



Stress hormones link food availability and population processes in seabirds

A. S. Kitaysky^{1,*}, J. F. Piatt², J. C. Wingfield³

¹Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, Alaska 99775, USA

²USGS Alaska Science Center, 1011 East Tudor Road, Anchorage, Alaska 99503, USA

³Department of Biology, University of Washington, Seattle, Washington 98195, USA

ABSTRACT: Catastrophic population declines in marine top predators in the northern Pacific have been hypothesized to result from nutritional stress affecting reproduction and survival of individuals. However, empirical evidence for food-related stress in wild animals is frequently lacking or inconclusive. We used a field endocrinology approach to measure stress, identify its causes, and examine a link between stress and population processes in the common murre *Uria aalge*. We tested the empirical relationship between variations in the stress hormone corticosterone (CORT) and food abundance, reproduction, and persistence of individuals at declining and increasing colonies in Cook Inlet, Alaska, from 1996 to 2001. We found that CORT secretion in murre is independent of colony, reproductive stage effects, and gender of individuals, but is directly negatively correlated with abundance of their food. Baseline CORT reflected current food abundance, whereas acute stress-induced CORT reflected food abundance in the previous month. As food supply diminished, increased CORT secretion predicted a decrease in reproductive performance. At a declining colony, increased baseline levels of CORT during reproduction predicted disappearance of individuals from the population. Persistence of individuals in a growing colony was independent of CORT during reproduction. The obtained results support the hypothesis that nutritional stress during reproduction affects reproduction and survival in seabirds. This study provides the first unequivocal evidence for CORT secretion as a mechanistic link between fluctuations in food abundance and population processes in seabirds.

KEY WORDS: Corticosterone · Food availability · Stress · Seabirds · Population processes

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

The identification of causes and consequences of stress in populations of wild animals is a fundamental ecological problem. Food limitations have long been suggested to control seabird population dynamics by altering the survival and reproductive performance of individuals (Lack 1966). During the past 3 decades, catastrophic population declines have occurred among some seabirds in the northern Pacific (Hunt & Byrd 1999). It has been hypothesized that deterioration of food resources during reproduction resulted in food-related stress, which in turn reduced fitness of marine top predators (Merrick et al. 1987, Hunt et al. 1996, Piatt & Anderson 1996). However, an empirical relationship between food availability and stress has not

been previously quantified in free-living seabirds, and the direct effect of food-related stress on reproduction and survival of individuals has yet to be elucidated. The present paper provides the first unequivocal evidence for food-related stress as a mechanistic link between fluctuations in food abundance during reproduction and population processes in seabirds.

Traditional methods for measuring food-related stress in free-living seabirds are not always effective. In this context, food-related stress can be defined as changes in the physiological condition of individuals that experience a shortage of food that impairs their ability to reproduce successfully. Alternatively, less severe food shortages may allow reproduction to proceed, but low post-fledging survival of young raised on low quality/quantity diets may precipitate reproduc-

*Email: ffask@uaf.edu

tive failure (Kitaysky et al. 2006) and/or affect their recruitment to breeding populations (Thompson & Ollason 2001). More importantly, breeding during sub-optimal foraging conditions may be detrimental to post-reproductive survival of adults (e.g. Kitaysky et al. 2001b, Golet et al. 2004). In long-lived animals, food-related stress is most likely to affect reproductive success (e.g. Kitaysky & Golubova 2000) or the survival of young rather than that of adults (Williams 1966). Yet, in some species, young may tolerate large fluctuations in food supply and fledge successfully despite severe food shortages (e.g. Kitaysky 1999, Wanless et al. 2005, Benowitz-Fredericks et al. 2006, Kitaysky et al. 2006), and survival of chicks may be affected by factors independent of food supplies, such as predation and inclement weather (e.g. Lloyd 1979, Regehr & Montevecchi 1997). In others, parents buffer their young from variations in food availability by increasing their effort in foraging during food shortages (Shea & Ricklefs 1995, 1996, Zador & Piatt 1999, Kitaysky et al. 2000, 2001b). Furthermore, long-lived seabirds do not recruit to breeding colonies until they are several years old and frequently forego reproductive attempts (e.g. Mougouin et al. 1997); therefore, a time series of several decades is required to assess the consequences of current environmental conditions on future population dynamics (Thompson & Ollason 2001). Thus, empirical evidence for the direct effects of food-related stress on seabird reproduction and survival is difficult to obtain while using traditional methods. In this study, we used a field endocrinology approach to measure stress, identify its causes, and to examine the hypothesized link between food-related stress and population processes in the common murre *Uria aalge*—one of the most abundant seabirds in the North Pacific.

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. 1999a, 2001a, Pravosudov et al. 2001, Lynn et al. 2003, Clinchy et al. 2004, Pravosudov & Kitaysky 2006). Specifically, baseline CORT was found to be proportional to the severity of experimentally induced nutritional deficits in the young of several species of seabirds (reviewed in Kitaysky et al. 2003). In adult free-living birds, experimental food supplementations also reduced CORT secretion (Lanctot et al. 2003, Clinchy et al. 2004). However, effects of food supplementation on CORT in adults were not consistent across the reproductive season (e.g. Lanctot et al. 2003), probably reflecting temporal changes in the natural food availability and/or physiological transitions of birds between different stages of reproduction (Kitaysky et al. 1999b, Wingfield & Kitaysky 2002). Also,

there is a possibility of synergistic effects of food-related stress with other ecological factors, such as predator and parasite pressures (e.g. Clinchy et al. 2004, Roaaf et al. 2006), inclement weather (Wingfield et al. 1997), and changes in parental effort at different stages of a bird's reproductive cycle (Kitaysky et al. 1999b).

The field endocrinology approach potentially offers an opportunity to discriminate between short-term and chronic effects of food stress on free-living individuals. Baseline CORT concentrations (measured in the blood of undisturbed birds immediately after capture) increase quickly (within hours or days) in response to a food shortage (Lynn et al. 2003, Edwards 2004). During prolonged food shortages, when animals are exposed to chronically elevated baseline CORT secretion, their adrenal function 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 (wk) than baseline CORT (d) (Kitaysky et al. 2001a, 2005). In seabirds, acute stress-induced CORT is expected to correspond to food availability and baseline CORT measures taken several weeks earlier (Kitaysky et al. 2001a).

The goals of the present study were (1) to measure physiological stress and to identify its causes in breeding seabirds and (2) to establish a link between stress during reproduction and the patterns of fecundity and persistence of individuals in a population. The specific objectives were (a) to assess variability in CORT secretion between colonies (with declining versus increasing numerical trajectories during the past 2 decades) within a single population, among years (1996 to 2001) and reproductive stages (egg-laying, incubation, and chick-rearing), and in relation to gender of individuals; (b) to directly measure intra-seasonal and inter-annual changes of food abundance in the vicinities of colonies (1996 to 1999); and (c) to determine colony-wide reproductive performances at the various stages of reproduction (1996 to 2001) and persistence of individuals in a colony (1997 to 2001).

MATERIALS AND METHODS

We conducted the present study at 2 major seabird colonies in Cook Inlet, Gulf of Alaska, from May to September in 1996 to 2001. The colonies are about 100 km apart and are situated in oceanographically distinct habitats (Robards et al. 1999, 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). Common murrens *Uria aalge* breeding on these colonies are morphologically and genetically indistinguishable (J. F. Piatt & V. Friesen unpubl. data; S. V. Drovetski, A. S. Kitayski, J. F. Piatt unpubl.). Currently, common murrens are much more numerous on Gull Island (4000 breeding pairs) compared to Duck Island (1200 breeding pairs). However, the numbers of birds breeding on these islands changed drastically over the past 3 decades—they steadily declined at Duck Island ($-8.9\% \text{ yr}^{-1}$) and increased at Gull Island ($+9.1\% \text{ yr}^{-1}$) (Piatt 2002). From 1998 to 2001, the survival estimates of adult murrens were consistently lower at Duck Island (90.8%) than at Gull Island (94.0%) (Piatt 2004).

