

Food availability and population processes: severity of nutritional stress during reproduction predicts survival of long-lived seabirds

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Summary

1. Life-history theory predicts a trade-off between costs of current reproduction and future survival of individuals. Studies of short-lived animals in general support this prediction. However, the effect of nutritional stress during reproduction on survival of long-lived animals is poorly understood.

2. We examined the link between nutritional stress, fecundity and return to a breeding colony (hereafter 'survival') of black-legged kittiwakes (*Rissa tridactyla*) at two colonies with contrasting patterns in adult survival, fecundity, and numerical trends.

3. We tested the observational (at Duck and Gull Is., Cook Inlet, Northern Gulf of Alaska) and experimental (at Middleton I., Gulf of Alaska) relationships between variations in the secretion of the stress hormone corticosterone (CORT) and food abundance. Then, we examined the relationships between nutritional stress (as reflected in CORT), reproduction, and survival of individuals.

4. On average, CORT was higher in kittiwakes breeding on Duck I. (declining, low fecundity, high survival) compared to those breeding on Gull I. (increasing, high fecundity, low survival).

5. At both colonies, CORT was directly negatively correlated with food abundance quantified at sea. Experimental feeding of individuals *ad libitum* resulted in a reduction of CORT in birds breeding on Middleton I. These results suggest that CORT is a reliable measure of food availability and defines nutritional stress (*stress*) in kittiwakes.

6. On Gull I., where survival is low (86%), production of young declined as *stress* increased. On Duck I., where survival is high (93%), parents always failed in raising young, though they experienced a wide range of *stress* levels.

7. Survival of individuals is linked to their CORT levels during reproduction. High levels of CORT predicted disappearance of individuals from both colonies.

8. The results support the hypothesis that nutritional stress during reproduction affects both survival and reproduction in long-lived animals. However, even within a species the ways in which survival and reproduction trade-off against each other may vary among populations. Results suggest that reproductive consequences of nutritional stress might differ between declining and increasing populations, which should be tested. We conclude that severity of nutritional stress during reproduction is one of the major factors defining population processes in kittiwakes.

Key-words: corticosterone, disturbance, kittiwake, life-history theory, stress hormone, trade-off

Introduction

The identification of causes and consequences of stress in populations of wild animals is a fundamental ecological

problem. During the past three decades, precipitous population declines have occurred among some seabirds in the North Pacific (Byrd, Schmutz & Renner 2008). It has been hypothesized that a long-term deterioration of food resources during reproduction resulted in food-related stress, which in turn reduced fitness of marine top-predators (Merrick, Loughlin & Calkins 1987; Piatt & Anderson

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1996; Piatt *et al.* 2007; Hunt *et al.* 2008). However, relationships between food availability and stress have been quantified only rarely in free-living animals (in seabirds, see Kitaysky, Piatt & Wingfield 2007), and the direct effect of food-related stress on survival of individuals has yet to be elucidated (Oro & Furness 2002; Grosbois & Thompson 2005; Sandvik *et al.* 2005). Here we provide observational and experimental evidence for food-related stress as a mechanistic link between fluctuations in food abundance during reproduction and survival of black-legged kittiwakes (*Rissa tridactyla*) at two colonies with contrasting patterns in numerical trends, adult fecundity and survival.

Food limitations have long been suggested to control seabird population dynamics via alteration of adult survival and fecundity (Lack 1966). Life-history theory predicts a trade-off between costs of current reproduction and future survival (Stearns 1992), and in long-lived seabirds, nutritional limitations are expected to affect fecundity rather than survival (Cairns 1987). Data from several systems support this prediction: changes in food abundance did not appear to affect adult survival in the herring gull *Larus argentatus* (Pons & Migot 1995); the Audouin's gull *Larus audouinii* (Oro, Pradel & Lerberston 1999; Oro *et al.* 2004); black-legged kittiwakes in Shoup Bay, Gulf of Alaska, (Golet *et al.* 2004); or in black-legged kittiwakes, common murre *Uria aalge*, and Atlantic puffins *Fratercula artica* in Hornoya, western Barents Sea (Sandvik *et al.* 2005). Yet, in other systems, i.e. black-legged kittiwakes in Shetland (Oro & Furness 2002); thick-billed murre *Uria lomvia* and razorbills *Alca torda* in Hornoya, western Barents Sea (Sandvik *et al.* 2005); common murre in Cook Inlet, Alaska, (Kitaysky, Piatt & Wingfield 2007), and little auks *Alle alle* at Kongsfjorden, Norway, (Welcker *et al.* 2009), parents experienced reduced survival in response to sub-optimal foraging conditions during reproduction. Surprisingly, these studies suggest that different populations of the same species of long-lived seabirds may resolve the survival/reproduction tradeoff differently.

Food shortages during reproduction are known to cause nutritional stress in adults of several species of seabirds, including kittiwakes (i.e. Kitaysky, Wingfield & Piatt 1999a; Buck, O'Reilly & Kildaw 2007; Benowitz-Fredericks, Shultz & Kitaysky 2008; Doody *et al.* 2008). Furthermore, several studies have linked nutritional stress and survival of affected individuals (Romero & Wikelski 2000; Kitaysky, Piatt & Wingfield 2007). However, the effect of nutritional stress during reproduction on survival of long-lived seabirds is still poorly understood. The issue is at least two-fold: (i) the trade-off between the life-history traits, such as adult survival and reproduction, may vary among closely-related species and populations within a species (i.e. Oro & Furness 2002 and Golet *et al.* 2004 for kittiwakes); and (ii) definitions, measures and interpretations of 'stress' vary drastically across studies (reviewed in Sapolsky, Romero & Munck 2000; Wingfield & Kitaysky 2002; Romero 2004; Romero, Dickens & Cyr 2009). Furthermore, given the multitude of factors (and logistical difficulties) determining food availability in marine environments (i.e. Cairns 1987), most studies rely on qualitative

('good' vs. 'poor') rather than quantitative measures of food availability. However, the relationship between adult survival and food availability is likely to depend on the severity of nutritional stress incurred by breeding individuals (predicted – Erikstad *et al.* 1998; observed – Kitaysky, Piatt & Wingfield 2007). Thus, the mixed evidence on the relationship between adult survival and food availability may be the result of observing study systems under different levels of nutritional limitation.

Traditional methods for measuring food-related stress in free-living seabirds are not always effective (Piatt *et al.* 2007). In this context, food-related stress can be defined as changes in the physiological condition of individuals experiencing a shortage of food that affects their fecundity and/or post-reproductive survival. In this study we used a field endocrinology approach to measure stress, identify its causes and to examine the hypothesized link between severity of food-related stress and population processes. Birds respond to food stress by increasing secretion of the steroid hormone corticosterone (CORT, the primary avian glucocorticoid). Results of controlled experiments suggested a direct relationship between food availability and secretion of stress hormones in birds (Kitaysky *et al.* 1999b; Kitaysky, Wingfield & Piatt 2001; Pravosudov *et al.* 2001; Lynn, Breuner & Wingfield 2003; Pravosudov & Kitaysky 2006). In free-living birds, food abundance was directly negatively correlated with CORT (Kitaysky, Piatt & Wingfield 2007), and experimental food supplementations also reduced CORT secretion (Lanctot *et al.* 2003; Clinchy *et al.* 2004). However, effects of food supplementation on CORT are not consistent across the reproductive season (e.g. Lanctot *et al.* 2003), probably reflecting the severity of nutritional limitations incurred by breeding individuals. Specifically, the effect of supplementation would be apparent only if natural food availability is limiting and causing nutritional stress in non-supplemented (control) individuals.

The field endocrinology approach offers an opportunity to discriminate between short-term and chronic effects of food stress on free-living individuals (Kitaysky, Piatt & Wingfield 2007). Baseline (measured in the blood of undisturbed birds immediately after capture) CORT concentrations increase quickly (within hours-days) in response to a food shortage (Lynn, Breuner & Wingfield 2003; Edwards 2004). During prolonged food shortages, when animals are exposed to chronically elevated baseline CORT secretion, their adrenal capacity is enhanced (Akana *et al.* 1992; Dallman *et al.* 2004), which results in higher maximum CORT production in response to a standardized stressor (capture, handling and restraint, *sensu* Wingfield 1994; hereafter called 'acute stress'). Thus acute stress-induced CORT levels may provide an integrative measure of an individual's nutritional history over longer time periods (weeks) than baseline CORT (days) (Kitaysky, Piatt & Wingfield 2007). This is relevant to a study of the relationship between adult survival and food availability because the magnitude of the adrenocortical response to an acute standardized stressor might reflect the duration of an individual's exposure to sub-optimal foraging conditions. In other words, baseline CORT provides evidence of a short-

term exposure to food shortages, whereas acute stress-induced CORT indicates the duration and severity of food shortages. Both measures of CORT have been shown to correlate negatively with survival of animals; however, in some cases, a negative correlation between acute stress-induced, but not baseline, CORT and survival was found (Romero & Wikelski 2001; Blas *et al.* 2007), whereas in others baseline CORT was found to predict survival (Brown *et al.* 2005; Kitaysky, Piatt & Wingfield 2007). Since survival is likely to depend on the severity and duration of a food shortage, both measures of nutritional stress might be useful.

The goals of this study were: (i) to quantify a relationship between variations in food abundance and nutritional stress in breeding seabirds, and (ii) to test a link between severity of stress during reproduction and the patterns of fecundity and survival of individuals.

