

Exxon Valdez Oil Spill
Restoration Project Final Report

Are Corticosterone Levels a Good Indicator of Food Availability and
Reproductive Performance in a Kittiwake Colony?

Restoration Project 01555
Final Report

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Study History: Restoration Project 01555 was initiated in 2000 as a single year study of the use of stress hormones in seabirds as a gauge of ocean forage conditions and a predictor of subsequent reproductive performance. There have been no other annual reports.

Abstract. We examined the use of corticosterone to gauge forage availability and predict reproductive performance in black-legged kittiwakes (*Rissa tridactyla*) breeding in the Gulf of 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 pairs that were not fed. Corticosterone levels were a good predictor of forage availability in some situations. In general, higher corticosterone levels were found in birds that lacked breeding experience and in birds sampled shortly after arriving from their wintering grounds. Supplemental feeding did not affect corticosterone levels in most cases. We also investigated whether corticosterone and other factors 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. Although corticosterone level successfully predicted reproductive performance in some cases, this parameter was not the best predictor overall. Counts of active nests with eggs or chicks may be more reliable estimates of the actual productivity of the colony.

Key Words: Alaska, Black-legged Kittiwake, corticosterone, endocrinology, hormones, seabirds, stress, reproduction, *Rissa tridactyla*

Project Data: Endocrinology, diet and supplementation, and reproductive data associated with kittiwakes at Middleton Island are in digital (Microsoft Excel™) format and under the custodial responsibility of Richard Lanctot, U.S. Fish and Wildlife Service, Migratory Bird Management, 1011 East Tudor Road, MS 201, Anchorage, Alaska 99503 (phone: 907-786-3609, fax: 907-786-3641, E-mail: Richard_lanctot@fws.gov).

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EXECUTIVE SUMMARY

Recently, field endocrinologists have suggested using circulating levels of corticosterone as a gauge of forage conditions and a predictor of reproductive performance in seabirds. Because reproductive performance appears to be closely tied to forage availability in seabirds, it seems reasonable to expect that seabirds living in poor food environments to have high basal levels of corticosterone and to have poor reproductive effort and performance. These relationships have been supported qualitatively for black-legged kittiwakes (*Rissa tridactyla*) living in a food-rich and food-poor colony of Cook Inlet, Alaska. Unfortunately, corticosterone is responsive to a variety of physical, seasonal and environmental factors that may confound inter-colony comparisons. Therefore careful study designs are needed before any cause and effect relationships that include corticosterone levels and other biological factors are made.

To assess whether circulating levels of corticosterone could be used to gauge forage availability in seabirds, we monitored black-legged kittiwakes breeding at an abandoned tower on Middleton Island in the Gulf of Alaska during 1999 and 2000. We modeled the relationship between baseline levels of corticosterone and a suite of individual (e.g., sex, weight) and temporal (e.g., year, breeding stage) characteristics from the sampled birds. Because it is difficult to measure and thus relate natural food availability to corticosterone levels, we provided supplemental food to a sample of pairs and compared their corticosterone levels with pairs that were not fed. We next related the corticosterone levels from our sample of birds to the subsequent reproductive performance of the colony. We used a modeling approach to determine how corticosterone, along with other individual and temporal parameters, would predict whether a bird successfully laid eggs, hatched eggs, and fledged young.

Data were collected at 220 artificial nest sites constructed along the sides of the tower. The use of one-way glass sliding windows allowed birds to be captured easily and nest contents monitored accurately (e.g., laying of eggs, hatching of eggs, and fledging of chicks). Supplemental food (capelin) was provided to a sample of pairs nesting at these sites. Birds were captured shortly after arriving at the colony, and during egg formation, incubation, and chick-rearing. Birds were measured, weighed and sampled for blood within three minutes of capture. Baseline levels of corticosterone were determined for each bird using a 125I double-antibody RIA kit. The natural diet of kittiwakes was quantified by comparing the frequency and biomass of different quality prey items present in regurgitations of adults and chicks collected during each breeding stage of each year. We also used the amount of supplemental capelin consumed by fed kittiwakes as an index of natural food supplies, under the assumption that birds would eat less supplemental food when natural food supplies were good.

