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RESEARCH

Hormonal stress responses in a species with female offspring desertion – testing the brood value hypothesis

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Abstract

Parental investment reflects a trade-off between current reproductive effort and future breeding opportunities. According to the brood value hypothesis, as the 'cost-to-replace' a brood increases, hormonal stress responses should be attenuated to ensure the maintenance of care. We examined how stress-induced prolactin (PRL) and corticosterone (CORT) levels – accounting for baseline concentrations – vary in relation to sex, breeding stage, laying date, clutch/brood size, and days relative to hatching in the Whiskered Tern *Chlidonias hybrida*, a species exhibiting obligate female desertion during the chick-rearing and post-fledging periods. We accounted for individual and seasonal variation by including body condition, laying date, and clutch size as additional covariates. While mean PRL levels did not differ between breeding stages, PRL dynamics diverged significantly following hatching. During incubation, stress-induced PRL remained stable and symmetrical between the sexes. Post-hatching, however, male responsiveness remained constant, whereas females exhibited a rapid down-regulation of the PRL stress response in relation to chick age, independent of baseline variation. This physiological shift likely facilitates offspring desertion – a strategy rendered viable by low predation pressure and effective male compensation, both of which reduce the relative value of the brood for females. Conversely, stress-induced CORT remained stable across both sexes and stages, contradicting the predicted attenuation of the hypothalamic-pituitary-adrenal (HPA) axis. CORT responsiveness was primarily predicted by individual baseline levels, suggesting a consistent hormonal phenotype rather than flexible adjustment. Ultimately, the brood value hypothesis was only partially supported; transitions in parental care appear to be mediated through the sex-specific modulation of prolactin rather than adjustments to the HPA axis.

Significant Statement

According to the brood value hypothesis, as the 'cost-to-replace' a brood increases, hormonal stress responses should be attenuated to ensure the maintenance of care. We tested this in the Whiskered Tern *Chlidonias hybrida*, a species where females exhibit obligate brood desertion. Our study reveals a critical divergence in hormonal dynamics: while corticosterone responses remained stable across breeding stages and sexes, prolactin (PRL) responsiveness was sex-specifically modulated post-hatching. Specifically, females exhibited a rapid down-regulation of the PRL stress response as chicks aged – a physiological shift that likely facilitates their departure. These findings provide partial support for the brood value hypothesis, suggesting that transitions in parental care and desertion strategies are mediated through prolactin dynamics rather than the HPA axis.

Keywords Corticosterone · Prolactin · Brood value hypothesis · Stress · Parental investment · Desertion

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Introduction

According to life-history theory, organisms must strategically allocate limited resources between competing functions, such as reproduction and self-maintenance (Stearns 1992). The "cost of reproduction" model (Williams 1966) predicts a fundamental trade-off where current investment may jeopardise future survival and reproductive potential. In species with biparental care, this often manifests as a conflict of interest, as one mate may maximise fitness at the partner's expense (Székely et al. 1996; Lessells 2012). Endocrine mechanisms are thought to be the main mediators of these decisions by orchestrating behavioural responses to environmental risks and parental demands (Bókony et al. 2009; Hau et al. 2010; Angelier and Wingfield 2013; Taff and Vitousek 2016).

The endocrine stress response is a key regulator of reproductive effort. Stressors – such as food shortages, harsh weather, or predation – activate the hypothalamic-pituitary-adrenal (HPA) axis, rapidly increasing circulating corticosterone (CORT) (Wingfield 2004; Wingfield and Sapolsky 2003). While moderately elevated CORT promotes foraging and brood provisioning, high concentrations can trigger an 'emergency life-history stage', redirecting resources towards immediate self-preservation (Landys et al. 2006; Breuner 2008; Williams 2012). Complementary to CORT, stressors also modulate prolactin (PRL), a hormone essential for incubation and chick provisioning (Buntin et al. 1999; Angelier and Chastel 2009; Smiley 2019; Hope et al. 2020). While CORT relates to survival, PRL reflects investment in offspring (Angelier and Chastel 2009). Stress typically induces a PRL decline; if levels drop below a critical threshold, parental motivation wanes, often leading to nest desertion (Groscolas et al. 2008; Angelier et al. 2009, 2016; Thierry et al. 2013; Angelier 2024).

The stress response may be down-regulated when such modulation provides fitness benefits to individuals (Wingfield and Sapolsky 2003; Angelier and Chastel 2009). Because stress response redirects energy from breeding towards survival, its magnitude is expected to covary with current brood value (e.g., Wingfield and Sapolsky 2003; Bókony et al. 2009). The brood value hypothesis (Heidinger et al. 2006; Lendvai et al. 2007; Bókony et al. 2009) proposes that endocrine stress responses vary according to the current brood's contribution to an individual's lifetime fitness. Central to this hypothesis is the 'cost-to-replace' the current reproductive attempt; as the season progresses or offspring age, the opportunities for renesting diminish, thereby increasing the relative value of the current brood. Consequently, when brood value is high, the stress response should be attenuated – characterised by reduced CORT elevation and mitigated PRL decline – to ensure that parental care is not compromised (Wingfield and Sapolsky 2003; Bókony et al. 2009; Angelier 2024). This perceived value depends on life-history strategies, seasonal timing, brood quality, and parental condition. This hypothesis has been supported by several correlative and experimental studies in free-living birds at both interspecific (Bókony et al. 2009; Hau et al. 2010) and intraspecific levels (Chastel et al. 2005; Angelier et al. 2007; Lendvai et al. 2007, 2015; Lendvai and Chastel 2008; Goutte et al. 2011; Schmid et al. 2013; Wojczulanis-Jakubas et al. 2018).