Blood sample collection and CORT assays. Birds were captured from their nesting sites using noose poles. In each year, birds were sampled during daylight hours every 2 wk from June to September (except that in 1996 birds were sampled only once on Gull Island at the incubation stage). Reproductive stages (egg-laying, incubation, and chick-rearing) and breeding status of birds were verified by the presence of a brood patch, egg, or chick at the capture site. For all birds ($n = 523$), initial blood samples were taken within 3 min of capture. It takes at least 3 min for levels of CORT to begin to rise in the blood in response to a stressor (Romero & Reed 2005) so this first sample provides a baseline measure of circulating CORT and does not reflect the stress induced by capture. Some birds ($n = 276$) 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 that 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 capture, handling, and restraint stressor) reflects the birds' ability to produce CORT. Approximately half of all birds were released after collection of the baseline sample; therefore, sample sizes are smaller for maximum 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 corticosterone. While being held, all birds were banded with metal US Fish and Wildlife bands and a combination of colored plastic bands, which ensured that no individual was sampled twice and allowed us to monitor individual birds.

Hormone assay. Total corticosterone was measured using a radioimmunoassay. For each sample, 20 μl 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 (average hormone recovery was 95%) was used to correct final values. Samples were reconstituted in PBSG-buffer (PBS supplemented with gelatin) and combined with antibody and radiolabel in a radioimmunoassay. Dextran-coated charcoal was used to separate antibody-bound hormone from unbound hormone. Inter- and intra-assay variations were $<4\%$ and 2% , respectively.

Beach seines. We conducted the concurrent measurements of food abundance and CORT on a regular schedule (approximately every 2 wk), which allowed us to examine the relationship between CORT levels and food abundances during 3 different time intervals: within the current 2 wk, within the current month, and during the previous month (i.e. CORT measurements lagged behind food measurement with a period of 1 mo). We used beach seines to measure forage fish abundance in waters adjacent to breeding colonies where birds foraged. Beach seines effectively and non-selectively sample shallow, inshore waters with smooth bottoms (Cailliet et al. 1986). Samples were collected about every 2 wk during May through September, 1996 to 1999 (detailed methods are described in Robards et al. 1999 and Abookire et al. 2000). Nets were deployed from a small boat and set parallel to shore, about 25 m from the beach. Seine catch per unit effort (CPUE) mirrored patterns of fish abundance offshore in mid-water trawls and hydro-acoustic surveys (Robards et al. 1999, Abookire et al. 2000, Piatt 2002). CPUE was calculated as the total catch of all fish per seine averaged by site and day. Catches consisted of sand lance *Ammodytes hexapterus* Pallas, Pacific herring *Clupea harengus pallasii*, Salmonidae, Osmeridae, and Gadidae. The body length of forage fishes sampled in beach seines in general matched those of fishes captured by birds (Piatt 2002). These fish species comprised $>90\%$ of the seabirds' diets during this study (Kitaysky et al. 1999a, Piatt 2002). CPUE data were $\log(x + 1)$ transformed to meet assumptions required for parametric statistical procedures.

Reproductive performance. We examined relationships between CORT levels and estimates of reproductive performance. Timing of breeding and reproductive performance were measured at all colonies from 1996 to 2001. Reproductive parameters were assessed using study plots and standardized methods (Birkhead & Nettleship 1982). Breeding parameters were calculated as the mean of plot means. We monitored 5 and 9 plots containing an average of 20 and 13 nest sites (sites with eggs, range 8 to 40) at Gull and Duck

Islands, respectively. Plots were checked every 1 to 2 d at Gull and every 3 d at Duck Island. We observed the status of nests from observation points on each island using binoculars at close range from hides. We quantified timing of breeding as the mean of plot medians for lay date. We calculated hatching success as the number of eggs laid that hatched, fledging success as the number of chicks fledged per egg laid, and reproductive success as the number of chicks fledged per nest. Chicks were considered to have fledged successfully if they disappeared from the nest site ≥ 15 d after hatching because 15 d is the minimum nest departure age for common murre chicks and we never observed mortality in older chicks.

Survival study. We examined the relationship between baseline CORT levels in individuals during a given reproductive season and the presence of those individuals at the colony during subsequent reproductive seasons. We distinguished 'persistence of individuals in a colony' (hereafter called 'persistence') from survival, because we did not survey all colonies in the region and thus were not able to distinguish between mortality and emigration if a bird was subsequently absent from the colony at which it was banded. Furthermore, at least 1 individual banded as a breeder at Duck Island was observed on Gull Island during subsequent years, confirming the possibility for movement of breeding birds between the focal colonies. To measure persistence of birds in a colony, we employed traditional methods. Specifically, we captured adult breeding birds (actively attending a nest site, egg, or chick) and marked them using a numbered stainless steel band and a unique combination of colored plastic leg bands. We collected blood from captured individuals for CORT and genetic analysis of gender, and took measurements of their body mass and skeletal elements. In subsequent years, we conducted re-sighting by intense daily searches throughout the colony for about 6 wk yr⁻¹, starting before egg-laying and continuing until re-sighting curves reached a plateau, indicating that all marked birds had been encountered (Hatch et al. 1993). Several years of re-sighting effort are recommended to ensure re-sighting of individuals that have been present in a colony but may be missed if re-sighting effort is limited to only 1 or 2 subsequent years (Lebrereton et al. 1992). With 5 yr of effort (including 4 yr of banding followed by 4 yr of re-sighting), and using only individuals with complete re-sighting histories, we were able to distinguish among 3 scenarios of a bird's persistence in a colony in relation to its baseline CORT during that current reproductive season. Specifically, individuals were either: (1) re-sighted at the colony in the following year (hereafter 're-sighted'); (2) skipped the following year, but were re-sighted during 2 sub-

sequent years ('skipped'); or (3) were not re-sighted during the following season or during 2 subsequent years ('disappeared').

Sex determination. To identify bird gender, we extracted genomic DNA from blood samples following the salt-extraction protocol described in Medrano et al. (1990) and modified as in Sonsthagen et al. (2004). We amplified the DNA of 271 individuals using standard polymerase chain reaction (PCR) conditions with the P8/P2 primer set to determine the gender of each bird based on the chromo-helicase-binding domain (CHD) gene. Sex was assigned based on the absence (male: ZZ) or presence (female: ZW) of the band for the *W* chromosome. For quality control purposes, approximately 20% of samples was re-extracted and re-processed.

Data analysis. All analyses were conducted using the SYSTAT and STATISTICA statistical packages. Data were log-transformed to meet assumptions for normal distribution and homogeneity of variance. Statistical analyses consisted of the following steps.

Measuring stress and identifying its causes: First, to examine whether differences in stress are intrinsic to a colony (Duck vs. Gull Island) and/or to the reproductive stage (egg-laying, incubating, and/or chick-rearing), we used univariate conventional ANOVA, where CORT was a dependent variable, and colony, reproductive stage, and year with interaction terms were factors. Second, we used ANCOVA with factors identified as significant in the previous step, and food abundances during current 2 wk (F2W), current mo (FCM), and previous mo (FPM) as covariates. Separate models were run for baseline and maximum CORT levels, and the Bonferroni adjustment of probabilities for multiple comparisons was used. Third, we used the information-theoretic approach to identify suitable models for predicting stress (CORT) in adult murrelets (Burnham & Anderson 1998, Anderson et al. 2000). Specifically, we examined a relative contribution of colony, reproductive stage, year, gender, body mass, and F2W, FCM and FPM, based on ANOVA, multiple regression, and ANCOVA approximating models. We had not planned to use the information-theoretic approach when we initiated the data collection; thus, we had no *a priori* reasons to focus on any particular sets/combinations of parameters and included all combinations of factors in our approximating models. We tested 83 approximating models in these analyses (we did not test models that included combinations of all interactions among different factors). We calculated the Akaike information criterion (AIC) 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 ($N/K \leq 40$; 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 . We used multi-model inference and determined the set that includes the best model in 95% of all samples (Burnham & Anderson 1998). Finally, to elucidate the importance of food abundance in determining CORT levels, we used linear regression analyses of means of the colony-specific CORT measured within the current 2 wk against mean food abundances measured either during the current 2 wk, current mo, or during a previous mo, whichever was included in the best fitting model according to the information-theoretic analyses, had a highest beta-weight within the best model, and was also identified as the best predicting variable in univariate analyses.

