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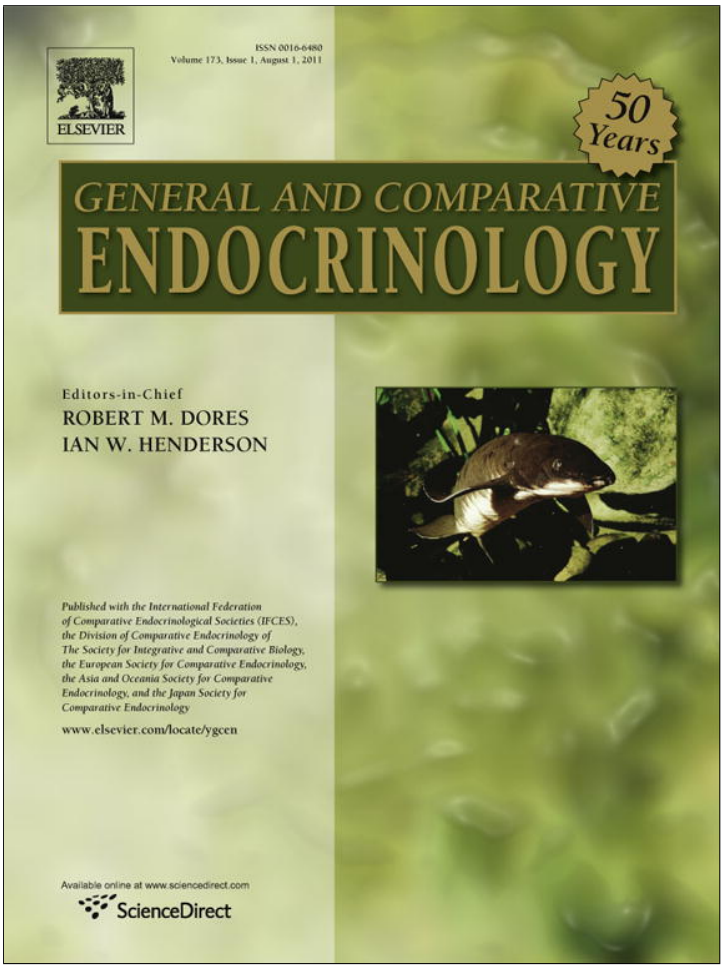

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California gull chicks raised near colony edges have elevated stress levels

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ABSTRACT

Coloniality in nesting birds represents an important life history strategy for maximizing reproductive success. Birds nesting near the edge of colonies tend to have lower reproductive success than individuals nesting near colony centers, and offspring of edge-nesting parents may be impaired relative to those of central-nesting parents. We used fecal corticosterone metabolites in California gull chicks (*Larus californicus*) to examine whether colony size or location within the colony influenced a chick's physiological condition. We found that chicks being raised near colony edges had higher fecal corticosterone metabolite concentrations than chicks raised near colony centers, but that colony size (ranging from 150 to 11,554 nests) had no influence on fecal corticosterone levels. Fecal corticosterone metabolite concentrations also increased with chick age. Our results suggest that similarly aged California gull chicks raised near colony edges may be more physiologically stressed, as indicated by corticosterone metabolites, than chicks raised near colony centers.

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1. Introduction

The physiological condition of birds is often influenced by changes in their local environment, and these physiological responses can be measured by endocrinological parameters. Prominent among these physiological responses is the hypothalamic–pituitary–adrenal (HPA) stress response, which in birds results in increased circulating levels of the corticosterone hormone during periods of environmental stress [69,71]. The development of the HPA response varies among bird species [see; 36,53,57,64], but it is thought to be well developed and functional soon after hatching in semi-precocial species [29]. Elevated corticosterone concentrations are thought to allow individuals to manage a specific stressor via physiological and behavioral modifications, but sustained levels of high corticosterone concentrations can impair individuals [38,56]. Corticosterone can promote the breakdown of stored energy through protein catabolism [7], and elevated corticosterone concentrations can influence the behavior of juvenile birds, such as increased aggression and begging rates [30,31,48]. These physiological and behavioral modifications which are mediated by altered levels of circulating corticosterone provide individuals with the ability to limit the negative impacts of short-term environmental stressors, such as starvation, risk of predation, and inclement weather [68,69]. Although beneficial over short time periods, elevated corticosterone concentrations in juvenile birds can have long-term negative consequences, including reduced cognitive abilities [31,32], mate attractiveness [41], and survival [9].