Interspecific comparisons have shown that short-lived birds often dampen their stress responses to maximise current reproductive success (Bókony et al. 2009). In contrast, long-lived species typically act as 'prudent parents' (Drent and Daan 1980; Bókony et al. 2009), prioritising adult survival through robust stress responses (Williams 1966; Angelier and Chastel 2009). At the intraspecific level, studies have demonstrated that endocrine stress responses are higher when parents attend less valuable (i.e. smaller or poor-quality) broods than when tending larger or higher-quality ones (Lendvai et al. 2007; Lendvai and Chastel 2008). Brood value generally increases as the season progresses (Breuner et al. 2013) and as parents transition from incubation to chick-rearing (Montgomerie and Weatherhead 1988; Wojczulanis-Jakubas et al. 2018). However, this value is also shaped by the potential for future reproductive attempts within the same or subsequent seasons (Angelier et al. 2020). In species with flexible parental care systems, the perceived value of the current brood may diverge between the sexes if one parent can desert without significantly compromising offspring survival (Székely et al. 1996). Conversely, parents in poor condition may perceive the costs of care as prohibitive, leading to stronger stress responses to safeguard self-maintenance (Ledwoń et al. 2019, 2022a). Furthermore, the sex providing less parental care often exhibits higher stress responses than the more heavily investing sex (reviewed in Bókony et al. 2009).

According to the brood value hypothesis hormonal modulation should be sex specific based on relative parental investment (Wingfield et al. 1998). In many species, particularly within the Charadriiformes, desertion is a common behavioural strategy whereby one parent – typically the female – departs before offspring independence (Székely et al. 1996; Ledwoń and Neubauer 2017). This strategy is generally not triggered by acute environmental stressors and does not necessarily compromise overall breeding success. Instead, for the deserting sex, the perceived value of the current brood may decline relative to the fitness benefits

of early departure (Kosztolányi et al. 2012). For instance, in Little Auks (*Alle alle*), females – the deserting sex – exhibit higher absolute CORT and lower baseline PRL than males; conversely, males show a more pronounced PRL stress response, which likely reinforces parental commitment (Wojczulanis-Jakubas et al. 2018). Similarly, in Whiskered Terns *Chlidonias hybrida*, males maintain higher stress-induced PRL, potentially serving as a physiological buffer against desertion (Ledwoń et al. 2022a). However, because static hormone snapshots often fail to predict individual desertion (Kosztolányi et al. 2012), it is crucial to examine fine-scale temporal dynamics across breeding stages while accounting for baseline concentrations to isolate the true magnitude of the stress response.

We tested brood value hypothesis in the Whiskered Tern, a long-lived waterbird characterised by obligate female desertion (Ledwoń and Neubauer 2017). Central to this framework is the expectation that perceived offspring value increases with age as the 'cost-to-replace' rises (Montgomerie and Weatherhead 1988). While previous research on this species focused on absolute hormone levels during chick-rearing (Ledwoń et al. 2022a), a comprehensive test requires evaluating the physiological transition from the shared, symmetrical investment of incubation to the divergent parental roles of the chick-rearing phase.

We predicted an attenuated stress response (lower CORT, higher PRL) as the season progresses, manifested both as a trend within breeding stages and as a shift between phases. During incubation, when parents share equally in nest protection (Ledwoń 2010), we expected no significant sex differences in hormonal profiles. In contrast, during chick-rearing – as males become primary providers and females prepare to desert – we predicted a divergence in stress reactivity: a consistent attenuation in males and a heightened response in females, reflecting the increasing costs of care relative to the declining brood value for the deserting sex. In our analytical approach, we treated the hormonal response as a plastic trait associated with both parental state and offspring development. Building on findings of comparable baseline levels between sexes (Ledwoń et al. 2022a), we focused on the modulation of the acute stress response. This reactivity is hypothesized to reflect the physiological plasticity required for life-history trade-offs more dynamically than baseline concentrations alone (Taff and Vitousek 2016). To isolate this response while accounting for individual variation and potential ceiling effects, we controlled for baseline levels as a covariate. Finally, we incorporated laying date, body condition, and brood size as control variables, as these factors further calibrate the perceived value of the brood and the parent's capacity for care.