Materials and methods

LONG-TERM OBSERVATIONAL STUDY

We conducted this study at two major seabird colonies in Cook Inlet, Gulf of Alaska, from May–August in 1996–2002. The colonies are about 100 km apart and are situated in oceanographically distinct habitats (Robards *et al.* 1999; Robards, Rose & Piatt 2002). Duck Island (west side of Cook Inlet; 60°09'N, 152°34'W) is surrounded by weakly stratified, relatively warm estuarine waters, whereas Gull Island (east side of Cook Inlet; 59°35'N, 151°19'W) is surrounded by colder, oceanic waters with warm surface layers that result from runoff (Robards *et al.* 1999). Kittiwakes are more numerous on Duck I. colonies (approx. 10 000 breeding pairs) compared to Gull I. colonies (approx. 5000 breeding pairs). However, the numbers of birds breeding steadily declined at Duck Island (−4.3% per year) and increased at Gull Island (+8.8% per year) over the last three decades (Piatt & Harding 2007; Piatt *et al.* 2007). During this study, fecundity of kittiwakes was relatively higher on Gull I. (0.599 chicks/breeding pair) than on Duck I. (0.016 chicks/breeding pair); whereas adult mortality was consistently lower at Duck I. (6.7% pa) than at Gull I. (14.5% pa) (Piatt 2004; Piatt & Harding 2007).

In Cook Inlet, birds were captured from their nests using 9-m long noose poles. In each year, we aimed to sample 10 birds approximately every 2 weeks during May–August. At each colony and sampling period, an effort was made to minimize disturbance to focal birds prior to their capture and to evenly distribute sampling among the pool of accessible nests across the colony. Logistically our samplings goals were not always possible and consequently we did not sample birds in all years/stages (Fig. 1). Reproductive stages (from egg-laying through hatching, hereafter called 'incubation', and chick-rearing) and breeding status of birds were verified by the presence of eggs or chicks at the capture site.

EXPERIMENTAL STUDY

Free-living black-legged kittiwakes nest on a modified radar tower on Middleton Island (Gulf of Alaska, 59°26'N, 146°20'W). All nest sites are on wooden ledges that were constructed on the outside face of the tower, and can be accessed from inside the tower (see Gill & Hatch 2002 for details). Nest sites are individually fitted with a sliding one-way mirror that permits access to individual nests sites from within the tower. Each site is equipped with a PVC feeding tube which allows

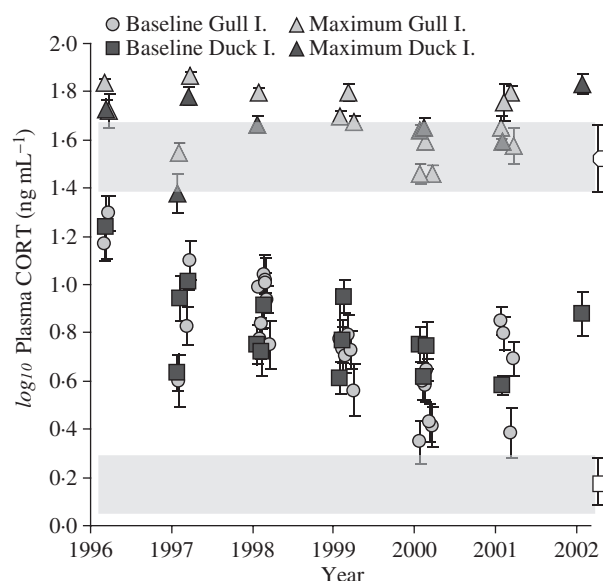


Fig. 1. Inter-annual (1996–2002) and intra-seasonal (grouped by sampling dates) dynamics of baseline ($n = 419$) and maximum ($n = 186$) CORT (mean \pm SE) in black-legged kittiwakes breeding on Duck and Gull Islands, Cook Inlet, Alaska. Open symbols and shaded areas denote (mean \pm SD) baseline CORT (open square) and maximal CORT (open circle) in adult black-legged kittiwakes experimentally fed *ad libitum* on Middleton I. ($n = 19$).

supplementary food provisioning to nest occupants. During the reproductive season of 2004, each day, birds (parents and their chicks) at 'fed' nests were given fish 3 times per day at 0900, 1400 and 1800. At each feeding, whole capelin (*Mallotus villosus*) were offered one at a time, until nest occupants refused to take additional fish. Birds at this site are marked with unique combinations of leg bands. Birds (19 supplementary fed and 13 control individuals) were captured during chick-rearing by sliding a wire leg hook under the window – legs hooks prevented departure for the several seconds needed to open the window and bring the bird inside the tower for blood sampling.

BLOOD SAMPLING

For all birds (419 in Cook Inlet and 32 on Middleton I.), initial blood samples were taken within 3 min of capture [on average, 2.18 ± 0.77 (SD) and 1.8 ± 0.78 (SD) min, in Cook Inlet and Middleton I. respectively]. In general for birds, it takes at least 3 min for levels of CORT to begin to rise in the blood in response to capture (reviewed in Romero & Reed 2005). In this study, the time after capture, within 3 min following the capture, did not affect CORT levels (Cook Inlet: $R^2 = 0.0002$, $F_{1,417} = 0.069$, $P = 0.794$; Middleton I.: $R^2 = 0.0023$, $F_{1,30} = 0.068$, $P = 0.796$). In Cook Inlet, the duration of colony disturbance (e.g. an investigator's presence in the vicinity of breeding cliffs prior to capture of a focal individual) also did not affect CORT levels in blood samples taken within three minutes after capture (see Appendix S1 in Supporting Information). Thus, we considered the first sample (taken within 3 min after capture) as a baseline measure of circulating CORT. Some birds in Cook Inlet and all the birds on Middleton were then held in breathable mesh bags and additional blood samples were taken at 10, 30 and 50 min post-capture. Because the rate at which CORT levels rise can differ among individuals (e.g. Cockrem & Silverin 2002; Cockrem 2004), for each bird we chose the sampling point which yielded the highest levels of CORT; in all cases this was the 30 or 50 min sample. This parameter

(maximum CORT level attained in response to a standardized stressor, hereafter called 'maximum CORT') reflects the birds' ability to produce CORT. All bleeds were taken from the brachial vein, blood samples were kept on ice until centrifugation to separate the plasma from the red blood cells. Plasma was drawn off red blood cells and kept frozen until assayed for CORT. While being held, birds were measured and banded with metal US Fish and Wildlife bands and a unique combination of colour plastic bands, which ensured that no individual was sampled twice and allowed us to monitor individual birds (see below).

Despite the different (and potentially less disturbing) capture method, levels of CORT in blood samples (baseline and acute stress-induced) of birds on Middleton I. were within the range of CORT levels previously reported in long-term studies of free-living black-legged kittiwakes captured using noose poles (Buck, O'Reilly & Kildaw 2007; Shultz & Kitaysky 2008; also see Appendix S2 in Supporting Information). Thus, the different capture techniques were not likely to bias comparisons of CORT levels between Middleton I and Cook Inlet kittiwakes.

HORMONE ASSAY

Total corticosterone was measured using a radioimmunoassay (as previously described in Kitaysky, Wingfield & Piatt 1999a). For each sample, 20 μ L of plasma were equilibrated with 2000 cpm of tritiated corticosterone prior to extraction with 4.5 mL distilled dichloromethane. After extraction, percent tritiated hormone recovered from each individual sample was used to correct final values. Samples were reconstituted in PBSG-buffer and combined with antibody and radiolabel in a radioimmunoassay (for general references on methodology see Wingfield & Farner 1975; Wingfield & Kitaysky 2002). Inter-assay variation, measured by assaying the 1 ng mL⁻¹ of corticosterone standard in each assay, was less than 10% and it did not co-vary with differences measured in plasma.

BEACH SEINES AND MID-WATER TRAWLS

We conducted the concurrent measurements of food abundance and CORT on a regular schedule, which allowed us to examine the relationship between CORT levels and food abundances during within the current week (June–August of 1996–1999) for beach seines and within the current 2 weeks (late June – early August of 1996–1999) for mid-water trawls. We used beach seines to measure forage fish abundance in waters adjacent to breeding colonies where birds foraged, and mid-water trawls within a foraging range of kittiwakes (50 km) around each colony (for general methods see Cailliet, Love & Ebeling 1986; detailed methods are described in Robards *et al.* (1999), Abookire, Piatt & Robards (2000), Abookire & Piatt (2005)). Seine catch-per-unit-effort (CPUE) mirrored patterns of fish abundance offshore in mid-water trawls (CPUE) and hydro-acoustic surveys (Robards *et al.* 1999; Abookire, Piatt & Robards 2000; Piatt 2002). CPUEs were calculated as the total catch of all fish per seine averaged by site and sampling period. Catches consisted (>99%) of sand lance (*Ammodytes hexapterus* Pallas), pacific herring (*Clupea harengus pallasii*), and *Salmonidae*, *Osmeridae*, and *Gadidae* (Piatt *et al.* 2007). The body length of forage fishes sampled in beach seines in general matched the size of ones captured by birds (Piatt 2002). These fish species comprised >90% of seabirds diets during this study (Kitaysky, Wingfield & Piatt 1999a; Piatt 2002). CPUE data were $\log(x + 1)$ transformed to meet assumptions required for parametric statistical procedures (Zar 1999).

REPRODUCTIVE PERFORMANCE

We examined relationships between CORT levels and estimates of reproductive performance at all colonies from 1996–2001. Reproductive parameters were assessed using study plots and standardized methods (Piatt *et al.* 2007). Breeding parameters were calculated as the mean of plot means. We quantified timing of breeding as the mean of plot medians for lay date. We calculated laying success as the number of nests with eggs per number of active nests, hatching success as the number of eggs laid that hatched, and fledging success as the number of chicks fledged per number of chicks hatched. Chicks were considered to have 'fledged' successfully if they disappeared from the nest site \geq 32 days after hatching, because 32 days is the minimum nest departure age for black-legged kittiwake chicks in our study and we never observed mortality in chicks older than 32 days. Fledging success of birds breeding on Middleton I. in 2004 was estimated using the same protocol.

