Corticosterone in very young seabird chicks (*Rissa tridactyla*) is sensitive to environmental variability and responds rapidly and robustly to external challenges

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Abstract.

In birds, patterns of development of the adrenocortical response to stressors vary among individuals, types of stressors, and species. Since there are benefits and costs of exposure to elevated glucocorticoids, this variation is presumably a product of selection such that animals modulate glucocorticoid secretion in contexts where doing so increases their fitness. In this study, we evaluated hypothalamic-pituitary-adrenal (HPA) activity in first-hatched free-living seabird nestlings (black-legged kittiwakes, *Rissa tridactlya*) at a critical early age when food availability may drive the establishment of important parent-offspring and intra-brood dynamics. We experimentally supplemented parents with food ("fed") and measured chick baseline corticosterone secretion at 5 days post-hatch (of the ~45 day nestling period) and capacity to rapidly increase corticosterone in response to an acute challenge (handling and a 15 min restraint in a bag). We also used topical administration of corticosterone to evaluate the ability of chicks to downregulate physiologically relevant corticosterone levels on a short (minutes) time scale. We found that 5 day old chicks are capable of releasing corticosterone in proportion to the magnitude of the challenge, showing differences in baseline between parental feeding treatments (supplementally-fed vs control), moderate increases in response to handling, and a larger response to restraint (comparable to restraint-induced levels found in adults) that also differed between chicks from fed and control nests. The topical application of exogenous corticosterone resulted in an increase of circulating levels similar to the restraint-induced levels. The corticosterone application also induced the downregulation of HPA responsiveness to the acute challenge of handling. Parental supplemental feeding did not affect absorbance/clearance or negative feedback. Thus, while endogenous secretion of corticosterone in 5 day old chicks is sensitive to environmental context, other aspects of the HPA function, such as rapid negative feedback and/or the ability to clear acute elevations in corticosterone, are not. We conclude that 5 day old kittiwake chicks are capable of robust adrenocortical responses to novel challenges, and are sensitive to parental food availability, which may be transduced behaviorally, nutritionally, or via maternal effects. Questions remain about the function of such rapid, large acute stress-induced increases in corticosterone in very young chicks.

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1. Introduction -

The activity of the vertebrate hypothalamo-pituitary adrenal (HPA) axis is often considered in terms of costs and benefits. At a basal level, activity of the axis and the consequent release of glucocorticoid hormones is mandatory for survival and normal development (Wada, 2008), and the ability to rapidly increase glucocorticoids allows animals to maintain or reestablish homeostasis in the face of internal or external challenges (Sapolsky et al., 2000). While developmental exposure to glucocorticoids can increase fitness, presumably by better-preparing offspring for environmental conditions (Crino and Breuner, 2015), prolonged exposure to glucocorticoids during development (whether chronic or repeated acute elevations) can be associated with costs (Kitaysky et al., 2003; Sapolsky and Meaney, 1986; Schoech et al., 2011). Thus, as with any process presumably shaped by selection, developing animals should only increase glucocorticoids when doing so increases fitness (i.e., benefits outweigh costs). In birds, there is variation among species in the age at which chicks begin to respond to environmental challenges by activating the HPA axis and releasing corticosterone (e.g. Adams et al., 2008; Bebus et al., 2020; Wada et al., 2007), as well as variation in which stimuli can elicit an HPA axis response from nestlings (e.g. Lynn and Kern, 2018, 2014). The existence and duration of a post-hatch "hypo-sensitive" period (the "stress non-responsive period" in mammals) of relatively low HPA axis responsiveness in many altricial (Bebus et al., 2020; Jones et al., 2021; Sims and Holberton, 2000; Wada et al., 2009, 2007) and some semi-altricial (Blas et al., 2006; Fiske et al., 2013) species is thought to protect young chicks who are both vulnerable to excessive glucocorticoid exposure and too early in development to benefit from elevated glucocorticoids because they have life-histories that leave them unable to change physiology or behavior in sufficiently rapid or appropriate ways to increase fitness (Fiske et al., 2013; Sims and Holberton, 2000; Torres-Medina et al., 2019; Wada, 2008; Wada et al., 2007). In this study, we examined sources of variation in HPA axis activity in very young semi-precocial seabird chicks with a life-history that involves complex early-life social dynamics that may be influenced by glucocorticoids (reviewed in Smiseth et al., 2011).

For nest bound chicks that compete with siblings for limited parental resources via begging, aggression, and, in some species, siblicide, corticosterone may be a relevant mediator of social behavior (Loiseau et al., 2008; Vallarino et al., 2006). Across vertebrates, glucocorticoid

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elevation is associated with metabolic function and challenges to energy balance (Jimeno and Verhulst, 2023). While glucocorticoids in adults are thought to help mediate the tradeoffs associated with allocating resources between self-maintenance and reproduction to maximize fitness (Bókony et al., 2009), chicks should be selected to maximize survival and optimize somatic growth such that they can successfully recruit to the breeding population. In some avian species, survival and optimal growth can require intense intra-brood competition at a very young age. These species may be selected for HPA activation early in postnatal life, despite potential costs of elevating glucocorticoids during development.

Semi-precocial black-legged kittiwake (*Rissa tridactyla*) chicks reside in cliffside nests and rely on parental food provisioning for ~40-45 days before fledging (Hatch et al., 2020). Both parents forage at sea and deliver regurgitated meals to chicks multiple times a day. Chicks engage in facultative siblicide, where the first-hatch chick (hereafter "A-chick") often out-competes the second-hatched chick (hereafter "B-chick") and monopolizes parental food resources. A-chicks accomplish this by interrupting B-chick begging and feeding bouts, driving them out of the nest with repeated attacks, or killing them outright (Braun and Hunt, 1983; reviewed in Dickins, 2021). Most often siblicide occurs during the first 10 days post-hatch, with chicks capable of intense aggression just a few days after hatching (Braun and Hunt, 1983). While there are dozens of hypotheses about the evolution of brood reduction, most of them center on maximizing fitness when resources are limited (Morandini and Ferrer, 2015). Thus, unlike more "helpless" altricial nestlings, very young kittiwake chicks have a behavioral repertoire that is likely to be sensitive to energy balance and resource availability, and therefore may be modulated by glucocorticoids.

Black-legged kittiwake physiology has been studied intensively, including several investigations of HPA activity (both baseline and restraint-induced elevations of circulating corticosterone) in captive and free-living chicks (Table 1). Captive studies demonstrated clear consequences of food intake (both quality and quantity) on HPA activity of older chicks (29-31 days) subject to several weeks of experimental diets (Kitaysky et al., 1999), with low quality/quantity diet treatments dramatically increasing both baseline and restraint-induced corticosterone, but there was no change in baseline corticosterone with age in captive chicks fed *ad libitum* (Table 1).

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However, these captive chicks were raised in isolation, without any of the natural, complicated social interactions (with parents and siblings) encountered in the wild. Sensitivity to food intake may also have driven the interannual and intercolony differences observed in free-living 12-15 day old chicks (Brewer et al., 2010, 2008), though experimental food supplementation to free-living kittiwake nests at a different colony did not generate large differences in corticosterone in at least some breeding seasons (J. Schultner et al., 2013; Young et al., 2017), potentially a consequence of high natural food availability to control (unsupplemented) adults in those years. Overall, corticosterone release in kittiwake chicks appears to be responsive to environmental and social context at a variety of ages. However, all but one of these studies (Merkling et al., 2014; baseline corticosterone only) measured corticosterone in chicks that had already passed the most critical developmental window in terms of competition and resource monopolization, which occurs between age 3 and 10 days post hatch (Merkling et al. 2014). For example, intrabrood aggression drops to very low levels by 10 days post hatch (Leclaire et al., 2011; White et al., 2010), and 62-80% of B chicks who died during the years of this study did so when both chicks were 10 days of age or younger (unpubl.). Thus, this early stage of development is critical for fitness, yet information about adrenocortical physiology at this age is lacking.