We used the information-theoretic approach to identify suitable models and parameters for predicting baseline levels of corticosterone and assessing the relative importance of parameters in determining the probability of kittiwakes laying eggs, hatching eggs, and fledging young. This approach has the advantages of (1) allowing information from more than one model to be used (i.e., no single null hypothesis is accepted or rejected based on *P*-values), (2) providing an estimate of the formal likelihood of each model, and (3) providing a measure of precision that incorporates model selection uncertainty. The last advantage allows us to estimate parameter and variance values for each parameter that is biological meaningful, and determines the relative importance of each parameter as a predictor of baseline levels of corticosterone and of kittiwake reproductive performance.

Regurgitation and food consumption results indicated 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 in the beginning of the breeding season in both years. In 1999, regurgitated food items suggested natural food conditions might have improved during incubation, although the increase in supplemental capelin consumption through chick rearing suggests forage availability may have remained low. In contrast, capelin consumption decreased during incubation and then increased during chick rearing in 2000, indicating better natural forage conditions were present (although variable) during the latter stages of breeding in that year. Baseline levels of corticosterone were collected on 126 adult kittiwakes in 1999 and 157 adult kittiwakes in 2000, respectively. A minimum of ten, but as many as 30 males or females, were sampled during each breeding stage. Roughly half were supplementally fed, and about three-fourths had prior breeding experience at the tower. Sampling birds in both years did not affect their corticosterone levels across years. A bootstrap analysis indicated that corticosterone values from males and females belonging to the same pair, when sampled during the same stage or year, were independent of one another.

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 (arrival to chick-rearing stages). On a relative scale, breeding stage and experience contributed most to model construction. Higher baseline levels of corticosterone were found in birds without prior tower breeding experience and when sampled during the early breeding stages. A second modeling exercise that investigated supplemental feeding effects on corticosterone identified a model with 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. As predicted supplementally fed birds had lower corticosterone values than unfed birds, although this difference was only about 1 ng/ml.

We next conducted analyses to determine what parameters best predicted whether a bird would lay eggs, hatch eggs and fledge young. For birds sampled during arrival, the most important parameters for predicting whether these birds would reproduce were breeding experience, body weight and sample year. During the egg formation stage, the most important parameters for predicting whether these birds would reproduce were breeding experience, sample year, and body weight. Of the birds sampled during incubation, body weight was the most important parameter for predicting whether these birds would hatch eggs and fledge young. Univariate analyses indicated corticosterone level was a good predictor of whether birds laid eggs during the arrival and egg formation stages, but was a poor predictor of hatching success during the incubation stage. An analysis that included only experienced breeders during the arrival stage found that those that laid eggs had significantly lower corticosterone values than those that did not. There were inadequate sample sizes to conduct a similar test for inexperienced breeders.

To evaluate directly the effects of supplemental feeding, we compared baseline levels of corticosterone and productivity parameters between supplementally fed and unfed kittiwakes during each breeding stage and year. Baseline levels of corticosterone were not significantly different between fed and unfed birds during most stages and years. In contrast, many of the reproductive parameters differed significantly between fed and unfed birds, especially in 1999. Fewer differences were found in 2000, although lay date was later, egg volume was smaller, and adult attendance was lower in the unfed birds.

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 baseline levels of corticosterone. Higher baseline levels of corticosterone were found in 1999, during the early breeding stages, and in inexperienced birds. Poor natural food conditions early in 1999 and 2000 may offer a partial explanation for the initially high corticosterone levels within each breeding season. Such a cause and effect response, however, does not explain why corticosterone levels were similar between fed and unfed birds during egg formation in 1999, even though supplemental food consumption and regurgitation data suggested 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. Further, this apparent cause and effect response does not explain why fed birds during incubation in 1999 and 2000 had similar corticosterone levels, and yet, their measures of productivity, which 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 provide 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. It seems likely that many of these inexperienced birds were searching for nest sites or future mates. Prospecting birds are 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. Established site holders are expected to defend against prospectors in such situations because retaining a nest site and mate from prior years enhances reproduction. Thus, inexperienced birds are likely to have elevated corticosterone levels. The fact that experienced breeders had high corticosterone levels in 1999 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.