SURVIVAL

We examined the relationship between CORT levels in individuals during a given reproductive season and presence of those individuals at the colony during subsequent reproductive seasons. We distinguished our estimate of survival from an estimate of 'true' survival, because we did not survey all colonies in the region and thus are not able to distinguish between mortality and emigration (Oro *et al.* 2004) when a bird was subsequently absent from the colony at which it was banded. To measure survival of birds at all three colonies, we captured adult breeding birds (actively attending a nest-site, egg or chick) and marked them (as described above). We collected blood from captured individuals for CORT and genetic analysis of gender (only a sub-sample of birds was genetically sexed, see below). In subsequent years we conducted re-sighting by intense daily searches throughout the colony for about 6 weeks per year, starting at egg-laying and continuing until re-sighting curves reached a plateau, indicating that all marked birds present at the site had been encountered (Hatch, Roberts & Fadley 1993). Several years of re-sighting effort are recommended to ensure re-sighting of individuals that were present in a colony but may be missed if re-sighting effort is limited to only one or two subsequent years (Lebrereton *et al.* 1992). With 5 years of effort, including 4 years (1996–2000) of banding followed by 4 years (1997–2001) of re-sighting, and using only individuals with complete re-sighting histories, we were able to distinguish among three scenarios of a bird's persistence in a colony in relation to its CORT during current reproductive season. Specifically, individuals were either: (i) re-sighted at the colony in the following year (hereafter 're-sighted'); (ii) skipped the following year but were re-sighted during one or both of the two subsequent years ('skipped'); or (iii) were not re-sighted during the following season and during two subsequent years ('disappeared').

SEX DETERMINATION

To identify gender of birds, we extracted genomic DNA from blood samples following the salt-extraction protocol described in Medrano, Aasen & Sharrow (1990) and modified as in Sonsthagen, Talbot & White (2004). We amplified DNA of 206 individuals using standard polymerase chain reaction (PCR) conditions using the P8/P2 primer set to determine gender of each bird, based on the chromo-helicase-binding domain (CHD) gene (Griffiths *et al.* 1998). Sex was assigned based on the absence (male:ZZ) or presence (female:ZW) of the band for the *W*

chromosome. For quality control purposes, DNA from approximately 20% of samples was re-extracted and re-processed.

DATA ANALYSIS

All analyses were conducted using STATISTICA statistical package. Data were log-transformed to meet assumptions for parametric tests (Zar 1999). Statistical analyses consisted of the following steps.

Measuring stress and identifying its causes

First, to examine whether differences in baseline CORT are intrinsic to a colony (Duck I. vs. Gull I.), and/or to the reproductive stage (incubating and/or chick-rearing), we used the information-theoretic approach to identify suitable models for predicting stress (CORT) in adults (Burnham & Anderson 1998; Anderson, Burnham & Thompson 2000). Specifically, we examined the relative contribution of colony, reproductive stage, and year, based on ANOVA, multiple regression, and ANCOVA approximating models. We tested 10 approximating models in this analysis (Table 1). We calculated the Akaike Information Criterion for each approximating model using the formula $AIC = N \ln(\sigma^2) + 2K$, where N is sample size, σ^2 is residual sum of squares from a model divided by N , and K is the number of parameters estimated in each model. We converted AIC to AIC_c values, which is recommended when sample sizes are small relative to the number of parameters being estimated (Burnham & Anderson 1998). The model with the lowest AIC_c was considered the best. Then we calculated the Akaike weights (W_i) for each model using the formula: $W_i = (\exp(-0.5 \times \Delta_i) / \sum_{r=1}^R \exp(-0.5 \times \Delta_r))$. These values indicate the approximate probabilities that model i is the best model in the set of models considered, and the relative likelihood that model i is better than model j is W_i/W_j . Second, we used ANCOVA of the best approximating model identified in the previous step and food abundances during current week as a covariate. Finally, to elucidate importance of food abundance in determining CORT levels, we used linear regression analyses of mean colony-specific CORT measured within current week against mean food abundances measured during same time period (2 weeks period in case of mid-water trawl CPUE).

Testing the relationships between CORT and reproductive performance

We relied on estimates of reproductive performance derived on a colony-wide (in case of Middleton 'treatment-wide') basis. In Cook Inlet, concurrent sampling of birds for determination of CORT and reproductive performance was done on different groups of birds to avoid

possible effects of capture on estimates of reproductive performance. Relationships between baseline CORT levels and measures of the reproductive performance were similar between Cook Inlet colonies at the incubation stage (parallelism of slopes tests with P -values > 0.1). We used correlation analyses to examine relationships between means of colony/year/stage specific CORT and reproductive performance values for incubation pooling data for both colonies. The relationship between CORT and reproductive performance at the chick-rearing stage was different between Cook Inlet colonies, therefore we conducted ANCOVA (homogeneity of slopes model) followed by correlation analyses separately for each colony.

Testing the relationships between CORT and survival

A detailed comparison of adult kittiwakes' survival between Duck and Gull colonies has been conducted (Piatt 2004; Piatt *et al.* 2007). The specific goal of the current study was to determine survival of individuals in relation to food-related stress they have experienced, and thus we used a sub-set of all available data that included only individuals with complete re-sighting histories that were also sampled for CORT and not otherwise manipulated ($n = 281$). We used a two-way ANOVA with baseline CORT levels as a dependent variable and colony, fate of birds (re-sighted, skipped, and disappeared as defined above) and interaction between colony and fate as factors. To test the effect of gender, we included sex of individuals as a factor; sample sizes were not sufficient to examine this relationship for each colony. Sample sizes were also not sufficient to examine maximum CORT levels in relation to re-sighting categories with colony (or sex) as a factor, therefore that test was conducted separately on data limited to Gull I. only and on data pooled for both colonies. For pair-wise comparisons of the means we used Tukey HSD post-hoc tests.

Testing the effect of supplemental feeding on CORT

We conducted ANOVAS on baseline and maximum CORT where treatment was used as factor. Average age of chicks was similar between treatments and was not included in analyses.

Results

CORT LEVELS – OBSERVATIONAL STUDY

Baseline corticosterone

Information-theoretic modelling. The information-theoretic approach identified a model with Year, Colony, Stage, and

Table 1. Models of baseline levels of CORT ($n = 419$) in black-legged kittiwakes breeding on Duck and Gull Island colonies during 1996–2002 using theoretic information criteria

Variables	K	ΔAIC_c	SSE	W_i	Evidence ratio
Colony, year, stage, colony \times year, colony \times stage	9	0.000	36.184	0.430	1.00
Colony, year, stage, colony \times year	7	1.294	36.659	0.225	1.91
Colony, year, stage	5	2.419	37.122	0.128	3.35
Colony, year	4	3.253	37.378	0.085	5.09
Year	3	3.550	37.587	0.073	5.90
Stage, year	4	3.991	37.444	0.058	7.36
Colony, stage	4	50.776	41.867	0.000	106150689950.39
Stage	3	53.841	42.380	0.000	491497167134.04
Colony	3	56.388	42.639	0.000	1756213128015.96
Constant	2	57.026	42.911	0.000	2415670074444.53

Table 2. Effects of year, colony, reproductive stage and CPUE (food abundance in terms of catch per unit effort) on baseline CORT in black-legged kittiwakes breeding on Duck I. and Gull I

Factor	d.f.	MS	d.f.	<i>F</i>	<i>P</i>
	Effect	Effect	Error		
(a) Model with no measures of food abundance included (<i>n</i> = 419)					
Year	1	3.314	414	37.82	0.000000
Colony	1	0.674	414	7.69	0.005798
Stage	1	0.665	414	7.58	0.006146
Colony × year	1	0.673	414	7.68	0.005836
Colony × stage	1	0.475	414	5.42	0.020402
(b) Model with food abundance measured by beach seine CPUE (<i>n</i> = 153)					
Year	1	0.533	146	6.49	0.011909
Colony	1	0.153	146	1.86	0.174152
Stage	1	0.000	146	0.00	0.995971
Colony × year	1	0.126	146	1.53	0.218372
Colony × stage	1	0.025	146	0.30	0.585172
Beach seine CPUE	1	0.379	146	4.61	0.033502
(c) Model with food abundance measured by mid-water trawl CPUE (<i>n</i> = 49)					
Colony	1	0.022	46	0.35	0.556846
Mid-water trawl CPUE	1	1.280	46	20.35	0.000044
Colony × mid-water trawl CPUE	1	0.025	45	0.40	0.531407

Colony × stage and Colony × year interaction terms as the best approximating model for variations in baseline CORT of kittiwakes breeding in Cook Inlet (Table 1).

Univariate analysis of the best approximating model. Corticosterone declined during the observation period 1996–2002 (Fig. 1; year effect: $\beta = -0.34$; Table 2a); average CORT level over the duration of the study was higher on Duck I. compared to Gull I. (colony effect: $\beta = +0.09$; Table 2a), and it was also higher during late season compared to early season (stage effect: $\beta = +0.08$; Table 2a). Significant interaction terms (Colony × year and Colony × stage effects; Table 2a) indicate that inter-colony differences in CORT were not always consistent between years and reproductive stages, and suggest that fluctuations in baseline CORT can not be attributed to the effects of colony and reproductive stage *per se*, rather they reflected changes in ecological factors. Including a measurement of food (beach seine CPUE) as a covariate in the best approximating model confirmed this. Specifically, the effects of Colony, Stage, Colony × year, and Colony × stage disappeared and the effect of year diminished when variations in food abundance was controlled for (Table 2b).