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Table 1. Review of studies measuring corticosterone in first-hatched black-legged kittiwake (*Rissa tridactyla)* chicks. Superscript letters indicate whether corticosterone radioimmunoassays were conducted using the same antibody (a = Esoterix, b = Biogenesis) and/or in the same lab (a = Wingfield, UW, b = O'Reilly, UP, c = Chastel, CEBC, d = Kitaysky, UAF). Note that comparison of absolute levels across studies may only be appropriate if hormone assays were conducted in the same lab using the same antibody, given the variation generated by inter-laboratory differences in extraction and assay methods, as well as specificity of antibodies used (Fanson et al. 2007). "~" indicates that age is presented as approximate in some studies, or that hormone levels were estimated from figures.

Citation	Age (days)	Location	Baseline corticosterone (ng/mL)	Restraint-induced max corticosterone (ng/mL)	Sources of variation in corticosterone	No significant effect of …
[a/a]Kitaysky, Piatt et al. 1999	29-31	Captivity (*source - Alaska: Cook Inlet*)	4-5; food ad libitum	30; high food	(-) food intake; (-) body composition (lipid content)	—
			16; food restricted	100; food restricted		
[a/a]Kitaysky et al. 2001	~16	Alaska: Cook Inlet	~7	—	—	—
[a/a]Kitaysky et al. 2003 (*including unpubl. data*)	14-56 (weekly samples); 75	Captivity (*source - Alaska: Cook Inlet*)	2.9; food ad libitum	31 (@ 75 days only)	—	age
[a/b]Brewer et al. 2008; 2010	12-15	Alaska: Shoup Bay	3.3 - 7.4	~30-35 (peak: 10 min)	Year (highest in year of lowest productivity); colony	brood size; hatching order
[b/c]Merkling et al. 2014	5	Alaska: Middleton Island	~3-4	—	hatching order x experimental hatching asynchrony interaction; (-) growth rate	sex; body condition
[a/d]Schultner et al. 2013	25	Pacific - Alaska, Middleton Island	1.6; control	14.8; control	population	supplemental feeding, parental corticosterone manipulation
			1.4 food supplemented	10.3; food supplemented		
		Atlantic - Norway: Svalbard	3.4; control	26.2; control		
[a/d]Young et al. 2017	10	Alaska: Middleton Island	2.5	—	(-) age; hatching order; brood swapping	sex; food supplementation; brood enlargement
	25		1.5			

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2. Methods

2.1 Study site. This research was conducted in two years (2021 and 2022) at a free-living colony of black-legged kittiwakes nesting on a modified radar tower on Middleton Island, in the Gulf of Alaska (59°25'41.2"N 146°20'10.3"W). Details of the study site are described in Gill et al. (2002) and Gill and Hatch (2002), but in short: semi-partitioned nest sites on the outside face of the tower are equipped with sliding one-way mirrored glass windows. The sliding glass provides access to individual nests from inside the tower for monitoring and manipulation with minimal disturbance to neighboring nests. All nests are monitored twice daily for events including egg-laying, hatching, chick death, and fledging. Chicks are identified by hatch order using colored pen marks, applied on hatch day and refreshed every 5 days afterwards, when they are weighed and measured - thus ages are known to the day. Tower nest sites are inaccessible to both terrestrial and aerial predators.

2.2 Food supplementation. The tower is also the site of a long-term food-supplementation experiment in which a subset of nests (hereafter "fed") are provided with whole fish (either capelin (*Mallotus mallotus)* or herring *(Clupea spp.);* both preferred prey items) ad-libitum, 3 times per day for the entirety of the breeding season, beginning several weeks before egg-laying. Adults readily consume the supplemental food; chicks consume the food supplement once they are large enough to consume whole fish (never observed prior to 7 days post-hatch, thus chicks in this study were not yet directly consuming the supplement). Adults at fed nests continue to forage at sea but benefit from the supplementation in terms of reproductive success in most years (e.g. Kahane-Rapport et al., 2022). Occupants of control (hereafter "unfed") nests do not receive any supplemental food and rely solely on foraging at sea.

2.3 Time of day. In both years and regardless of treatment, all blood sampling occurred between 0600 and 0845, prior to the first daily supplemental feeding for fed nests, which occurred every day at 0900. All chicks had been briefly handled only once before: on hatch day for measurements and marking.

2.4 Experiment 1: Sources of variation in baseline corticosterone and response to restraint. In 2021, between 24 Jun and 7 Jul, chicks from unfed nests and fed nests containing 2 chicks were

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bled for baseline corticosterone ("undisturbed"; Table 2). Nests were sampled when the first-hatched chick (hereafter "A" chick) was 5 days old (second-hatched, or "B" chick ages varied from 2 to 5 days old). For each nest, both A and B chicks were removed simultaneously, the A chick was bled in < 3 min from initial disturbance (mean = 94 ± 36 s); tapping on the window to alert the brooding parent (to prevent startles that can dislodge chicks from the nest). Chicks were then weighed and measured, B chicks were returned to the nest and A chicks were placed in a breathable cloth bag in proximity to a space heater, since 5 day old chicks do not have full thermoregulatory capacity. 15 min after initial disturbance, A chicks were bled a second time to evaluate short-term adrenocortical response to restraint, then returned to their nest. Previous serial samples of restrained three-week old kittiwake chicks at this site found that corticosterone peaked at either 10 or 30 min (Kitaysky, unpubl.). In 2022, baseline blood samples were collected from A chicks between 29 Jun and 4 Jul for interannual comparisons.

2.5 Experiments 2 and 3: Responses to exogenous corticosterone. To bypass some of the challenges and constraints associated with the use of subcutaneous corticosterone implants (Torres-Medina et al, 2018) and minimize changes in HPA activity associated with handling, we used topical administration of corticosterone in dimethyl sulfoxide (DMSO) to rapidly elevate corticosterone with minimal disturbance. This manipulation allowed us to evaluate differences in glucocorticoid uptake and/or clearance, as well as negative feedback. DMSO is a polar solvent that has been used in veterinary and human medicine as a delivery vehicle for topical application of lipophilic compounds for decades (Kumar and Darreh-Shori, 2017; Patil, 2013). It is considered non-toxic, though it can have off-target cellular effects such as inhibition of acetylcholinesterase and is used by itself for a variety of conditions to reduce inflammation (Santos et al., 2003). In avian endocrinology, it has been used successfully for topical application of corticosterone (Busch et al., 2008; Pegan et al., 2019; Vitousek et al., 2018). In 2021 and 2022, 5 day old A chicks from either one- or two-chick nests were treated with a 20uL drop of either corticosterone in DMSO gel (hereafter "CORT" treatment) or DMSO gel (hereafter "DMSO" treatment; see section 2.6). CORT and DMSO gels were kept in physically different locations (and away from where chicks were bled) with dedicated pipettes, tip boxes, and glove boxes, to minimize the risk of corticosterone contamination. Chicks were treated by opening the nest window partway (causing the brooding

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parent to stand or briefly flush), reaching with a pipette into the nest, and gently touching the tip to the skin on the back of the A chick between the scapulae and dispensing the gel (see supplemental material for sample video clip). Application of the treatment usually took ~15 seconds from initial disturbance of nest site (tapping on window to alert brooding parent so it didn't flush and knock chicks from nest) to completion (closing of window), unless the brooding parent was particularly aggressive, in which case it could take up to 30 seconds to work around the adult. Parents resumed brooding within seconds of window closure. Chicks were not weighed until the final blood sample was taken; chicks were excluded from further analyses *a priori* if they weighed < 50 g, a threshold below which chicks have dramatically reduced survival.

2.5.1 Experiment 2: Effects of exogenous corticosterone on endogenous production (2021; Fig. 1). We used chicks from 1 or 2 chick fed and unfed nests (Table 2) and took a first blood sample 15 minutes after gel application, when the A chick was bled (in < 3 minutes from disturbance, average = 74 sec) and immediately returned to the nest. We removed the chick to take a second blood sample 15 min after the first sample (i.e., 30 min after gel treatment), to evaluate the effect of exogenous corticosterone on subsequent endogenous corticosterone production in response to handling during bleed #1. Finally, though DMSO is estimated to take at least 5 minutes to penetrate the skin and enter the bloodstream (Patil 2013), nothing is known about the acute time course of corticosterone uptake from topical DMSO application in young seabird chicks. Therefore we checked for very rapid changes in corticosterone by treating a small subset of chicks with topical CORT or DMSO and taking a single blood sample 5 minutes after treatment administration (Table 2).