Coloniality in seabirds is a common life history strategy that is thought to increase reproductive success via several mechanisms, including diluting the risk of predation [3,16,43], increasing the ability to thwart predators via mobbing [37,72], increased vigilance [11,43], sharing foraging information [65], and increasing the ability to find mates [16]. However, within a nesting colony, reproductive success can be highly variable. Birds nesting in the center of colonies often experience greater reproductive success than birds nesting near the edges of colonies [3,14,37,49].

Whereas the advantages of nesting in the center of colonies to improve reproductive success is well documented, it remains unclear whether there also are physiological benefits to raising offspring in the center of colonies. Few studies have investigated the physiological benefits associated with nest positioning within a seabird colony. Walker et al. [63] examined the physiological condition of adult magellanic penguins (*Spheniscu magellanicus*) and found no difference in body condition or in corticosterone concentrations between colonial penguins nesting in central versus edge locations. Yet, results might differ for seabird species that are flighted and expend considerably less energy travelling to the center of a colony, since penguins must walk substantial distances to travel to the center of a breeding colony relative to those that breed at the edge of colonies. Furthermore, we are aware of no other studies that have examined differences in corticosterone concentrations in chicks being raised in different parts of the colony.

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Herein, we examined whether colony size and the location within a colony that a chick was being raised influenced fecal corticosterone metabolite concentrations within California gull chicks (*Larus californicus*). The size of California gull colonies varies considerably throughout their range, with colonies ranging from fewer than 100 to over 11,544 nests in San Francisco Bay, California. Moreover, the densities of gull nests varies within colonies such that central nest locations typically are surrounded by much higher densities of nesting birds than towards the edge of the colony [46]. Specifically, we assessed fecal corticosterone metabolite concentrations in California gull chicks that were being raised within both central and edge colony locations, across a range of colony sizes from 150 to 11,554 nests. We additionally investigated whether chick age [47,59,61] and body condition [44] influenced fecal corticosterone metabolite levels.

2. Methods

2.1. Study species

California gulls are colonial nesters (defined as breeding among densely distributed territories that contain no resources other than nest sites) and have bi-parental care [73]. In the San Francisco Bay, breeding occurs from April through July. Females lay a clutch of 2–3 eggs, which they incubate for approximately 24–25 days, and the eggs hatch asynchronously, 1–2 days a part [8,73]. California gull chicks are semi-precocial [50] and fledge at 40–60 days of age [73].

2.2. Study area

We examined the physiological condition of California gull chicks at three California gull colonies within the Don Edwards San Francisco Bay National Wildlife Refuge, San Francisco Bay (37°26′N 121°58′W) during June 2010. There were approximately 46,000 breeding adult California gulls nesting at six breeding colonies in the South San Francisco Bay during 2010 [55]. We selected three of the six colonies for our study which spanned the range of colony sizes, including a small colony of 150 nests breeding on an island within a flooded, former, salt evaporation pond (A1), a medium sized colony of 3297 nests on salt pond islands (Coyote Hills, N2A/3A), and the largest colony of 11,554 nests within a dry former salt pond bed (A6) in San Francisco Bay [colony details in 1,2]. Colonies were located within the southern San Francisco Bay and were 5–14 km apart, and within a short flight distance (<14 km) of three local landfills (Tri-Cities, Newby Island, and Palo Alto Landfills) where gulls spend much of their time foraging during the breeding season [2].