Testing the relationships between CORT and reproductive performance: We relied on estimates of reproductive performance derived on a colony-wide basis. Concurrent sampling of birds for determination of CORT and reproductive performance has always been done on different groups of birds to avoid the possible effects of capture on estimates of reproductive performance. Relationships between CORT levels and measures of the reproductive performance were not different between the colonies (parallelism of slope tests with p -values > 0.1). We used Spearman correlation analyses to examine relationships between means of colony/yr/stage-specific CORT and reproductive performance values for egg-laying, early incubation, late incubation, and chick-rearing stages. Because CORT levels at earlier stages could affect reproductive performance at later stages (i.e. CORT during incubation may affect fledging success, etc.), we tested all possible combinations of these parameters.

Testing the relationships between CORT and persistence of birds in a colony: A detailed comparison of adult murre's survival between the Duck and Gull colonies has previously been conducted (Piatt 2004). The specific goal of this current study was to determine persistence of individuals in relation to the food-related stress they have experienced, and thus we used a sub-set of all available data that included only complete re-sighting histories for individuals that were sampled for CORT and were not otherwise manipulated ($n = 372$). We used a 2-way ANOVA with baseline CORT 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. For pair-wise comparisons of the means, we used Tukey honestly significant difference (HSD) post hoc tests.

RESULTS

Baseline CORT levels

Univariate analysis

There was a significant difference in baseline CORT among years (Fig. 1, see Table 1 for statistical analysis). There were no consistent differences between colonies and stages, rather seasonal dynamics differed among years, colonies, and stages (Table 1). Overall, baseline CORT levels changed in opposite ways between colonies (significant Year \times Colony interaction term); specifically, CORT decreased at Duck Island and increased at Gull Island during the study period (Fig. 1). Significant interaction terms between year, colony, and reproductive stage (Table 1) suggest that fluctuations in baseline CORT could not be attributed to the effects of colony and reproductive stage per se; rather, they reflected changes in ecological factors. ANCOVA with year as a factor and measurements of food abundance as covariates confirmed this. Specifically, the year effect became non-significant when controlled for variations in abundance of food (Table 1), whereas measurements of food abundance had highly significant effects on baseline CORT.

Information-theoretic modeling

The information-theoretic approach identified a model with food abundance as the best approximating model for baseline CORT (Table 2). Specifically, the model that included F2W (beta weight = -0.75), FCM (beta weight = 0.47), and FPM (beta weight = -0.28) was the top model. Other models including year, colony, stage, and sex of birds should probably not be discounted; however, Akaike weight for the top model was so much higher than that in the next best models (17 and 57 times better for Models 2 and 3, respectively), indicating that Model 1 was much better than Models 2 and 3. Overall, compared to other factors, F2W was by far the most important factor explaining variability in baseline CORT, as it was included as a factor in each of the top 10 models (Table 2). F2W alone explained 56% of the variability in baseline CORT (Fig. 2).

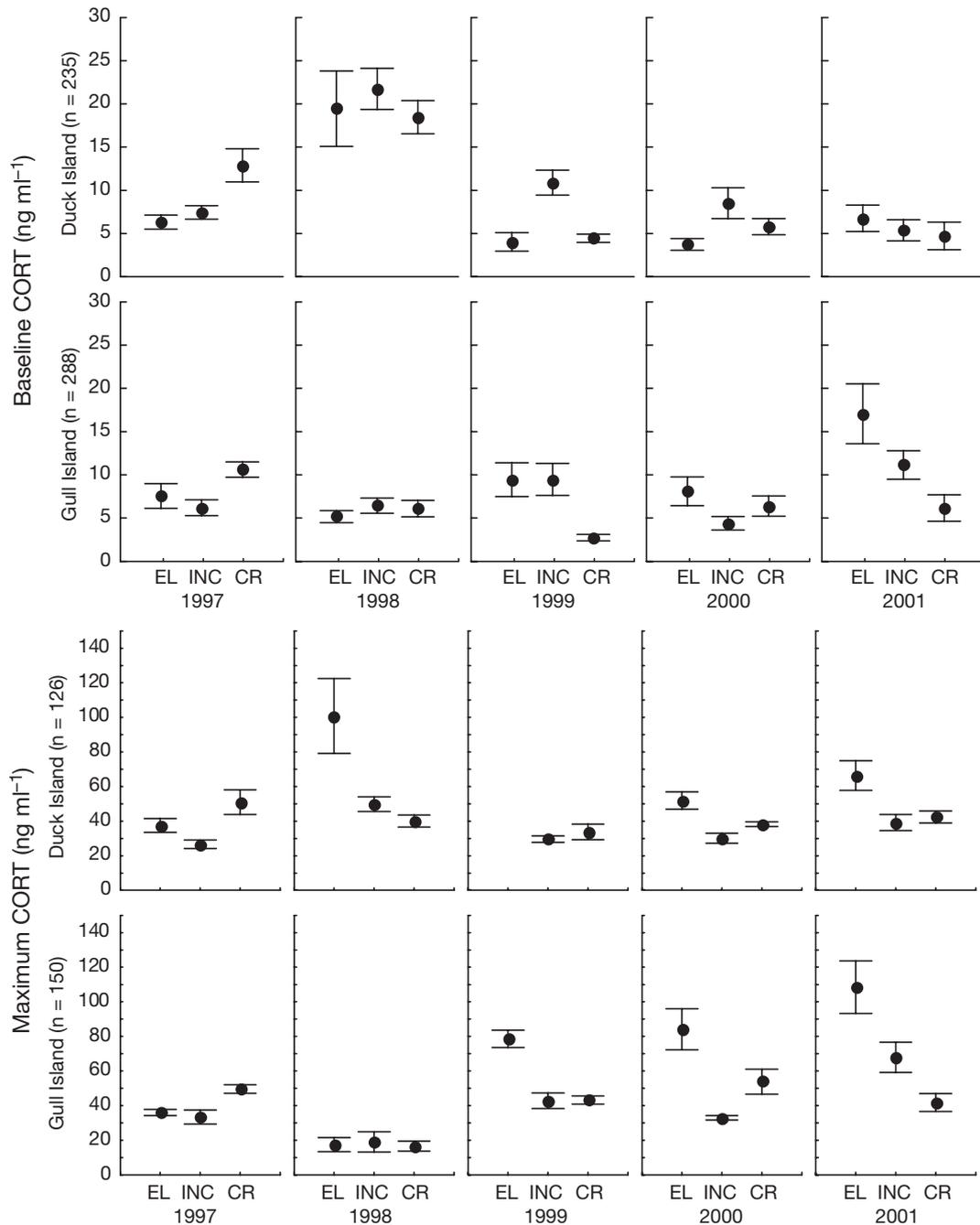


Fig. 1. *Uria aalge*. Inter-annual (1997 to 2001) and intra-seasonal dynamics of baseline and maximum corticosterone values (CORT; mean \pm SE) in common murre breeding at Duck and Gull Islands, Cook Inlet, Alaska. EL: egg-laying; INC: incubation, CR: chick-rearing

Maximum acute stress-induced CORT levels

Univariate analysis

There was a significant difference in maximum CORT among years and stages (Fig. 1, see Table 1 for statistical analysis). However, year and stage effects were not consistent between colonies. During

the study period, inter-annual changes in maximum CORT levels differed between colonies—they remained relatively constant at Duck Island and increased at Gull Island (Fig. 1). Significant interaction terms between year, colony, and reproductive stage (Table 1) suggest that fluctuations in the adrenocortical stress response could not be attributed to the colony and reproductive stage effects per se;