2.5.2 Experiment 3: Time course of exogenous corticosterone (Fig. 1). In 2022, we repeated the topical CORT experiment (mixing fresh batches of gel solutions using the same protocol), but only used chicks from 2-chick unfed nests. A subset of chicks were bled for the first time 15 min after dosing to confirm rapid increase in corticosterone in CORT group, and a different set of chicks was bled for the first time 60 min after dosing to evaluate chicks' ability to clear exogenous corticosterone from circulation.

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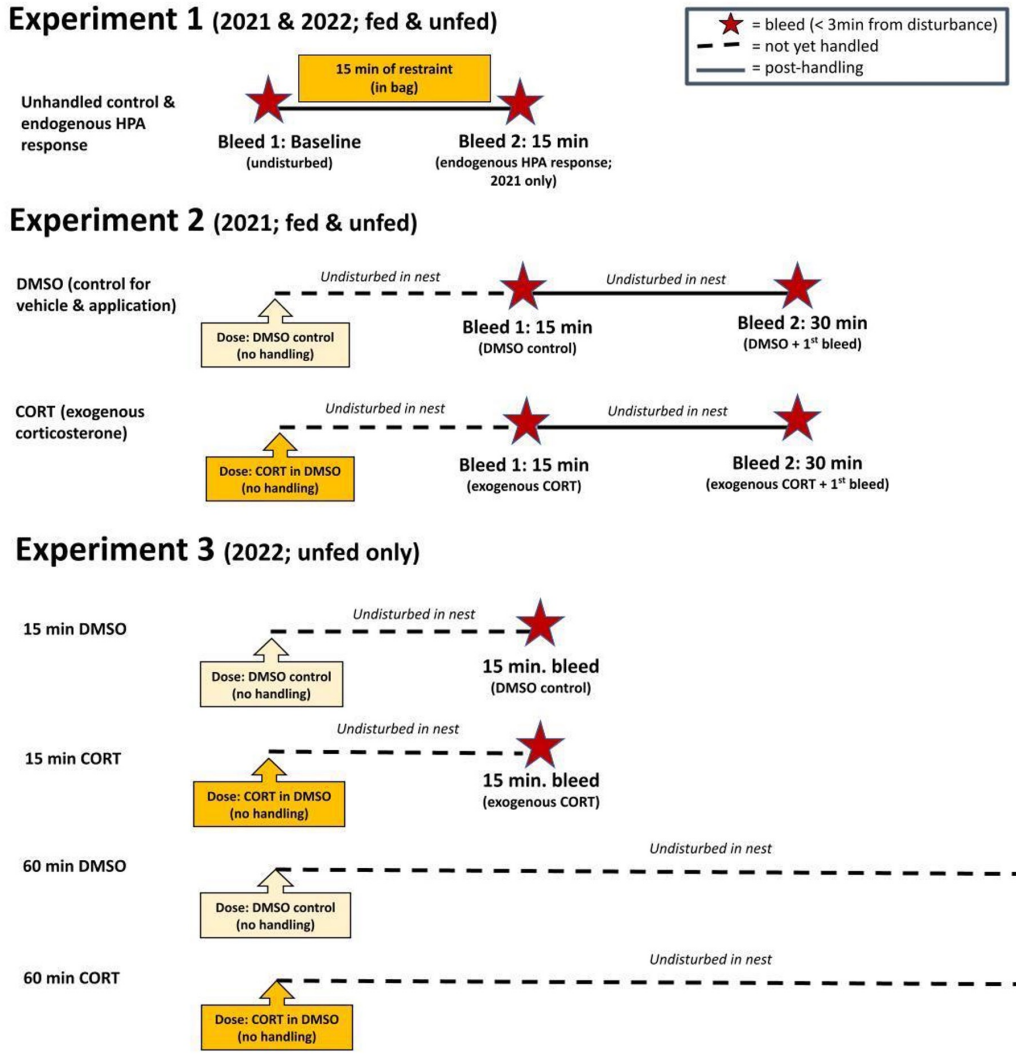

Figure 1. Experimental design. Timeline for blood sampling and topical hormone treatments of 5 day old black-legged kittiwake A-chicks.

2.6 Preparation of exogenous corticosterone treatments. Topical treatments were made following Pegan et al. (2019), though with a higher ratio of liquid DMSO to facilitate pipetting and surface area of contact on skin. In short, for the "CORT" treatment, powdered corticosterone (Sigma #27840) was dissolved in liquid DMSO, which was mixed with veterinary grade DMSO gel at a ratio of 4 mL : 6 grams to achieve a concentration of 5ug/µL. A control DMSO gel solution was made using the same ratio of liquid to gel DMSO, but with no corticosterone.

We used average body masses from 5 day old chicks measured in 2019 (90g) to anticipate that a 20 µL dose would deliver approximately 1µg corticosterone per gram of body mass (based on previous

experiments with topical corticosterone/DMSO in birds – Busch et al, 2008, Pegan et al. 2019). We used food coloring to visually confirm that vortexing rapidly and thoroughly dispersed liquid DMSO throughout the gel (though did not include dye in the final solutions). In the years of our study, average body mass of 5 day old chicks was lower than in 2019 (73g in 2021; 75g in 2022), such that 20µL of gel would have been a higher dose than intended. However, while 20µL of gel was drawn into each pipette tip, the viscosity of the gel meant that several drops were always left behind on the inside of the pipette tip. Repeated measurements in the lab using a microbalance to weigh pipetted DMSO gel mix (n = 20; compared to the weight of 20µL dispensed using a displacement syringe) indicated that an average of 12.4 ± 0.0019 µL of gel was delivered to each chick (57% of the dose originally calculated for 90g chicks). Thus, the average dose delivered to a 74g chick was 0.62 µg corticosterone/g body mass.

Table 2. Sample size for treatments and blood sampling of 5 day old first-hatched black-legged kittiwake (*Rissa tridactyla*) chicks in 2021 and 2022. DMSO and CORT treatments were applied topically; unfed and fed refers to supplemental food treatments to parents.

Time *(post-treatment)*	**Hormone treatment**	**Unfed** (*2021 / 2022*)	**Fed** (*2021 / 2022*)
0 min	Undisturbed†	19† / 10	17† / 12
5 min	DMSO	4 / 0	*NA*
	CORT	4 / 0	*NA*
15 min	Bag restraint†	19† / 0	17† / 0
	DMSO	16* / 11	11* / 0
	CORT	17* / 11	9* / 0
60 min	DMSO	0 / 14	*NA*
	CORT	0 / 14	*NA*

† *Same individuals sampled for undisturbed and 15 min bag restraint*
* *bled again @ 30 min for effects of treatment on response to handling*

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2.7 Blood sampling. Blood was collected in heparinized microhematocrit tubes following venipuncture of the alar vein using sterile 26G needles. Samples were refrigerated for up to 3 hours prior to centrifugation to separate erythrocytes from plasma, both of which were frozen at -20°C until transport off the island, when they were stored at -80°C until use.

2.8 Genetic sexing. Because 5 day old chicks are not sexually dimorphic yet their physiology may differ by sex, all chicks were genetically sexed from DNA extracted from erythrocytes (Qiagen DNeasy Blood and Tissue kits, Cat # 69556). We used primers and protocols for PCR and gel electrophoresis described in Merkling et al. (2012) to differentiate the sexes by number of bands.