Food abundance measured by two independent techniques was in both cases directly negatively correlated with baseline levels of CORT (Table 2b and c; Fig. 2).

Maximum acute stress-induced corticosterone

Maximum CORT levels were not different between colonies (Colony effect: $F_{1,181} = 0.98$, $P = 0.324$; Fig. 1). Maximum CORT levels were higher in chick-rearing compared to incubating birds (Stage effect: $F_{1,181} = 12.61$, $P = 0.0005$), and the stage effect was consistent between colonies (Colony × stage interaction term: $F_{1,181} = 1.99$, $P = 0.161$).

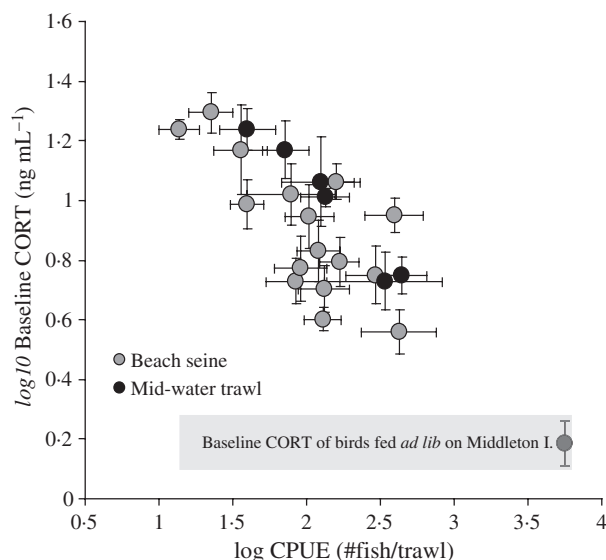


Fig. 2. The relationships between baseline CORT and food abundance in black-legged kittiwakes breeding on Duck and Gull Is. during 1996–1999 (mean ± SE; light grey circles – beach seine CPUE; black – mid-water trawl CPUE). Shaded area denotes baseline CORT (mean ± SD) in adult black-legged kittiwakes experimentally fed *ad libitum* on Middleton I. Baseline CORT (both colonies and all 4 years combined) levels were negatively correlated with both measures of food abundance – beach seine CPUE ($R^2 = 0.53$, $F_{1,15} = 15.66$; $P = 0.0014$, $N = 16$) and mid-water trawl CPUE ($R^2 = 0.96$, $F_{1,5} = 99.5$; $P = 0.0006$, $N = 6$).

Concurrent data for food abundance and maximum CORT were available for seven sampling periods only (both colonies and all years combined). Small sample sizes did not allow us to test the direct relationship between food abundance and maximum CORT. However, because baseline

CORT is a reliable proxy for food abundance (see above), we examined the relationships between max and baseline CORT levels. We found that max CORT was positively (but weakly) correlated with baseline CORT measured in the same individuals ($R^2 = 0.15$, $F_{1,189} = 33.4$, $P < 0.0001$; $n = 191$). Average colony-date specific maximum CORT levels were more strongly positively correlated with average colony-date specific baseline CORT measured 2 weeks prior ($R^2 = 0.38$, $F_{1,9} = 5.6$, $P = 0.042$; $n = 11$). These results suggest that maximum CORT is likely to reflect food availability within a period of days to weeks prior to sampling.

CORT LEVELS – EXPERIMENTAL STUDY

Baseline CORT levels were lower in individuals fed *ad libitum* compared to controls (Treatment effect: $F_{1,30} = 11.72$, $P = 0.0018$; Fig. 3a). Experimental treatment also affected the adrenocortical response to acute stress of handling and restraint - maximum CORT levels of individuals fed *ad libitum* were lower compared to those of controls (Treatment effect: $F_{1,30} = 10.36$, $P = 0.0031$; Fig. 3b). Baseline and maximum CORT of individuals fed *ad libitum* were lower than (i.e. baseline) or similar to (i.e. maximum) the lowest CORT levels measured in birds breeding in Cook Inlet (Figs 1 and 2). CORT levels of control individuals (unfed)

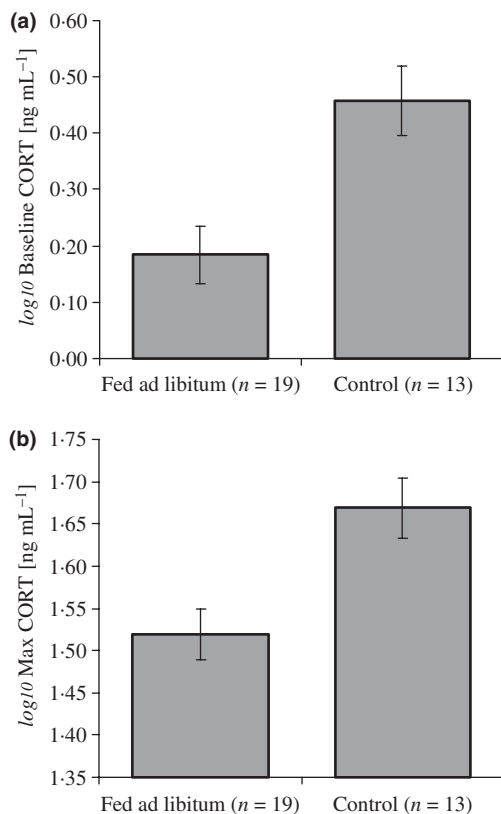


Fig. 3. Effect of experimental feeding *ad libitum* on (a) baseline and (b) maximum acute stress-induced levels of CORT (mean \pm SE) in black legged kittiwakes breeding on Middleton I.

were at the low end of the range of CORT levels measured in Cook Inlet (see Figs 1 and 3).

BASELINE CORT AND REPRODUCTIVE PERFORMANCE

Baseline CORT at the incubation stage was positively correlated with egg-laying chronology (high CORT associated with delayed egg-laying; $R = 0.87$, $P = 0.002$, $N = 9$; Fig. 4a), negatively correlated with laying success ($R = -0.75$, $P = 0.021$, $N = 9$), and was not significantly correlated with clutch size ($R = -0.51$, $P = 0.161$, $N = 9$) or hatching success ($R = -0.42$, $P = 0.267$, $N = 9$).

Striking inter-colony differences in the relationship between baseline CORT of brooding (chick-rearing birds) and colony-wide fledging success was found (Colony effect: $F_{1,5} = 88.9$, $P = 0.0002$; baseline CORT effect: $F_{1,5} = 9.92$, $P = 0.025$; Colony \times baseline CORT interaction term: $F_{1,5} = 13.51$, $P = 0.014$; Fig. 4b). On Gull I., baseline CORT was negatively correlated with fledging success ($R = -0.94$, $P = 0.018$, $N = 5$; Fig. 4b), whereas on Duck I. birds almost always completely failed regardless of baseline CORT (Fig. 4b). A comparison of reproductive performances of Middleton I. supplemental feeding and control treatments suggest that CORT was higher and fledging success was lower in controls compared to fed birds (Fig. 4b).

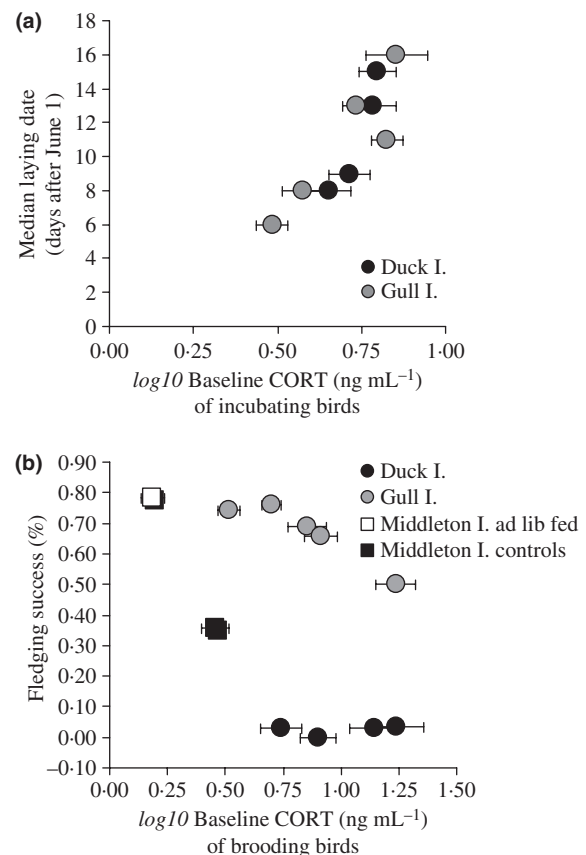


Fig. 4. The relationships between CORT (mean \pm SE) and colony-wide reproductive performance at (a) incubation and (b) chick-rearing.

CORT AND SURVIVAL

Baseline CORT, Cook Inlet. There was a significant difference in baseline CORT among re-sighted, skipped and disappeared birds at colonies in Cook Inlet (Re-sighting category effect: $F_{2,275} = 4.46$, $P = 0.012$; Fig. 5a). The relationship between baseline levels of CORT and re-sighting of kittiwakes at the colonies was similar between Duck and Gull colonies (Colony effect: $F_{1,275} = 0.33$, $P = 0.566$; Colony \times re-sighting interaction term $F_{2,275} = 0.35$, $P = 0.709$). Baseline CORT levels were higher among birds that were not re-sighted during three consecutive reproductive seasons (disappeared; Fig. 5a) compared to birds that were re-sighted during a following reproductive season (Tukey post-hoc $P < 0.001$). CORT levels in birds that skipped the next season but were re-sighted during the following two seasons were not different from those in birds that disappeared ($P = 0.146$) or were re-sighted ($P = 0.413$).

