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## Are corticosterone levels a good indicator of food availability and reproductive performance in a kittiwake colony?

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### Abstract

We evaluated the use of corticosterone to gauge forage availability and predict reproductive performance in black-legged kittiwakes (*Rissa tridactyla*) breeding in Alaska during 1999 and 2000. We modeled the relationship between baseline levels of corticosterone and a suite of individual and temporal characteristics of the sampled birds. We also provided supplemental food to a sample of pairs and compared their corticosterone levels with that of pairs that were not fed. Corticosterone levels were a good predictor of forage availability in some situations, although inconsistencies between corticosterone levels and reproductive performance of fed and unfed kittiwakes suggested that this was not always the case. In general, higher corticosterone levels were found in birds that lacked breeding experience and in birds sampled shortly after arriving from their wintering grounds. All parameters investigated, however, explained only a small proportion of the variance in corticosterone levels. We also investigated whether corticosterone, supplemental feeding, year of the study, breeding experience, body weight, and sex of a bird were able to predict laying, hatching, and fledging success in kittiwakes. Here, breeding experience, year of the study, and body weight were the best predictors of a bird's performance. Corticosterone level and supplemental feeding were good predictors of kittiwake reproductive performance in some cases. For example, corticosterone levels of birds sampled during the arrival stage reliably predicted laying success, but were less reliable at predicting hatching and fledging success. Counts of active nests with eggs or chicks may be more reliable estimates of the actual productivity of the colony. Supplemental feeding had strong effects on kittiwake productivity when natural forage was poor, but had little effect when natural forage was plentiful.

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Animals are thought to respond to unpredictable and disruptive change in their environment by modifying their behavior to promote survival. Behavior modification can include increased foraging, cessation of territoriality, reduced feeding or abandonment of young, and irruptive migration (Astheimer, Buttemer, and Wingfield, 1992; Silverin, 1998; Wingfield, Hunt, Breuner, Dunlap, Fowler, Freed, and Lepson, 1997). This behavior modification is thought to occur through the rapid activation of adrenocor-

tical tissue that results in an increase of circulating glucocorticosteroids (Harvey, Phillips, Rees, and Hall, 1984). Measurement of circulating levels of glucocorticosteroids in free-living animals can provide a method for determining whether an individual is stressed and for monitoring animals' response to unpredictable and disruptive environmental change (Wingfield et al., 1997).

Recently, field endocrinologists have suggested the use of circulating levels of corticosterone as a gauge of forage availability and a predictor of reproductive performance in seabirds (Wingfield et al., 1997; Kitaysky, Wingfield, and Piatt, 1999). Because reproductive performance appears to be closely tied to forage availability in seabirds (Baird, 1990; Cairns, 1987; Gill, Hatch, and Lanctot, 2002), it seems reasonable to expect seabirds living in poor food

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environments (or experiencing a sudden decrease in food availability) to have high basal levels of corticosterone and poor reproductive effort and performance. Following this prediction, Kitaysky et al. (1999) showed that black-legged kittiwakes (*Rissa tridactyla*) breeding at a colony where local food conditions were poor had higher corticosterone levels than kittiwakes breeding at a colony where local food conditions were good. Also as predicted, kittiwakes in the food-poor colony did much poorer reproductively than kittiwakes in the food-rich colony. Thus corticosterone measurements appear to have the potential to indicate food availability and predict the likelihood of reproducing successfully.

Despite the appeal of using corticosterone levels as indicators of individual health, this hormone has the disadvantage of being responsive to a variety of physical, seasonal, and environmental factors. For example, corticosterone can be affected by an individual's body weight, body condition, and gender (Fowler, Wingfield, Boersma, and Sosa, 1994; Wingfield et al., 1997; Wingfield, Ramos-Fernandez, Nunez-de la Mora, and Drummond, 1999). Corticosterone levels also may change within a breeding season (Wingfield et al., 1997) or within a breeding stage if food availability or the level of parental care changes. Additional environmental factors that may affect corticosterone levels include pollution (Fowler, Wingfield, and Boersma, 1995), habitat conditions (Marra and Holberton, 1998), predation (Eilam, Dayan, Ben-Eliyahu, Schulman, Shefer, and Hendrie, 1999), and extreme weather conditions (Romero, Reed, and Wingfield, 2000). These latter factors are especially troublesome when comparing corticosterone levels across colonies. The preferred approach for studying the relationship between corticosterone and other biological factors would be an experimental manipulation that alters only the factor (e.g., food) thought to increase corticosterone levels while standardizing as many other factors as possible (e.g., habitat, predation).

In our study, we modeled the relationship between baseline levels of corticosterone from black-legged kittiwakes sampled at a uniquely accessible colony and a suite of individual (e.g., sex, weight) and temporal parameters (e.g., year, breeding stage). Because it was difficult to measure and compare natural food availability to corticosterone levels, we experimentally provided supplemental food to a sample of pairs and compared their corticosterone levels with that of pairs that were not fed. We predicted that fed birds would have lower corticosterone levels than unfed birds, although our experimental setup could not prevent unfed birds from feeding naturally in the ocean surrounding the colony. Consequently, when natural food conditions were good, we expected to find little or no difference in corticosterone levels between fed and unfed kittiwakes.

To determine whether corticosterone levels were good predictors of a bird's subsequent reproductive performance, we related the corticosterone levels from our sample of birds to the subsequent reproductive performance of all

kittiwakes breeding at the colony. As above, we used a modeling approach to determine whether corticosterone, along with other individual and temporal parameters, predicted whether a bird successfully laid eggs, hatched eggs, and fledged young. We also compared corticosterone levels and reproductive performance of pairs that were and were not fed.

## Materials and methods

### *Study animal, site, and food supplementation*

Black-legged kittiwakes are long-lived, pelagic, cliff-nesting seabirds that breed in colonies (Cullen, 1957; Danchin and Nelson, 1991) throughout the arctic and subarctic regions of both the Pacific and the Atlantic oceans (Harrison, 1983). The fact that adults obtain food from the nearby ocean for themselves and their brood make them an ideal species for evaluating how corticosterone levels relate to forage conditions and reproductive performance. This study was conducted in an abandoned Air Force radar tower on Middleton Island (59° 26'N, 146° 20' W) in the north-central Gulf of Alaska. Artificial nest sites created on the upper walls could be viewed from inside the tower through a sliding pane of one-way mirror glass. The artificial nest sites ensured that habitat quality was uniform across all sites. The vertical tower prevented avian predators from preying on adults, eggs, or young. In 1999 and 2000, we provided excellent quality supplemental food (i.e., capelin, *Mallotus villosus*, weighing about 22–25 g each) to a sample of pairs nesting at these sites by hand feeding them. Adults were fed until satiated three times a day (08:00, 14:00, and 18:00 h). The number of capelin consumed by the pair was recorded during each feeding. Supplemental feeding was begun on May 9 in both years and lasted until pairs failed to nest, lost their eggs or chicks, or their young fledged. On average pairs were fed for 32 and 19 days prior to laying eggs in 1999 and 2000, respectively (based on mean lay dates for fed birds). All fed pairs were located on 2 (1999) or 3 (2000) of the 12 walls of the tower. These walls were selected a priori so the nest site selection of a pair dictated whether it would be fed or not. Walls with fed birds were adjacent to walls with unfed birds. Clumping fed sites in this manner does not decrease the independence of the sites but lessens the likelihood of food stealing by unfed birds (V. Gill and S. Hatch, unpublished data).