Table 1. *Uria aalge*. Effects of year, colony, reproductive stage, and food abundance on baseline and maximum corticosterone (CORT) in common murre breeding on Duck Island and Gull Island from 1997 to 2001

Factor	df effect	MS effect	df error	F	p	Bonferroni significance
Baseline CORT (ANOVA)						
Year	4	1.638	493	17.39	<0.00001	Yes
Colony	1	0.249	493	2.65	0.10428	No
Stage	2	0.275	493	2.93	0.05475	No
Year × Colony	4	1.831	493	19.45	<0.00001	Yes
Year × Stage	8	0.417	493	4.43	0.00003	Yes
Colony × Stage	2	0.477	493	5.07	0.00664	No
Colony × Year × Stage	8	0.145	493	1.54	0.13993	No
Baseline CORT—effect of food abundance (ANCOVA)						
Year	3	0.261	295	2.74	0.04382	No
Food (current 2 wk)	1	5.064	295	53.15	<0.00001	Yes
Food (current mo)	1	1.099	295	11.53	0.00077	Yes
Food (previous mo)	1	1.115	295	11.70	0.00071	Yes
Maximum CORT (ANOVA)						
Year	4	0.505	266	13.60	<0.00001	Yes
Colony	1	0.041	266	1.11	0.29394	No
Stage	2	0.626	200	21.34	0.00001	Yes
Year × Colony	4	0.894	266	24.07	0.00001	Yes
Year × Stage	6	0.193	200	6.59	0.00001	Yes
Colony × Stage	2	0.007	200	0.24	0.79020	No
Colony × Year × Stage	6	0.061	200	2.09	0.05658	No
Maximum CORT—effect of food abundance (ANCOVA)						
Year	3	0.277	115	6.98	0.00025	Yes
Stage	2	0.098	115	2.47	0.08927	No
Food (current 2 wk)	1	0.002	115	0.06	0.81509	No
Food (current mo)	1	0.039	115	0.99	0.32086	No
Food (previous mo)	1	0.794	115	20.02	0.00001	Yes

CORT and reproductive performance

Baseline CORT at the egg-laying and incubation stages was negatively correlated with hatching, fledging success, and overall productivity (Table 3). Baseline CORT at incubation was also positively correlated with phenology of egg-laying—in other words, baseline CORT was higher during years with relatively late egg-laying (Table 3). Baseline CORT at chick-rearing was not correlated with indices of reproductive performance. Maximum CORT levels at early and late incubation were negatively correlated with hatching and fledging success, and maximum CORT at late incubation was negatively correlated with overall productivity (Table 3). Maximum CORT values at egg-laying and chick-rearing were not correlated with indices of reproductive performance (Table 3). Maximum CORT was not correlated with phenology of egg-laying (Table 3).

rather, maximum CORT levels reflected changes in ecological factors. ANCOVA with year and stage as factors, and measurements of food abundance as covariates confirmed this suggestion. Specifically, the effect of stage disappeared and the effect of year diminished when those factors were controlled for variations in food abundance, whereas FPM had a highly significant effect on maximum CORT (Table 1).

Information-theoretic modeling

The information-theoretic approach identified a model with FPM (beta weight = -0.85), year (beta weight = 0.20), colony (beta weight = 0.54), and stage (beta weight = -0.44) as the best approximating model for maximum CORT (Table 2). The second best model also included sex (beta weight = -0.10) of the birds. Year and FPM were the most important among the top 10 models. FPM alone explained 31 % of the variability in maximum CORT (Fig. 2).

Table 2. *Uria aalge*. Models of baseline and maximum levels of corticosterone (CORT) in common murre breeding on Duck and Gull Island colonies from 1997 to 1999, using theoretic-information criterion. Food abundance during: current 2 wk (F2W); current mo (FCM); previous mo (FPM). Ev. ratio: evidence ratio

Variables	K ^a	ΔAIC _c ^a	SSE	W _i ^a	Ev. ratio
Baseline CORT (n = 271)					
F2W, FCM, FPM	5	0.00	0.097	0.879	1.0
F2W, stage	4	5.66	0.100	0.052	17.0
F2W, year, stage	5	8.07	0.100	0.016	56.5
F2W, stage, sex	5	8.71	0.101	0.011	78.0
F2W, colony, stage	5	8.75	0.101	0.011	79.3
F2W, FCM	4	9.61	0.102	0.007	122.2
F2W	3	10.10	0.103	0.006	156.4
F2W, FPM	4	10.75	0.102	0.004	216.3
F2W, year, colony, stage	6	11.08	0.101	0.003	254.7
F2W, year, stage, sex	6	11.17	0.101	0.003	266.3
Maximum CORT (n = 110)					
FPM, year, colony, stage	6	0.00	0.035	0.601	1.0
FPM, year, colony, stage, sex	7	0.86	0.034	0.391	1.5
FPM, year	4	10.31	0.039	0.003	173.2
FPM, year, colony	5	12.10	0.039	0.001	424.8
FPM, year, stage	5	12.39	0.039	0.001	491.2
FPM, year, sex	5	13.14	0.040	0.001	713.0
FPM, year, colony, sex	6	14.95	0.040	0.000	1763.3
FPM, year, stage, sex	6	15.41	0.040	0.000	2220.3
Year	3	18.17	0.043	0.000	8805.2
Body mass, year	4	19.41	0.043	0.000	16365.1

^aDefined in 'Data analysis'

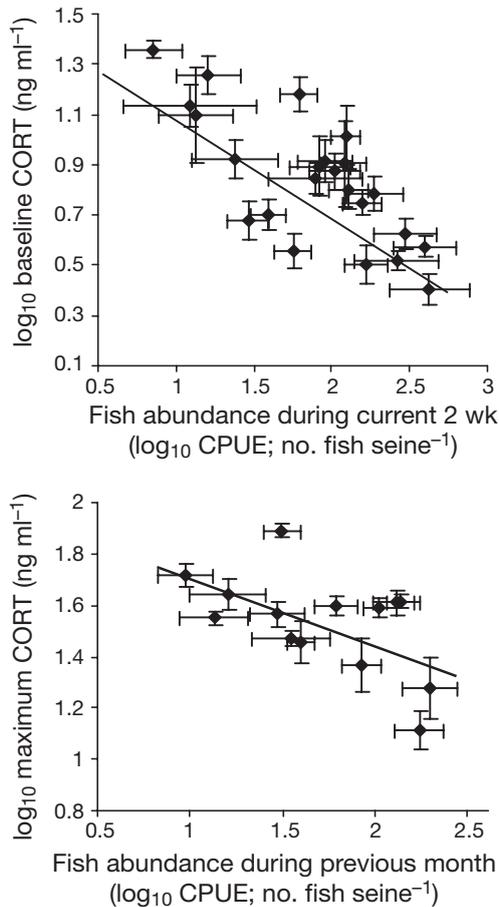


Fig. 2. *Uria aalge*. Relationships between corticosterone (CORT) and food abundance in common murres breeding on Duck and Gull Islands, from 1996 to 1999 (mean \pm SE). Lines represent slopes of linear regression analyses of mean CORT levels and mean fish abundance during current 2 wk for baseline ($R^2 = 0.56$, $F_{1,22} = 27.08$; $p < 0.0001$, $N = 23$, both colonies and all 4 yr combined) and during previous month for maximum CORT ($R^2 = 0.31$, $F_{1,13} = 5.26$; $p = 0.040$, $N = 14$, both colonies and all 4 yr combined). CPUE: catch per unit effort

Table 3. *Uria aalge*. Relationships between corticosterone (CORT) and reproductive performance (colony/year/stage-specific values) in common murres breeding on Duck and Gull Islands, from 1996 to 2001. Reported numbers are Spearman correlation coefficients and sample sizes (in parentheses); statistically significant relationships ($p < 0.05$) indicated in bold