2.3. Chick sampling

We sampled gull chicks when they were approximately two to three weeks of age. We sampled 10–27 individuals from each of two locations per colony (colony edges or centers), within each of the three breeding colonies (n = 111 individual chicks). We used non-invasive fecal sampling to measure corticosterone metabolite concentrations in California gull chicks. Corticosterone metabolite concentrations in fecal material represent steroid concentrations from within 1–3 days [4,21,22,39]. Concentrations of corticosterone metabolites are lower in feces than in circulating levels due to rapid and extensive metabolization before excretion [66] and have been shown to be effective biomarkers of stress responses in birds associated with increased brood size [17], food limitation [25], human disturbance [4,60], increased temperatures [35], and others. We did not use corticosterone concentrations in blood plasma because of the short time-frame that blood samples represent, and logistically not being able to sample all chicks within 3 min of disturbing the breeding colony [51,52].

For each sampled chick, we measured short tarsus length (middle of midtarsal joint to the end of tarso-metatarsus), flattened wing length, exposed culmen length, ninth primary length, and mass. All measurements were to the nearest 0.01 mm using digital calipers or a wing ruler, except mass, which was measured to the nearest 1.0 g using a spring scale. Based on the length of the ninth primary feather, we estimated that chicks were 12–22 days of age when they were sampled [27,58]. Chicks were held in shaded and screenlined poultry cages until processing within 30 min of capture (model 5KTC, Murray McMurray Hatchery, Webster City, IA). From each chick, we extracted approximately 2 ml of fecal material either directly from the cloaca using a micropipette or after fecal samples were voided on clean aluminum foil. Fecal samples were stored in labeled micro-centrifuge tubes and placed on wet ice in the field and later frozen in the lab at −20 °C until corticosterone metabolite analysis was conducted within 78 days. Each chick was banded with a uniquely numbered aluminum US Geological Survey leg band and Darvic color bands to facilitate recapture. All chicks at each of the three colonies were captured and sampled within a seven day time period in order to minimize any potential changes in corticosterone metabolite concentrations associated with environmental variables not measured in the study (e.g., changing food availability over time). We sampled chicks at the center and edges of each colony within three hours to minimize any time of day variation in corticosterone metabolite concentrations [56,62] and bile production and excrement [18,19].

2.4. Validation study

To validate the determination of excreted corticosterone metabolites in our Correlate-EIA™ Corticosterone Enzyme Immunoassay kit (EIA), we used a capture-and-handling stress protocol [70]. Briefly, three California gull chicks were held in the cages for an additional 60 min after their initial handling for measurements and fecal samples before they were released to increase their potential for elevated corticosterone metabolite concentrations. We then recaptured each of these chicks 8 and 24 h after their initial capture and, at each of the two recapture events, we re-sampled their fecal material to measure corticosterone metabolite concentrations. Chicks were released at their location of capture.

2.5. Measurement of corticosterone metabolites

Corticosterone metabolite concentrations were measured following procedures outlined by Möstl et al. [40] and Palme [42]. Briefly, wet fecal samples (~0.75 g subsamples) were homogenized for one-minute and then mixed with 5.0 ml of 95% ethanol and vortexed for 30 min. To minimize potential bias associated with variation in fecal corticosterone metabolite concentrations associated with urinary and fecal materials [13,40] we did not analyze samples that were exclusively urinary liquids. Variation in our fecal samples was likely minimal because the forms of excreta are mixed in the cloaca of birds [33]. Samples were then centrifuged (15 min, 2500*g*), the supernatant was transferred to a new vial and was then evaporated under nitrogen gas. Corticosterone metabolites were then resuspended in diluted extraction buffer and measured using the Correlate-EIA™ Corticosterone kit [25,54] following the manufacturer's instructions (Assay Design, Inc., Ann Arbor, MI). The Correlate-EIA™ Corticosterone kit used a donkey anti-sheep IgG microtiter plate, and a sheep polyclonal corticosterone EIA antibody as a standard. Cross reactivity for these EIA kits are considered low and reported for desoxycorticosterone (12.3%), progesterone (0.2%), tetrahydrocorticosterone (0.7%), aldosterone (0.6%), cortisol (0.4%), progesterone (0.2%), cortisone

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(<0.1%), and estradiol (<0.1%; Assay Design, Inc., Ann Arbor, MI). The minimum detectable level of corticosterone metabolites was 0.02 ng/g (Assay Design, Inc., Ann Arbor, MI).