### *Capture and measurement of reproductive performance*

Adults and young were captured and processed according to conditions listed in Federal Fish and Wildlife Permits and State of Alaska Scientific Permits issued to the U.S. Geological Survey's Alaska Science Center. Adults could be captured quickly from within the building assuring no precapture disturbance that could artificially inflate baseline

levels of corticosterone. Most adults were captured and individually marked at the tower. For each adult, culmen, diagonal tarsus, natural wing, and head and culmen combined were measured. The sex of adults was determined from morphological measurements, behavior, and genetics (Jodice, Lanctot, Gill, Roby, and Hatch, 2000). We used the weight of a bird as an estimate of the bird's body condition because the selection of models and the relative importance of parameters in explaining both corticosterone levels and breeding performance changed little whether condition, as measured by weight divided by culmen length, instead of weight, was used in the analyses. Further, there was a strong positive association between body weight and body condition ( $r = 0.93$ ,  $N = 282$ ,  $P = 0.0001$ ). We classified birds as experienced breeders if they had been captured while nesting at the tower during 1 or more years prior to the year of sampling. Inexperienced birds had never been captured at the tower although they may have bred elsewhere.

Nest sites were checked twice daily for the presence of laid and hatched eggs and fledged (i.e., first observed flight or 40 days) or dead young. The clutch size and egg order were accurately known in all instances. Laying date was defined as the date on which the first egg of a nest was laid. Adult attendance at nests was quantified at a sample of nests by recording the number of adults at each nest during incubation and chick rearing (see Gill et al., 2002, for methods). We also recorded the clutch size and volume of the A and B eggs combined (using Coulson's [1963] formulas). For pairs within each feeding treatment, we determined laying success (whether at least one egg was laid), hatching success (percentage of eggs laid that hatched), and fledging success (percentage of chicks hatched that fledged). We also calculated average growth rates (grams/day) for chicks belonging to fed and unfed pairs using linear regression analysis of weights collected every 5 days when chicks were between 5 and 25 days old. Chick growth curves approximated a straight line during this age interval.

#### *Corticosterone study design and sampling*

Between April and mid August in 1999 and 2000, we captured birds at four stages: "arrival" (within 5 days of birds arriving at the colony), "egg formation" (within 10 days prior to the first egg being laid, cf., Neuman, Chardine, and Porter, 1998), "incubation" (13–19 days after the first egg was laid), and "chick rearing" (19–22 days after the first chick was hatched). Individuals were captured opportunistically within "fed" and "unfed" treatment groups until adequate sample sizes were obtained for each capture stage. Birds were captured primarily between 10:00 and 13:00 h but attendance patterns required some birds to be captured at other times (sampling occurred from 08:04 to 19:15 h, with  $\bar{X} \pm SE = 12:47 \pm 00:09$ ,  $N = 283$ ). Sampling times did not affect corticosterone levels ( $F_{1,281} = 0.99$ ,  $P = 0.32$ ,

$R^2 = 0.003$ ) and did not differ between birds that were and were not supplementally fed ( $F_{1,281} = 3.2$ ,  $P = 0.075$ ,  $R^2 = 0.01$ ). Although diurnal changes in corticosterone levels have been reported, these changes are typically very small (Silverin, 1998).

Approximately 100–200  $\mu\text{l}$  of blood was drawn from the basilic vein of the wing of each adult within 3 min after capture was initiated. Birds were released after measurements and banding and typically returned to their nest site within 1 to 10 mins. Average collection time was  $96.3 \pm 1.6$  (SEM,  $N = 283$ ) s. Blood samples collected in fewer than 3 min were considered to reflect baseline levels of corticosterone (a significant increase in baseline levels of corticosterone occurred in samples drawn over a longer period of time; R. Lanctot and V. Gill, unpublished data). Blood samples were centrifuged within 1–2 h of collection and the separated plasma was stored below freezing until transported on dry ice to the Laboratory of Immuno-Neuroendocrinology at the University of Leuven in Belgium. Baseline total corticosterone levels were assayed directly and blindly for each sample using a  $^{125}\text{I}$  double-antibody RIA kit available from ICN Biomedicals, Inc. (Costa Mesa, CA). This assay is highly sensitive and specific (i.e., cross-reactivity to testosterone is 0.10%, to  $5\alpha\text{-DHT}$  is 0.01%, and to  $17\beta\text{-estradiol}$  is  $<0.01\%$ ). Although it is becoming increasingly important to determine the levels of corticosterone binding globulin, free steroids, and corticosteroid receptor levels (Deviche, Breuner, and Orchinik, 2001), we only measured total corticosterone concentrations (as is the case in many other studies). Our measures of total corticosterone levels are also unlikely to present problems with protein binding and interference from high lipid levels (ICN Biomedicals, Inc., unpublished data). The kit was developed for rats and mice (ICN Biomedicals, Inc.) and has been tested for parallelism in a wide variety of animal taxa (e.g., chickens [*Gallus domesticus*]; Geris, Kotanen, Berghman, Kuhn, and Darras, 1996). The concentrations of corticosterone in the provided standards ranged between 0.125 and 5 ng/ml. We followed the manufacturer's protocol in all cases except for dilution of plasma samples. We diluted the plasma samples 1:6 or 1:11, yielding an effective working interval between 0.75 and 30 ng/ml for samples diluted 1:6 and between 1.4 and 55 ng/ml for samples diluted 1:11, respectively. The dilution curves have been shown to follow the standard curve in previous research (Geris et al., 1996). Some samples (18 [14.3%] in 1999 and 6 [3.8%] in 2000, respectively) contained corticosterone levels at or below the minimum detection limit (1.4 ng/ml in 1999 and 0.75 ng/ml in 2000). We chose to use these minimum values in our subsequent analyses because the values were close to zero and therefore provided useful information, and including them had little effect on a reanalysis of our results. A nested analysis of variance indicated that most of the variation in corticosterone was due to variation among birds rather than duplicate measures within birds (i.e., 1.34 and 1.36% of the variance in 1999 and 2000, respectively, was due to re-

peated measures within birds). The inter- and intraassay CVs were 7.2 and 7.1%, respectively. For all individuals, we used the average of two corticosterone measurements made on each sample within a single assay.

#### *Within-season and between-year natural food availability*

To evaluate how natural food supply may have mediated our supplemental feeding treatment, we quantified the availability and quality of natural food items in two ways during each breeding stage of 1999 and 2000. First, we compared the frequency and biomass of different prey items present in opportunistically collected regurgitations of adults and chicks at each stage. We classified prey into poor, fair, good, and excellent quality categories, using published energy densities of forage fish (Anthony, Roby and Turco, 2000; Van Pelt, Piatt, Lance, and Roby, 1997) and unpublished data (D. Roby, pers. comm.). A list of prey belonging to each class is available from R. Lanctot. In addition to the four breeding stages listed above, we added a “pre-egg” stage that consisted of regurgitations collected prior to the 10-day egg formation stage but after the arrival stage. We then determined the percentage of occurrence and biomass of each prey quality category for breeding stages and years. For occurrence estimates, each species was counted only once per regurgitation. No effort was made to collect regurgitations during the arrival stage in 1999 and few were obtained during particular stages in 2000. Given that we did not systematically lavage birds, regurgitations could only be used as a qualitative estimate of prey availability. Accordingly, prey that occurred frequently and in large amounts within regurgitation samples was assumed to be more common in the environment. No effort was made to convert regurgitation data to caloric intake values due to the qualitative nature of the data.