Parameter	Egg-laying phenology	Hatching success	Fledging success	Productivity
Baseline CORT				
Egg-laying	0.69 (8)	-0.73 (8)	-0.87 (8)	-0.76 (9)
Incubation	0.78 (9)	-0.82 (9)	-0.80 (9)	-0.80 (10)
Early chick-rearing	0.83 (9)	-0.79 (9)	-0.82 (9)	-0.79 (10)
Late chick-rearing	0.48 (8)	-0.34 (8)	-0.45 (8)	-0.37 (9)
Maximum CORT				
Egg-laying	0.39 (7)	-0.53 (7)	-0.61 (7)	-0.52 (8)
Incubation	0.59 (9)	-0.78 (9)	-0.83 (9)	-0.63 (10)
Early chick-rearing	0.42 (9)	-0.77 (9)	-0.72 (9)	-0.67 (10)
Late chick-rearing	-0.26 (8)	-0.02 (8)	0.00 (8)	-0.02 (9)

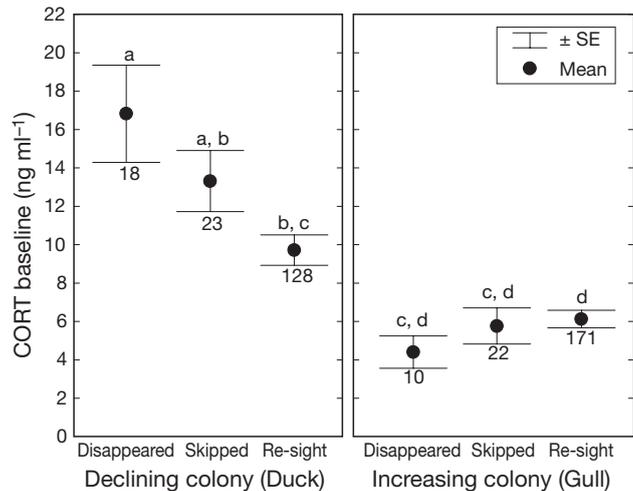


Fig. 3. *Uria aalge*. Persistence of individuals at declining (Duck Island) and increasing (Gull Island) colonies of common murres breeding in Cook Inlet, Alaska, from 1997 to 2001, in relation to their baseline corticosterone value (CORT; mean \pm SE). A significant difference between groups with different re-sighting histories is indicated by a change in lettering above the SE bars. Numbers below the SE bars represent sample sizes

CORT and persistence of individuals in the colony

The relationship between baseline levels of CORT and re-sighting of murres at the colonies was different between Duck and Gull colonies (colony \times re-sighting interaction term $F_{2, 366} = 5.53859$, $p = 0.004$; Fig. 3). At Duck Island colony, baseline levels were significantly higher among birds that were not re-sighted during 3 consecutive reproductive seasons (disappeared) compared to birds that were re-sighted during a following reproductive season (Tukey post hoc $p = 0.005$). CORT levels in birds that skipped the next season but were re-sighted during the following 2 seasons were not different from those in birds that disappeared ($p = 0.960$) or were re-sighted ($p = 0.066$) at the declining Duck Island colony. There were no differences in baseline CORT among re-sighted, skipped, and disappeared birds at the increasing Gull Island colony ($p > 0.267$; Fig. 3).

DISCUSSION

Fluctuations in availability of food have long been hypothesized to play a major role in regulating seabird populations. In the present study we used a field endocrinology approach to measure stress, identify its causes, and to examine the hypothesized

link between food-related stress and population processes in the common murre *Uria aalge*. A long-term series of measurement of stress and food abundance allowed us to establish: (1) a direct link between changes in food abundance and stress status of individuals, (2) negative effects of food-related stress on fecundity, and (3) negative effects of food-related stress on persistence of individuals in a declining colony.

CORT as a measure of food-related stress

CORT is an important regulator of carbohydrate, lipid, and protein metabolism and thus is expected to play a role during nutritional limitations (reviewed in Sapolsky et al. 2000, Romero 2004). Consequently, several studies suggested that CORT may provide information on the stress status of individuals in relation to the abundance of their food (Kitaysky et al. 1999a, Romero & Wikelski 2000, Lanctot et al. 2003, Clinchy et al. 2004). However, the idea of using CORT as a direct measure of food availability in free-living animals was controversial (e.g. Lanctot et al. 2003). First, CORT production in birds may reflect population-specific parameters and/or endogenous changes in the physiology of individuals at different stages of their life cycle (i.e. Wingfield 1994, Romero et al. 1997, Kitaysky et al. 1999b, Romero 2002). Second, CORT may be released in response to a wide range of adverse environmental conditions (Wingfield 1994, Wingfield et al. 1997). It was also not well known whether elevated levels of CORT would only be associated with catastrophic events, such as famine (i.e. Romero & Wikelski 2000); CORT may also reflect moderate changes in food supplies.

In the current study we have addressed at least some of these concerns and present the first empirical evidence for CORT secretion as a quantitative link between changes in food abundance and stress status in free-living seabirds. Contrary to the first argument, a long-term series of data in our study revealed that secretion of CORT reflects changes in ecological conditions rather than changes that are specific for a particular colony or reproductive stage. We did not find a consistent effect of the colony across years (Fig. 1). Our results show clearly that baseline and acute stress-induced levels of CORT may change in all possible ways among stages (see Fig. 1). We conclude that studies of seasonal changes in the adrenocortical function might yield equivocal results if they are based on short time series that do not cover a full range of environmental conditions. This study calls for a revision of the conclusion regarding the intrinsic contribution of the reproductive stage as a driving force for changes in adrenal activity.

In contrast to the second argument, our results show that in breeding common murres the variability in

CORT levels is largely explained by the variations in food supply (Fig. 2). Specifically, 2 different analytical approaches used in this study confirmed this: univariate analyses 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. The information-theoretic analyses also identified models that included measures of food abundance as the best approximating models for CORT. We are not arguing that other factors do not contribute to changes in CORT in seabirds. It might well be that sickness, parasite infestations, and agonistic social interactions contribute greatly to variation in CORT secretion in seabirds. However, in our study, we sampled only actively breeding individuals; in other words, our sampling was 'biased' toward healthy individuals because all others that were sick, heavily parasitized, or had not accumulated sufficient resources to participate in reproduction were not sampled. Furthermore, our sampling was limited to 'socially established' individuals that have succeeded in securing a nest site, mate, egg, or chick, and others that had failed at those stages were also not sampled. Our selective sampling may explain why the variations in food were by far the most important factors determining CORT secretion in common murres in this study. We would argue that the selection criteria used in our study are not only appropriate, but are strictly required to examine a functional link between food-related stress and population processes in seabirds. We would also argue that, although changes in food abundance explained a large portion of variability in CORT, our assessment of food availability was probably far from the ideal. Specifically, although it is arguably the best practical way to measure temporal and spatial changes in food resources in marine environments, beach seine trawling has provided us with the information on food abundance only. Yet, food availability is the only true measure of foraging conditions in animals, and it may vary depending on distribution and density of patches, distance from a breeding colony, energetic density of prey, etc. Thus, food abundance as we measured it was still only a proxy for food availability, and a significant effect of year on CORT levels (at least in case of the maximum CORT) may easily reflect this imperfection in our measurements of food resources. If food availability rather than food abundance could be measured in marine environments, we expect an even higher proportion of variability in CORT would have been explained by variations in food resources.

