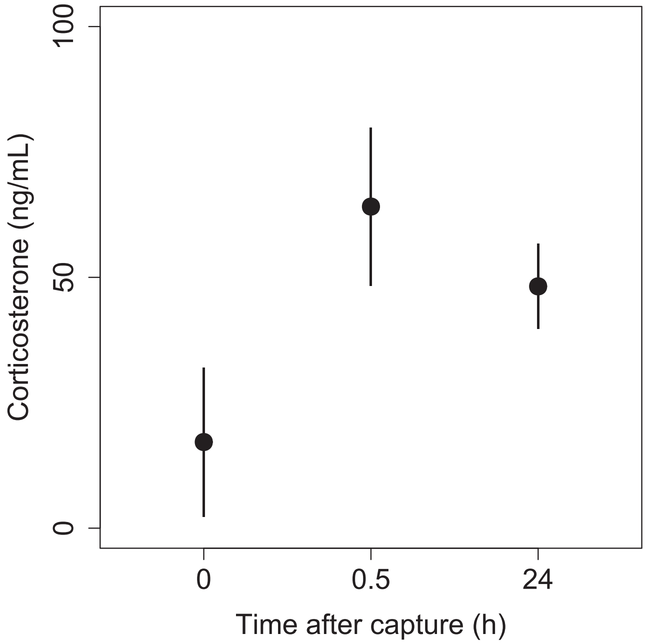

Fig. 4. Relationships between corticosterone concentration and stress duration (0 – baseline, 0.5 h after capture, 24 h after capture) in adult Whiskered Terns in 2017. Symbols – model-averaged means, whiskers – 95% confidence intervals.

Table 4

Model-averaged coefficients and unconditional standard errors from generalized linear models used to explain variation in the corticosterone concentration in 2017 in relation to the duration of stress (three levels: no stress – baseline concentration, 30 min and 24 h after capture), body condition, sex and their interactions.

Parameter	Estimate	SE	z	*p*
Intercept	17.172	7.73	2.221	**0.026**
Condition	−0.403	0.9224	0.437	0.662
Stress: 30 min	46.938	9.616	4.881	**<0.001**
Stress: 24 h	31.035	7.782	3.988	**<0.001**

captivity were negatively correlated with body condition in females but not in males (Fig. 8, Table 9 and Table A8).

None of the 9 males released after being held in captivity for 24 h deserted, whereas 4 (29%) of the 14 females kept in captivity for 24 h deserted (G = 4.50, df = 1, p = 0.03). There were no differences in stress-induced (24 h after capture) concentrations of either hormones between males, females that deserted, and females that returned to the nest after prolonged stress (Table 10).

4. Discussion

4.1. Baseline prolactin and corticosterone concentrations

Baseline concentrations of plasma prolactin decreased significantly and to similar extents with advancing brood age in both sexes of Whiskered Tern (Fig. 5). This pattern has been observed in many precocial species (Oring et al., 1986; 1988; Gratto-Trevor et al., 1990; Boos et al., 2007; Angelier and Chastel, 2009; Williams, 2012). In contrast, we did not find any significant correlation between the baseline corticosterone concentrations and brood age. It is in line with other studies, in many species there is no significant relationship or else the direction of this correlation differs strongly among species (e.g. Kitaysky et al., 1999; Love et al., 2014; Williams, 2012; Wojczulanis-Jakubas et al., 2013).

We predicted that offspring desertion by female Whiskered Terns should be related to lower baseline concentrations of prolactin. However, we failed to detect any differences in baseline prolactin concentrations between sexes during the brooding period. We studied baseline hormone concentrations in parent birds only up to about the 7th day of chick life because it is impossible to catch adults later in order to collect blood. Hence, we cannot rule out the possibility that sexual differences in baseline prolactin concentrations may become apparent later, when the chicks are older and when desertion events by females become more common. In support of our results, no differences were found in prolactin and corticosterone concentrations between males and females in three other species of Charadriiformes with dominant female desertion – Little Auk (Dovekie) *Alle alle*, Kentish Plover *Charadrius alexandrinus* and Semipalmated Sandpiper *Calidris pusilla* – (Gratto-Trevor et al., 1990; Kosztolányi et al., 2012; Wojczulanis-Jakubas et al., 2013). In all these studies (including ours), hormone concentrations were never assessed shortly before desertion, so we cannot exclude that the hormonal-mediated changes leading to brood desertion take place rapidly; this would be difficult to measure in wild populations.