We conducted a standard assay validation, which included an assessment of parallelism, recovery of exogenous corticosterone, and intra- and inter-assay precision to confirm that the EIAs accurately measured corticosterone metabolites in fecal samples [5,21,54]. All fecal samples were analyzed within 78 days of collection to avoid any issues with changes in metabolite concentrations associated with longer storage times [24,28].

2.6. Statistical analyses

To validate EIA test kits for fecal corticosterone metabolites, we performed a serial dilution of fecal corticosterone metabolites from California gull chicks and tested for equality of slopes (parallelism) between the gull and corticosterone standard using a general linear model. Similar slopes between serially diluted fecal corticosterone metabolite samples and standards demonstrated that the EIA kits were in fact measuring the parameter as purported by the manufacturer.

We used an information-theoretic approach [12] and generalized linear models in SAS (PROC GLM; [34]) to determine which variables influenced California gull chick fecal corticosterone metabolite concentrations. We built and ranked competing candidate models which included colony size (small, medium, and large), location within colony (edge vs. center), chick age (length of ninth primary feather), chick mass, and the interaction colony size × location within colony. We included the age index in all models that included mass in order to account for variation in a chick's structural size associated with age; therefore the mass variable should be interpreted as an index of the chick's body condition relative to it's size. We $\log_e$-transformed corticosterone metabolite concentrations to improve normality.

We used Akaike's information criterion adjusted for small samples sizes (AIC_c) and considered the model with the lowest AIC_c value to be the most parsimonious [12]. We determined the relative ranking of each model by subtracting each candidate model's AIC_c value from the best model. We calculated Akaike weights (w_i) to assess the weight of evidence that the selected model was the best model in the set of models considered [12]. We also calculated variable weights by summing Akaike weights across all models that included the variable to assess the relative importance of each variable. We calculated the model averaged estimates for coefficients and 95% confidence interval for each parameter across all models [12] and back transformed all estimates. We reported back transformed model averaged least squares means ± standard error (SE) for fecal corticosterone metabolites concentrations. Standard errors were calculated using the Delta method [67].

3. Results

3.1. Corticosterone metabolite validation studies

Serial dilutions of California gull chick fecal corticosterone metabolite extracts yielded displacement parallel to the standard corticosterone curve ($F_{3,10} = 0.50$, $P = 0.62$), demonstrated that the EIA kits were in fact measuring metabolites correctly as purported by the manufacturer. Mean recovery of the added exogenous corticosterone spike was 89.5% ± 8.1 (SE). Inter- and intra-assay coefficients of variation for corticosterone internal standards were 7% and 9%, respectively. Corticosterone metabolite concentrations of chicks captured and handled to induce a stress response (following our stress induction protocol) all increased over baseline metabolite concentrations after 8 h and then returned to near baseline concentrations after 24 h from their initial capture (Fig. 1).

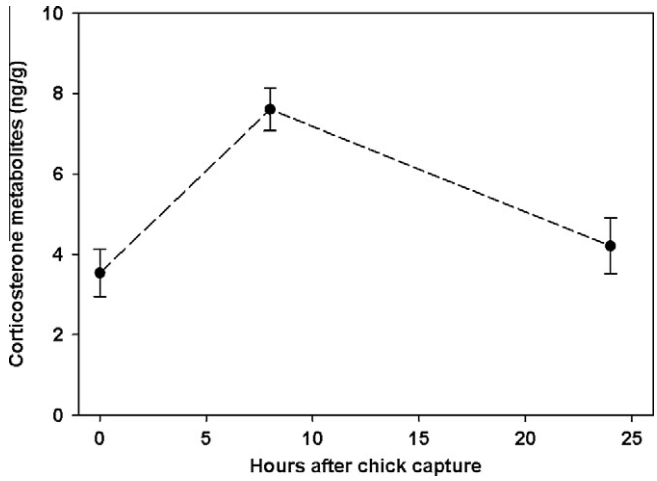

Fig. 1. Baseline (0 h) and stress-induced (>0 h) fecal corticosterone metabolite concentrations (ng/g) of three California gull chicks in San Francisco Bay, California. Chicks were stressed by capturing and holding them in shaded and screen-lined poultry cages for 1 h, then releasing them and re-capturing them 8 and 24 h after their initial capture.