Methods

Study species

The Whiskered Tern is a long-lived, socially and genetically monogamous, migratory, and single-brooded waterbird that nests colonially on marshes and fish ponds (Ledwoń et al. 2013; Gochfeld et al. 2020; Ledwoń and Szczys 2022b). While replacement clutches occur if initial attempts fail, parental investment is high: males provide courtship feeding, and females lay a three-egg clutch weighing approximately one-third of their body mass (Ledwoń 2010; Ledwoń and Neubauer 2018; Ledwoń et al. 2023). Incubation (ca. 21 days) and the subsequent brooding of young chicks are shared equally by both parents (Spina 1982; Paillisson et al. 2007; Ledwoń 2010; Ledwoń and Neubauer 2017). Chicks remain in the nest for approximately 19–21 days, followed by a prolonged period of post-fledging parental care lasting several weeks (Ledwoń and Neubauer 2017). During the biparental chick-rearing stage, males provide about 25% more food than females. This asymmetry in investment precedes obligate female desertion. The process is characteristically protracted, taking place between the early chick-rearing and post-fledging stages. The timing of female desertion varies: about half of the females depart between day 5 and 21 of the chick-rearing period, while the rest remain until fledging and depart within two weeks of the chicks taking flight. Hatching and fledging success in studied population remain high (83% and 81%, respectively), with no increase in offspring mortality in male-only nests. Since only 5% of females renest, desertion likely benefits self-maintenance or early migration rather than immediate reproductive gain (Ledwoń et al. 2023).

Study site and field work

Fieldwork was conducted in 2016 and 2017 at Za Stodołami pond (approx. 16 ha; 50°01'20.1"N 19°24'00.5"E, Poland), which hosted a colony of approximately 100 breeding pairs each year. Nests were built on the floating leaves of fringed water lily *Nymphoides peltata* and distributed across almost the entire pond surface, typically spaced a few metres apart. Nest monitoring commenced during early incubation (Ledwoń et al. 2022a). To ensure precise determination of hatching dates, the colony was visited 2–3 times per week, with increasing frequency as the expected hatching dates approached. Hatching dates were determined primarily by the presence of wet, newly hatched chicks or a craks on the eggshells (indicating hatching within 24 h). Additionally, hatching dates were estimated based on known laying

dates of fresh eggs (assuming a 21-day incubation period) or by measuring chick wing length, following the methods of Ledwoń and Neubauer (2017) and Banach et al. (2021). Furthermore, egg flotation was used to predict the hatching window, allowing us to focus on specific nests during subsequent visits (Betleja 2003). Together, these methods enabled us to determine the hatching date of the oldest chick with high precision. Only nests meeting these high-precision criteria were included in the study; from this pool, nests were selected randomly for adult trapping to ensure a representative sample of the colony. To facilitate consistent monitoring and ensure offspring safety, all nests in the colony were enclosed with circular plastic mesh fences (1.3 m in diameter, 0.6 m in height, and 1 cm mesh size) lined with plastic foil (Ledwoń et al. 2015, 2016). Enclosures were installed gradually, starting at least seven days after clutch completion, to allow the birds to acclimatize. These structures were essential for chick survival, as they prevented them from swimming away in response to disturbance during colony visits; without enclosures, chicks entering the water could easily become chilled, lost, or attacked by aggressive conspecifics. For welfare purposes, wooden boards were placed inside enclosures as resting platforms, as natural vegetation-based platforms often disintegrated as chicks grew older. Adults were trapped using roof traps (1.2 × 1.2 m) installed on the enclosures during late incubation or the downy chick stage. To minimize the risk of nest abandonment, trapping did not commence until at least 14 days after clutch completion. Furthermore, trapping was no longer feasible after the chicks reached seven days of age, as adults became increasingly reluctant to enter the traps. This methodology has previously been shown to have no adverse effects on breeding success or bird behaviour (Ledwoń 2010; Ledwoń et al. 2015, 2016).

Baseline and acute stress

Following a standardised capture-and-restraint protocol (Wingfield 1994), we collected an initial blood sample (~250 µl) from the brachial vein within three minutes of capture (mean ± SD: 123.02 s ± 32.87, $n = 64$) to estimate baseline hormone levels (Ledwoń et al. 2022a). There was no significant correlation between baseline CORT or PRL concentrations and the time from capture to first sampling (Appendix 1: Fig. S1). To estimate stress-induced hormone levels, birds were kept in cloth bags for 30 min before a second ~250 µl sample was collected from the opposite wing, exactly 30 min after the initial capture, with timing strictly monitored using stopwatches started immediately upon the bird's restraint. We aimed to maintain maximum speed and efficiency during the field procedures (reminiscent of the agility seen in film Crouching Tiger, Hidden Dragon). The total volume of blood remained below 1% of the bird's body mass. After the second sampling, each individual was ringed, weighed, and measured (bill and head length). All birds were then immediately released. During subsequent colony inspections, we monitored breeding success in both sampled nests and those where no adults were trapped to ensure the procedure had no adverse effects. It was not possible to record data blind because our study involved focal animals in the field.

Blood samples and hormonal analyses

Blood samples were stored in a portable cooler on ice at approximately 4 °C and centrifuged within 6 h of collection (relative centrifugal force: 2680 × g for 10 min). The resulting plasma was collected, stored at −20 °C, and analysed within six months. Molecular sexing was performed using CHD gene markers with F2550/R2718 and P2/P8/P0 primers, with each sample tested at least twice to ensure reliability (Griffiths et al. 1998; Fridolfsson and Ellegren 1999; Banach et al. 2021). Hormone concentrations were measured by radioimmunoassay at the Centre d'Études Biologiques de Chizé (France), as previously described in Lormée et al. (2003); Angelier et al. (2006); Ledwoń et al. (2022a). All concentrations were measured in duplicate. The intra-assay coefficients of variation (CV) were 8.58% for prolactin and 9.19% for corticosterone, while the inter-assay CV for corticosterone was 8.78%.