Our findings that there are no differences between the sexes in baseline prolactin level are consistent with the general idea that prolactin reflects the amount of parental activity (Angelier and Chastel, 2009; Angelier et al., 2016b), since both sexes in Whiskered Tern participate in brooding and chick feeding (Ledwoń, 2010; Ledwoń and Neubauer, 2017) until the females desert the brood. In birds, parental care and prolactin levels are intrinsically and functionaly linked.

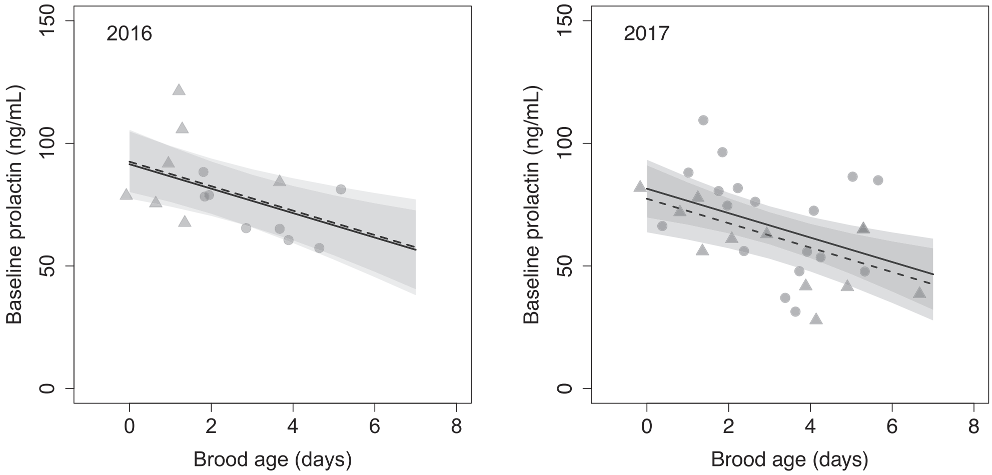

Fig. 5. Relationships between baseline prolactin concentration and brood age in Whiskered Tern in 2016 and 2017. Lines and shaded areas – model-averaged means with 95% confidence intervals, symbols – original measurements of individual birds. Circles, solid line – females; triangles, dashed line – males. Symbols have been jittered slightly around their original positions on X axis (Brood age) to reduce overlap.

Table 5
Model-averaged coefficients and unconditional standard errors from generalized linear models used to explain variation in the baseline prolactin concentration in relation to brood age, year, sex and body condition, as well as the sex-body condition, brood age and sex-year interactions.

Parameter	Estimate	SE	z	*p*
Intercept	91.489	7.336	12.472	**<0.001**
Brood age	−4.985	1.585	3.145	**<0.01**
Year: 2017	−9.985	7.087	1.409	0.159
Sex: male	1.014	7.299	0.139	0.889
Sex: male-Year: 2017	−5.112	10.338	0.494	0.621

Prolactin is known to trigger parental behavior while parental-related stimuli (contact with the egg or the chick) also stimulate prolactin secretion (Sockman et al. 2006; Angelier and Chastel 2009; Angelier et al., 2016b; Smiley 2019). For example, no differences between the sexes in baseline prolactin concentrations were found in species with equal male and female care (Angelier and Chastel, 2009; Williams, 2012), but males of polyandrous species with predominant male care had higher prolactin concentrations (Gratto-Trevor et al., 1990; Oring et al., 1986; 1988). In this study, we did not examine the relationship between hormonal concentrations and parental care (time budget, provisioning rate) at an individual level. This aspect will be relevant in future studies to test whether prolactin concentrations are a proxy of the degree of parental commitment.

We found no difference in baseline corticosterone concentrations between male and female chick-rearing Whiskered Terns, suggesting that females are not more constrained than males (Bonier et al., 2009; Williams, 2012). However, and interestingly, we found that baseline corticosterone concentrations were negatively correlated with body

Table 6
Model-averaged coefficients and unconditional standard errors from generalized linear models used to explain variation in the stress-induced prolactin concentration (30 min after trapping) in relation to brood age, year, sex and body condition, as well as the sex-body condition, sex-brood age and sex-year interactions.