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 suggests that corticosterone and supplemental feeding can, in limited situations, also be useful predictors of performance. For example, there were large differences 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 removing the effect of breeding experience. 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. Corticosterone levels and supplemental feeding, however, were not the best predictors of productivity when both years and all breeding stages were evaluated.

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. Unfortunately, like baseline levels of corticosterone, a bird's sensitivity to the capture stress protocol may change with season, reproductive state, and body condition of individuals. The need to hold birds and repeatedly sample them for blood may also lead to artificially low reproductive performance, making it impossible to evaluate how the adrenocortical response to stress relates to reproductive performance.

Our results suggest that baseline levels of corticosterone have the potential for use as an indicator of forage availability. To be a useful measure, however, corticosterone levels would have to be reasonably predictive under all ecological conditions and across breeding stages. At a minimum, this technique requires intensive sampling of birds over a range of good and bad food conditions, and possibly during different breeding stages, to furnish a realistic baseline against which measured corticosterone values can be compared.

The value of baseline levels of corticosterone as a predictor of reproductive performance also has its limitations. Given that baseline levels of corticosterone are reflective of current forage conditions and that these conditions can change through a breeding season, measures of corticosterone from birds during egg formation are unlikely to indicate breeding performance of birds during latter stages. Changes in forage conditions within years will also limit the ability of other parameters, such as body weight and breeding experience, to predict reproductive performance. Other more traditional parameters such as counts of active nests with eggs or chicks may be simpler and more reliable, given they estimate the actual productivity of a colony.