Hormone analysis was performed on 63 individuals for PRL and 59 for CORT (Appendix 1: Table S1). Birds were captured in 2016 ($n_{PRL} = 20$, $n_{CORT} = 16$) and 2017 ($n = 43$ for both). Samples spanned incubation ($n_{PRL} = 18$, $n_{CORT} = 15$) and chick-rearing ($n_{PRL} = 45$, $n_{CORT} = 44$), including 28 males and 35 females for PRL, and 27 males and 32 females for CORT.

Data analysis

We analysed factors influencing stress-induced PRL and CORT levels using linear models (LM). To account for the hierarchical structure of the breeding cycle, we employed a nested design, where clutch/brood age (days relative to the hatching date) was nested within the breeding stage (incubation vs. chick-rearing), separately for each sex (see R code script in Appendix 2). All stress-induced concentrations were log-transformed to meet the assumptions of normality and homoscedasticity. Instead of analysing the magnitude of the stress response (stress-induced minus baseline levels), we modelled stress-induced concentrations with baseline levels included as a covariate. This approach avoids the mathematical coupling inherent to difference scores and allows us to control for individual variation in baseline physiological

state. Preliminary analyses confirmed a strong correlation between baseline levels and the calculated magnitude of the stress response ($r>0.92$ in both cases, $p<0.001$). Including baseline as a covariate also helps control for potential ceiling effects, thereby isolating the effects of life-history stage and parental traits on the stress-induced output. PRL and CORT concentrations were analysed in separate models because they represent distinct physiological pathways. Preliminary analyses confirmed that there was no significant correlation between baseline levels of these two hormones (Pearson's $r=-0.05$, $p=0.71$, $n=60$), nor between their stress-induced concentrations ($r=-0.08$, $p=0.58$), justifying their treatment as independent variables (see also Wojczulanis-Jakubas et al. 2018).

We employed a full-model strategy, retaining all a priori selected biological predictors regardless of statistical significance. This approach ensures robust parameter estimation and avoids the inherent biases associated with automated model selection or model averaging. To maintain time-series continuity while accounting for the distinct physiological drivers of each phase (incubation vs. chick-rearing), both breeding stages were integrated into a single analytical framework using a nested interaction structure (for the R script, see Appendix 2). Specifically, we included a fixed interaction between sex and breeding stage (incubation vs. chick-rearing) to capture differences in mean stress-induced CORT and PRL concentrations. To estimate stage-specific slopes, we included a nested term (sex : days relative to hatching %in% breeding stage), with incubation defined as the period from day−7 to -1, and chick-rearing from day 0 to 7 (where day 0 represents the hatching date). This design effectively isolated the unique hormonal dynamics of the chick-rearing period from those of incubation, while providing a rigorous statistical test for physiological shifts during the transition from eggs to chicks. To account for individual and seasonal variation, we included body condition (mass-total head length residuals), clutch/brood size (number of eggs or chicks), and within-year standardised laying dates (measured in days elapsed from 1st May each year) as additive control variables. These were included as main effects without further interactions, as preliminary diagnostics showed no evidence of stage-specific shifts in their influence, and this parsimonious structure maintained a robust ratio of observations to estimated parameters. All continuous covariates were mean-centered prior to analysis to ensure meaningful intercepts and improve model stability. Random effects were not required, as each individual and nest was sampled only once. 'Year' was not included as a categorical or random factor because with only two study years and unequal sample sizes, the model would be unable to reliably estimate among-year variance, often leading to a singular fit. Instead, inter-annual variation was accounted for by including body condition and laying dates as covariates. This approach effectively controls for the primary biological drivers of annual differences – namely, physiological state and breeding phenology – while maintaining model stability and a robust ratio of observations to parameters.

Significance of main effects and interactions was assessed using Type III sums of squares to account for the unbalanced design. Where significant interactions were found, we explored them using post-hoc pairwise comparisons of marginal means to compare sexes within each breeding stage and stage-specific trends (slopes for day relative to hatching) using the *emmeans* and *emtrends* functions (Lenth 2024). All results from log-transformed models were back-transformed to the response scale for biological interpretation. Model assumptions were verified using the DHARMa package (Hartig 2022). Visual inspection of scaled residuals and formal diagnostic tests confirmed that model assumptions of normality and homoscedasticity were met (Appendix 1: Figs S2, S3). Multicollinearity was minimal, with all adjusted Generalized Variance Inflation Factors (GVIF) below 1.9, indicating that the structural correlation between interactions and main effects did not compromise model stability. Analyses were performed in R 4.4.3 (R Core Team 2025).