Parameter	Estimate	SE	z	*p*
Intercept	42.484	5.174	8.211	**<0.001**
Brood age	−3.126	1.333	2.346	**0.019**
Sex: male	9.503	4.629	2.053	**0.040**
Year: 2017	1.452	3.543	0.410	0.682

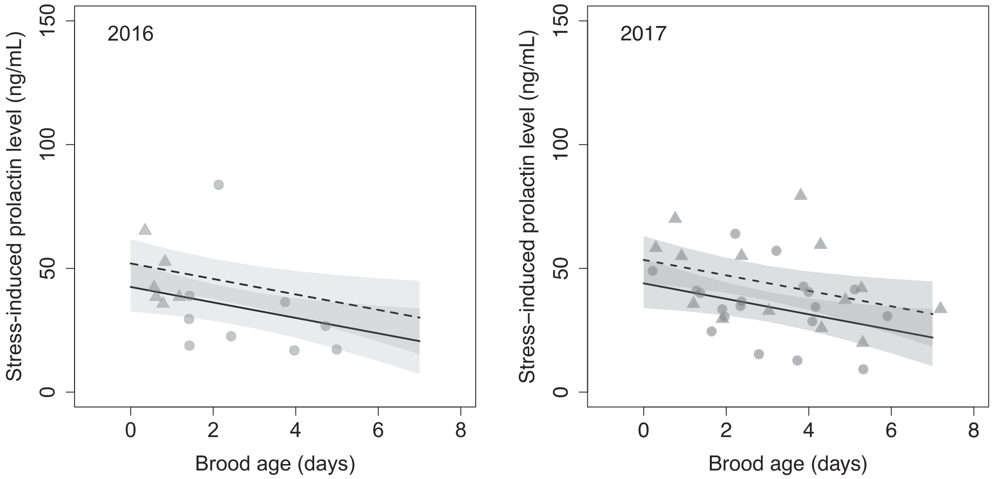

Fig. 6. Relationships between stress-induced prolactin concentration (30 min after capture) and brood age in Whiskered Tern in 2016 and 2017. Lines and shaded areas – model-averaged means with 95% confidence intervals, symbols – original measurements of individual birds. Circles, solid line – females; triangles, dashed line – males. Symbols have been jittered slightly around their original positions on X axis (Brood age) to reduce overlap.

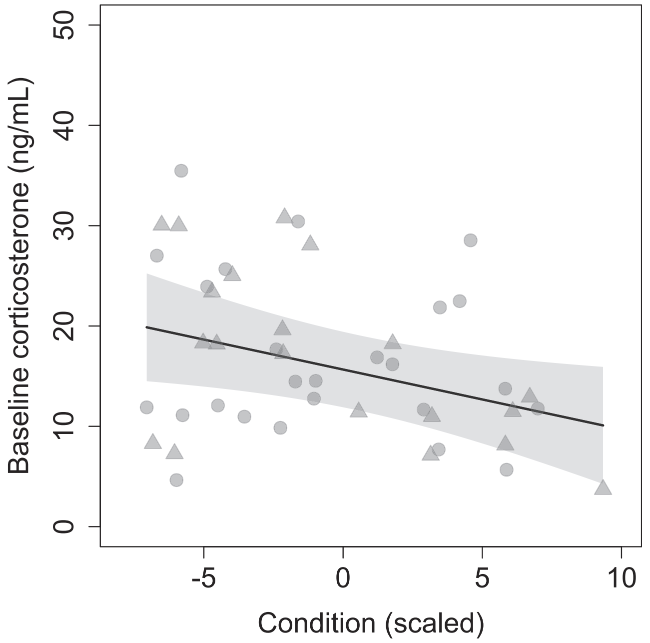

Fig. 7. Relationships between baseline corticosterone concentration and body condition in Whiskered Tern. Line and shaded area – model-averaged mean with 95% confidence intervals, symbols – original measurements of individual birds. Circles– females; triangles – males.