Second, we compared the average amount of supplemental capelin taken by adult and young kittiwakes during each breeding stage in 1999 and 2000. Consumption was averaged within a nest site and stage. We assumed that birds would eat more supplemental food when natural food supplies were low (indicating their inability to satisfy their requirements by foraging naturally; see Gehlbach and Roberts, 1997). A strong negative correlation between the amount of food consumed by fed birds and the productivity of unfed birds over a 6-year period supports this assumption (Spearman  $r = -1.0$ ,  $N = 6$ ,  $P = <0.0001$ ; S. A. Hatch and V. A. Gill, unpublished data). Overall, we predicted elevated baseline levels of corticosterone to be present in unfed kittiwakes during reproductive stages when the quantity and quality of natural food were limited. In contrast, we predicted kittiwakes that were supplementally fed to have consistently low baseline levels of corticosterone regardless of the natural food supply.

#### *Statistics*

##### *Predicting baseline levels of corticosterone*

We used the information-theoretic approach to identify suitable models for predicting baseline levels of corticosterone in kittiwake adults (Anderson, Burnham, and Thompson, 2000; Burnham and Anderson, 1998). We conducted ANOVA or ANCOVA analyses to examine the relationship between baseline levels of corticosterone and feeding treatment, study year, breeding stage, sex, weight, and breeding experience. Corticosterone levels were investigated in two ways. First, we examined natural changes in corticosterone levels throughout the entire breeding season (Analysis 1). Because feeding did not occur during the arrival stage, we excluded all supplementally fed birds sampled at later stages as their corticosterone levels may have been altered. Second, we focused on how corticosterone levels might be affected by supplemental feeding (Analysis 2). Because birds were not fed during the arrival stage, we restricted our analyses to data collected after that stage. We included all combinations of parameters in our models because we had no a priori reason to exclude particular states of any parameter or combinations of parameters. We did not test models that had all possible combinations of interactions among the parameters.

We calculated the Akaike Information Criterion (AIC) for each model using the formula  $AIC = N \log_e(\sigma^2) + 2K$ , where  $N$  is sample size,  $\sigma^2$  = residual sum of squares from the ANCOVA or ANOVA divided by  $N$ , and  $K$  = number of parameters estimated in each approximating model. AIC values were converted to  $AIC_c$  values when sample sizes were small relative to the number of parameters being estimated (i.e.,  $N/K \leq 40$ ; Burnham and Anderson 1998:76). The model with the lowest AIC (or  $AIC_c$ ) was considered the best. Next we calculated the Akaike weights ( $W_i$ ) using the formula:  $W_i = (\exp(-0.5 \cdot \Delta_i)) / \sum_{r=1}^R (\exp(-0.5 \cdot \Delta_r))$ . These values indicate the approximate probabilities that model  $i$  is the best model in the set of models considered. The relative likelihood that one model is better than another is simply  $W_i/W_j$ .

We used multimodel inference and determined the set of models that includes the best model in 95% of all samples (Burnham and Anderson, 1998). Using this subset of models, we calculated unconditional estimates for coefficients and standard error terms for each parameter across all models using the formulas

$$\hat{\theta}_a = \sum_{i=1}^R \hat{\pi}_i \hat{\theta}_i \quad \text{and}$$

$$SE(\hat{\theta}) = \sum_{i=1}^R \hat{\pi}_i \sqrt{\hat{\text{var}}(\hat{\theta}_i | M_i) + (\hat{\theta}_i - \hat{\theta}_a)^2}.$$

Here  $\hat{\pi}_i$  was approximated with  $W_i$ ,  $\hat{\theta}_i$  was approximated with  $b1$  (the parameter estimate),  $\hat{\text{var}}(\hat{\theta}_i | M_i)$  was approximated by the SEM of  $b1$ , and  $M$  referred to the model.

Finally, we determined the relative importance of each parameter by summing the Akaike weights over all models that included that particular parameter (Burnham and Anderson, 1998).

#### *Predicting reproductive success*

We also used the information-theoretic approach to assess the relative importance of parameters in determining the probability of kittiwakes laying eggs, hatching eggs, and fledging young. The parameters of interest included the year of the study, breeding experience, body weight, corticosterone level, sex, and for birds sampled after the arrival stage, whether they were supplementally fed. We used logistic regression to generate AIC values for each of the 32 or 64 models possible (depending on the breeding stage) and then generated Akaike weights ( $W_i$ ) as described above. Logistic regression was used because it differentiated birds that did and did not lay eggs, hatch eggs, and fledge young (i.e., all yes/no information). Akaike weights were then summed over all models that included a particular parameter. For simplicity, we do not present the 95% confidence set of models or parameter estimates.

Conventional ANOVA procedures were used to test for (1) changes in supplemental capelin consumption among breeding stages and year, (2) the relationship among weight, breeding stage, and breeding experience, and (3) differences in corticosterone levels among kittiwakes that laid eggs, hatched eggs, and fledged young relative to kittiwakes that did not. Student *t* tests and Mann–Whitney *U* tests were used to compare productivity parameters between supplementally fed and unfed kittiwake pairs. Where applicable, we used two-tailed tests and a *P* value of 0.05 to determine significance. Data were transformed when necessary to meet assumptions of statistical tests. Information-theoretic derivations and other statistical analyses were conducted with PC-SAS 7.0 (SAS Institute, Inc., 1998) and SYSTAT 7.0 (SYSTAT, 1997).

## **Results**

#### *Natural and supplemental food supply*

The quality of prey regurgitated by black-legged kittiwakes varied among breeding stages and years (Fig. 1). Although there were no data for the arrival stage in 1999, the pre-egg stage had a large percentage of poor to fair quality prey. The arrival stage in 2000 also had fair quality prey in over half of the samples. By egg laying, most of the food regurgitated consisted of good quality prey. These good conditions lasted throughout the remainder of the breeding season in both years, although poor and fair quality prey showed up occasionally during egg formation and chick rearing in 1999 and during chick rearing in 2000.

A total of 48 kittiwake pairs in 1999 and 70 kittiwake pairs in 2000 were supplementally fed (Fig. 2). Overall,

kittiwakes ate significantly more supplementally fed capelin in 1999 than in 2000 (year effect:  $F_{1,288} = 200.6$ ,  $P < 0.0001$ , Fig. 2). Capelin consumption increased throughout the breeding season in 1999, meeting roughly 60% of daily food requirements during chick rearing (243 g/419 g; see Gabrielson, Klaassen, and Mehlum, 1992). In contrast, food consumption decreased during incubation and then increased again during chick rearing in 2000 (stage effect:  $F_{2,288} = 34.1$ ,  $P < 0.0001$ , Fig. 2). These differences in food consumption also resulted in a significant year  $\times$  stage interaction ( $F_{2,288} = 24.9$ ,  $P < 0.0001$ ).

The regurgitation and supplemental feeding results suggest that 1999 had poorer natural food conditions, both in the beginning and throughout chick rearing, than in 2000. Poor to fair quality food occurred in regurgitations at the beginning of the breeding season in both years. Regurgitation food items suggest that natural food conditions may have improved thereafter, although the increase in supplemental capelin consumption through chick rearing in 1999 suggests that forage availability may have remained low in that year. In contrast, capelin consumption decreased during incubation and then increased during chick rearing in 2000, indicating that better natural forage conditions were present (although variable) during the latter stages of breeding in that year.