In a smaller dataset ($N = 175$; data for both colonies were combined for this analysis because an insufficient number of known sex individuals among 'skipped' and 'disappeared' birds were sampled at Duck I.), where sex of birds was determined, there was still a significant effect of re-sighting (Re-sighting category effect: $F_{2,169} = 4.49$, $P = 0.013$). There were no differences in baseline CORT among re-sighted,

skipped and disappeared males and females (Sex effect: $F_{1,169} = 0.073$, $P = 0.788$; Sex \times re-sighting interaction term $F_{2,169} = 0.16$, $P = 0.852$).

Maximum CORT, Cook Inlet. There was a significant difference in maximum CORT among re-sighted, skipped and disappeared birds at Gull I. (Re-sighting category effect: $F_{2,61} = 4.03$, $P = 0.023$). Sex of birds did not affect this relationship (Sex effect: $F_{1,43} = 0.91$, $P = 0.765$). There was also a significant difference in maximum CORT among re-sighted, skipped and disappeared birds when data for both colonies were pooled (Re-sighting category effect: $F_{2,84} = 4.63$, $P = 0.012$; Fig. 5b). For the later dataset, maximum CORT levels were higher among birds that were not re-sighted during three consecutive reproductive seasons (disappeared; Fig. 5b) compared to birds that were re-sighted during a following reproductive season (Tukey post-hoc $P = 0.018$). CORT levels in birds that skipped next season but were re-sighted during the following two seasons were not different from those in birds that disappeared ($P = 0.276$) or were re-sighted ($P = 0.616$).

Baseline and maximum CORT, Middleton I. All controls and experimentally fed individuals ($n = 32$) were re-sighted during the following season (Fig. 6).

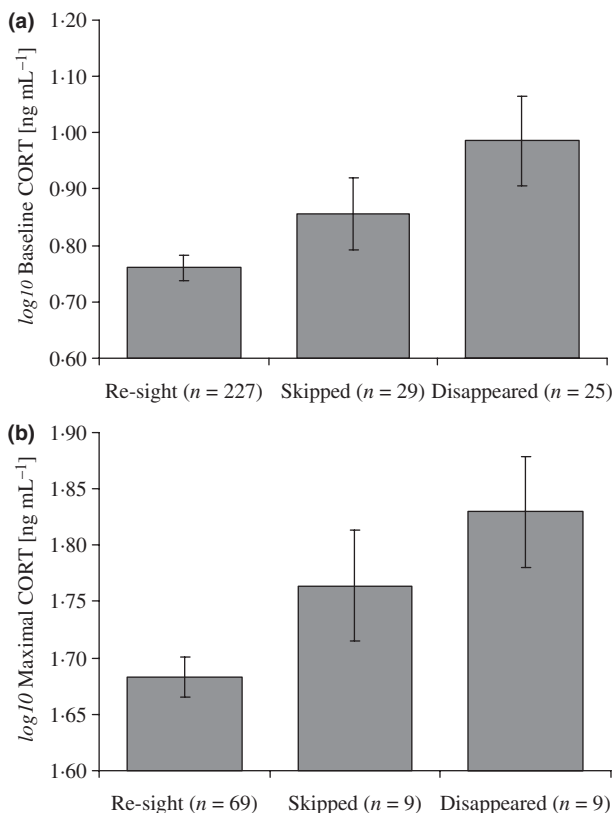


Fig. 5. Survival of adult black-legged kittiwakes in colonies on Duck & Gull Is. in relation to their (a) baseline CORT; and (b) maximal acute stress-induced CORT. CORT shown as mean \pm SE, sample sizes (n) in groups with different re-sighting histories are reported in parenthesis.

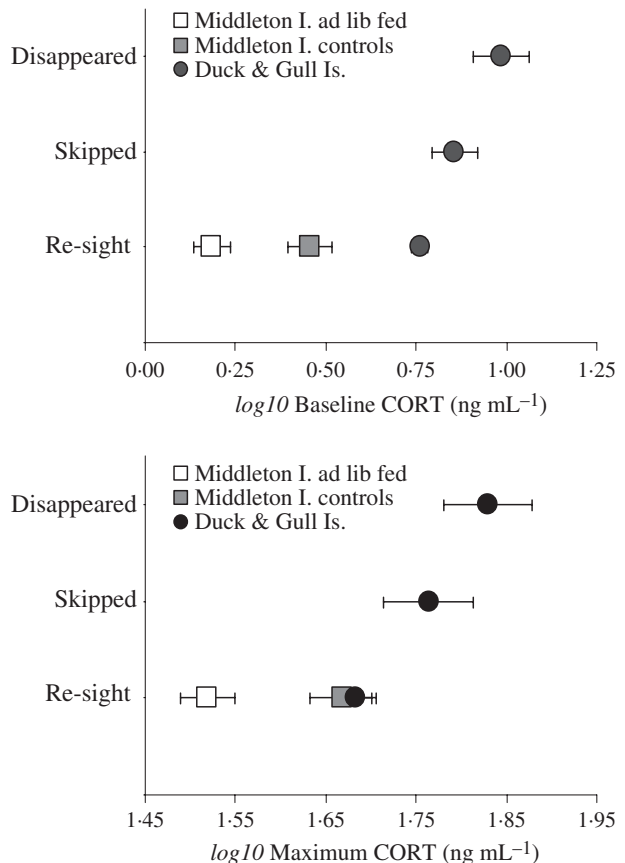


Fig. 6. Re-plot of data from Figs 3 and 5 to illustrate the idea that survival of black-legged kittiwakes depends on food availability in a 'threshold' manner. CORT levels (upper panel – baseline; low panel – maximum acute stress-induced) are used as proxy for food availability.

Discussion

Fluctuations in availability of food have long been hypothesized to play a major role in regulating seabird populations. In this study we used a field endocrinology approach to measure stress, identify its causes, and examine the hypothesized link between food-related stress and population processes in the black-legged kittiwake. A long-term series of measurement of stress and food abundance, and a controlled experiment manipulating food intake of free-ranging individuals, allowed us to establish (i) a direct link between changes in food abundance and stress status of individuals; (ii) negative effects of food-related stress on fecundity; and (iii) negative effects of food-related stress on local survival of individuals. Results support the study hypothesis: nutritional stress affected fecundity and survival of individuals. Severity of stress determined how specific fitness components were affected – initial increases of nutritional stress resulted in fecundity losses, whereas further deterioration of foraging conditions affected adult survival. The most interesting finding is that although kittiwakes incurred comparable nutritional stress levels at both colonies, Gull I. kittiwakes continued to invest in reproduction under sub-optimal conditions, which probably resulted in overall elevated post-breeding mortality at that colony (Piatt *et al.* 2007). In contrast, over the same range of conditions Duck I. kittiwakes consistently failed in their reproductive efforts, and exhibited higher survival (Piatt *et al.* 2007). This suggests that, even within a species and geographic region, the ways in which survival and reproduction trade-off against each other may vary among colonies.

CORT AS A MEASURE OF NUTRITIONAL STRESS

Corticosterone is an important regulator of energy metabolism and thus is expected to fluctuate during nutritional limitations (reviewed in Sapolsky, Romero & Munck 2000; Romero 2004). Consequently, several studies suggested that CORT may provide information on the stress status of individuals in relation to abundance of their food (Kitaysky, Wingfield & Piatt 1999a; Romero & Wikelski 2000; Lanctot *et al.* 2003; Clinchy *et al.* 2004; Kitaysky, Piatt & Wingfield 2007). However, using CORT as a direct measure of food availability in free-ranging animals has been somewhat controversial (e.g. Lanctot *et al.* 2003). One concern is that CORT production in birds may reflect population-specific parameters and/or endogenous changes in physiology of individuals at different stages of their life cycle (i.e. Wingfield 1994; Romero, Ramenofsky & Wingfield 1997; Kitaysky *et al.* 1999b; Romero 2002; Landys, Ramenofsky & Wingfield 2006). Another possibility is that CORT may be released in response to a wide range of adverse environmental conditions unrelated to food (Wingfield 1994; Wingfield, Bruener & Jacobs 1997). It was also not well known whether elevated levels of CORT would only be associated with famine (i.e.

Romero & Wikelski 2000), or might also reflect moderate changes in food supplies (i.e. Kitaysky, Piatt & Wingfield 2007).

We have previously addressed some of these concerns using observational studies of free-ranging seabirds (Kitaysky, Piatt & Wingfield 2007; Benowitz-Fredericks, Shultz & Kitaysky 2008; Shultz & Kitaysky 2008). In this current study we present further observational and experimental evidence for CORT secretion as a quantitative link between changes in food abundance and stress status in seabirds. Contrary to the first argument, a long-term series of data in our study revealed that secretion of CORT does not reflect changes that are specific for a particular colony or reproductive stage. Although CORT levels were on average higher on Duck I. compared to Gull I., we did not find a consistent effect of the colony across years (Fig. 1). Our results show clearly that patterns of CORT secretion may change in all possible ways among stages (see Fig. 1), and therefore do not reflect endogenous physiological cycles, or consistent patterns generated by triggers associated with reproductive stages. Results of this study are consistent with results for common murre (Kitaysky, Piatt & Wingfield 2007); thick-billed murre *Uria lomvia* and least auklets *Aethia pusilla* (Benowitz-Fredericks, Shultz & Kitaysky 2008), and kittiwakes (Buck, O'Reilly & Kildaw 2007; Shultz & Kitaysky 2008), and do not support the earlier suggestion (Kitaysky, Wingfield & Piatt 1999a) that the intrinsic contribution of reproductive stage is one of the driving forces for changes in the adrenal activity in long-lived seabirds.