The field endocrinology approach offers the possibility to discriminate between short- and long-term changes in food resources, and provides a measure of recovery from food-related stress in free-living indi-

viduals. Baseline CORT increases quickly (within hours or days) in response to experimentally induced food shortages (Kitaysky et al. 2001a, Lynn et al. 2003, Edwards 2004). Supporting this, concurrent measurements of CORT and food abundance in this study identified that baseline CORT is directly correlated with changes in current food abundance. On the other hand, the adrenocortical stress response integrates changes in food abundance over longer time periods. During prolonged food shortages, when animals are exposed to chronically elevated baseline CORT secretion, their adrenal function is enhanced (Akana et al. 1992, Dallman et al. 2004), which results in higher maximum CORT production in response to a standardized stressor (Kitaysky et al. 2001a). Accordingly, acute stress-induced CORT levels of common murrelets in the present study were best explained by changes in food abundance during the previous month. Thus, acute stress-induced CORT levels provide an integrative measure of an individual's nutritional history over longer time periods (wk) than baseline CORT (d). In a parallel study of free-living adult black-legged kittiwakes, we found that baseline CORT was also directly related to changes in food abundance during the current 2 wk, whereas their adrenocortical stress response was best correlated with changes in baseline CORT or food abundance during the current month (A. S. Kitaysky, J. F. Piatt unpubl. data). Similar results were also obtained for juvenile kittiwakes and common murrelets—their adrenocortical stress response reflected experimentally controlled nutritional history during a 3 to 4 wk period (Kitaysky et al. 1999a, 2001a). Whether the adrenocortical stress response is related to the severity of food shortages or the recovery from nutritional stress is allometrically related to body size of animals is not currently known. Thus, although it is clear that recent past nutritional history of birds at large defines the magnitude of the adrenocortical response to acute stressors, at least in the species of seabirds we have examined, future controlled experiments should examine the possibility that the time required to recover from food shortages depends on an animal's body size.

To conclude, multiple controlled experiments and observations of adrenal function in wild birds suggested that CORT secretion may be used to assess food stress in seabirds. Results obtained in this current study provide unequivocal evidence for a direct quantitative relationship between natural variability in food and the adrenocortical function in wild seabirds. We conclude that with careful sampling criteria, CORT can be used as a reliable measure of food-related stress and to gauge relative food availability in free-living seabirds. CORT can be used as an ecological indicator, as it is relatively easy to measure, not invasive, and responsive to food shortages in a predictable manner.

It is also very important that we can measure CORT as frequently as desired, unlike other 'remote' processes like food availability.

Food-related stress affects fecundity

Although corticosterone production may reflect the intensity of a stressor, the question remained whether naturally occurring levels of CORT are relevant to reproduction of wild animals (i.e. Lanctot et al. 2003, Lormee et al. 2003). We found a persistent 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 current study provides direct support for the hypothesis that food-related stress during reproduction can contribute to decreased fecundity of seabirds. Specifically, we consistently found negative relationships between CORT and reproductive performance at various stages of reproduction, both within and between colonies. This relationship may be causal. CORT is involved in the regulation of body maintenance processes, in part by modifying the behavior of individuals in accordance with ecological and life-history events (Wingfield & Kitaysky 2002). In particular, an increase in baseline CORT in parent seabirds changes the allocation of resources away from reproductive processes (by decreasing parental care) and towards body maintenance (by increasing foraging; Kitaysky et al. 2001b). Accordingly, in this study, baseline CORT was a reliable predictor of performance at the current stage (except at chick-rearing). Baseline CORT was a better predictor of reproductive performance compared to maximum CORT. According to correlation analyses, relationships between baseline CORT and reproductive performance were significant in 11 out of 16 possible combinations, while maximum CORT was significant only in 5 out of 16 possible combinations (Table 3). It is not surprising, however, because the effects of CORT on fecundity are expressed via behavioral modifications; and increases in baseline CORT have been shown to induce behavioral changes, whereas maximum CORT represents only the bird's capacity for stronger physiological and behavioral responses to environmental perturbations. Whether this potential would be realized or not depends on current environmental conditions.

Food-related stress affects persistence of individuals in a colony

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). Furthermore, to establish an effect of food-related stress during reproduction on persistence of adults in a population, one should be able to determine the relative contribution of factors affecting survival of adults during different stages of their life (i.e. during reproductive or post-reproductive stages), which is difficult (Fredericksen et al. 2004). This is of critical importance, however, as effects of stress during reproduction may not manifest for a prolonged period after a stressful event has already passed (Hunt & Byrd 1999, Kitaysky et al. 2001b, Golet et al. 2004).

Several studies have shown a negative relationship between endogenous CORT and survival of individuals (Romero & Wikelski 2000, Brown et al. 2005). During El Niño events, increased adrenocortical function in marine iguanas was negatively correlated with their subsequent survival (Romero & Wikelski 2000). In this case, an El Niño-induced famine was most likely a causal factor inducing increased CORT secretion and survival. However, El Niño may be characterized as a catastrophic event, and whether a relationship between CORT and survival would be observed under less drastic declines in foraging conditions remains to be shown. In another well-studied system, the cliff swallow, higher CORT secretion was related to higher mortality of individuals (Brown et al. 2005). At least in some cases, increased CORT secretion in swallows could be attributed to a decrease in food availability and/or to metabolic challenges induced by heavy parasite loads in individuals (Raouf et al. 2006). However, because food abundance was not quantified in this system, the relative contribution of various factors (i.e. food-related stress and parasite infestation) to survival of adult swallows has not been established.

We found that persistence of individuals in a declining colony is driven by food-related stress during the reproductive period (Fig. 3). Specifically, individuals that disappeared from this colony had higher levels of CORT compared to individuals that were re-sighted (Fig. 3). This result supports the hypothesis that population processes and the main factor contributing to population dynamics in seabirds—adult persistence in a colony—are constrained by food resources. The results of re-sighting at a declining colony maybe interpreted in 2 ways: (1) food stress and/or elevated CORT is detrimental to the survival of affected individuals and murrelets that disappeared from the colony; (2) food stress and/or elevated CORT induced birds to skip reproduction or relocate. In this second 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 the colony

was associated with nutritional stress during reproduction.

We also found that persistence of individuals in an increasing colony (Gull Island) is independent of foraging conditions during the reproductive season. These contrasting results for colonies with opposite numerical trends might be explained by several mutually non-exclusive mechanisms. First of all, it is possible that common murrelets from the focal colonies over-winter in different regions and are exposed to different environmental conditions. Although we cannot rule out this possibility, it is highly unlikely because of a close physical proximity of the colonies and the absence of population differentiation between them. Second, there is a possibility that murrelets breeding at a declining colony are older individuals compared to those breeding at an increasing colony. Specifically, analyses of survival and recruitment of common murrelets in Cook Inlet indicate that during the last 2 decades there was virtually no recruitment of young into the colony at Duck Island, in contrast to high recruitment and immigration into the Gull Island colony (Piatt 2004, S. V. Drovetski, A. S. Kitaysky, J. F. Piatt unpubl.). A senescent decline in survival of common murrelets has been previously demonstrated (Crespin et al. 2006) and, in combination with the results of this current study, it may suggest that nutritional stress during reproduction has a stronger effect on senescent individuals (breeding at Duck Island) compared to on young individuals (breeding at Gull Island). However, existing evidence argues against this hypothesis. Crespin et al. (2006) showed that senescence affects both survival and reproduction in the common murre. Thus, survival and breeding success of ageing birds at Duck Island are expected to be lower than at Gull Island. However, although survival probabilities were consistently lower at Duck Island, the declining colony (Piatt 2004), reproductive performance of murrelets did not differ between Gull and Duck colonies (Piatt 2002). Furthermore, because food abundance was lower in the vicinity of Duck Island compared to Gull Island (at least from 1996 to 1999; Piatt 2002), murrelets breeding there have performed better than expected compared to birds breeding at the food-rich Gull Island colony (Piatt 2002). This conflicting evidence for a possible differential effect of food limitations on senescent versus young individuals requires further examination. Finally, common murrelets breeding at Duck Island could be higher quality and/or more experienced individuals than those breeding at Gull Island. Recent studies of seabirds suggest substantial heterogeneity in quality of individuals breeding at the same colonies (e.g. Cam et al. 1998, 2002). Considering the almost exponential increase in numbers of common murrelets at Gull Island and the steady decline at Duck Island, it is plausible that het-

erogeneity in quality of individuals is higher at Gull Island compared to Duck Island. Factors affecting adult survival probably consist of predictable/unavoidable (e.g. climate-driven changes in food resources) and unpredictable/random (e.g. collision with a rock) elements. Thus, the persistence of high-quality experienced breeders at Duck Island is mostly a result of unavoidable factors (food limitations), whereas random effects prevail in determining the persistence of low-quality inexperienced breeders at the Gull Island colony.