INTRODUCTION

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 et al. 1992, Wingfield et al. 1997, Silverin 1998). This behavior modification is thought to occur through the rapid activation of adrenocortical tissue that results in an increase of circulating glucocorticosteroids (Harvey et al. 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 using circulating levels of corticosterone as a gauge of forage availability and a predictor of reproductive performance in seabirds (Wingfield et al. 1997, Kitaysky et al. 1999). Because reproductive performance appears to be closely tied to forage availability in seabirds (Cairns 1987, Baird 1990, Gill et al. 2002), it seems reasonable to expect seabirds living in poor food environments (or experiencing a sudden decrease in food availability) to have high basal levels of corticosterone and to have 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 worse 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 et al. 1994, Wingfield et al. 1997, Wingfield et al. 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 et al. 1995), habitat conditions (Marra and Holberton 1998), predation (Eilam et al. 1999), and extreme weather conditions (Romero et al. 2000). These latter factors are especially troublesome when comparing corticosterone levels across colonies. The preferred approach to study 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 pairs that were not fed. We predicted that fed birds would have lower corticosterone levels than unfed birds, although our experimental set-up 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 sub arctic regions of both the Pacific and 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 (0800, 1400, 1800 hrs). The number of capelin consumed by the pair was recorded during each feeding. Supplemental feeding was begun on May 9 both years and lasted until pairs either 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 two (1999) or three (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, U. S. Geological Survey, unpubl. 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 pre-capture 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 et al. 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 one 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 was 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 or not 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 (g/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. 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 et al. 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 hrs but attendance patterns required some birds to be captured at other times (sampling occurred from 08:04 to 19:15 hrs, 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 μ l of blood was drawn from the basilic vein of the wing of each adult within 3 minutes after capture was initiated. Birds were released after measurements and banding, and typically returned to their nest site within 1 to 10 minutes. Average collection time was 96.3 ± 1.6 (SEM, $N = 283$) seconds. Blood samples collected in less 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, U. S. Geological Survey, unpubl. data). Blood samples were centrifuged within 1-2 hrs 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 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 5α -DHT is 0.01% and to 17β -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 et al. 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., unpubl. 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 et al. 1996). A separate laboratory analysis on black-legged kittiwake plasma reflected good parallelism with the standard curve and plasma loading tests showed an average recovery of 98%. The concentrations of corticosterone in the provided standards ranged between 0.125 ng/ml 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. Some samples (18 [14.3%] in 1999 and 6 [3.8%] in 2000, respectively) contained corticosterone levels below the minimum detection limit (1.4ng/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 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 repeated measures within birds). The inter- and intra-assay CVs were 16% and 8%, 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 et al. 2000, Van Pelt et al. 1997) and unpublished data (D. Roby, U. S. Geological Survey, pers. comm.). Poor prey consisted of walleye pollock *Theragra chalcogramma*, Pacific cod *Gadus macrocephalus*, sculpins (Cottidae), sablefish *Anoplopoma fimbria*, prowlfish (Zaproridae), octopus (Cephalopoda), shrimp (Decapoda), isopods, and copepods. Fair prey consisted of salmonids *Oncorhynchus* sp., pricklebacks (Stichaeidae), euphausiids *Thysanoessa* sp., amphipods (Gammaridae), squid (Gonatidae) and polychaetes (loaded with gonads). Good prey consisted of Pacific herring *Clupea harengus*, Pacific sand lance *Ammodytes hexapterus*, capelin, smelt (Osmeridae), offal, while excellent prey consisted of lantern fish (Myctophidae). 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 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, U. S. Geological Survey, unpubl.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 was 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 (Burnham and Anderson 1998, Anderson et al. 2000). This statistical approach has the advantages of (1) allowing information to be used from more than one model (i.e., models are ranked in their relative ability to explain corticosterone levels and thus no single null hypothesis is accepted or rejected; Anderson et al. 2000), (2) providing an estimate of the formal likelihood of each model given the data, and (3) providing a measure of precision that incorporates model selection uncertainty. The last advantage allows us to estimate parameter and variance values for each parameter that is biologically meaningful (e.g., effect sizes or estimated corticosterone values for fed and unfed birds can be determined). Further, the relative importance of each parameter as a predictor of corticosterone can be determined through a model-averaging technique. In effect, this statistical approach does not rely on strict P values to include or eliminate potential parameters, but rather weighs the importance of each parameter relative to each other and strives to separate biologically from statistically significant results (Yoccoz 1991). We chose not to use traditional statistical approaches because initial analyses indicated the number and identity of the parameters used in the model changed the significance, and thus inclusion or exclusion, of any one parameter. This result occurred because none of the parameters explained much of the variance in corticosterone levels and reproductive performance.

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. Even with this restriction, we had 32 models for Analysis 1 and 64 models for Analysis 2.

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, σ^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 and the relative rank of the remaining models was determined by rescaling the AIC_c values such that the model with the lowest AIC_c had a value of zero. Rescaling was done using the formula:

$\Delta_i = AIC_i - \min AIC$. Next we calculated the Akaike weights (W_i) using the formula:

$$W_i = (\exp(-0.5 * \Delta_i)) / \sum_{r=1}^R (\exp(-0.5 * \Delta_r)).$$

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 (i.e., model i relative to model j).

Following Burnham and Anderson (1998), we used multi-model inference and determined the set of models that includes the best model in 95% of all samples. This set includes all models where the cumulative sum of the Akaike weights, when ordered from lowest to highest, sum to approximately 0.95. Using this subset of models, we next calculated unconditional estimates for coefficients and standard error terms for each parameter across all models using the formulas:

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

Here $\hat{\pi}_i$ was approximated with W_i , $\hat{\theta}_i$ was approximated with $b1$ (the parameter estimate), $\text{var}(\hat{\theta}_i | M_i)$ was approximated by the SEM of $b1$, and M referred to the model. This model averaging technique allows information on parameter and standard error estimates to be combined across all models within the 95% subset. For the one continuous variable, weight, we used the Type III sum of square parameter estimates and associated standard errors provided by SAS 7.0 (using the "solution" function) to represent the slope of corticosterone in relation to weight. When weight was not a parameter in the model, we used a value of zero for the parameter and standard error estimates. For the remaining categorical variables, we generated predicted corticosterone values for each level of each parameter for each of the 95% best-fit model equations. These predicted values were then used to generate a coefficient estimate and standard error value for each level of each parameter (e.g., year parameter had values for 1999 and 2000) with each of the 95% subset of models. 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 or not. Although our main objective was to determine whether corticosterone was a good predictor of a bird's subsequent performance, we wanted to investigate the relative importance of corticosterone compared to other parameters that might influence kittiwake productivity. Thus, 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 between 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 was 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 et al. 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*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 natural food conditions may have improved thereafter, although the increase in supplemental capelin consumption through chick rearing in 1999 suggests 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 better natural forage conditions were present (although variable) during the latter stages of breeding in that year.

Measurement and Predictors of Base-line 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.

Analysis 1, Natural Variation.--Base-line 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 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).

Parameter and standard error estimates (Table 3) indicated 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 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 found 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 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 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 analysis 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 much lower. The high levels of corticosterone detected in experienced breeders during the arrival stage in 1999 suggested natural food was especially poor during this time (Fig. 4).

Analysis 2, Food Supplementation.--Base-line levels of corticosterone from kittiwakes that were supplementally fed varied from 0.8 to 23.1 ng/ml ($\bar{X} \pm SE = 4.5 \pm 0.4$, $N = 112$) 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 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 corticosterone 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 less than 10% of the variation in corticosterone, our analyses indicated 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 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 (± 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 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 ± 1.6 versus 6.1 ± 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 ± 0.7 versus 11.6 ± 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 (± 0.4 SEM) days after adults were sampled for blood. However, three and five 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 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 ± 0.6 versus 7.4 ± 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 amongst 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 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 (non-significantly) 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 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 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 two years supports the idea that 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 et al. 1998, Golet and Irons 1999). 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 non-stressful 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 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 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 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 et al. 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 provide 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 et al. 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 between 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 Reproductive Performance

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 suggests 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 removing the effect of breeding experience. 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 and Hatch 2002, Gill et al. 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 productivity 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 non-breeding 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 et al. 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 et al. (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 minutes 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 et al. 1994a, Wingfield et al. 1994b). 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).

CONCLUSIONS

Our results suggest that baseline levels of corticosterone have the potential for use as an indicator of forage availability. This was especially true for birds sampled shortly after arriving at Middleton in each year of our study. For corticosterone to be a useful measure, however, it would have to be reasonably predictive under all ecological conditions and across breeding stages. At a minimum, this technique requires intensive sampling of birds over a range of good and bad food conditions, and possibly during different breeding stages, to furnish a realistic baseline against which corticosterone values can be compared. Our results suggest corticosterone is most affected during extremely poor forage conditions.

The value of baseline levels of corticosterone as a predictor of reproductive performance also has its limitations. Given that baseline levels of corticosterone are reflective of current forage conditions and that these conditions can change through a breeding season, measures of corticosterone from birds during egg formation are unlikely to indicate breeding performance of birds during latter stages. Changes in forage conditions within years will also limit the ability of other parameters, such as body weight and breeding experience, to predict reproductive performance. Other more traditional parameters such as counts of active nests with eggs or chicks may be simpler and more reliable, given they estimate the actual productivity of a colony.

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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 ¹	Sample size (male / female)	No. nest sites sampled	No. individuals (fed / unfed)	Breeding experience (no / yes)
<u>1999</u>						
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
<u>2000</u>						
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

¹ Number of days before or after the first egg of a clutch was laid; day 0 = date of first egg in a clutch.

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	<i>R-square</i>	<i>K</i>	RSS	<i>AIC^l</i>	Δ_i	W_i	Cum. Sum of W_i
<u>Analysis 1: Natural Variation ²</u>							
(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
<u>Analysis 2: Food Supplementation ³</u>							
(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

Table 2. Continued.

¹ AIC values converted to AIC_c when $n / K \leq 40$.

² 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.

³ Analysis 2 models the 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 ($\hat{\theta}_a$)¹ 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. 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).