In contrast to the second argument that a multitude of environmental factors is concurrently affecting the adrenal activity, our results show that in breeding black-legged kittiwakes the variability in CORT levels is largely explained by the variations in food supply (Fig. 2). Specifically, the analytical approach used in the observational component of this study confirmed this: univariate analyses of the best approximating model (based on the information-theoretic analysis) showed that colony and reproductive stage had no effect on CORT levels when these factors (with a potentially inherent effect on CORT secretion) were controlled for changes in food availability (Table 2). Results of the controlled experiment on free-ranging kittiwakes on Middleton I. provided unequivocal evidence supporting the observational studies – individuals fed *ad libitum* had the absolute minimal (zero nutritional stress) CORT compared to those measured in Cook Inlet (this study) and in the Bering Sea (Shultz & Kitaysky 2008; see Appendix S2 in Supporting Information). All of our sampling was 'biased' toward fit breeders because individuals that were sick, heavily parasitized or had not accumulated sufficient resources to participate in reproduction, were not at the colonies to be sampled. Similar to our earlier study (Kitaysky, Piatt & Wingfield 2007), we would argue that the selection criteria we used to sample birds are essential to examine a functional link between food-related stress and population processes in seabirds. We would also argue that even the best possible sampling of food abundance in marine environments (including beach seine and mid-water trawls we

used in this study) would not measure food availability. Yet, food availability is the only true measure of foraging conditions for animals, and it varies depending on vertical distribution and density of patches, distance from a breeding colony, energetic density of prey, etc. (i.e. Cairns 1987). For example, we found that foraging conditions of surface-foraging kittiwakes, and pursuit-diving auklets and murres breeding at the same colonies often varied in opposite ways – what was a ‘good’ season for one species was a ‘bad’ season for another and *vice versa* (Kitaysky *et al.* 2000; Benowitz-Fredericks, Shultz & Kitaysky 2008).

To conclude thus far, multiple controlled experiments and observations of adrenal function in wild birds suggested that CORT secretion may be used to assess nutritional stress in breeding seabirds. Results obtained earlier (Kitaysky, Piatt & Wingfield 2007) and in this current study (observational and experimental) provide strong evidence for a direct quantitative relationship between natural variability in food and the adrenocortical function in breeding seabirds of different phylogenetic lineages, life-history traits and foraging ecology. This study quantified the levels of nutritional stress from ‘zero-stress’ in birds fed *ad libitum* on Middleton I. to ‘maximum-stress’ in birds that disappeared from the breeding populations in Cook Inlet. CORT secretion is a reliable measure of food-related stress and can be used to gauge relative food availability in free-ranging seabirds.

FOOD-RELATED STRESS AFFECTS FECUNDITY

The question remained whether naturally occurring levels of nutritional stress are relevant to reproduction of wild animals (i.e. Lanctot *et al.* 2003; Lormee *et al.* 2003; Criscuolo *et al.* 2005; Angelier *et al.* 2007a; but see Silverin 1986; Buck *et al.* 2007; Love *et al.* 2004; Angelier *et al.* 2007b; and *in press*). We found a negative relationship between increased CORT secretion and fecundity. Because we were able to identify the changes in food abundance as a major factor affecting CORT, this study provides direct support for the hypothesis that food-related stress during reproduction can contribute to decreased fecundity of seabirds. The relationship between CORT and fecundity depends on severity of nutritional limitations and it may be causal. CORT is involved in regulation of body maintenance processes in part by modifying behaviour of individuals in accordance with ecological and life-history events (Wingfield & Kitaysky 2002; McEwen & Wingfield 2003; Landys, Ramenofsky & Wingfield 2006; Romero, Dickens & Cyr 2009). In particular, an increase in baseline CORT in parent seabirds changes allocation of resources away from reproductive processes (by decreasing parental care) and towards body maintenance (by increasing foraging; Angelier *et al.* 2007b; Kitaysky, Wingfield & Piatt 2001). Supporting this, several studies (Harding, Piatt & Shmutz 2007; Harding *et al.* 2007; Piatt *et al.* 2007) found that seabirds’ allocation time to attending their chicks at the colony is sensitive to declines in food abundance. Thus, CORT secretion might

be a physiological mechanism (direct or in synergy with other hormones, i.e. prolactin – Angelier *et al.* 2009, *in press*) linking changes in food availability and parental resource allocation in seabirds (Kitaysky, Wingfield & Piatt 2001; Angelier *et al.* 2007b; Bokony *et al.* 2008).

Yet, the relationship between nutritional stress and fecundity is not always linear in the black-legged kittiwake. At the beginning of the reproductive season, Duck I. and Gull I. kittiwakes responded similarly to changes in food availability – increased nutritional stress affected timing and success of egg-laying in a linear fashion on both colonies (Fig. 4). Lanctot *et al.* (2003) also reported low laying success in kittiwakes with elevated CORT. These observations corroborate the earlier prediction (Drent & Daan 1980) that seabirds should respond to food shortages by delaying reproduction until they accumulated sufficient resources to initiate breeding (also see Shultz *et al.* 2009 for empirical support of this prediction). However, we observed a drastic difference in responses to nutritional stress between Gull I. and Duck I. birds during chick-rearing. At Gull I., high levels of stress induced a reduction but never a complete failure of birds in raising young, but Duck I. birds experienced complete failure over the entire range of stress levels. As predicted (Cairns 1987; Erikstad *et al.* 1998; Piatt *et al.* 2007), reproductive responses of Middleton and Duck Is. kittiwakes to nutritional stress appeared to be a negative exponential function (a small increase in stress triggered a large reduction in reproductive performance, Fig. 4). Coupled with observations of low survival probabilities in Gull I. birds compared to Duck and Middleton Is. birds (Hatch, Roberts & Fadley 1993; Piatt *et al.* 2007), this scenario suggests that Duck I. birds might be pursuing a long-term strategy (and fewer individuals are willing to incur survival costs under sub-optimal conditions), whereas Gull I. birds are investing in reproduction despite survival costs associated with high nutritional stress. This is interesting as it suggests intra-specific flexibility in life-history strategies (‘slow-reproducing but long-lived’ vs. ‘fast-reproducing but short-lived’) of a long-lived animal (Pugesek 1990). Because Duck and Middleton Is. colonies experienced drastic population declines during the last three decades, and Gull I. colony increased exponentially during the same period, selection against fast-living behavioural phenotypes or their immigration from the declining colonies seem possible (Erikstad *et al.* 1998). Several studies suggested that Atlantic and Pacific populations of black-legged kittiwakes represent extremes of such slow-fast continuum – Atlantic kittiwakes reproduce at a high rate and experience low survival, with the opposite observed for Pacific kittiwakes (i.e. Frederiksen, Harris & Wanless 2005; Suryan *et al.* 2009). However, an interesting observation we made in this study is that presumably fast-living Gull I. birds experienced low survival while their fecundity was still low compared to Atlantic kittiwakes (Piatt *et al.* 2007). Whether or not these strategies are associated with population trajectories, are evolutionarily stable, or reflect genetic, epigenetic or demographic (i.e. age) differences among kittiwakes breeding on our study colonies is not currently known.

FOOD-RELATED STRESS AFFECTS SURVIVAL OF INDIVIDUALS

It is not well understood whether or not food is a major cause of changes in adult seabird survival (Aebischer & Coulson 1990; Sandvik *et al.* 2005). To establish how food-related stress during reproduction affects survival of adults, food availability should be measured, which is difficult (Cairns 1987; Oro & Furness 2002; Piatt *et al.* 2007). This study suggests that monitoring CORT levels in breeding individuals might offer a solution to this critical issue. Results of this study show that low food availability resulting in severe nutritional stress (defined by the magnitude, baseline CORT, and by the duration, maximum CORT) is an important factor determining return of kittiwakes to a breeding colony. Specifically, individuals that 'disappeared' from the colonies had higher baseline and maximum acute stress-induced levels of CORT compared to individuals that were 're-sighted' (Fig. 6). However, unlike effects of nutritional stress on fecundity (i.e. laying success), adult survival in kittiwakes is likely to be affected by deteriorating food availability in a 'threshold manner' (*sensu* Piatt *et al.* 2007; Fig. 6). Survival of adults was not affected within a relatively wide range of initial increases in nutritional stress (Fig. 6). However, as nutritional stress reached a certain threshold, survival of adults dropped precipitously, as Erikstad *et al.* (1998) predicted in their theoretical model for long-lived birds breeding in a stochastic environment. This result supports the hypothesis that population processes, and the main factor contributing to population dynamics in seabirds – adult survival – are constrained by food resources during reproduction. These results maybe interpreted in two ways: (i) food stress and/or elevated CORT is detrimental to the survival of affected individuals and birds that disappeared from the colony died. Chronically elevated CORT secretion might be causal in determining survival of individuals. Several studies have shown a negative relationship between endogenous CORT and survival of animals (Romero & Wikelski 2000; Brown *et al.* 2005; Blas *et al.* 2007; Kitaysky, Piatt & Wingfield 2007). Experimentally simulated chronic stress (using exogenous corticosterone application) resulted in high mortality of kittiwakes (Kitaysky, Wingfield & Piatt 2001). (ii) Food stress and/or elevated CORT induced birds to skip reproduction or relocate. In the latter case, CORT may be functioning as an anti-stress mechanism allowing long-lived birds to avoid being stressed by skipping reproduction or permanently leaving the food-poor colony (Wingfield & Kitaysky 2002). Either way, the disappearance of breeders from a colony was associated with severity of nutritional stress they incurred during reproduction.