#### *Measurement and predictors of baseline levels of corticosterone*

We sampled blood from 126 adult kittiwakes in 1999 and 157 adult kittiwakes in 2000 (Table 1). Individuals were sampled only once within a year, and 46 birds (19.4% of the 237 birds) were sampled in both years. Sampling birds in both years did not affect their corticosterone levels across years (interyear pearson correlation = 0.07,  $N = 46$ ,  $P = 0.64$ ). This was true even when birds sampled during the same breeding stage were compared (interyear Spearman correlation = 0.21,  $N = 12$ ,  $P = 0.52$ ). The number of nests and birds sampled (differentiated by sex, feeding treatment, and breeding experience) and dates at which they were sampled are listed in Table 1. Thirty-six nest sites in 1999 and 38 nest sites in 2000 had both members of a pair sampled. Of these, 19 pairs in 1999 (30.2% of birds sampled in that year) and 11 pairs in 2000 (14.0%) were captured during the same breeding stage. A bootstrap analysis indicated that corticosterone values from males and females belonging to the same pair, when sampled during either the same stage or year, were essentially independent of one another. This analysis compared corticosterone values of males and females from known pairs to males and females randomly placed together. For this reason we did not exclude samples taken from members of the same nesting pair and did not include “pair” as a variable in our subsequent analyses.

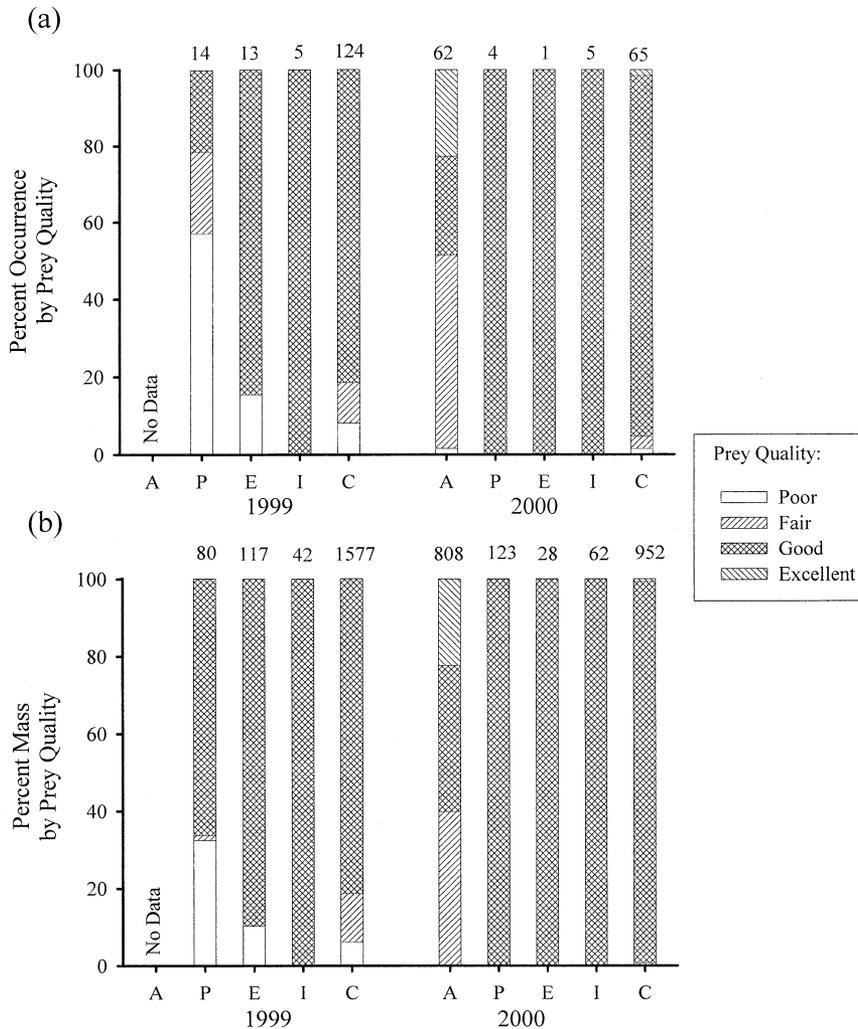


Fig. 1. Percentage occurrence (a) and mass (b) of prey quality categories in regurgitations of black-legged kittiwake adults and chicks on Middleton Island in 1999 and 2000. Bars depict arrival (A), pre-egg formation (P), egg formation (E), incubation (I) and chick-rearing (C) stages. Numbers above bars are the total number (a) and overall mass (b) in grams of prey items in the sample. Prey species comprising each prey quality type are available from the senior author.

*Analysis 1, natural variation*

Baseline levels of corticosterone in unfed kittiwakes varied from 0.8 to 30 ng/ml ( $\bar{X} \pm SE = 6.2 \pm 0.4$ ,  $N = 171$ ) throughout the study. The information-theoretic approach identified a model with year, breeding stage, weight, and breeding experience as the best approximating model for baseline levels of corticosterone (Table 2). However, the Akaike weight was relatively low and not much larger than  $W_i$  values for the next best models, indicating that model 1 was only slightly better than models 2 and 3. Based on the ratio of Akaike weights (i.e.,  $W_i/W_j$ ), model 1 was between 1.5 and 10.8 times better than the alternative models. The fact that 8 of the original 32 models were needed to ensure inclusion of the best model in 95% of all samples indicated that the parameters (and thus models) used to predict baseline levels of corticosterone in this study were rather poor. This conclusion is confirmed by the small percentage of variation in corticosterone explained by parameters in each model (note low  $R^2$  values, Table 2).

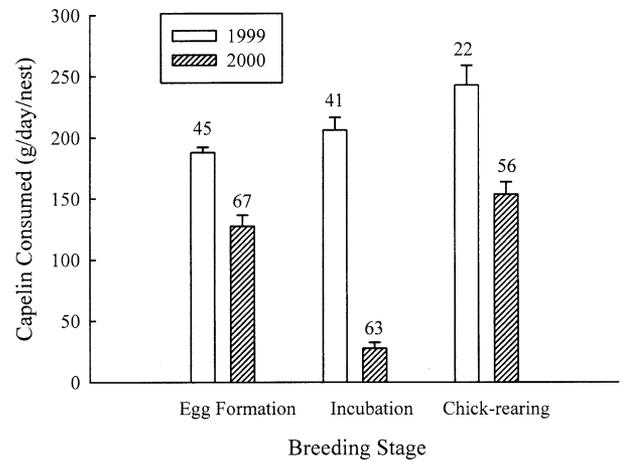


Fig. 2. Supplemental capelin consumed by black-legged kittiwakes per day per nest ( $\bar{X} \pm SEM$ ) during three stages of breeding in 2 years on Middleton Island. Sample sizes (number of nests) are shown above bars.

Table 1  
Numbers of black-legged kittiwakes sampled for baseline levels of corticosterone during 1999 and 2000 on Middleton Island, Alaska

Breeding stage	Sampling period	Day in breeding season <sup>a</sup>	Sample size (male/female)	No. nest sites sampled	No. individuals (fed/unfed)	Breeding experience (no/yes)
1999						
Arrival	10 April	−73 to −51	10/10	19	0/20	0/20
Egg formation	28 May to 13 June	−10 to 0	24/30	40	20/34	20/34
Incubation	16 June to 7 July	14 to 17	14/11	21	13/12	6/19
Chick rearing	17 July to 11 Aug	19 to 21	14/13	26	11/16	4/23
Total			62/64		44/82	30/96
2000						
Arrival	11–15 April	−61 to −39	26/29	38	0/55	13/42
Egg formation	22 May to 5 June	−7 to 0	9/10	19	8/11	2/17
Incubation	5–30 June	13 to 19	18/19	35	18/19	8/29
Chick rearing	12–21 July	19 to 22	22/24	38	22/24	1/45
Total			75/82		48/109	24/133

<sup>a</sup> Number of days before or after the first egg of a clutch was laid; day 0 = date of first egg in a clutch.