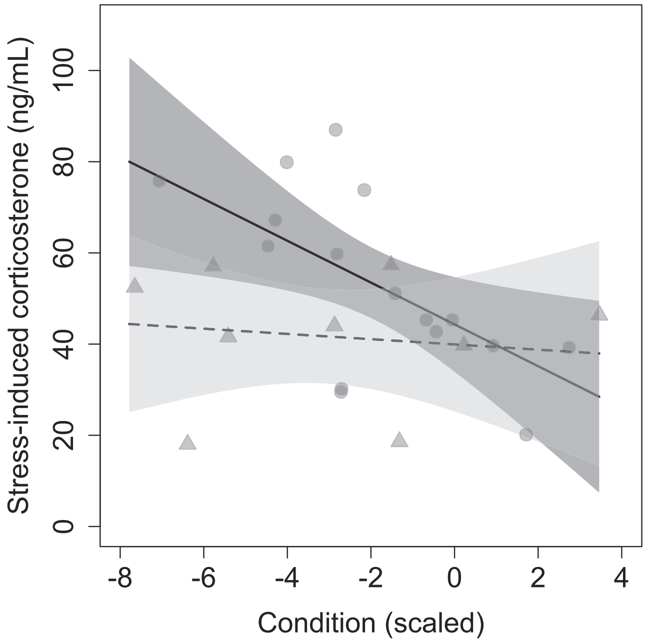

Fig. 8. Relationships between stress-induced (24 h after capture) corticosterone concentration and body condition in Whiskered Tern in 2017. Lines and shaded areas – model-averaged means with 95% confidence intervals, symbols – original measurements. Circles, solid line – females; triangles, dashed line – males.

Table 7
Model-averaged coefficients and unconditional standard errors from generalized linear models used to explain variation in the baseline corticosterone concentration in relation to brood age, year, sex and body condition, as well as the sex-body condition, sex-brood age and sex-year interactions.

Parameter	Estimate	SE	z	*p*
Intercept	15.663	1.961	7.986	**<0.001**
Condition	−0.597	0.259	2.242	**0.025**
Brood age	0.272	0.548	0.488	0.625

Table 8
Model-averaged coefficients and unconditional standard errors from generalized linear models used to explain variation in the stress-induced corticosterone concentration (30 min after trapping) in relation to brood age, year, sex and body condition, as well as the sex-body condition, sex-brood age and sex-year interactions.

Parameter	Estimate	SE	z	*p*
Intercept	58.174	4.203	13.841	**<0.001**
Sex: male	4.112	4.754	0.865	0.387
Condition	0.018	0.305	0.061	0.952
Condition-sex: male	−0.161	0.540	0.298	0.765
Brood age	0.211	0.740	0.285	0.776
Year: 2017	−0.641	2.460	0.261	0.794

Table 9
Model-averaged coefficients and unconditional standard errors from generalized linear models used to explain variation in the stress-induced corticosterone concentration (24 h after trapping) in relation to sex, body condition and the sex-body condition interaction.

Parameter	Estimate	SE	t	*p*
Intercept	43.242	4.900	8.825	**<0.001**
Sex: male	−1.734	8.468	−0.205	0.840
Condition	−5.155	1.581	−3.260	**0.003**
Sex: male-Condition	5.099	2.185	2.333	**0.030**

Table 10
Prolactin and corticosterone concentrations (bootstrapped means and 95% confidence intervals) in Whiskered Terns in relation to the behavioural reaction for prolonged stress (24 h in captivity).

Sex and category	Hormone [ng/ml]	
	Prolactin	Corticosterone
Males	33.4 (21.0–45.8)	45.5 (36.0–53.6)
Females that returned to the nest	31.7 (19.6–45.7)	47.5 (36.7–58.2)
Females that deserted	20.4 (10.4–33.3)	51.1 (36.4–64.8)

condition in both sexes, supporting the idea that corticosterone concentrations could be a proxy of the amount of body reserves (Lynn et al. 2010) in birds. Such a decline in body condition frequently occurs during the demanding chick-provisioning period, when parents are energetically constrained and actively reduce their body mass to increase foraging efficiency (Romero, 2002).

4.2. *Stress-induced prolactin and corticosterone concentrations*

The decrease in prolactin concentrations in response to stress was expected (Fig. 3), as it had been previously reported in a great many of species (Angelier and Chastel, 2009, but see Wojczulanis-Jakubas et al., 2013). Interestingly, the prolactin concentrations reached after 24 h of captivity (prolonged stress) were similar to those reached after 30 min of restraint (Fig. 3). This suggests that prolactin concentrations decrease to a lower threshold following stress and that they remain unchanged even if the stressor is maintained. The pattern of corticosterone stress responses after 30 min of acute stress is consistent with the one widely reported for many bird species (e.g. Bókony et al., 2009; Wingfield, 1994; Vitousek et al., 2019). Such an acute corticosterone response is generally thought to allow an individual to cope physiologically and behaviourally with perturbations in the environment (Wingfield et al., 1998; Angelier and Wingfield, 2013). Interestingly, the corticosterone concentrations reached after 24 h of captivity were lower than those reached after 30 min of restraint, although they were still higher than the baseline corticosterone level (Fig. 4). This reduction of corticosterone concentrations during the 24 h following the initial stressor is likely due to the activation of the corticosterone negative feedback that limits the secretion of corticosterone by the adrenal glands (Taff et al., 2018).