Results

Prolactin

The global model for stress-induced PRL was statistically significant ($F_{11,51}$ = 2.66, $p=0.009$), explaining 22.7% of the variance (adjusted $R^2=0.227$; Table 1). We found a highly significant interaction between sex and breeding

Table 1 Results of nested general linear models (Type III sums of squares) evaluating factors influencing stress-induced prolactin (PRL) and corticosterone (CORT) concentrations in the Whiskered Tern *Chlidonias hybrida*

Predictor	df	F (PRL)	*p* (PRL)	F (CORT)	*p* (CORT)
Baseline Hormone	1	1.79	0.187	6.31	**0.015**
Body Condition	1	0.02	0.892	2.48	0.122
Sex	1	0.55	0.463	0.40	0.529
Breeding Stage	1	1.01	0.320	1.57	0.216
Clutch/Brood Size	1	0.00	0.963	0.97	0.329
Laying Date	1	0.08	0.774	1.52	0.223
Sex × Breeding Stage	1	13.68	**<0.001**	2.64	0.111
Sex × (Days Relative to Hatching ∈ Breeding Stage)	4	3.02	**0.026**	0.47	0.761

Significant *p*-values ($p<0.05$) are shown in bold. Global model for PRL: $F_{11,51}=2.66$, $p=0.009$, adj.$R^2=0.227$; Global model for CORT: $F_{11,47}=1.62$, $p=0.125$, adj.$R^2=0.105$

stage ($F_{1,51}$ = 13.68, p < 0.001), as well as a significant interaction between sex and days relative to hatching nested within breeding stage ($F_{4,51}$ = 3.02, p = 0.026). Analysis of estimated marginal means showed that overall mean PRL concentrations did not differ significantly between sexes within either stage (incubation: p = 0.282; chick-rearing: p = 0.736; Appendix 1: Tables S2, S3). Although females exhibited higher estimated marginal mean levels during incubation (68.1 ng/ml) compared to males (37.6 ng/ml), this difference did not reach statistical significance due to high individual variance (Table S2 in Appendix 2). Specifically, post-hoc trend analysis revealed a significant decline in stress-induced PRL levels as chicks aged in females during the chick-rearing phase (β = −0.168, p = 0.005; Table 2), while no such significant trend was observed in males during the same period (β = −0.084, p = 0.10; Table 2; Fig. 1). During the incubation stage, PRL concentrations showed no significant linear relationship with days relative to hatching for either sex (all p > 0.50). Other factors, including baseline PRL levels, body condition, clutch/brood size, and laying date, were not significant predictors of stress-induced PRL concentrations (Table 1).

Table 2 Post-hoc trend analysis (estimated marginal means of trends) showing the slopes (β) of stress-induced prolactin (PRL) concentrations in relation to the number of days relative to hatching in Whiskered Terns *Chlidonias hybrida*

Breeding Stage	Sex	Slope (β)	SE	t-ratio	*p*
Incubation	Female	0.021	0.180	0.12	0.908
Incubation	Male	-0.045	0.062	-0.73	0.468
Chicks	Female	**-0.168**	0.056	-3.01	**0.005**
Chicks	Male	-0.084	0.051	-1.65	0.104

Significant p-values (p < 0.05) are shown in bold. Slopes (β) represent the daily rate of change in log-transformed hormone levels. The breeding cycle is expressed as days relative to hatching (day 0): incubation (days −7 to −1) and chick-rearing (days 0 to 7). SE = Standard Error; df = 51

Corticosterone

The global model for stress-induced CORT did not reach overall statistical significance ($F_{11,47}$ = 1.62, p = 0.125, adj. R^2 = 0.105; Table 1). However, baseline CORT concentrations emerged as the only significant predictor within the model ($F_{1,47}$ = 6.31, p = 0.015), indicating that the acute stress response was partially dependent on initial physiological state. None of the other main effects or interactions significantly influenced CORT levels in our sample. Specifically, there was no significant interaction between sex and breeding stage ($F_{1,47}$ = 2.64, p = 0.11; Table 1), nor did the days relative to hatching significantly influence CORT levels within either stage (p = 0.76; Table 1). Environmental and individual factors, such as body condition, laying date, and clutch size, also failed to explain significant variation in stress-induced CORT concentrations (all p > 0.12; Table 1).

Discussion

Prolactin

Regarding stress-induced PRL, mean concentrations did not differ overall between the incubation and chick-rearing periods. While this lack of a seasonal increase initially appears to contradict the brood value hypothesis, the result was driven by a significant interaction between sex and breeding stage. This suggests that the transition from eggs