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References

- Abookire, A.A. & Piatt, J.F. (2005) Oceanographic conditions structure forage fishes into lipid-rich and lipid-poor communities in lower Cook Inlet, Alaska, USA. *Marine Ecology Progress Series*, **287**, 229–240.
- Abookire, A.A., Piatt, J.F. & Robards, M.D. (2000) Nearshore fish distributions in an Alaskan estuary in relation to stratification, temperature and salinity. *Estuarine, Coastal and Shelf Science*, **51**, 45–59.
- Aebischer, N.J. & Coulson, J.C. (1990) Survival of the kittiwake in relation to sex, year, breeding experience and position in the colony. *Journal of Animal Ecology*, **59**, 1063–1071.
- Akana, S.F., Dallman, M.F., Bradbury, M.J., Scribner, K.A., Strack, A.M. & Walker, C.D. (1992) Feedback and facilitation in the adrenocortical system – Unmasking facilitation by partial inhibition of the glucocorticoid response to prior stress. *Endocrinology*, **131**, 57–68.
- Anderson, D.R., Burnham, K.P. & Thompson, W.L. (2000) Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management*, **64**, 912–923.
- Angelier, F., Moe, B., Weimerskirch, H. & Chastel, O. (2007a) Age-specific reproductive success in a long-lived bird: do older parents resist stress better? *Journal of Animal Ecology*, **76**, 1181–1191.
- Angelier, F., Clement-Chastel, C., Gabrielsen, G.W. & Chastel, O. (2007b) Corticosterone and time-activity budget: an experiment with Black-legged kittiwakes. *Hormones and Behavior*, **52**, 482–491.
- Angelier, F., Clement-Chastel, C., Welcker, J., Gabrielsen, G.W. & Chastel, O. (2009) How does corticosterone affect parental behavior and reproductive success? A study of prolactin in black-legged kittiwakes. *Functional Ecology*, **23**, 784–793.
- Benowitz-Fredericks, M.Z., Shultz, M.T. & Kitaysky, A.S. (2008) Stress hormones suggest opposite trends of food availability for planktivorous and piscivorous seabirds in 2 years. *Deep Sea Research II*, **55**, 1868–1876.
- Blas, J., Bortolotti, G.R., Tella, J.L., Baos, R. & Marchant, T.A. (2007) Stress response during development predicts fitness in a wild, long-lived vertebrate. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 8880–8884.
- Bokony, V., Lendvai, A.Z., Liker, A., Angelier, F., Wingfield, J.C. & Chastel, O. (2008) Stress response and the value of reproduction: are birds prudent parents? *American Naturalist*, **173**, 589–598.
- Brown, C.R., Brown, M.B., Raouf, S.A., Smith, L.C. & Wingfield, J.C. (2005) Effects of endogenous steroid hormone levels on annual survival in cliff swallows. *Ecology*, **86**, 1034–1046.
- Buck, C.L., O'Reilly, K.M. & Kildaw, S.D. (2007) Interannual variability of Black-legged kittiwakes productivity is reflected in baseline corticosterone levels. *General and Comparative Endocrinology*, **150**, 430–436.
- Burnham, K.P. & Anderson, D.R. (1998) *Model Selection and Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York.
- Byrd, G.V., Schmutz, J.A. & Renner, H.M. (2008) Contrasting population trends of piscivorous seabirds in the Pribilof Islands: a 30-year perspective. *Deep Sea Research II*, **55**, 1846–1855.
- Cailliet, G.M., Love, M.S. & Ebeling, A.W. (1986) *Fishes: A Field and Laboratory Manual on Their Structure, Identification and Natural History*. Wadsworth Publishing Company, Belmont, California, 194 pp.
- Cairns, D.K. (1987) Seabirds as indicators of marine food supplies. *Biological Oceanography*, **5**, 261–271.
- Clinchy, M., Zanette, L., Boonstra, R., Wingfield, J.C. & Smith, J.N.M. (2004) Balancing food and predator pressure induces chronic stress in songbirds. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **271**, 2473–2479.
- Cockrem, J.F. (2004) Conservation and behavioral neuroendocrinology. *Hormones and Behavior*, **48**, 492–501.
- Cockrem, J.F. & Silverin, B. (2002) Variation within and between birds in corticosterone responses of great tits (*Parus major*). *General and Comparative Endocrinology*, **125**, 197–206.
- Criscolo, F., Chastel, O., Bertile, F., Gabrielsen, G.W., Le Maho, Y. & Raclot, T. (2005) Corticosterone alone does not trigger a short-term behavioral shift