As in the case of the baseline prolactin concentrations, we found that the stress-induced prolactin level (30 min after capture) decreased in relation to brood age. Importantly, stress-induced prolactin concentrations were higher in males than in females, although the difference was not great (Fig. 6). Because elevated prolactin concentrations are thought to support the maintenance of parental care under stress (Hope et al., 2020), this hormonal result could explain why male parents may be more resistant to stress and less likely to desert the brood than female parents during the chick-rearing period. This tallies with our prediction that females should have lower stress-induced prolactin concentrations than males during the chick-rearing period. It has been assumed that the level of prolactin in response to a standardized stressor is a surrogate measure of parental investment (Angelier and Chastel, 2009). The higher prolactin level after stress in males than in females suggests that the former are more strongly driven to provide parental care and are probably more resistant to stress as regards the continuation of parental care during chicks rearing period. The differences of the stress response in prolactin level between the sexes suggest that fitness value of current brood is higher for males than for females – obviously, since in this species the females desert while the males continue parental care.

Our results suggest that males should be less risk-averse than females, so they should also be less sensitive to stressors in order to ensure their greater involvement in the chick-rearing and post-fledgling periods. Our results generally confirm that no males deserted in response to prolonged stress, whereas females deserted at a high rate. It seems that elevated prolactin concentrations in males may play an important role in maintaining parental care. This statement may be corroborated by the fact that prolactin concentrations after prolonged stress (24 h in captivity) were lower in females that deserted than in males and in females that did not desert after being held in captivity (Tab. 10). This difference was not statistically significant, however, possibly because of a lack of statistical power.

Interestingly, the corticosterone concentrations reached after 24 h of captivity were negatively correlated with body condition, although this relation was sex-dependent and only apparent in females (Fig. 8). Elevated corticosterone concentrations during a stressful event are known to trigger behavioural and physiological responses that lead to reduced parental investment, and even to the cessation of parental activities (Angelier et al., 2007; Kitaysky et al., 1999; Spée et al., 2011; Thierry et al., 2013). In this respect, higher corticosterone concentrations in females in poor body condition after acute stress (24 h after capture) are generally consistent with the data we obtained during the removal experiment (Ledwoń et al., 2019), since in stressed females the probability of provoked offspring desertion increased significantly with decreasing body condition, whereas stressed males deserted at a low rate, regardless of body condition.

In summary, prolactin and corticosterone baseline concentrations did not differ between the sexes in Whiskered Tern, a species where offspring desertion by females is part of the natural breeding system. The decrease in both baseline and stress-induced prolactin concentrations with advancing brood age suggests that differences between the sexes in hormone concentrations could occur shortly before desertion and that female desertion could be a rapid process. Our results indicate that higher prolactin concentrations after acute stress in males than in females may be involved in the maintenance of parental care. This higher prolactin level indicates that males are more resistant to stress as regards the continuation of parental care. Both the behavioural and hormonal responses of females seem to indicate that they are more sensitive to stressful situations during chicks rearing period. Thus, the finding that sexes and individuals exhibit different physiological and behavioural responses to the same stressful situation suggests that they face other constraints or trade-offs. Future studies could further investigate the role of hormone concentrations in the life histories of other species, especially in the context of sexual differences in the abandonment of parental care, particularly during the post-fledging period.

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CRediT authorship contribution statement

Mateusz Ledwoń: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Funding acquisition, Project administration, Visualization, Writing – original draft. **Adam Flis:** Investigation, Methodology, Writing – review & editing. **Agata Banach:** Investigation, Methodology, Writing – review & editing. **Grzegorz Neubauer:** Formal analysis, Methodology, Visualization, Writing – review & editing. **Frédéric Angelier:** Formal analysis, Methodology, Funding acquisition, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ygcen.2021.113943.

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