2.9 Corticosterone assays. Corticosterone was measured blind to treatment using radioimmunoassay, following the protocol described in Kitaysky et al. (2007). In short, plasma was equilibrated with tritiated corticosterone, extracted using dichloromethane, and assayed in duplicate. 2021 and 2022 samples were run in separate assays (three and one assays in 2021 and 2022, respectively), but all samples from the same chick were run in the same assay, with treatments distributed across assays. Each assay included a standard treated identically to samples to calculate interassay variability (interassay CV = 2.7%). Final corticosterone values were corrected for the percent of tritiated corticosterone lost during extraction (average recovery for 2021 = 96% +/- 3.18%, for 2022 = 92% +/- 2.96%) and were log-transformed to normalize their distribution prior to statistical analysis.

2.10 Data analysis. We first determined whether brood size (one or two chicks) affected baseline corticosterone concentrations using a Welch's two-sample t-test. To test which ecological and biological factors affect five-day old chicks' baseline corticosterone and response to handling stress (including whether there is a response) we used a model selection approach. From a set of a priori candidate models of interest (Table 3) we used Akaike's Information Criterion (Burnham and Anderson, 2004) to identify the top performing model(s), defined as all models with AIC scores with a difference of < 2 from the top performing model. We calculated the effect size for the variables from each best fit model and considered any variable with an effect size whose 95% confidence interval does not overlap zero as statistically significant. We calculated AIC scores in R

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(v. 4.2.1, R Core Team 2022) using packages *AICcmodavg* (Mazarolle 2023) and *effectsize* (Ben-Shachar et al., 2020).

We used Analysis of Covariance and mixed effects Analysis of Variance with post-hoc comparisons to test the effect of DMSO and exogenous CORT application. We report p-values and F statistics from a Type III ANOVA using Satterthwaite's method for modeled variables, and p-values from post-hoc Tukey contrasts. We analyzed data in R (v. 4.2.1, R Core Team 2022) packages *lmerTest* (for mixed effects ANOVA, Kuznetsova et al. 2017) and *multcomp* (for ANCOVA and post-hoc contrasts Hothorn et al., 2008). We considered variables and contrasts with p-values < 0.05 as significant.

3. Results

3.1 Experiment 1: Sources of variation in HPA activity

3.1.1 Sources of variation in baseline corticosterone (Years: 2021 and 2022). There was no difference in A chick baseline CORT between one- and two-chick nests ($t_{18.16}$= -0.06, p = 0.95), so brood size was omitted from subsequent analyses. Chick body condition did not differ between years ($F_{1,55}$ = 1.69, p = 0.2), or treatments ($F_{1,54}$ = 1.77, p = 0.28). Model comparison indicated strong support for an effect of feeding treatment that differed between years, with both top models including the year*treatment interaction (Table 3). Post-hoc analyses indicated significant effects of year, treatment and their interaction - baseline CORT was higher in unfed nests (effect size ± 95% confidence interval from top model: 0.99 ± 0.58, 1.41) but more so in 2021 than 2022 (-0.73 ± -1.16, -0.31), and was higher in both fed and unfed birds in 2022 (0.57 ± 0.27, 0.87). The next best performing model included body condition; however it was not an informative predictor on its own (-0.0042 ± -0.32, 0.31). Body condition did explain some of the variability with respect to treatment (Fig 2) and so was included as a covariate in subsequent analyses.

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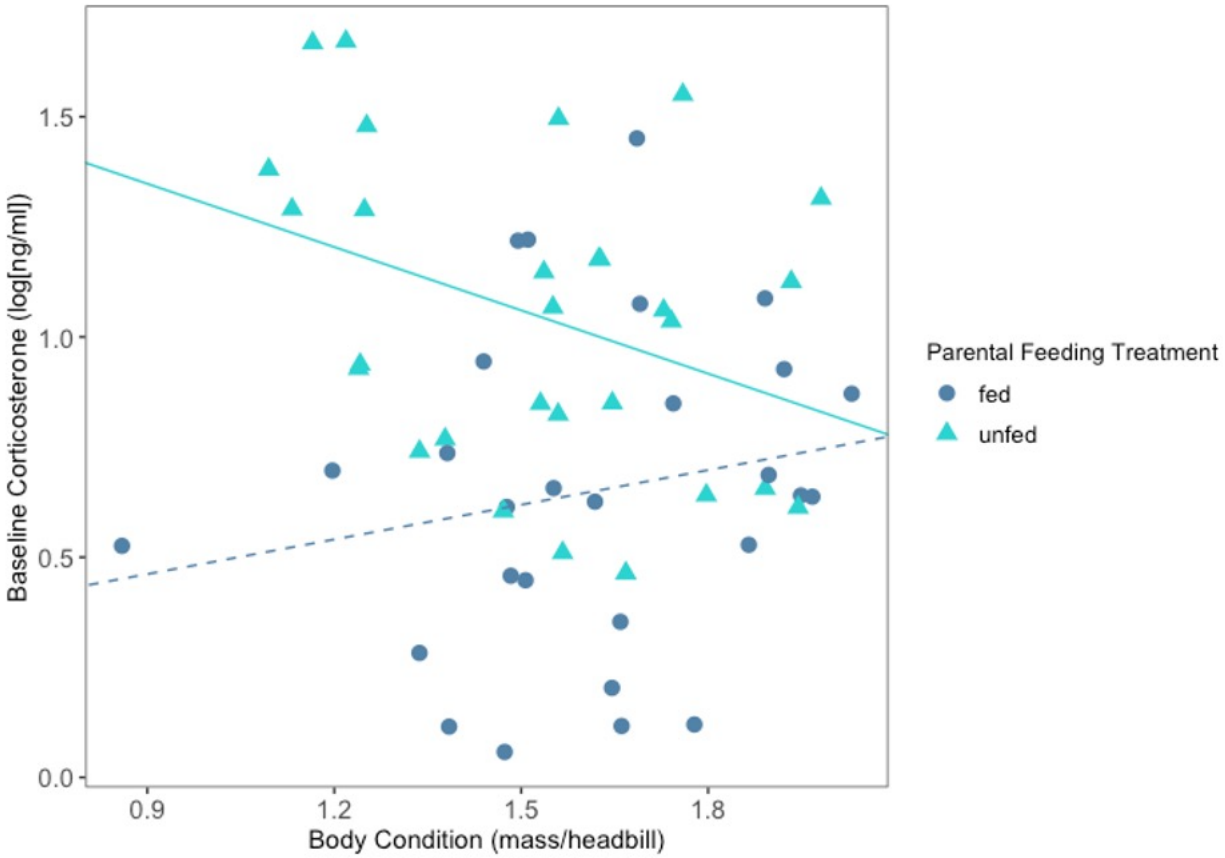

Figure 2. Body condition and baseline corticosterone. Body condition of 5 day old first-hatched kittiwake chicks was negatively related to baseline corticosterone levels, but this relationship was eliminated in nests where parents were food-supplemented. Solid line = significant, dashed = non-significant.

Table 3. Model selection results of variables affecting baseline corticosterone ("CORT") secretion of 5-day old chicks and *a priori* justification for model inclusion. Treatment = food supplementation to parents (fed or unfed).