Parameter and standard error estimates (Table 3) indicated that year, breeding stage, and breeding experience had strong effects on baseline levels of corticosterone based on the lack of overlap in predicted corticosterone values (Table 3). Birds sampled in 1999 had higher corticosterone levels

than birds sampled in 2000, particularly during the arrival and egg formation stages (Table 3, Fig. 3). Similarly, inexperienced birds had higher corticosterone levels than experienced birds, especially during the arrival and egg laying stages (Table 3, Fig. 3). Because corticosterone levels were

Table 2

Model selection statistics (see text) from ANOVA and ANCOVA analyses of corticosterone levels in black-legged kittiwakes sampled on Middleton Island in 1999 and 2000

Model	$R^2$	$K$	RSS	$AIC^a$	$\Delta_i$	$W_i$	Cum. sum of $W_i$
Analysis 1: natural variation <sup>b</sup>							
(1) Year, stage, weight, experience	0.209	8	3847.76	547.20	0	0.335	0.335
(2) Year, stage, experience	0.205	7	3868.54	547.34	0.83	0.221	0.556
(3) Year, stage, weight, experience, sex	0.210	9	3843.91	549.26	2.06	0.119	0.675
(4) Stage, weight, experience	0.187	7	3959.08	549.84	2.64	0.089	0.765
(5) Year, stage, experience, sex	0.205	8	3868.47	550.23	3.03	0.074	0.838
(6) Stage, weight, experience, sex	0.189	8	3946.52	551.51	4.31	0.039	0.877
(7) Stage, experience	0.177	6	4004.58	551.77	4.56	0.034	0.911
(8) Year, stage, weight	0.176	7	4008.99	551.98	4.78	0.031	0.942
Analysis 2: food supplementation <sup>c</sup>							
(1) Stage, weight	0.081	5	2783.95	548.27	0	0.209	0.209
(2) Year, stage, weight	0.086	6	2768.68	549.25	0.98	0.128	0.338
(3) Stage, weight, experience	0.083	6	2776.60	549.85	1.57	0.096	0.434
(4) Stage, weight, sex	0.083	6	2777.07	549.88	1.61	0.094	0.528
(5) Stage, weight, fedtrt	0.081	6	2783.93	550.39	2.12	0.073	0.600
(6) Year, stage, weight, sex	0.089	7	2759.68	550.72	2.45	0.062	0.662
(7) Year, stage, weight, experience	0.089	7	2759.82	550.74	2.46	0.061	0.723
(8) Year, stage, weight, fedtrt	0.086	7	2768.45	551.38	3.11	0.044	0.768
(9) Stage, weight, experience, sex	0.085	7	2771.07	551.58	3.30	0.040	0.808
(10) Stage, weight, experience, fedtrt	0.083	7	2776.57	551.99	3.71	0.033	0.840
(11) Year, stage, weight, experience, sex	0.083	7	2776.96	552.02	3.74	0.032	0.873
(12) Stage, weight, sex, fedtrt	0.091	8	2752.43	552.34	4.07	0.027	0.900
(13) Year, stage, weight, sex, fedtrt	0.089	8	2759.15	552.85	4.58	0.021	0.921
(14) Year, stage, weight, experience, fedtrt	0.089	8	2759.79	552.90	4.62	0.021	0.942

<sup>a</sup>  $AIC$  values converted to  $AIC_c$  when  $n/K \leq 40$ .

<sup>b</sup> Analysis 1 models the natural variation in baseline levels of corticosterone through all breeding stages. Parameters included in the model are year, stage, weight, breeding experience, and sex (supplementally fed birds are excluded).  $N = 170$  or  $171$  in each model.

<sup>c</sup> Analysis 2 models variation in baseline levels of corticosterone from egg formation through chick rearing. Birds sampled upon arriving at the colony are excluded from analysis. Parameters included in the model are year, stage, weight, breeding experience, sex, and feeding treatment (fedtrt);  $N = 207$  for all models.

Table 3

Coefficient ( $\hat{\theta}_a$ )<sup>a</sup> and standard error estimates (model averaging approach with ANOVA and ANCOVA) for each parameter affecting baseline levels of corticosterone (ng/ml) in black-legged kittiwakes breeding on Middleton Island in 1999 and 2000

Parameter	$\hat{\theta}_a$	SE( $\hat{\theta}_a$ )	$\hat{\theta}_a \pm SE(\hat{\theta}_a)$	Importance
Analysis 1: natural variation				
Year				0.800
1999	6.72	0.32	6.40 to 7.04	
2000	5.78	0.38	5.41 to 6.16	
Stage				0.999
Arrival	9.02	0.16	8.86 to 9.18	
Egg formation	5.52	0.29	5.24 to 5.81	
Incubation	4.77	0.23	4.53 to 5.00	
Chick rearing	4.30	0.14	4.16 to 4.44	
Breeding experience				0.923
Inexperienced	8.51	0.32	8.19 to 8.83	
Experienced	5.60	0.20	5.40 to 5.80	
Sex				0.266
Female	6.40	0.28	6.12 to 6.69	
Male	6.04	0.26	5.78 to 6.31	
Weight	-0.006	0.009	-0.015 to 0.003	0.649
Analysis 2: food supplementation				
Year				0.383
1999	4.91	0.17	4.74 to 5.08	
2000	4.27	0.15	4.13 to 4.42	
Stage				0.967
Egg formation	5.05	0.15	4.90 to 5.19	
Incubation	4.89	0.11	4.78 to 5.00	
Chick rearing	3.90	0.09	3.81 to 3.99	
Breeding experience				0.326
Inexperienced	5.57	0.25	5.32 to 5.82	
Experienced	4.36	0.11	4.25 to 4.47	
Sex				0.308
Female	4.74	0.13	4.61 to 4.88	
Male	4.45	0.14	4.31 to 4.59	
Weight	-0.02	0.006	-0.03 to -0.02	0.992
Feeding treatment				0.259
Fed	4.21	0.10	4.11 to 4.32	
Unfed	4.91	0.10	4.81 to 5.02	

Note. Models contained in the 95% confidence set (see Table 1) were used for model averaging. The relative importance of each parameter is listed in the far right column (1.0 = most important, 0.0 = least important).

<sup>a</sup> For weight,  $\hat{\theta}_a$  is the average slope of the line describing the relationship between corticosterone and weight.

especially high during the arrival stage in both years, we investigated how breeding experience and year affected corticosterone level independently. This approach allowed us to evaluate the lack of samples from inexperienced breeders during the arrival stage in 1999. We found that experienced breeders in 1999 had unusually high corticosterone levels—comparable to those levels detected in inexperienced breeders in 2000 (Fig. 4). Further scrutiny revealed that inexperienced breeders tended to weigh less than experienced birds. This was especially noticeable when comparing experienced and inexperienced birds during egg formation. There was little effect of sex and weight on baseline levels of corticosterone. This is revealed by the overlap in corticosterone values predicted for each sex and the fact that the estimated slope of the regression equation involving weight and corticosterone approximated zero (indicating no relationship; Table 3). The relative importance ranking of each parameter also indicated that year, breeding

stage, and breeding experience contributed most to model construction (Table 3).