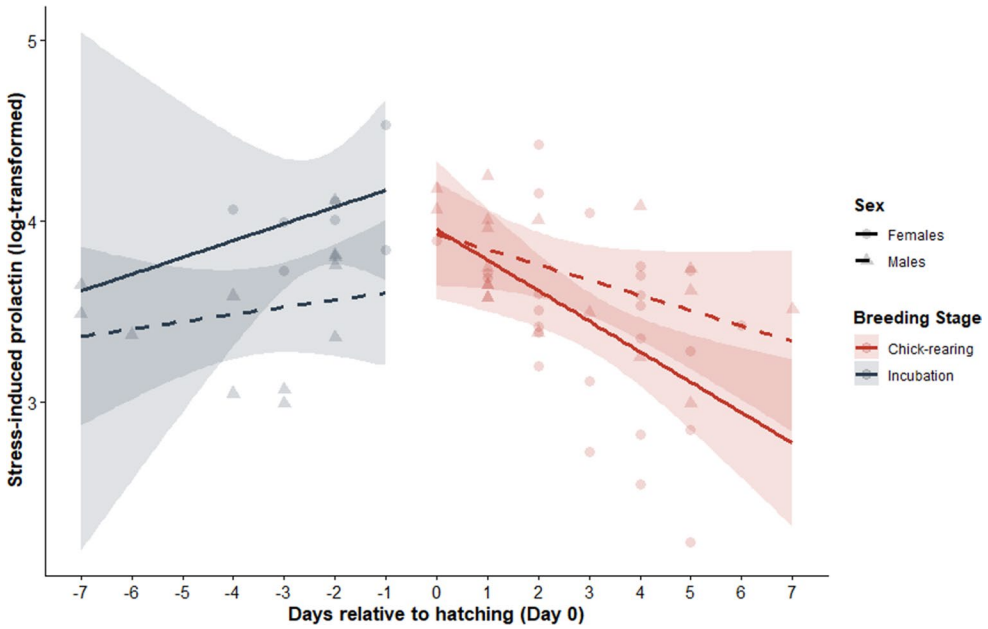

Fig. 1 Predicted trends in stress-induced prolactin (PRL) concentrations during the breeding cycle of the Whiskered Tern *Chlidonias hybrida*. Day 0 represents the hatching date. Shaded areas denote 95% confidence intervals. A significant decline in stress-induced PRL was observed in females during the chick-rearing period (β = −0.168, p = 0.005; Table 2)

to chicks does not involve a uniform species-level shift, but rather a divergent physiological response between the sexes. According to the brood value hypothesis, resistance to stress should increase as the reproductive value of the clutch or offspring rises (Montgomerie and Weatherhead 1988; Bókony et al. 2009).

Whilst we initially predicted an increase in PRL over the studied period of incubation, the observed stability aligns with patterns reported in many precocial and semi-precocial species (Angelier et al. 2016). As the probability of hatching increases, late-stage clutches represent a higher brood value; therefore, maintaining consistently high, stable PRL levels despite acute stressors may function to preserve parental commitment when the payoff of continued incubation is at its peak. The absence of a significant positive trend in stress-induced PRL relative to clutch age aligns with findings by Riou et al. (2010) in the Puffinus puffinus. This suggests that instead of a continuous linear increase, the physiological "buffer" predicted by the brood value hypothesis may reach a stable plateau shortly before hatching. Although caution is warranted because our sampling was restricted to the final week of incubation to mitigate desertion risk, the lack of a significant correlation in our cross-sectional data likely reflects that, at this late stage, reproductive value is already effectively maximised (Angelier et al. 2016). This interpretation remains consistent with the core tenets of the hypothesis, which posits that parental investment should scale with the "cost-to-replace" the offspring. Experimental work on Mallards *Anas platyrhynchos* has shown that the probability of brood desertion following stress declines as incubation progresses (Ackerman and Eadie 2003), a trend also observed in several seabird species (Fisher 1971; Boersma 1976; Bourgeon et al. 2006). Taken together, these findings suggest that whilst the perceived value of the brood increases most dramatically during the early and middle stages of incubation, it may settle into a consistently high and stable state as eggs approach hatching. In the Whiskered Tern, maintaining this hormonal plateau ensures that parental commitment is at its maximum when the transition to the even more valuable chick-rearing stage is imminent.

Consistent with our predictions and the brood value hypothesis, neither mean concentrations nor slopes of stress-induced PRL during late incubation differed significantly between the sexes (Table 2; Appendix 1: Tables S2, S3). This lack of significant differences reflects the equal parental investment required at this stage; in the Whiskered Tern, both sexes share diurnal incubation and nest protection (Ledwoń 2010), and the loss of either parent invariably leads to nest failure. Furthermore, the opportunities for renesting appear symmetrical, as birds typically remain in the same pairs for subsequent breeding attempts (Ledwoń 2010; Ledwoń et al. 2023). A similar lack of sex differences in the prolactin stress response during incubation has been reported in the related Little Auk, where biparental cooperation is equally indispensable for reproductive success (Wojczulanis-Jakubas et al. 2018). In our cross-sectional sample, such results support the principle that when parental duties and future reproductive potential are symmetrical, endocrine stress-modulation should not diverge (O'Reilly and Wingfield 2001; Bókony et al. 2009). While we acknowledge that the limited sample size during the incubation stage warrants a cautious interpretation, the observed physiological synchrony is consistent with the biology of the species and the high perceived value of the clutch at this stage. Maintaining this hormonal plateau ensures that parental commitment is maximised shortly before hatching, when the 'cost-to-replace' the clutch is at its peak – a key prediction of the brood value hypothesis. While higher absolute PRL in females has been reported in other species (Angelier and Chastel 2009; Angelier 2024), potentially due to varying receptor densities (Farrar et al. 2022), females in our study exhibited a non-significant tendency towards higher average concentrations than males during this period (Appendix 1: Table S2). Consequently, our data suggest a broadly similar physiological pattern between the sexes during this phase of shared responsibility.