Model	**K**	**AICc**	**Delta AICc**	**AICc Wt**	***a priori* justification**
Treatment*Year	5	38.93	0	0.56	Effects of parental nutritional status depend on interannual environmental variability
Year*Treatment*Body Condition	9	39.66	0.73	0.39	The effect of parental nutritional status on the relationship between chick energy stores and CORT varies interannually
Full Two-Way Interaction Model	12	44.31	5.38	0.04	

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Year+Treatment*Body Condition	6	48.37	9.45	0	Interannual environmental variation affects CORT, but parental nutritional status also modulates the impact of chick energy stores on CORT
Treatment	3	49.35	10.43	0	Parental nutritional status affects CORT
Treatment*Body Condition	5	49.36	10.44	0	Parental nutritional status modulates the impact of chick energy stores on CORT
Year+Treatment+Body Condition	5	49.83	10.91	0	CORT is affected by interannual environmental variability, parental nutritional status, and chick energy stores
Treatment+Sex	4	50.25	11.32	0	CORT is affected by parental nutritional status and chick sex.
Treatment+Body Condition	4	51.27	12.35	0	Both chick energy balance and parental nutritional status affect chick CORT
Year*Treatment+Body Condition+Sex	6	51.36	12.44	0	CORT is affected by interannual environmental variability, parental nutritional status, chick energy balance and sex
Treatment*Sex	5	52.39	13.46	0	Parental nutritional status affects CORT in male and female chicks differently
Null (intercept only) Model	2	62.82	23.9	0	None of these variables explain variation in CORT
Year	3	63.14	24.21	0	CORT reflects interannual environmental variability
Year+Body Condition	4	63.5	24.58	0	CORT reflects both energy balance and interannual environmental variability
Body Condition	3	63.82	24.9	0	CORT reflects energy balance
Year*Body Condition	5	64.08	25.16	0	The effect of chick energy balance on CORT is modulated by interannual environmental variability
Sex	3	64.1	25.18	0	CORT reflects sex-specific differences
Body Condition*Sex	5	64.14	25.22	0	CORT reflects energy balance in sex-specific ways
Year+Sex	4	64.55	25.63	0	CORT reflects both sex and interannual environmental variability
Body Condition+Sex	4	65.55	26.62	0	CORT reflects both energy balance and sex
Year*Sex	5	66.76	27.83	0	Male and female chicks respond differently to impacts of interannual environmental variability on CORT

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3.1.2 Endogenous corticosterone secretion in response to restraint (Year: 2021). After 15 min of restraint in a bag, 5 day old chicks increased corticosterone by 44.98 ± 5.13 (SE) ng/mL to 51.02 ± 17.94 ng/mL (fed) and by 35.57 ± 3.8 ng/mL to 54.73 ± 10.71 ng/mL (unfed; Fig. 3, 4B). The top model for corticosterone after 15 min of restraint included the interaction between baseline CORT and feeding treatment (effect size: 1.55 ± 0.65, 2.44; Table 4). In nests where parents were supplementally fed, higher baseline CORT was associated with lower HPA response - this was not the case in unfed nests. The next best performing model included all two-way interaction terms and indicated that body condition was negatively correlated with chicks' HPA response (effect size: -0.57 ± -1.05, -0.08).

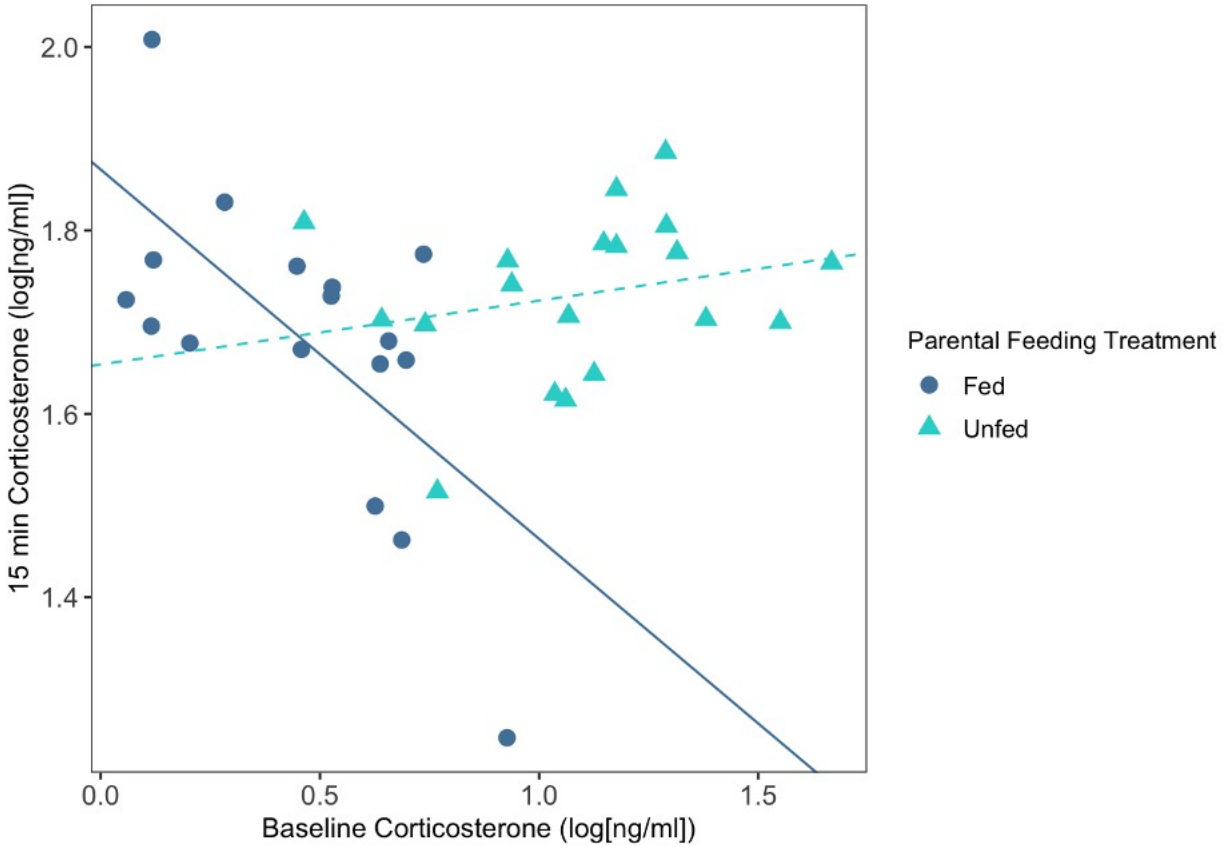

Figure 3. Baseline and restraint-induced corticosterone. Baseline corticosterone of 5 day old kittiwake chicks was negatively correlated with corticosterone levels after 15 min bag restraint, but only in chicks from nests where parents received supplemental feeding ("Fed"). Chicks from Fed nests had lower baseline corticosterone to begin with (see figure 4A). Solid line = significant, dashed = non-significant.

Table 4. Model selection results of variables affecting CORT response to 15 minutes of restraint in 5 day old chicks. Baseline CORT is log-transformed. Treatment = food supplementation to parents (fed or unfed). *A priori* justification is the same as in Table 3 with the addition of baseline CORT: a chick's baseline physiological state affects their response to a stressor, and that response may exist in parallel or be modified by the other study variables.

Model	K	AICc	Delta AICc	AICcWt
Treatment*Baseline CORT	5	-49.38	0	0.66
Two-Way Interaction Model without Sex	8	-47.29	2.09	0.23
Body Condition	3	-42.28	7.1	0.02
Treatment+Body Condition+Baseline CORT	5	-41.24	8.14	0.01
Null (intercept only) Model	2	-41.23	8.15	0.01
Treatment+Body Condition	4	-40.84	8.54	0.01
Treatment+	4	-40.27	9.11	0.01
Treatment	3	-40.16	9.22	0.01
Body Condition+Baseline CORT	4	-39.86	9.52	0.01
Sex+Body Condition	4	-39.83	9.55	0.01
Sex	3	-39.28	10.1	0
Treatment*Body Condition	5	-38.96	10.41	0
Baseline CORT	3	-38.87	10.51	0
Treatment+Sex+Body Condition+Baseline CORT	6	-38.86	10.52	0
Treatment*Body Condition+Baseline CORT	6	-38.81	10.57	0
Treatment+Sex	4	-38.16	11.22	0
Treatment+Sex+Body Condition+Baseline CORT	5	-37.67	11.7	0
Treatment*Sex	5	-37.26	12.12	0
Sex*Body Condition	5	-37.15	12.23	0
Sex*Baseline CORT	5	-36.96	12.42	0
Sex+Baseline CORT	4	-36.8	12.58	0
Full Two-Way Interaction Model including Sex	12	-32.27	17.1	0

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3.3 Experiment 2: Exogenous corticosterone and negative feedback (Year: 2021, fed and unfed nests).