It is extremely important to be able to distinguish among the scenarios described above, as it would allow us to predict responses of colonies with differential numerical trajectories to future environmental perturbations. For instance, a colony of murrelets at Gull Island has increased from a few to 1000s of individuals during the last 3 decades, probably due to the sudden appearance of relatively unlimited food supplies resulting from climate-driven changes in the ecosystems of the Gulf of Alaska (Anderson & Piatt 1999). Because of food-rich environments, birds of varying quality were able to reproduce successfully at this colony. If environmental conditions return to a prior state of the ecosystem, an unprecedented decline in numbers of breeding murrelets would be observed at this colony due to an increased proportion of inferior phenotypes. Whether individuals that would not be able to sustain breeding at the Gull Island colony would move somewhere else or die is not clear.

From 1996 to 1999, directly measured food abundance was higher in the vicinity of Gull Island compared to Duck Island (Piatt 2002). However, during the last 2 yr of observations (2000 and 2001), both measures of CORT tended to be higher in murrelets on Gull Island than on Duck Island (Fig. 1). This suggests that during our study we probably witnessed the beginning of a regime shift in the ecosystem of Cook Inlet. Thirty years ago, breeding murrelets were much more numerous on Duck Island compared to Gull Island, probably reflecting former abundances of food in the vicinities of those colonies (Piatt & Anderson 1996). Based on changes in food availability (as gauged by CORT), we predict that again Gull Island is becoming a food-poor colony, whereas Duck Island is becoming a food-rich colony.

Acknowledgements. This study was supported by a grant from EVOS Trustees Council; financial support during manuscript preparation was also provided by NPRB, NSF EPSCoR, USGS, and Institute of Arctic Biology, University of Alaska, Fairbanks. We are grateful to E. Kitaiskaia for performing hormonal assays and to M. Benowitz-Fredericks and M. Shultz for enthusiastic discussions and their help with many aspects of this paper. We thank S. Talbot for expertly conducting genetic sexing. Thank you to A. Abookire, M. Arumitsu, J. Benson, D. Black, L. Ochikubo, A. Chapman, J. Figurski, M.

Gray, A. Harding, G. Hoffman, C. Hovnanian, B. Keitt, R. Kitaysky, M. Litzow, K. Mangel, A. Nielsen, R. Papish, M. Post, M. Schultz, M. Shultz, G. Snegden, B. Smith, T. Van Pelt, M. Wada, S. Wang, J. Wetzel, S. Wright, S. Zador, and S. Zuniga for their great field work. This study was approved by the IACUC, University of Washington.

LITERATURE CITED

- Abookire AA, Piatt JF, Robards MD (2000) Nearshore fish distributions in an Alaskan estuary in relation to stratification, temperature and salinity. *Estuar Coast Shelf Sci* 51: 45–59
- Aebischer NJ, Coulson JC (1990) Survival of the kittiwake in relation to sex, year, breeding experience and position in the colony. *J Anim Ecol* 59:1063–1071
- Akana SF, Dallman MF, Bradbury MJ, Scribner KA, Strack AM, Walker CD (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 DR, Burnham KP, Thompson WL (2000) Null hypothesis testing: problems, prevalence, and an alternative. *J Wildl Manag* 64:912–923
- Anderson PJ, Piatt JF (1999) Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Mar Ecol Prog Ser* 189:117–123
- Benowitz-Fredericks MZ, Kitaysky AS, Thompson CW (2006) Growth and resource allocation by common murre (*Uria aalge*) chicks in response to experimentally restricted diets. *Auk* 123:722–734
- Birkhead TR, Nettleship DN (1982) The adaptive significance of egg size and laying date in thick-billed murrelets *Uria lomvia*. *Ecology* 63:300–306
- Brown CR, Brown MB, Raouf SA, Smith LC, Wingfield JC (2005) Effects of endogenous steroid hormone levels on annual survival in cliff swallows. *Ecology* 86:1034–1046
- Burnham KP, Anderson DR (1998) Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York
- Cailliet GM, Love MS, Ebeling AW (1986) Fishes: a field and laboratory manual on their structure, identification and natural history. Wadsworth, Belmont, CA
- Cam E, Hines JE, Monnat J-Y, Nichols JD, Danchin E (1998) Are adult nonbreeders prudent parents? The kittiwake model. *Ecology* 79:2917–2930
- Cam E, Cadiou B, Hines JE, Monnat J-Y (2002) Influence of behavioral tactics on recruitment and reproductive trajectory in the kittiwake. *J Appl Stat* 29:163–185
- Clinchy M, Zanette L, Boonstra R, Wingfield JC, Smith JNM (2004) Balancing food and predator pressure induces chronic stress in songbirds. *Proc R Soc Lond B* 271:2473–2479
- Cockrem JF (2004) Conservation and behavioral neuroendocrinology. *Horm Behav* 48:492–501
- Cockrem JF, Silverin B (2002) Variation within and between birds in corticosterone responses of great tits (*Parus major*). *Gen Comp Endocrinol* 125:197–206
- Crespin L, Harris M, Leberon J-D, Frederiksen M, Wanless S (2006) Recruitment to a seabird population depends on environmental factors and population size. *J Anim Ecol* 75:228–238
- Dallman MF, Akana SF, Strack AM, Scribner KS, Pecoraro N, La Fleur SE, Houshyar H, Gomez F (2004) Chronic stress-induced effects of corticosterone on brain: direct and indirect, stress: current neuroendocrine and genetic approaches. *Ann N Y Acad Sci* 1018:141–150