The decrease in baseline levels of corticosterone through the breeding season qualitatively reflected the changes in food quality detected in the regurgitation samples but did not reflect changes in supplemental food consumption (Figs. 1, 2, and 3). For example, when regurgitation samples suggested that natural food conditions were fair to poor (i.e., arrival and pre-egg formation), baseline corticosterone levels were relatively higher. As the quality of food improved, corticosterone levels decreased as might be predicted. These analyses did not test directly for this relationship, however, as we had no parameter within the models that reflected natural food availability. However, corticosterone levels did not increase with supplemental food consumption increases that occurred through chick rearing in 1999. In fact, corticosterone levels remained low and were similar to those recorded in 2000 when supplemental food consumption was

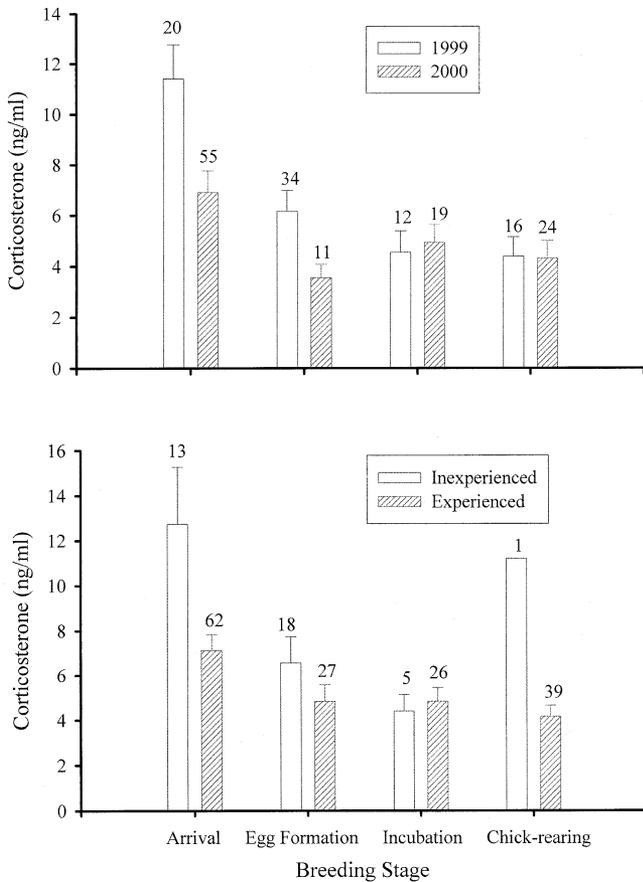


Fig. 3. Baseline levels of corticosterone ( $\bar{X} \pm \text{SEM}$ ) in black-legged kittiwake adults sampled during four stages of breeding on Middleton Island in 1999 and 2000 (top) and in relation to prior breeding experience (bottom; data from 1999 and 2000 are combined). In both cases, birds that were supplementally fed are excluded.

much lower. The high levels of corticosterone detected in experienced breeders during the arrival stage in 1999 suggested that natural food was especially poor during this time (Fig. 4).

*Analysis 2, food supplementation*

Baseline levels of corticosterone from kittiwakes that were supplementally fed varied from 0.8 to 23.1 ng/ml ( $\bar{X} \pm \text{SE} = 4.5 \pm 0.4$ ,  $N = 112$ ) throughout the study. The information-theoretic approach identified a model with only breeding stage and body weight as the best approximating model for the baseline levels of corticosterone measured in birds from egg formation to chick rearing (Table 2). As in the above analysis, the Akaike weight was relatively low and not much larger than  $W_i$  values for other models. The ratio of Akaike weights between models (i.e.,  $W_i/W_j$ ) indicated that model 1 was between 1.6 and 9.9 times better than the alternative models. The fact that 14 of the original 64 models were needed to ensure inclusion of the best model in 95% of all samples indicated that the parameters (and thus models) used to predict baseline levels of corti-

sterone in this study were poor. The extremely low  $R^2$  values associated with each model reaffirmed this conclusion (Table 2).

Bearing in mind that these models explained fewer than 10% of the variation in corticosterone, our analyses indicated that a small change in baseline levels of corticosterone was associated with all six parameters investigated (Table 3). Predicted values differed the most for birds sampled during different breeding stages or for birds with different breeding experiences. As predicted, supplementally fed birds had lower corticosterone values than unfed birds, although this difference was only about 1 ng/ml. The importance values calculated for each parameter indicated that breeding stage and weight were the most important, albeit marginal, parameters affecting baseline levels of corticosterone (Table 3). Heavier birds and birds sampled during chick rearing had lower corticosterone levels. The remaining parameters had low importance values (Table 3).

*Predictors of reproductive performance*

*Arrival stage*

Of the birds sampled during arrival, 51 (68%) subsequently laid egg(s), 45 (60%) hatched at least one egg, and 42 (56%) fledged at least one young. Eggs were laid an average of 49.2 ( $\pm 1.2$  SEM) days after adults were sampled for blood. Information-theoretic modeling indicated that the most important parameters for predicting whether a kittiwake would be involved in the production of eggs were breeding experience, body weight, sample year, corticosterone level, and sex of the bird (Table 4). The relative importance of the same parameters changed slightly when predicting whether a kittiwake would hatch eggs or fledge young. In these cases, breeding experience and the year in which the bird was sampled were most important, with sex, corticosterone level, and body weight being much less important (Table 4). These analyses did not include a parameter that measured natural food availability or supplemental

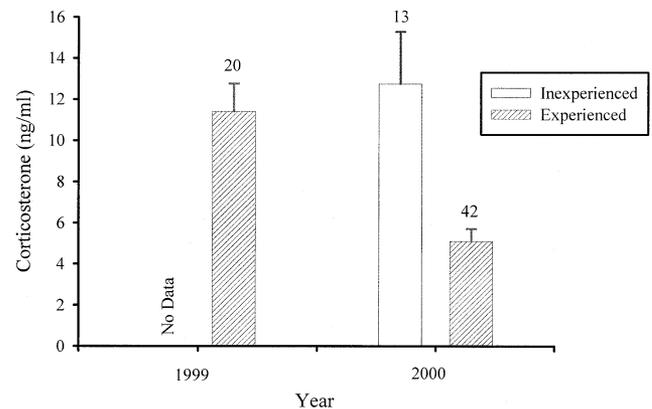


Fig. 4. Baseline levels of corticosterone ( $\bar{X} \pm \text{SEM}$ ) in black-legged kittiwake adults sampled shortly after arriving at Middleton Island in 1999 and 2000 in relation to prior breeding experience.