3.3.1 Response to exogenous corticosterone treatment. Topical application of corticosterone had a significant effect on plasma corticosterone ($F_{5, 87} = 115.63$, $p < 0.0001$, controlled for effect of body condition $F_{1, 87} = 87.18$, $p = 0.05$, with individual as a random effect). Post-hoc tests showed that the CORT treatment elevated circulating corticosterone compared to undisturbed baseline ($p < 0.001$) and to the DMSO treatment ($p < 0.001$), but the identical application of DMSO alone did not elevate corticosterone compared to undisturbed baseline ($p = 0.996$), confirming that neither DMSO nor the topical administration procedure evoked significant changes in HPA activity. The topical application-induced elevation of circulating corticosterone was within a physiologically-appropriate range: it was slightly (but significantly; $p = 0.009$) lower than levels secreted endogenously in response to 15 minutes of restraint (Fig 4A/B). Feeding treatment had a strong effect on corticosterone levels 15 min after exogenous corticosterone application ($F_{1,50} = 4.56$, $p = 0.037$, controlling for body condition $F_{1,50} = 0.34$, $p = 0.56$) - chicks from fed nests had much lower circulating corticosterone 15 min after the topical hormone application (25.46 +/- 6.39 ng/mL) than chicks from unfed nests (40.97 +/- 5.54 ng/mL; Fig 4A). This difference between fed and unfed groups mirrored the difference between them in the baseline group: i.e. unfed corticosterone was 12 ng/mL higher than fed at baseline. A separate subset of chicks bled 5 min after gel application showed no significant difference between the DMSO and the CORT treatments ($t_5 = -1.07$, $p = 0.33$).

3.3.2 Effects of exogenous treatment on endogenous response to handling (Year: 2021, second bleed). Both the CORT and DMSO-treated chicks increased circulating corticosterone at the second bleed (30 min after topical gel application and 15 min after the first bleed) compared to their respective first bleeds (post-hoc comparison from mixed-effects ANCOVA, DMSO $p < 0.001$, CORT $p = 0.02$; Fig 4C). Although the corticosterone in the CORT treated group remained higher ($p = 0.003$; Fig 4B), the increase from the first to the second bleed was larger in the DMSO treatment ($F_{1,50} = 8.6626$, $p = 0.005$; Fig 4C).

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In addition, DMSO and CORT treated chicks from fed nests had lower corticosterone at both the first ($F_{1,50} = 5.17$, $p = 0.03$) and second bleed ($F_{1,50} = 4.56$, $p = 0.04$) compared to those from unfed nests (in both cases controlling for body condition, though body condition was not significant; bleed 1: $F_{1,50} = 0.12$, $p = 0.45$; bleed 2: $F_{1,50} = 0.02$, $p = 0.56$; Fig 4A/B). However, the differences in bleed 2 corticosterone levels between parental feeding treatments were additive: i.e. not larger than the difference between fed and unfed at the 1st bleed (15 min after gel application; $F_{1,49} = 1.2688$, $p = 0.26$), and there were no differences between feeding treatments in the magnitude of change within CORT or DMSO treatments (Fig 4C). Finally, the increase in corticosterone 15 min after the brief disturbance of handling and bleeding was much lower than the increase in corticosterone after 15 min of continuous bag restraint ($F_{2.82} = 21.29$, $p < 0.0001$).

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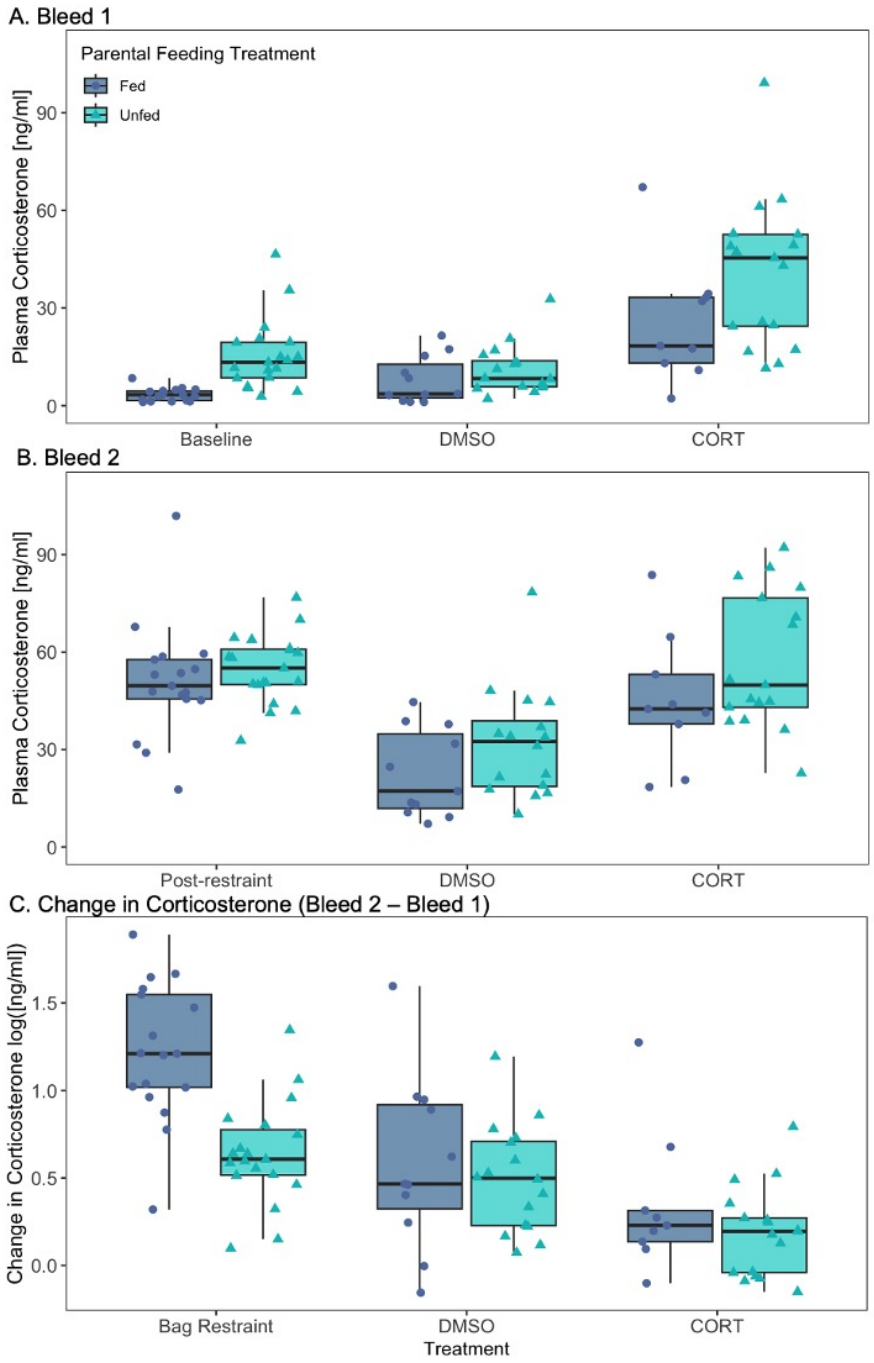

Figure 4. Hormone treatments and repeated blood samples. Circulating corticosterone levels in 5 day old kittiwake chicks by parental feeding status and chick treatment. A) Bleed 1 is an undisturbed baseline bleed for the control group (< 3 min) and 15 min after topical treatments for the DMSO (DMSO gel) and CORT (corticosterone dissolved in DMSO gel) groups. B) Bleed 2 is after 15 min of continuous bag restraint for the control group, and 15 min after the first bleed for the DMSO and CORT groups (treated chicks were returned to nests between bleed 1 and bleed 2). C) Change in corticosterone levels between the first and second bleed. All statistical analyses were performed using log-transformed data, but raw data are shown for panels A and B.

3.4 Experiment 3. Clearance of exogenous corticosterone (Year: 2022, unfed nests only, each chick bled only once). Circulating corticosterone in DMSO-treated chicks bled for the first time 15 or 60 min after treatment did not differ from undisturbed baseline corticosterone (Tukey Contrasts, p = 1 and 0.63 respectively; Fig 5). Corticosterone in the CORT treatment was higher than baseline and DMSO at both 15 (p = 0.01 and 0.007) and 60 min post-treatment (p = 0.02 and <0.001) and was not different between the 15- and 60-min groups (p = 0.97).