- Edwards AE (2004) Proximate and ultimate constraints on breeding in seabirds. PhD thesis, University of Washington, Seattle, WA
- Frederiksen M, Wanless S, Harris MP, Rothery P, Wilson L (2004) The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes. *J Appl Ecol* 41:1129–1139
- Golet GH, Schmutz JA, Irons DB, Estes JA (2004) Determinants of reproductive costs in the long-lived black-legged kittiwake: a multiyear experiment. *Ecol Monogr* 74: 353–372
- Hatch SA, Roberts BD, Fadley BS (1993) Adult survival of black-legged kittiwakes *Rissa tridactyla* in a Pacific colony. *Ibis* 135:247–254
- Hunt GL, Byrd GV (1999) Marine bird populations and carrying capacity of the eastern Bering Sea. In: Loughlin TR, Otani K (eds) *Dynamics of the Bering Sea*. University of Alaska Sea Grant, Fairbanks, AK, p 631–650
- Hunt GL Jr, Decker MB, Kitaysky AS (1996) Fluctuations in the Bering Sea ecosystem as reflected in the reproductive ecology and diets of kittiwakes on the Pribilof Islands, 1975 to 1991. In: Greenstreet SPR, Tasker ML (eds) *Aquatic predators and their prey*. Fishing News Books, Oxford, p 142–153
- Kitaysky AS (1999) Metabolic and developmental responses of alcid chicks to experimental variation in food intake: functional significance of juvenile traits in varying environments. *Physiol Zool* 72:462–473
- Kitaysky AS, Golubova EG (2000) Climate change causes contrasting trends in reproductive performance of planktivorous and piscivorous alcids. *J Anim Ecol* 69:248–262
- Kitaysky AS, Piatt JF, Wingfield JC, Romano M (1999a) The adrenocortical stress-response of black-legged kittiwake chicks in relation to dietary restrictions. *J Comp Physiol B* 169:303–310
- Kitaysky AS, Wingfield JC, Piatt JF (1999b) Food availability, body condition and physiological stress response in breeding black-legged kittiwakes. *Funct Ecol* 13:577–584
- Kitaysky AS, Hunt GL, Flint EN, Rubega MA, Decker MB (2000) Resource allocation in breeding seabirds: responses to fluctuations in their food supply. *Mar Ecol Prog Ser* 206:283–296
- Kitaysky AS, Kitaiskaia EV, Wingfield JC, Piatt JF (2001a) Dietary restriction causes chronic elevation of corticosterone and enhances stress-response in red-legged kittiwake chicks. *J Comp Physiol B* 171:701–709
- Kitaysky AS, Wingfield JC, Piatt JF (2001b) Corticosterone facilitates begging and affects resource allocation in the black-legged kittiwake. *Behav Ecol* 12:619–625
- Kitaysky AS, Kitaiskaia EV, Piatt JF, Wingfield JC (2003) Benefits and costs of increased corticosterone secretion in seabird chicks. *Horm Behav* 43:140–149
- Kitaysky AS, Romano MD, Piatt JF, Wingfield JC, Kikuchi M (2005) The adrenocortical response of tufted puffin chicks to nutritional stress. *Horm Behav* 47:609–619
- Kitaysky AS, Kitaiskaia EV, Wingfield JC, Piatt JF (2006) A mechanistic link between chick diet and decline in seabirds? *Proc R Soc Lond B* 273:445–450
- Lack D (1966) *Population studies of birds*. Clarendon Press, Oxford
- Lanctot RB, Hatch SA, Gill VA, Eens M (2003) Are corticosterone levels a good indicator of food availability and reproductive performance in a kittiwake colony? *Horm Behav* 43:489–502
- Lebrerton JD, Burnham KD, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: case studies and recent advances. *Ecol Monogr* 62:67–118
- Lloyd CS (1979) Factors affecting breeding of razorbills *Alca torda* on Skokholm. *Ibis* 121:165–176
- 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
- Lynn SE, Breuner CW, Wingfield JC (2003) Short-term fasting affects locomotor activity, corticosterone, and corticosterone binding globulin in a migratory songbird. *Horm Behav* 43:150–157
- Medrano JF, Aasen E, Sharrow L (1990) DNA extraction from nucleated red blood cells. *Biotechniques* 8:43
- Merrick RL, Louphlin TR, Calkins DG (1987) Decline in abundance of the northern sealion, *Eumetopias jubatus*, in Alaska, 1956–86. *Fish Bull* (Wash DC) 85:351–365
- Mougin JL, Jouanin C, Roux F (1997) Intermittent breeding in Cory's shearwater *Calonectris diomedea* of Selvagem Grande, North Atlantic. *Ibis* 139:40–44
- Piatt JF, Anderson PJ (1996) Response of common murres to the Exxon Valdez oil spill and long-term changes on the Gulf of Alaska marine ecosystem. In: Rice SD, Spies RB, Wolfe DA, Wright BA (eds) *Exxon Valdez Oil Spill Symp Proc*. Am Fish Soc Symp 18: 720–773
- Piatt JF (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, AK
- Piatt JF (2004) Survival of adult murres and kittiwakes in relation to forage fish abundance. Final report to Exxon Valdez Oil Spill Restoration Project (Restoration Project 00338). U.S. Geological Survey, Anchorage, AK
- Pravosudov VV, Kitaysky AS (2006) Effects of nutritional restrictions during post-hatching development on adrenocortical function in western scrub-jays (*Aphelocoma californica*). *Gen Comp Endocrinol* 145:25–31
- Pravosudov VV, Kitaysky AS, Wingfield JC, Clayton NS (2001) Long-term unpredictable foraging conditions and physiological stress response in mountain chickadees (*Poecile gambeli*). *Gen Comp Endocrinol* 123:324–331
- Raouf SA, Smith LC, Brown MB, Wingfield JC, Brown CR (2006) Glucocorticoid hormone levels increase with group size and parasite load in cliff swallows. *Anim Behav* 71: 39–48
- Regehr HM, Montevecchi WA (1997) Interactive effects of food shortage and predation on breeding failure of black-legged kittiwakes: indirect effects of fisheries activities and implications for indicator species. *Mar Ecol Prog Ser* 155:249–260
- Robards MD, Piatt JF, Kettle AB, Abookire AA (1999) Temporal and geographic variation in fish communities of lower Cook Inlet, Alaska. *Fish Bull* (Wash DC) 97:962–977
- Robards MD, Rose GA, Piatt JF (2002) Growth and abundance of Pacific sand lance, *Ammodytes hexapterus*, under differing oceanographic regimes. *Environ Biol Fish* 64: 429–441
- Romero LM (2002) Seasonal changes in plasma glucocorticoid concentrations in free-living vertebrates. *Gen Comp Endocrinol* 128:1–24
- Romero LM (2004) Physiological stress in ecology: lessons from biomedical research. *Trends Ecol Evol* 19:249–255
- Romero LM, Wikelski M (2000) Corticosterone levels predict survival probabilities of Galapagos marine iguanas during El Niño events. *Proc Natl Acad Sci USA* 98:7366–7370
- Romero LM, Reed JM (2005) Collecting baseline corticosterone samples in the field: is under 3 min good

- enough? *Comp Biochem Physiol A* 140:73–79
- Romero LM, Ramenofsky M, Wingfield JC (1997) Season and migration alters the corticosterone response to capture and handling in an Arctic migrant, the white-crowned sparrow (*Zonotrichia leucophrys gambelii*). *Comp Biochem Physiol* 116:171–177
- Sandvik H, Erikstad KE, Barrett R, Yoccoz NG (2005) The effect of climate on adult survival in five species of North Atlantic seabirds. *J Anim Ecol* 74:817–831
- Sapolsky RM, Romero ML, Munck AU (2000) How do glucocorticoids influence stress responses? integrative, permissive, suppressive, stimulatory, and preparation actions. *Endocr Rev* 21:55–89
- Shea RE, Ricklefs RE (1995) An experimental test of the idea that food supply limits growth rate in tropical seabirds. *Am Nat* 125:116–122
- Shea RE, Ricklefs RE (1996) Temporal variation in growth performance in six species of tropical, pelagic seabirds. *J Anim Ecol* 65:29–42
- Sonsthagen SA, Talbot SL, White CM (2004) Gene flow and genetic characterization of northern goshawks breeding in Utah. *Condor* 106:826–836
- Thompson PM, Ollason JC (2001) Lagged effects of ocean climate change on fulmar population dynamics. *Nature* 413:417–420
- Wanless S, Harris MP, Redman P, Speakman JR (2005) Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Mar Ecol Prog Ser* 189:117–123
- Williams GC (1966) Natural selection, the costs of reproduction and a refinement of Lack's principle. *Am Nat* 100: 687–692
- Wingfield JC (1994) Modulation of the adrenocortical response to stress in birds. In: Davey KG, Peter RE, Tobe SS (eds) *Perspectives in comparative endocrinology*. National Research Council of Canada, Ottawa, p 520–528
- Wingfield JC, Kitaysky AS (2002) Endocrine responses to unpredictable environmental events: stress or anti-stress hormones? *Integr Comp Biol* 42:600–609
- Wingfield JC, Bruener C, Jacobs J (1997) Corticosterone and behavioral responses to unpredictable events. In: Harvey S, Etches RJ (eds) *Perspectives in avian endocrinology*. Society for Endocrinology, Bristol, p 267–278
- Zador SG, Piatt JF (1999) Time-budgets of common murrelets at a declining and increasing colony in Alaska. *Condor* 101:149–152

Editorial responsibility: Howard Browman (Associate Editor-in-Chief), Storebø, Norway

*Submitted: September 28, 2006; Accepted: December 23, 2006
Proofs received from author(s): October 13, 2007*