In our study, the transition to chick-rearing revealed that the hormonal stability observed during late incubation does not persist post-hatching. Instead of the population-level increase predicted by a simplified brood value hypothesis, our high-resolution approach revealed a sex-specific down-regulation of the PRL stress response within the first week. Crucially, this shift was exclusive to females (Table 2). In contrast, stress-induced PRL in males remained independent of offspring age. By accounting for exact brood age (days relative to hatching), we avoided the arbitrary thresholds typical of many previous studies (e.g. Riou et al. 2010).

For males, these stable levels align with the brood value hypothesis, which posits that parental investment is maintained when the current offspring contribute significantly to an individual's lifetime fitness. Since the male remains the primary – and often sole – caregiver later in the season (Ledwoń and Neubauer 2017), the current brood represents a terminal investment for the season, with its relative value remaining at a peak. While the absolute fitness loss of a failed brood is equal for both sexes, the male's sustained PRL levels reflect the lack of viable future reproductive opportunities within the same year, effectively increasing the "cost-to-replace" the current attempt from his perspective. In females, this rapid down-regulation likely reflects a physiological preparation for desertion. While we acknowledge that our sampling was limited to the first seven days – a period when desertion remains rare (Ledwoń and Neubauer 2017), our results suggest that the internal shift in how

females value the brood begins well before they actually depart. By down-regulating PRL sensitivity, females may maintain the physiological plasticity required to prioritise their long-term survival or future reproductive opportunities. In this context, the divergence in PRL response does not contradict the brood value hypothesis but rather highlights how the "perceived value" of the current brood scales with the parent's future reproductive potential and the availability of alternative care.

In our study population, low predation pressure and high food abundance ensure high breeding success even after female desertion, primarily due to effective male compensation (Ledwoń and Neubauer 2017). Such stable conditions likely minimise the fitness costs of parental flexibility, as brood survival is not compromised by the departure of one parent. This flexibility is facilitated by the observed sex-specific endocrine shift, which may act as a regulatory precursor to desertion. By down-regulating PRL early, females may reduce their parental investment once the brood's survival is effectively secured by the male. From the perspective of the brood value hypothesis, this suggests that as the marginal value of further female care diminishes, the physiological commitment to the current brood is scaled back accordingly.

Our findings further suggest a decoupling of baseline PRL levels from the subsequent stress response. By including baseline concentrations as a covariate, we demonstrated that they do not significantly predict stress-induced PRL levels. This independence suggests an intrinsic regulation of pituitary sensitivity to acute stressors, rather than a functional dependency on circulating baseline concentrations. Such a pattern contrasts with the Little Auk, where the PRL stress response is so strongly coupled with baseline levels that it exhibits a shift in directionality (Wojczulanis-Jakubas et al. 2018).

This re-evaluation provides a critical refinement of the hormonal patterns reported by Ledwoń et al. (2022a). While that initial analysis identified a general decline in both baseline and stress-induced PRL levels in both sexes during the early chick-rearing period, with males maintaining higher absolute concentrations, our present approach reveals that the underlying regulatory mechanisms differ fundamentally. By decoupling the stress response from baseline variation, we demonstrate that the decline in females is not a passive by-product of falling baseline levels, but a distinct regulatory shift representing a sex-specific physiological adjustment.

Finally, our results align with those for the Kentish Plover (*Charadrius alexandrinus*), where no sex differences in mean stress-induced PRL were found around hatching (Kosztolányi et al. 2012). However, point-sample studies (e.g. Kosztolányi et al. 2012; Wojczulanis-Jakubas et al. 2018) may overlook the sex-specific dynamics revealed by our high-resolution approach. While mean concentrations in our study did not differ between the sexes, the interaction between sex and offspring age revealed a fundamental divergence. In the Kentish Plover, stress-induced PRL levels – which decrease under stress, as in the present study – remained similar between deserting females and caring males (Kosztolányi et al. 2012). Conversely, in the Little Auk, where stress-induced PRL levels increase, males exhibit a significantly higher response magnitude than females (Wojczulanis-Jakubas et al. 2018). Our findings demonstrate that even when absolute levels appear symmetrical at a single time-point, the underlying regulatory trajectories differ, reflecting an asymmetrical cost of replacing the brood.

Corticosterone

Contrary to our predictions, stress-induced CORT levels did not vary between breeding stages, nor were they influenced by clutch or brood age within those stages. Notably, our models revealed that stress-induced CORT concentrations were positively correlated with baseline levels. This result aligns with findings in the Little Auk, where the magnitude of the CORT stress response was also strongly and positively related to baseline concentrations across both breeding stages (Wojczulanis-Jakubas et al. 2018). Such a correlation suggests a consistent individual endocrine profile, or 'hormonal phenotype', where an individual's reactivity to acute stressors remains tied to its baseline state, rather than being reprogrammed by the specific demands of the breeding phase or offspring age.