- in incubating female Common Eiders, but does modify long-term reproductive success. *Journal of Avian Biology*, **36**, 306–312.
- Dallman, M.F., Akana, S.F., Strack, A.M., Scribner, K.S., Pecoraro, N., La Fleur, S.E., Houshyar, H. & Gomez, F. (2004) Chronic stress-induced effects of corticosterone on brain: direct and indirect. *Stress: Current Neuroendocrine and Genetic Approaches. Annals of the New York Academy of Sciences*, **1018**, 141–150.
- Doody, L.M., Wilhelm, S.I., McKay, D.W., Walsh, C.J. & Storey, A.E. (2008) The effects of variable foraging conditions on common murre (*Uria aalge*) corticosterone concentrations and parental provisioning. *Hormones and Behavior*, **53**, 140–148.
- Drent, R.H. & Daan, S. (1980) The prudent parent: energetic adjustments in avian breeding. *Ardea*, **6**, 225–252.
- Edwards, A.E. (2004) *Proximate and Ultimate Constraints on Breeding in Seabirds*. PhD thesis. University of Washington, Seattle, WA.
- Erikstad, K.E., Fauchald, P., Tveraa, T. & Steen, H. (1998) On the costs of reproduction in long-lived birds: the influence of environmental variability. *Ecology*, **79**, 1781–1788.
- Frederiksen, M., Harris, M.P. & Wanless, S. (2005) Inter-population variation in demographic parameters: a neglected subject? *Oikos*, **111**, 209–214.
- Gill, V. & Hatch, S.A. (2002) Components of productivity in black-legged kittiwakes *Rissa tridactyla*: response to supplemental feeding. *Journal of Avian Biology*, **33**, 113–126.
- Golet, G.H., Schmutz, J.A., Irons, D.B. & Estes, J.A. (2004) Determinants of reproductive costs in the long-lived Black-Legged Kittiwake: a multiyear experiment. *Ecological Monographs*, **74**, 353–372.
- Griffiths, R.M., Double, C., Orr, K. & Dawson, R.J.G. (1998) A DNA test to sex most birds. *Molecular Ecology*, **7**, 1071–1075.
- Grosbois, V. & Thompson, P.M. (2005) North Atlantic climate variation influences survival in adult fulmars. *Oikos*, **109**, 273–290.
- Harding, A.M.A., Piatt, J.F. & Schmutz, J.A. (2007) Seabird behavior as an indicator of food supplies: sensitivity across the breeding season. *Marine Ecology Progress Series*, **352**, 269–274.
- Harding, A.M.A., Piatt, J.F., Schmutz, J.A., Shultz, M.T., van Pelt, T.I., Kettle, A.B. & Speckman, S.G. (2007) Prey density and the behavioral flexibility of a marine predator: the common murre (*Uria aalge*). *Ecology*, **88**, 2024–2033.
- Hatch, S.A., Roberts, B.D. & Fadley, B.S. (1993) Adult survival of Black-legged Kittiwakes *Rissa tridactyla* in a Pacific colony. *Ibis*, **135**, 247–254.
- Hunt Jr, G.L., Stabeno, P.J., Strom, S. & Napp, J.M. (2008) Patterns of spatial and temporal variation in the marine ecosystem of the southeastern Bering Sea, with special references to the Pribof Domain. *Deep Sea Research II*, **55**, 1919–1944.
- Kitaysky, A.K., Piatt, J.F. & Wingfield, J.C. (2007) Stress hormones link food availability and population processes in seabirds. *Marine Ecology Progress Series*, **352**, 245–258.
- Kitaysky, A.S., Wingfield, J.C. & Piatt, J.F. (1999a) Food availability, body condition and physiological stress response in breeding Black-legged Kittiwakes. *Functional Ecology*, **13**, 577–584.
- Kitaysky, A.S., Wingfield, J.C. & Piatt, J.F. (2001) Corticosterone facilitates begging and affects resource allocation in the Black-legged Kittiwake. *Behavioral Ecology*, **12**, 619–625.
- Kitaysky, A.S., Piatt, J.F., Wingfield, J.C. & Romano, M. (1999b) The adrenocortical stress-response of Black-legged Kittiwake chicks in relation to dietary restrictions. *Journal of Comparative Physiology B*, **169**, 303–310.
- Kitaysky, A.S., Hunt, G.L., Flint, E.N., Rubega, M.A. & Decker, M.B. (2000) Resource allocation in breeding seabirds: responses to fluctuations in their food supply. *Marine Ecology Progress Series*, **206**, 283–296.
- Lack, D. (1966) *Population Studies of Birds*. Clarendon Press, Oxford, UK.
- Lancot, R.B., Hatch, S.A., Gill, V.A. & Eens, M. (2003) Are corticosterone levels a good indicator of food availability and reproductive performance in a kittiwake colony? *Hormones and Behavior*, **43**, 489–502.
- Landys, M.M., Ramenofsky, M. & Wingfield, J.C. (2006) Action of glucocorticoids at a seasonal baseline as compared to stress-related levels in the regulation of periodic life processes. *General and Comparative Endocrinology*, **148**, 132–149.
- Lebererton, J.D., Burnham, K.D., Clobert, J. & Anderson, D.R. (1992) Modeling survival and testing biological hypotheses using marked animals: case studies and recent advances. *Ecological Monographs*, **62**, 67–118.
- Lormee, H., Jouventin, P., Trouve, C. & Chastel, O. (2003) Sex-specific patterns in baseline corticosterone and body condition changes in breeding Red-footed Boobies *Sula sula*. *Ibis*, **145**, 212–219.
- Love, O.P., Breuner, C.W., Vezina, F. & Williams, T.D. (2004) Mediation of a corticosterone-induced reproductive conflict. *Hormones and Behavior*, **46**, 59–65.
- Lynn, S.E., Breuner, C.W. & Wingfield, J.C. (2003) Short-term fasting affects locomotor activity, corticosterone, and corticosterone binding globulin in a migratory songbird. *Hormones and Behavior*, **43**, 150–157.
- McEwen, B.S. & Wingfield, J.C. (2003) The concept of allostasis in biology and biomedicine. *Hormones and Behavior*, **43**, 2–15.
- Medrano, J.F., Aasen, E. & Sharrow, L. (1990) DNA extraction from nucleated red blood cells. *BioTechniques*, **8**, 43.
- Merrick, R.L., Louphlin, T.R. & Calkins, D.G. (1987) Decline in abundance of the northern sealion, *Eumetopias jubatus*, in Alaska, 1956–86. *Fishery Bulletin*, **85**, 351–365.
- Oro, D. & Furness, R. (2002) Influences of food availability and predation on survival of kittiwakes. *Ecology*, **83**, 2516–2528.
- Oro, D., Pradel, R. & Lebererton, J.-D. (1999) The effects of nest predation and food availability on life history traits in Audouin's gull. *Oecologia*, **118**, 438–445.
- Oro, D., Cam, E., Pradel, R. & Matinez-Abrain, A. (2004) Influence of food availability on demography and local population dynamics in a long-lived seabird. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **271**, 387–396.
- Piatt, J.F. (ed.) (2002) *Response of Seabirds to Fluctuations in Forage Fish Density*. Final Report to Exxon Valdez Oil Spill Trustee Council (Restoration Project 00163M) and Minerals Management Service (Alaska OCS Region). Alaska Science Center, U.S. Geological Survey, Anchorage, Alaska. 406 pp.
- Piatt, J.F. (2004) *Survival of Adult Murres and Kittiwakes in Relation to Forage Fish Abundance*. Exxon Valdez Oil Spill Restoration Project Final Report (Restoration Project 00338), U.S. Geological Survey, Anchorage, Alaska.
- Piatt, J.F. & Anderson, P.J. (1996) Response of Common Murres to the Exxon Valdez oil spill and long-term changes on the Gulf of Alaska marine ecosystem. *Exxon Valdez Oil Spill Symposium Proceedings* (eds S.D. Rice, R.B. Spies, D.A. Wolfe & B.A. Wright) pp. 720–737. American Fisheries Society Symposium 18, Bethesda, Maryland.
- Piatt, J.F. & Harding, A.M.A. (2007) Population ecology of seabirds in Cook Inlet. *Long-Term Ecological Change in the Northern Gulf of Alaska* (ed Robert Spies), pp. 335–352. Elsevier, Amsterdam.
- Piatt, J.F., Harding, A.M.A., Shultz, M., Speckman, S.G., van Pelt, I.I., Drew, G.S. & Kettle, A.B. (2007) Seabirds as indicators of marine food supplies: Cairns revisited. *Marine Ecology Progress Series*, **352**, 221–234.
- Pons, J.-M. & Migot, P. (1995) Life-history strategy of the herring gull: changes in survival and fecundity in a population subjected to various feeding conditions. *Journal of Animal Ecology*, **64**, 592–599.
- Pravosudov, V.V. & Kitaysky, A.S. (2006) Effects of nutritional restrictions during post-hatching development on adrenocortical function in western scrub-jays (*Aphelocoma californica*). *General and Comparative Endocrinology*, **145**, 25–31.
- Pravosudov, V.V., Kitaysky, A.S., Wingfield, J.C. & Clayton, N.S. (2001) Long-term unpredictable foraging conditions and physiological stress response in mountain chickadees (*Poecile gambeli*). *General and Comparative Endocrinology*, **123**, 324–331.
- Pugesek, B.H. (1990) Parental effort in the California Gul: tests of parent-offspring conflict theory. *Behavioral Ecology and Sociobiology*, **27**, 211–215.
- Robards, M.D., Rose, G.A. & Piatt, J.F. (2002) Growth and abundance of Pacific sand lance, *Ammodytes hexapterus*, under differing oceanographic regimes. *Environmental Biology of Fishes*, **64**, 429–441.
- Robards, M.D., Piatt, J.F., Kettle, A.B. & Abookire, A.A. (1999) Temporal and geographic variation in fish communities of lower Cook Inlet, Alaska. *Fishery Bulletin*, **97**, 962–977.
- Romero, L.M. (2002) Seasonal changes in plasma glucocorticoid concentrations in free-living vertebrates. *General and Comparative Endocrinology*, **128**, 1–24.
- Romero, L.M. (2004) Physiological stress in ecology: lessons from biomedical research. *Trends in Ecology and Evolution*, **19**, 249–255.
- Romero, L.M., Dickens, M.J. & Cyr, N.E. (2009) The reactive scope model – A new model integrating homeostasis, allostasis, and stress. *Hormones and Behavior*, **55**, 375–389.
- Romero, L.M., Ramenofsky, M. & Wingfield, J.C. (1997) Season and migration alters the corticosterone response to capture and handling in an Arctic migrant, the white-crowned sparrow (*Zonotrichia leucophrys gambelii*). *Comparative Biochemical Physiology*, **116**, 171–177.
- Romero, L.M. & Reed, J.M. (2005) Collecting baseline corticosterone samples in the field: is under 3 min good enough? *Comparative Biochemistry and Physiology A*, **140**, 73–79.
- Romero, L.M. & Wikelski, M. (2000) Corticosterone levels predict survival probabilities of Galapagos marine iguanas during El Nino events. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 7366–7370.

- Sandvik, H., Erikstad, K.E., Barrett, R. & Yoccoz, N.G. (2005) The effect of climate on adult survival in five species of North Atlantic seabirds. *Journal of Animal Ecology*, **74**, 817–831.
- Sapolsky, R.M., Romero, M.L. & Munck, A.U. (2000) How do glucocorticoids influence stress responses? Integrative, permissive, suppressive, stimulatory, and preparation actions *Endocrine Reviews*, **21**, 55–89.
- Shultz, M.T. & Kitaysky, A.S. (2008) Spatial and temporal dynamics of corticosterone and corticosterone-binding globulin are driven by environmental heterogeneity. *General and Comparative Endocrinology*, **155**, 717–728.
- Shultz, M.T., Piatt, J.F., Harding, A.M.A., Kettle, A.B. & Van Pelt, T.I. (2009) Seabird timing of breeding and reproductive performance reflect mismatched seasonal prey dynamics. *Marine Ecology Progress Series*, **393**, 247–258.
- Silverin, B. (1986) Corticosterone-binding proteins and behavioral effects of high plasma levels of corticosterone during breeding period. *General and Comparative Endocrinology*, **64**, 67–74.
- Sonsthagen, S.A., Talbot, S.L. & White, C.M. (2004) Gene flow and genetic characterization of northern goshawks breeding in Utah. *Condor*, **106**, 826–836.
- Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford.
- Suryan, R.M., Saba, V.S., Wallace, B.P., Hatch, S.A., Frederiksen, M. & Wanless, S. (2009) Environmental forcing on life history strategies: multi-trophic level response at ocean basin scales. *Progress in Oceanography*, **81**, 214–222.
- Welcker, J., Harding, A.M.A., Kitaysky, A.S., Speakman, J.R. & Gabrielsen, G.W. (2009) Daily energy expenditure increase in response to low nutritional stress in an Arctic-breeding seabird with no effect on mortality. *Functional Ecology*, **23**, 1081–1090.
- Wingfield, J.C. (1994) Modulation of the adrenocortical response to stress in birds. *Perspectives in Comparative Endocrinology* (eds K.G. Davey, R.E. Peter & S.S. Tobe), pp. 520–528, National Research Council of Canada, Ottawa, Canada.
- Wingfield, J.C., Bruener, C. & Jacobs, J. (1997) Corticosterone and behavioral responses to unpredictable events. *Perspectives in Avian Endocrinology* (eds S. Harvey & R.J. Etches), pp. 267–278, Society for Endocrinology, Bristol UK.
- Wingfield, J.C. & Farner, D.S. (1975) The determination of five steroids in avian plasma by radioimmunoassay and competitive protein binding. *Steroids*, **26**, 311–327.
- Wingfield, J.C. & Kitaysky, A.S. (2002) Endocrine responses to unpredictable environmental events: Stress or anti-stress hormones? *Integrative and Comparative Biology*, **42**, 600–609.
- Wingfield, J.C., Vleck, C.M. & Moore, M.C. (1992) Seasonal changes in the adrenocortical response to stress in birds of the Sonoran Desert. *Journal of Experimental Zoology*, **264**, 419–428.

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Supporting information

Additional Supporting information may be found in the online version of this article.

Appendix S1. Duration of colony disturbance prior to capture does not affect corticosterone levels of breeding black-legged kittiwakes.

Appendix S2. Different methods of capture do not influence corticosterone levels of breeding black-legged kittiwakes.

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