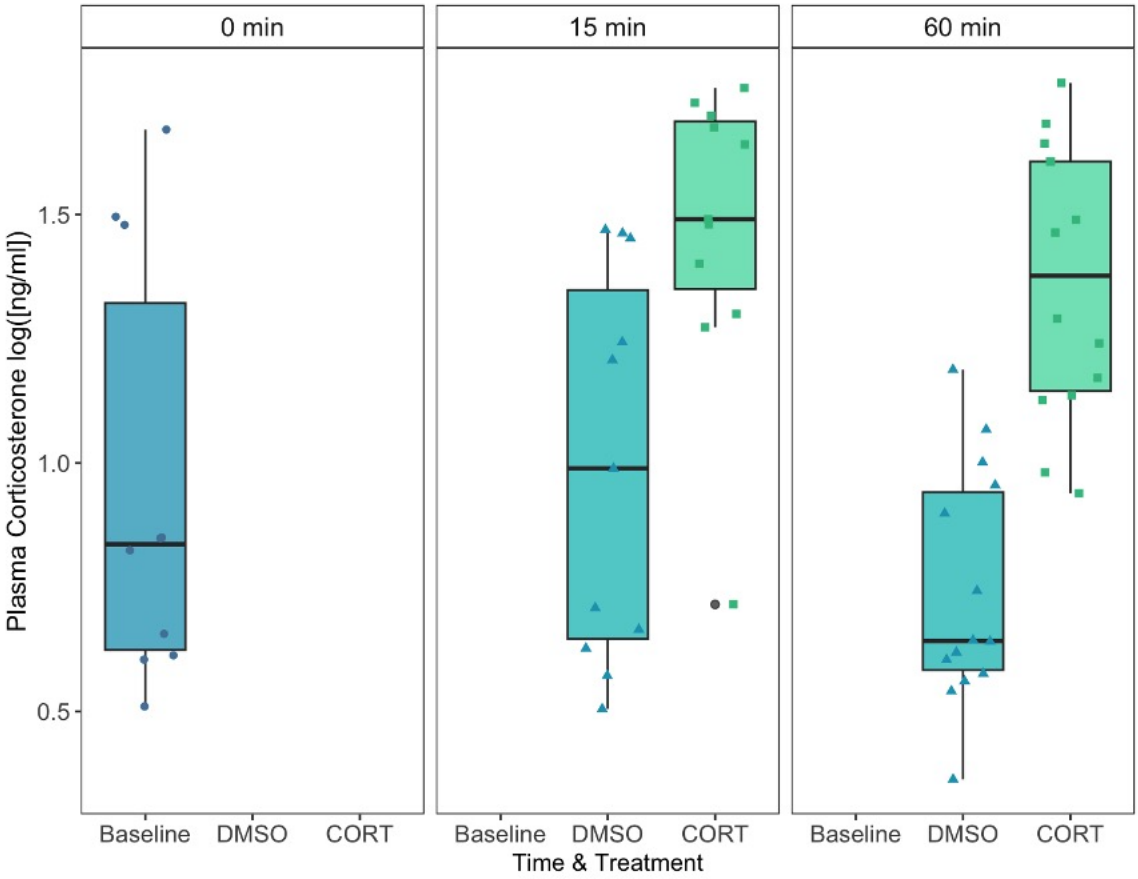

Figure 5. Time course for topical corticosterone. Corticosterone levels in 5 day old chicks from nests without parental food supplementation (unfed) at undisturbed baseline (< 3 min), 15 and 60 minutes after application of topical gel treatments. No chick was bled more than once. Statistical analyses were performed using log-transformed data but raw data are shown here.

4. Discussion

In this study, we found that very young chicks have HPA axes that a) can rapidly secrete a large amount of corticosterone and b) are sensitive to environmental and physiological context. Specifically, at 5 days post-hatch, just 10-15% of the way through the nestling stage, nutritional status of parents interacted with interannual variability and body condition to affect baseline HPA axis activity, though neither chick sex nor number of siblings did. Our study design minimized potential sources of variation in HPA activity by using known age, rank and sex kittiwake chicks, and sampling within a narrow hatch date range (< 2 weeks) and time of day (< 3 hours). Young chicks also mounted corticosterone responses proportional to the intensity of the challenge, with levels 15 min after a moderate challenge (brief handling for a bleed followed by return to the nest) that were higher than the undisturbed baseline, but lower than levels evoked by a more intense challenge (15 min of continuous restraint). Chick corticosterone levels after the 15 min restraint challenge were not only much higher than their baseline levels, but higher than any of the previously reported maximum values for chicks with the exception of much older, severely food-restricted captive chicks (though all previous studies that measured restraint-induced levels used chick older than 5 days; Table 1). Restraint-induced levels of corticosterone in chicks were comparable to (with some individuals higher than) maximal levels secreted by adult kittiwakes at this colony during 50 min of restraint (12 - 63 ng/mL; Kitaysky et al., 2010).

4.1 Food availability to parents and year effects. Despite the fact that 5 day old chicks are very early in development and parents should be able to meet their relatively low food needs at this stage, there were strong effects of year and parental supplemental feeding treatment on chick HPA activity. Baseline corticosterone was significantly lower in chicks from fed nests in one of two years. While an obvious explanation for this difference might be that the current nutritional status of parents is transmitted to chicks via differences in provisioning, which affects chick nutritional status and thereby their HPA activity, two lines of evidence indicate that this was a contributing factor but not the sole driver. First, parental food treatment had a strong effect in 202,1 even when chick body condition was controlled for statistically. Second, there were no significant differences in chick body condition between years or feeding treatments, yet their baseline circulating corticosterone levels differed between years. In fact, although climate indices and measures of reproductive success indicated that 2021 and 2022 were both years of

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intermediate reproductive success for kittiwakes at this site (S. Hatch, unpublished data), 2022 was a better year than 2021. Yet baseline corticosterone was higher in 2022 than in 2021, and in 2022 chicks from fed nests had corticosterone levels that were similar to unfed. Though reproductive success at the end of the season is temporally distant from conditions at 5 days post hatch, the mismatch between annual breeding success and young chick endocrine physiology suggest that the differences in chick baseline corticosterone are affected by food availability and additional, unmeasured factors.

There are several potential modulators of the relationship between chick corticosterone and current food availability. First, it could be a result of prenatal effects. Supplemental feeding at fed nests began before egg-laying, potentially interacting with early season or even overwinter environmental conditions in each year to influence egg composition (Benowitz-Fredericks et al., 2013). Variation in egg composition can affect chick HPA activity (Ahmed et al., 2014; Love and Williams, 2008; Schwabl and Partecke, 2020; Sockman et al., 2001) and may be a mechanism for intergenerational transmission of information that prepares chicks for the environment into which they are born (reviewed in Engqvist and Reinhold, 2016). In addition, adults show high nest site fidelity at this colony, thus most parents at fed and unfed nests have likely experienced the same feeding treatments in past years. This combination of early indicators of natural food availability during the pre-lay period (Whelan et al., 2021) and anticipated changes in food availability during chick-rearing based on prior experience may shape investment in reproduction (Shultz et al., 2009), and thus the programming of chicks' HPA axes. Second, the differences in HPA activity could be driven by post-natal behavioral cues from parents or siblings. While chick body condition indicated that parents seemed to be meeting the nutritional needs of their chicks at this early age regardless of the supplemental food treatment (but see 4.2), differences in competition from siblings or responsiveness of parents to begging may impact corticosterone secretion (Braasch et al., 2014; Dreiss et al., 2016). Finally, other aspects of interannual environmental variability could modulate the relationship between food availability and corticosterone by imposing additional energetic challenges. For example, weather can affect chick corticosterone (Crino et al., 2020; De Bruijn and Romero, 2018), as can ectoparasites (Dudek et al., 2021; Kitaysky, 2001; Quillfeldt et al., 2004).