Although CORT levels during incubation have been widely studied, few studies have addressed the brood-value hypothesis directly, and our results add to a body of literature characterised by significant discrepancies. For instance, while an attenuation of the CORT stress response toward the end of incubation has been reported (Viblanc et al. 2016), others have found the opposite trend (e.g. Adams et al. 2005; DuRant et al. 2013). These inconsistencies likely reflect multiple selective pressures; for example, the increasing energetic demands of incubation can elevate CORT levels, potentially masking brood-value effects (DuRant et al. 2013).

In our study, stress-induced CORT levels were not significantly predicted by chick age during the first seven days of chick-rearing. Although this short sampling window might limit the detection of long-term patterns, it represents the most biologically critical stage for the Whiskered Tern; chicks are highly dependent at this time, and female desertion typically begins during this period (days 5–7; Ledwoń 2010; Ledwoń and Neubauer 2017). The observed stability of CORT, which contrasts with the sex-specific shifts seen

in PRL, suggests that measuring circulating glucocorticoid levels alone may be insufficient to assess the role of the HPA axis in breeding decisions.

The physiological actions of CORT are mediated by additional mechanisms, including corticosteroid-binding globulins (CBG; Breuner et al. 2013), the density and location of glucocorticoid receptors (Romero 2004), and their associated cochaperones such as FKBP5 (Zimmer et al. 2021). Furthermore, recent studies highlight that the efficiency of CORT negative feedback may be more crucial in mediating parental decisions than absolute stress-induced levels (Angelier et al. 2015; Zimmer et al. 2019). Consequently, the stability of the CORT response in our study may reflect a complex trade-off between these unmeasured regulatory factors, maintaining a standardised 'stress signature' while other hormones, such as PRL, drive the fine-tuned behavioural shifts associated with female desertion.

Finally, we found no significant sex differences in the CORT stress response, which also fails to align with the brood value hypothesis. This is, however, partially consistent with phylogenetic analyses suggesting that CORT modulation is not always sex-linked in species with biased parental care (Bókony et al. 2009). While sex differences in CORT magnitude occur in some species (Schmid et al. 2013), their absence here supports the idea that circulating glucocorticoids do not act in isolation. Instead, parental decisions likely emerge from the integration of multiple endocrine signals, where stable CORT levels maintain basic physiological homeostasis while sex-specific shifts in PRL – as observed in our study - drive the fine-tuned behavioural transitions associated with nest desertion.

Other factors influencing the stress response

Contrary to our predictions, body condition, clutch/brood size, and laying date did not significantly influence stress-induced PRL or CORT (Table 1). The lack of a condition-dependent response is noteworthy, as the return probability of females following prolonged stress (24-hour holding in captivity) in this population is linked to their physical state (Ledwoń et al. 2019). However, our results demonstrate that acute endocrine reactivity remains stable across varying physical states. This stability may ensure consistent parental investment, buffering the brood against short-term fluctuations such as adaptive mass loss (Ledwoń et al. 2024).

Furthermore, we found no evidence that the stress response was attenuated in relation to clutch size or laying date, failing to corroborate the brood value hypothesis (Lendvai et al. 2007; Bókony et al. 2009). Theoretically, larger or later clutches represent a higher cost of replacement. However, in Whiskered Terns, lower survival of late-season offspring may offset their increasing seasonal value, nullifying the expected shift in hormonal response.

These results likely reflect a life-history strategy prioritising self-maintenance in a relatively long-lived species. Critically, as our cross-sectional data reflect population-level stability rather than individual plasticity, the lack of significant covarying effects suggests that sex and days relative to hatching – rather than environmental or individual factors – are the primary drivers of hormonal profiles.

Conclusions

Our study demonstrates that testing the brood value hypothesis in species with flexible parental care requires accounting for sex-specific strategies and the continuous dynamics of offspring development. We show that hormonal responses are governed by sex-dependent trade-offs rather than a uniform species-level pattern. While the HPA axis (CORT) remains stable, providing a consistent physiological background, the divergent dynamics of PRL after hatching reflect the shifting roles of the sexes. The rapid down-regulation of PRL in females, contrasted with the stable response in males, provides a physiological mechanism that may facilitate female desertion. These results suggest that in long-lived species, the endocrine system integrates offspring value with sex-specific life-history constraints to determine final reproductive decisions.

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Authors' contributions ML: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Funding acquisition, Project administration, Visualization, Writing – original draft. AF, AB: Investigation, Methodology, Writing – review & editing. ÁZL: Formal analysis, Writing – review & editing, FA: Formal analysis, Methodology, Funding acquisition, Writing – review & editing.

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Data availability The raw hormone data (corticosterone and prolactin concentrations) and additional supporting data for this study have been deposited in the Zenodo repository under the identifier DOI: 10.5281/zenodo.17750308 and are accessible at https://zenodo.org/records/17750309.

Declarations

Ethics approval and consent to participate All applicable international, national, and/or institutional guidelines for the use of animals were followed. The fieldwork was carried out under the approval of the Local Ethical Committee (permit no. 11/2016) and the Regional Directorate for Environmental Protection (permit no. OP-I.6401.211.2015.PKw).

Competing interests The authors declare no competing interests.

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