Table 4  
Breeding success and relative importance (1 = most important, 0 = least important) of parameters in predicting whether black-legged kittiwakes sampled at three stages of breeding would successfully lay eggs, hatch eggs, and fledge young on Middleton Island in 1999 and 2000

Breeding stage bird sampled and parameter measured	Reproductive measure		
	Lay eggs	Hatch eggs	Fledge young
<b>Arrival</b>			
% lay eggs ( $N = 75$ )	68.0	60.0	56.0
Year	0.72	0.93	0.93
Breeding experience	1.00	1.00	1.00
Body weight	0.80	0.27	0.25
Corticosterone	0.69	0.30	0.27
Sex	0.37	0.30	0.33
<b>Egg formation</b>			
% lay eggs ( $N = 73$ )	78.1	50.7	43.8
Year	0.46	0.68	0.79
Breeding experience	0.98	0.94	0.90
Body weight	0.86	0.31	0.34
Corticosterone	0.28	0.30	0.22
Feeding treatment	0.39	0.29	0.38
Sex	0.39	0.22	0.23
<b>Incubation</b>			
% hatch eggs ( $N = 62$ )	N/A	65.3	59.7
Year	N/A	0.37	0.27
Breeding experience	N/A	0.26	0.26
Body weight	N/A	0.85	0.96
Corticosterone	N/A	0.39	0.64
Feeding treatment	N/A	0.27	0.23
Sex	N/A	0.28	0.33

feeding since feeding began after birds were sampled for corticosterone. A univariate analysis revealed significantly higher corticosterone levels in birds that failed to lay eggs relative to those that successfully laid ( $12.4 \pm 1.6$  versus  $6.1 \pm 0.7$  ng/ml,  $t$  test with unequal variances = 3.68,  $df = 31.5$ ,  $P = 0.0009$ ). An analysis that included only experienced breeders found that those that laid eggs had significantly lower corticosterone values than those that did not ( $6.1 \pm 0.7$  versus  $11.6 \pm 1.8$  ng/ml,  $t$  test with equal variances = 3.38,  $df = 60$ ,  $P = 0.0013$ ). There were inadequate sample sizes to conduct a similar test for inexperienced breeders (i.e., 12 individuals failed to lay eggs and 1 laid eggs).

#### Egg formation stage

Fifty-seven (78.1%) of the birds sampled during the egg formation stage subsequently laid egg(s), 37 (50.7%) hatched at least one egg, and 32 (43.8%) fledged at least one young. Eggs were laid on average  $4.4 (\pm 0.4$  SEM) days after adults were sampled for blood. However, 3 and 5 birds laid eggs after the 10-day period in 1999 and 2000, respectively, and thus were not used in the study. Information-theoretic modeling indicated that breeding experience was the best predictor of whether a kittiwake sampled during egg formation would subsequently be involved with the

laying and hatching of eggs, as well as the fledging of young (Table 4). The next best predictors were the year in which a bird was sampled and the weight of the bird. Corticosterone level and feeding treatment varied from third to sixth best predictor of kittiwake productivity, depending on the measure (laying, hatching, or fledging success) being analyzed. As above, univariate analyses indicated significantly lower corticosterone levels in birds that laid eggs relative to those that did not lay eggs ( $4.4 \pm 0.6$  versus  $7.4 \pm 1.2$  ng/ml,  $t$  test with equal variances = 2.5,  $df = 71$ ,  $P = 0.016$ ). All of the experienced breeders sampled during the egg formation stage subsequently laid eggs. However, there was no significant difference in corticosterone values between successful and unsuccessful layers among the inexperienced breeders sampled during egg formation ( $P = 0.87$ ).

#### Incubation and chick-rearing stages

Of the birds sampled during incubation, 47 (65.3%) and 43 (59.7%) subsequently hatched eggs and fledged young, respectively. Information-theoretic modeling indicated that body weight was the best predictor of hatching and fledging success. The remaining parameters had much lower relative importance values. Corticosterone was ranked the second most important parameter, although a univariate analysis failed to find a significant difference in corticosterone levels between birds that hatched eggs and those that did not ( $P = 0.45$ ). Indeed, the levels of corticosterone were the opposite of what might be expected (assuming stressed birds are less prone to incubate eggs), with birds hatching eggs having (nonsignificantly) higher corticosterone levels.

All birds sampled during chick rearing raised their young to fledging. This prevented us from contrasting failed and successful birds at that stage.

#### Food supplementation effects

We compared baseline levels of corticosterone and productivity parameters between supplementally fed and unfed kittiwakes during each breeding stage and year (Table 5). Baseline levels of corticosterone were not significantly different between fed and unfed birds during most stages and years. The only exception was the chick-rearing stage in 1999, when fed kittiwakes had lower levels of corticosterone relative to unfed kittiwakes (although both groups had low corticosterone values overall). In contrast, many of the other reproductive parameters differed significantly between fed and unfed birds, especially in 1999 (Table 5). Fewer differences were found in 2000, although the laying date was later, egg volume was smaller, and adult attendance was lower in unfed birds. Despite having similar corticosterone levels, hatching success for fed birds in 1999 was nearly half that of both the fed and the unfed birds in 2000. The fact that laying and hatching success was much lower in 1999 relative to 2000, and that fledging success was similar between the 2 years, supports the idea that

Table 5  
Baseline levels of corticosterone (ng/ml) and reproductive performance of supplementally fed and unfed black-legged kittiwakes breeding on Middleton Island in 1999 and 2000<sup>a</sup>

Breeding stage	Parameter	1999			2000		
		Fed	<i>P</i> value	Unfed	Fed	<i>P</i> value	Unfed
Egg formation	Corticosterone	4.78 ± 1.17 (20)	NS	6.17 ± 0.82 (34)	3.03 ± 0.88 (8)	NS	3.55 ± 0.52 (11)
	Laying success	92% (48)	<0.001	37% (178)	94% (70)	NS	89% (152)
	Laying date	10 June ± 1.0 (44)	<0.001	18 June ± 0.6 (65)	28 May ± 0.66 (67)	<0.046	30 May ± 0.63 (135)
	Egg volume (cc)	46.3 ± 0.40 (73)	0.033	45.0 ± 0.50 (74)	47.0 ± 0.33 (129)	<0.001	44.9 ± 0.29 (255)
	Clutch size	1.68 ± 0.08 (44)	<0.001	1.14 ± 0.04 (65)	1.92 ± 0.05 (67)	NS	1.89 ± 0.03 (136)
Incubation	Corticosterone	4.27 ± 0.74 (13)	NS	4.53 ± 0.85 (12)	5.56 ± 1.11 (18)	NS	4.92 ± 0.70 (19)
	Hatching success	43% (76)	NS	56% (75)	72% (135)	NS	72% (261)
	Shift length (hs)	4.26 (29)	<0.001	11.95 (27)	4.74 (29)	NS	5.0 (32)
Chick rearing	Corticosterone	1.82 ± 0.20 (11)	0.011	4.38 ± 0.75 (16)	4.25 ± 0.83 (22)	NS	4.30 ± 0.69 (24)
	Fledging success	82% (33)	NS	79% (42)	87% (97)	NS	80% (188)
	A-chick growth (g/day)	16.4 ± 0.34 (22)	0.004	14.9 ± 0.34 (30)	15.9 ± 0.25 (52)	NS	15.9 ± 0.19 (104)
	% Adult attendance	56.2 ± 0.99 (21)	<0.001	41.8 ± 0.81 (26)	51.3 ± 0.54 (24)	<0.001	43.0 ± 1.35 (24)

Note. Values shown as means ± SE; sample sizes are in parentheses.

<sup>a</sup> NS, nonsignificant. Tests included Mann–Whitney *U*, Student *t* test, and one-way ANOVAs.

natural food conditions remained relatively poor until chick rearing in 1999.

## Discussion

### *Predictors of baseline levels of corticosterone*

This study found that the year and breeding stage at which a bird was sampled and the breeding experience of the sampled bird were the most important parameters in explaining natural variation in corticosterone measurements (Table 3). Higher baseline levels of corticosterone were found in 1999, during the early breeding stages, and in inexperienced birds. The breeding stage effect found in this study might be related to changes in reproductive costs experienced by kittiwakes as they establish nests, lay and incubate eggs, and then guard and feed young. Several research studies have shown adult kittiwakes to have higher energy expenditures and survival costs during the chick-rearing stage (Golet and Irons, 1999; Golet, Irons, and Estes, 1998). If the chick-rearing stage is stressful, one might predict higher corticosterone levels at this time. However, activities associated with chick rearing are likely to be natural and predictable, thus reducing the likelihood of birds being overly stressed. Our results would support the idea that chick rearing is a nonstressful event.