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4.2 Body condition. Control chicks (from unfed nests) in higher body condition had lower baseline corticosterone levels, and body condition was generally negatively correlated with restraint-induced corticosterone levels. While negative relationships between body condition or body mass and corticosterone has been frequently reported in birds, including adult black legged kittiwakes (Kitaysky et al. 1999) and red-legged kittiwake chicks (Kitaysky et al. 2001), a phylogenetically-controlled meta-analysis found no consistent relationship between baseline corticosterone and body condition in seabirds (Sorenson et al., 2017). In adult kittiwakes, low body condition can be associated with either low or high levels of corticosterone (Schultner et al., 2013) - the first because animals with a dependable food supply and low corticosterone can afford to avoid the costs of carrying extra weight (Rogers, 2015), and the second because severe food shortages elevate corticosterone, which mobilize and deplete reserves. Growing chicks are under different selection pressures than adults and may be less likely to benefit from maintaining a "lean" phenotype, though the relationships between growth and fitness in kittiwakes are complex and context-dependent (Vincenzi et al., 2013; Vincenzi and Mangel, 2013). Indeed, in this experiment the relationship between body condition and baseline corticosterone was eliminated by supplemental feeding. While some models predict that the relationships between glucocorticoids and phenotype will be obscured by high resource availability (Breuner and Berk, 2019), there were no differences in body condition between treatments in the young chicks included in this study. This indicates that at least at this age, factors in addition to internal indicators of energy reserves may modify chick HPA activity. For example, other aspects of interannual variability, such as weather, may be buffered to different extents by parents in fed and unfed nests. The negative relationship with response to restraint suggests that chicks in better condition may be able to buffer themselves from potential costs of elevated glucocorticoids exposure by downregulating their sensitivity to challenges. However, it is also worth noting that food intake can change tissue composition of chicks including increased water retention (Kitaysky et al., 1999) and, potentially, differences in rate of yolk absorption (Noy and Sklan, 2001), such that measures of body condition may not always provide an accurate proxy of nutritional status.

4.3 Sex. Though young kittiwake chicks are initially sexually monomorphic, males grow faster and are generally considered more costly for parents to rear (Merkling et al., 2012; Young et al.,

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2017). While the dimorphism manifests when chicks are older than 5 days (Merkling et al. 2012), the physiological substrates for these differences may be established earlier. Despite this possibility, we did not find strong evidence for an early effect of sex on HPA function. Whether such a difference manifests later in development or whether the subsequent effects of corticosterone differ by sex remains to be determined.

4.4 Sources of variation in restraint-induced corticosterone. The magnitude of the corticosterone response to restraint in chicks has been proposed to reflect consistent phenotypic variation in adrenocortical responsiveness with fitness implications, predicting subsequent recruitment and survival in at least one species (Blas et al. 2007). What drives variation in restraint-induced corticosterone levels in kittiwake chicks? Though we did not measure it here, HPA axis activity has a heritable component in many birds, with higher heritability of restraint induced levels than baseline levels (Beziers et al. 2019, Jenkins et al. 2014). While body condition may also play a role (see section 4.2), the strongest evidence in this study was for a negative relationship between baseline corticosterone and corticosterone after restraint, but only among chicks in the food-supplemented treatment. Chicks from the fed treatment secreted more corticosterone to reach similar levels as their counterparts from the unfed treatment after 15 min of restraint, despite starting at much lower baseline levels. While these results suggest that lower baseline corticosterone levels in fed chicks was not a consequence of a difference in adrenal capacity, they do not identify sources of interindividual variation within treatments.

Variation in adrenal capacity may be explained in part by the "facilitation" phenomenon, in which restraint-induced corticosterone levels reflect adrenal capacity as shaped by HPA activity in the recent past (Akana et al., 1992; Dallman et al., 2004, 1992; Kitaysky et al. 2007). In a study of adult kittiwakes, maximum restraint-induced corticosterone was correlated with food availability two weeks prior to sampling (Kitaysky et al., 2010). Though the adrenal capacity of five day old kittiwake chicks has had limited opportunity to be shaped by post-hatch experience, the HPA axis of avian embryos is active and capable of responding to stimuli (Jenkins and Porter, 2004) and its activity in chicks may be shaped by both prenatal and postnatal exposure to corticosterone (Benowitz-Fredericks et al. 2015; Marasco et al., 2016), as well as environmental context (Groothuis et al., 2020). Thus, it is possible that prenatal experience plays a role (see

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section 4.1) and the HPA responsiveness of 5 day old kittiwake chicks to restraint is determined by a combination of ontogenetic changes and embryonic/early post-hatch exposures to external cues.

4.5 Effects of exogenous glucocorticoids. We used topical corticosterone administration to evaluate rapid uptake, clearance and negative feedback of glucocorticoids. The ability to clear circulating glucocorticoids via a combination of negative feedback and metabolism is an important aspect of HPA function that likely has fitness consequences, as it allows animals to buffer themselves from costs of extended glucocorticoid exposure (Lattin and Kelly, 2020; Romero, 2004; Romero et al., 2009; Taff et al., 2018). Though the effects were not apparent after 5 minutes, topical corticosterone treatment elevated circulating corticosterone within a physiologically relevant range after 15 min. This elevation persisted for at least 60 min. In contrast, administration of the vehicle control (DMSO alone) did not change corticosterone levels, compared to undisturbed baseline levels, at any point.

We did not find evidence that chicks from fed and unfed nests processed exogenous corticosterone differently. The difference in levels of corticosterone between parental feeding treatments 15 min after administration of exogenous corticosterone was similar to the difference between them at baseline. However, the second bleed for the DMSO and CORT treated chicks provided evidence that a) exogenous corticosterone evoked rapid negative feedback on endogenous production (the magnitude of the handling-induced increase was higher in the DMSO control treatment compared to the CORT treatment) and b) the levels of negative feedback did not differ by parental feeding treatment (differences in corticosterone between CORT-treated chicks in fed and unfed nests at the 2nd bleed were the same magnitude as in the first bleed). Thus, while endogenous secretion of corticosterone in 5 day old chicks is sensitive to environmental context, other aspects of HPA function are not: rapid negative feedback and/or the ability to clear acute exogenous elevations in corticosterone. Though changes in sensitivity to negative feedback has been proposed as a potential mechanism to explain ontogenetic changes in HPA activity in chicks, this hypothesis was not supported in white storks (Torres-Medina et al., 2019). Similarly, our study suggests that it does not explain variation in HPA activity between

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young kittiwake chicks from fed and unfed nests, though age-related changes have not yet been tested.

4.6 Conclusion. The developmental trajectory of avian HPA axes has been hypothesized to be driven by a species' position on the altricial-precocial continuum (Blas et al., 2006), latitude (Jones et al., 2021), or by other aspects of life-history including provisioning strategies, but no consistent patterns have emerged (Sagar et al., 2019). The HPA axes of black-legged kittiwake chicks are sensitive to internal and external cues and are capable of mounting a large glucocorticoid response to an acute challenge (restraint) during a window of intense social interaction with both siblings and parents. While this is consistent with the hypothesis that glucocorticoids are important for species with intra-brood competition, the ability of young chicks to mount an adult-like HPA response to restraint has been found in a number of other seabird species that have one-egg clutches, including three species of petrels (Adams et al., 2008; Angelier et al., 2022; Sagar et al., 2019), three species of Alcids (Benowitz-Fredericks et al., 2015; Kitaysky et al., 2005; Will et al., 2015), and a congener of the black-legged kittiwakes studied here: the red-legged kittiwake (Kitaysky et al., 2001; though red-legged kittiwakes historically had larger clutch sizes). Thus, sibling competition cannot be the sole selective pressure on the development of HPA axis activity. A phylogenetically-controlled meta-analysis characterizing the ontogeny of HPA activity across species with varied ecologies and life-histories would be valuable for understanding the pressures and constraints on HPA axis development in birds. However, for species with very early activation of the axis, like kittiwakes, the next steps are to understand why young chicks are capable of such robust responses to acute challenges by characterizing the rapid metabolic and behavioral effects of elevated corticosterone in chicks.

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