3.2. Factors influencing gull chick corticosterone metabolites

The most parsimonious model explaining differences in California gull chick fecal corticosterone metabolite concentrations included the chick's location within colony (edge vs. center) and age (ninth primary feather length), with a model Akaike weight of 0.34 (Table 1). Three other models that included combinations of the chick's location within colony, age, and mass also provided reasonable fits to the data, although the log-likelihood values for these competing models did not improve substantially (Table 1). The weight of evidence suggested that the model containing the chick's location within the colony and age was 1.5, 2.3, and 2.6 times more likely than the next best models. Using variable weights to assess variable importance, we found that models containing chick age had a combined AIC_c weight of 0.95, followed by location within colony (0.61), mass (0.32), and colony size (0.13), indicating that chick age and location within the colony were the most important factors explaining chick fecal corticosterone metabolite concentrations. Model averaged least squares means indicated that fecal corticosterone metabolites were 44% higher at the edge of colonies than at the center of colonies ($\beta = 1.207$ [95% confidence interval = 1.029–1.415]; Fig. 2) and increased with chick age at a rate of 1% per 1 mm of ninth primary feather growth for feathers between 13 and 73 mm long ($\beta = 1.011$ [1.001–1.021]). Colony size and chick mass had a negligible effect on fecal corticosterone metabolites based on beta coefficient estimates with 95% CIs that overlapped 1.0 (small colony $\beta = 1.078$ [0.769–1.510], medium colony $\beta = 0.909$ [0.641–1.289], mass $\beta = 0.998$ [0.993–1.002]). Coefficient estimates that differed from 1.0 were considered evidence of effects.

4. Discussion

We found that corticosterone metabolite concentrations in California gull chicks were not related to colony size, but instead were related to the location that chicks were being raised within colonies. Mean fecal corticosterone metabolite concentrations in gull chicks raised near colony edges were 44% higher than chicks raised near colony centers. Increased fecal corticosterone metabolite concentrations reflect increased plasma corticosterone concentrations

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Table 1
Ranking of candidate models describing variables influencing fecal corticosterone metabolite concentrations in California gull chicks. Chicks were sampled at colony edges and colony centers at three nesting colonies that ranged in size from 150 to 11,554 nests in San Francisco Bay, California. Variables considered included colony size, location of chick within colony, age (as indexed with the length of the ninth primary feather), and mass.

Model structure	n	K[a]	Log likelihood	AIC_C[b]	ΔAIC_C[c]	w_i[d]
Location in colony + age	111	4	−166.66	341.70	0.00	0.34
Age	111	3	−168.19	342.60	0.90	0.22
Location in colony + age + mass	111	5	−166.36	343.30	1.60	0.15
Age + mass	111	4	−167.66	343.70	2.00	0.13
Colony size + location in colony + age	111	6	−166.40	345.60	3.90	0.05
Location in colony	111	3	−170.04	346.30	4.60	0.03
Colony size + location in colony + age + mass	111	5	−168.11	346.80	5.10	0.03
Colony size + age	111	7	−165.91	346.90	5.20	0.03
Colony size + age + mass	111	6	−167.55	347.90	6.20	0.02
Colony size + location in colony + colony size × location in colony	111	6	−168.50	349.80	8.10	0.00
Colony size + location in colony	111	5	−169.91	350.40	8.70	0.00
Colony size	111	4	−171.11	350.60	8.90	0.00
Global	111	9	−169.21	358.20	16.50	0.00
Intercept only	111	2	−181.19	366.50	24.80	0.00

[a] Number of estimated parameters in the model including the variance.
[b] Second-order Akaike's Information Criterium (AIC_c).
[c] The difference in the value between AICc of the current model and the value of the most parsimonious model.
[d] Likelihood of the model given the data, relative to models in the candidate set (model weights sum to 1.0).