Poor natural food conditions early in 1999 and 2000 may offer a partial explanation for the initially high corticosterone levels within each breeding season. Kitaysky et al. (1999) suggested that a high baseline level of corticosterone in kittiwakes at a food-rich colony during chick rearing was probably due to less abundant food at that stage in the

season. In our study, there appeared to be a positive relationship between the higher baseline levels of corticosterone of birds sampled during the arrival and egg formation stages (Fig. 3) and the poor natural food conditions present at that time (Figs. 1 and 2). This relationship was especially supported in 1999 when even experienced breeders had high corticosterone levels during the arrival stage (Fig. 4). Our analysis, unfortunately, could not directly test the relationship between natural food and corticosterone levels during the arrival stage. Nevertheless, two findings within our study suggest that corticosterone is not always a reliable indicator of forage conditions. First, corticosterone levels were similar between fed and unfed birds during the egg formation stage in 1999, even though supplemental food consumption and regurgitation data suggested that natural food conditions were poor. Indeed, unfed kittiwakes appeared to be food limited in that year, given their much lower breeding performance values. These reproductive measures are closely tied to the body condition of a bird and thus indirectly to the available food resources (i.e., through more difficult foraging; see e.g., Cairns, 1987; Monaghan, Uttley, Burns, Thaine, and Blackwood, 1989). Second, fed birds during incubation in 1999 and 2000 had similar corticosterone levels, and yet, measures of productivity (e.g., hatching success) that are likely to reflect natural forage conditions were much lower in 1999.

The large number of inexperienced birds captured during the arrival and egg formation stages provides a second explanation for the high corticosterone levels early in the season. Inexperienced kittiwakes had much higher corticosterone levels than birds with prior breeding experience at the tower during the first two stages of the breeding season (Fig. 3). It seems likely that many of these inexperienced

birds were searching for nest sites or future mates. Such prospecting is likely to incur aggression from long-term site holders or neighboring pairs, especially considering that prospectors were trying to establish themselves at a very productive, densely settled colony (Porter, 1990; Cadiou, Monnat, and Danchin, 1994). Established site holders are expected to defend against prospectors in such situations because retaining a nest site and mate from prior years enhances reproduction (Chardine, 1987; Fairweather and Coulson, 1995). Thus, inexperienced birds are likely to have elevated corticosterone levels. The fact that experienced breeders had high corticosterone levels in 1999 (Fig. 4) indicates that prior breeding experience alone cannot explain corticosterone levels and that other factors, such as forage availability, may combine with breeding experience to affect corticosterone levels. Inexperienced birds were difficult to capture later in the season as very few had acquired a nest site and managed to lay or hatch eggs. This fact made it difficult to evaluate the effect of breeding experience later in the breeding season.

The body weight of a bird was weakly related to corticosterone levels (0.02 ng/ml decrease in corticosterone per gram increase in weight). Body weight was especially important in explaining variation in corticosterone level from egg formation through chick-rearing stages. Kitaysky et al. (1999) found a similar negative relationship between body condition and baseline levels of corticosterone. Other studies have failed to find consistent relationships among body mass, fat reserves, and corticosterone levels in a variety of temperate and arctic species (in Silverin, 1998). Weight, like most of the other parameters explored in our study, explained only a small proportion of the total variance in corticosterone levels (Table 3).

#### *Predictors of kittiwake reproduction*

Among birds sampled during the arrival, egg formation, and incubation stages, the most important parameters for predicting laying, hatching, and fledging success were breeding experience, year, and body weight. However, our data suggest that corticosterone and supplemental feeding can, in limited situations, also be useful predictors of performance. For example, there were large differences (i.e., 6 ng/ml on average) in baseline levels of corticosterone in kittiwakes that subsequently laid eggs and those that did not when birds were sampled during the arrival stage. These differences continued to be true even after the effect of breeding experience was removed. Similarly, supplemental feeding appeared to enhance laying success and clutch and egg sizes during the early part of the 1999 breeding season when poor natural food conditions were present (similar patterns were found in 1996 and 1997; see Gill et al., 2002; Gill and Hatch, 2002). Further, supplementally fed kittiwakes had lower corticosterone values overall relative to unfed kittiwakes. Corticosterone levels and supplemental feeding, however, were not the best predictors of produc-

tivity when both years and all breeding stages were evaluated.

In our study, fed and unfed kittiwakes had corticosterone levels that were similar (and relatively low), but had dramatic differences in laying success, laying date, and egg and clutch size, especially in 1999 (Table 5). In contrast, corticosterone levels of birds sampled shortly after arriving at the colony (some 39 to 73 days prior to egg laying) were highly predictive of subsequent laying success. This was true whether birds were previous breeders at the colony or not. This suggests that physiological state of a bird coming out of the nonbreeding season may strongly affect the likelihood of a bird breeding in the upcoming summer. Previous researchers have reported higher basal levels of corticosterone in birds sampled during spring migration relative to fall migration, possibly reflecting the harsher physiological conditions experienced by birds preparing for breeding (Romero, Ramenofsky, and Wingfield, 1997). In our case, providing supplemental food, similar to what might be experienced if food conditions were suddenly to improve, was sufficient to stimulate breeding (e.g., compare laying success of fed and unfed birds in 1999, Table 5).

The unique colony site used in this study, while allowing easy data collection, arguably compromised our ability to relate corticosterone levels to reproductive performance by removing natural predation as a mechanism for egg and chick loss. We think this is unlikely for several reasons. First, predation has no effect on the number of pairs that lay eggs, the number of eggs laid within a clutch, or the size of the eggs. These parameters differed significantly between fed and unfed kittiwakes in this study, despite adults from these two groups having similar levels of corticosterone. Second, previous studies have shown egg and chick loss to be associated with declines in adult attendance, not predation directly (Hatch and Hatch, 1990). In both years of our study, we documented significantly higher attendance rates in fed versus unfed adult kittiwakes during chick rearing, although corticosterone levels from fed and unfed kittiwakes were the same (2000) or only slightly lower in fed birds (1999, although both fed and unfed birds had very low corticosterone levels). Finally, Kitaysky, Wingfield, and Patti (2001) found that adult kittiwakes implanted with corticosterone also showed reduced levels of nest attendance, although young survived equally well from experimental and control nests.

As an alternative to baseline levels of corticosterone (which is thought to reflect current stress levels), the adrenocortical response to stress has been suggested as a predictor of an individual's ability to cope with current and future stress (Wingfield, 1994). The approach entails holding a bird for up to 60 min and sampling blood at regular intervals. Birds that show a rapid increase in plasma levels of corticosterone during the protocol are considered less resistant to stress. This approach has the potential of providing additional predictive information that may not be present when just baseline levels are measured (i.e., whether

animals are adapted to a future stressful situation). Unfortunately, like baseline levels of corticosterone, a bird's sensitivity to the capture stress protocol has been documented to change with season, reproductive state, and body condition of individuals (Wingfield, Deviche, Sharbaugh, Astheimer, Holberton, Suydam, and Hunt, 1994a; Wingfield, Suydam, and Hunt, 1994b; O'Reilly and Wingfield, 2001). Holding birds for long periods and repeatedly sampling them may also preclude any attempt to relate an individual's corticosterone level to observed breeding performance because of increased predation of unattended nests (Sandvik and Barrett, 2001).

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