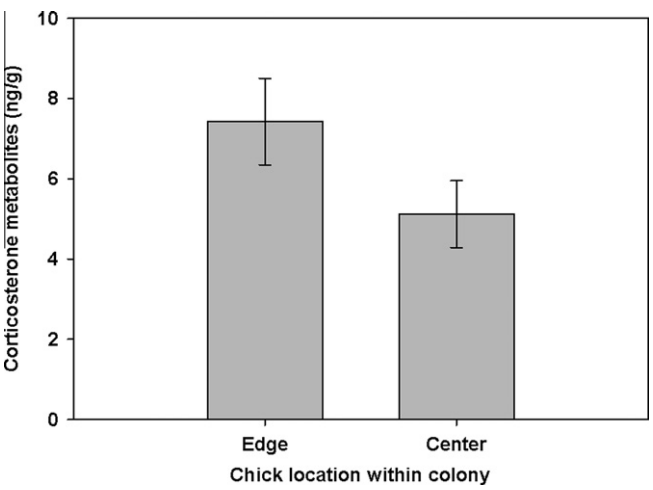

Fig. 2. Model averaged least squares mean ± SE fecal corticosterone metabolite concentrations (ng/g) in California gull chicks raised near the edge (n = 63) or center (n = 48) of colonies in San Francisco Bay, California.

[21,22,39]. Prolonged plasma corticosterone concentrations can cause muscle atrophy, neuronal cell death, and suppression of immune function [31,56]. For example, black-legged kittiwake (*Rissa tridactyla*) and red-legged kittiwake (*R. brevirostris*) chicks that had elevated corticosterone concentrations during the developmental period experienced impaired cognitive abilities associated with the ability to locate food [31,32]. Therefore, higher fecal corticosterone metabolite concentrations in California gull chicks being raised near colony edges might indicate individuals were in poorer physiological condition if these elevated fecal corticosterone metabolite concentrations reflect sustained increases in stress levels over time.

Older and more experienced adult California gulls tend to nest in the central regions of colonies, and younger less experienced breeders tend to be located near the edges of colonies [45,46]. In turn, less experienced and younger California gull parents tend to invest less in their offspring [45]. Bogdanova et al. [10] experimentally demonstrated that younger and less experienced Herring gulls (*Larus argentatus*) laid smaller eggs of poorer quality, with reduced albumin and water content, and this resulted in lower fledging success. Pugesek [45] found that younger and less experienced California gull parents provisioned their chicks less frequently and defended their territories less frequently than older and more experienced parents nesting in the center of colonies. Accordingly, California gull chicks raised near colony edges had higher fecal corticosterone metabolite concentrations and may have been more stressed than those chicks being raised in colony centers. Therefore, physiological condition might be one mechanism reducing reproductive success for birds nesting near colony edges.

We also found that older California gull chicks tended to have higher concentrations of fecal corticosterone than younger chicks, similar to other studies [see 47,59,61]. Previous studies have suggested that increased corticosterone concentrations with age may play a role in the breakdown of stored lipids used for growth in juvenile birds [15] and preparing for fledging [23,47,59]. Elevated fecal corticosterone metabolite concentrations in older chicks may also have been associated with increased movements of larger, non-flighted chicks [6]. California gull chicks move farther from nests as they age [73] and these movements often are associated with increased attacks from neighboring adults [20,26,73]. It remains unclear if the increases in corticosterone metabolites with chick age is a result of the increased movements and negative interactions with neighboring adults or if it has the effect of promoting increased breakdown of stored lipids to be used in growth.

The importance of location within colony (relative to the effect of age) on influencing fecal corticosterone metabolite concentrations suggests that California gull chicks raised near colony edges may have been exposed to increased stressors. The elevated corticosterone metabolite concentrations in chicks at colony edges may reflect an elevation in plasma corticosterone concentrations that allow a chick to respond to stresses associated with poorer quality parents. California gull chick fecal corticosterone metabolite concentrations were not related to body condition, suggesting that elevated corticosterone metabolite concentrations in chicks raised at the edges of colonies were not due to poor body condition. However, other, less-obvious physiological impairment such as reduced cognitive abilities [32] or survival [9] may occur with increased fecal corticosterone metabolite concentrations. Therefore, it remains unclear whether these elevated corticosterone metabolite levels will negatively impact chick fitness, and lead to lower reproductive success of gulls nesting near colony edges.

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