Parameter	$\hat{\theta}_a$	SE($\hat{\theta}_a$)	$\hat{\theta}_a \pm$ SE($\hat{\theta}_a$)	Importance
<u>Analysis 1: Natural Variation</u>				
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
<u>Analysis 2: Food Supplementation</u>				
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	

Table 3. Continued

¹ For weight, $\hat{\theta}_a$ is the average slope of the line describing the relationship between corticosterone and weight.

Table 4. Breeding success (top line of the Arrival, Egg formation, and Incubation sections) 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
<u>Arrival</u>			
% 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
<u>Egg formation</u>			
% 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
<u>Incubation</u>			
% 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

Table 5. Baseline levels of corticosterone (ng/ml) and reproductive success of supplementally fed and unfed black-legged kittiwakes breeding on Middleton Island in 1999 and 2000. ¹ Values shown as mean \pm SE; sample sizes in parentheses.

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

¹ NS = non-significant. Tests included Mann-Whitney U, student t-test and one-way ANOVAs.

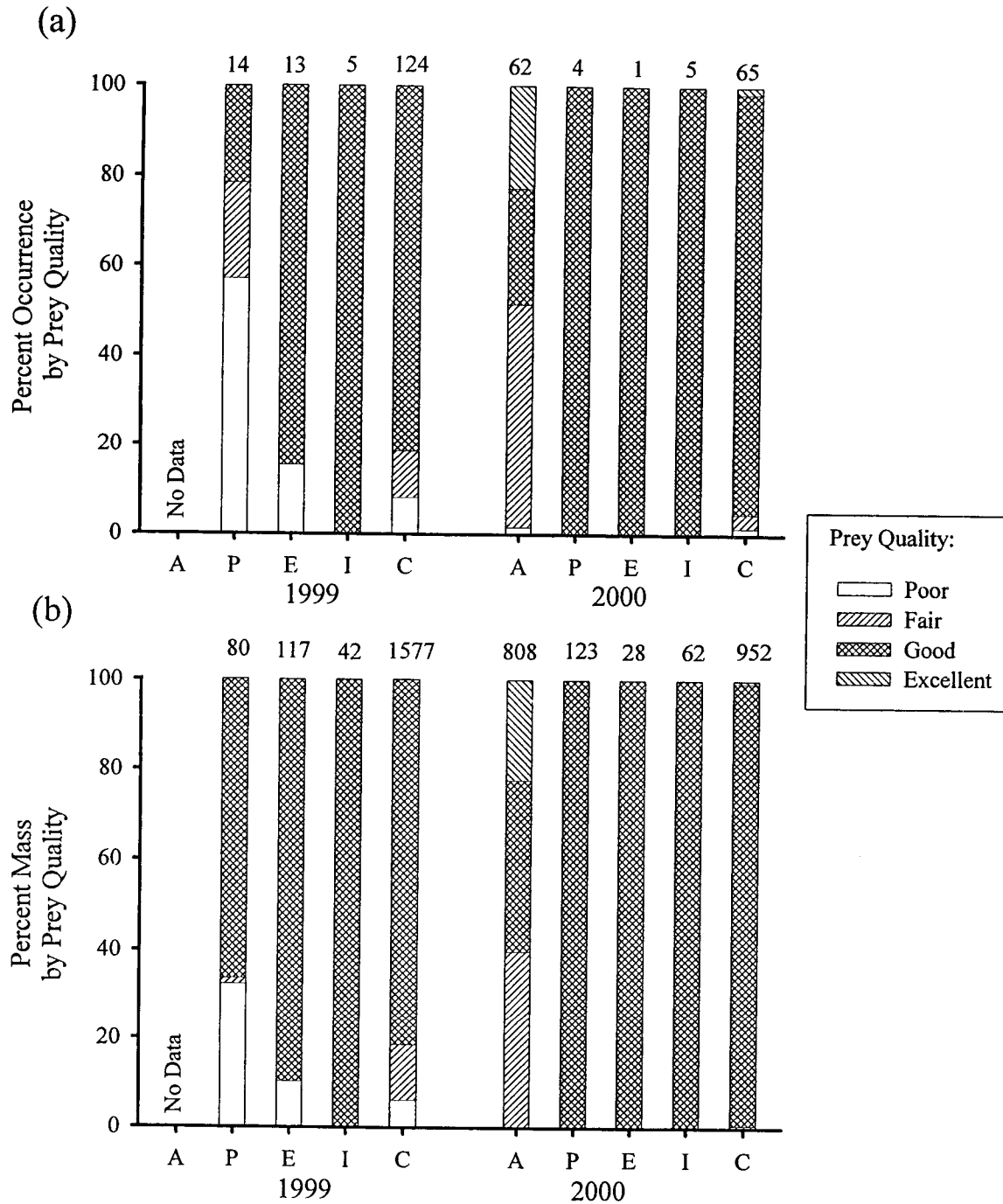


Figure 1. Percent occurrence (a) and mass (b) of prey quality categories in regurgitations of black-legged kittiwake adults and chicks on Middleton Island in 1999 and 2000. Bars depict arrival (A), pre-egg formation (P), egg formation (E), incubation (I) and chick-rearing (C) stages. Numbers above bars 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 listed in the text.

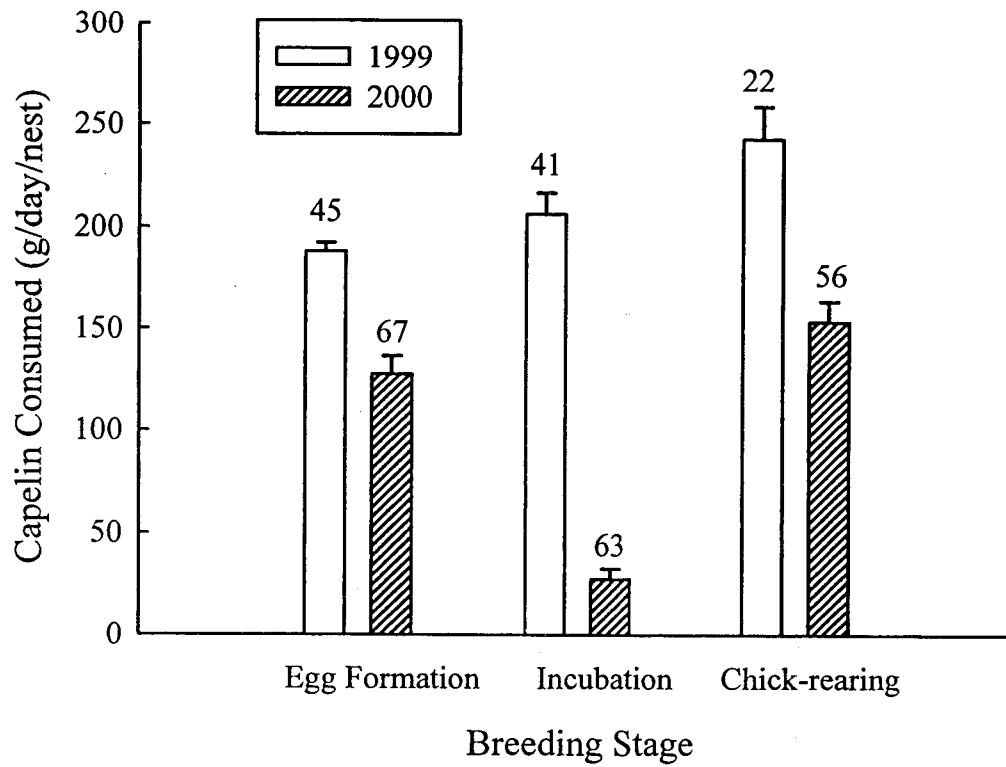


Figure 2. Supplemental capelin consumed by black-legged kittiwakes per day per nest ($\bar{X} \pm$ SEM) during three stages of breeding in two years on Middleton Island. Sample sizes (number of nests) are shown above bars.

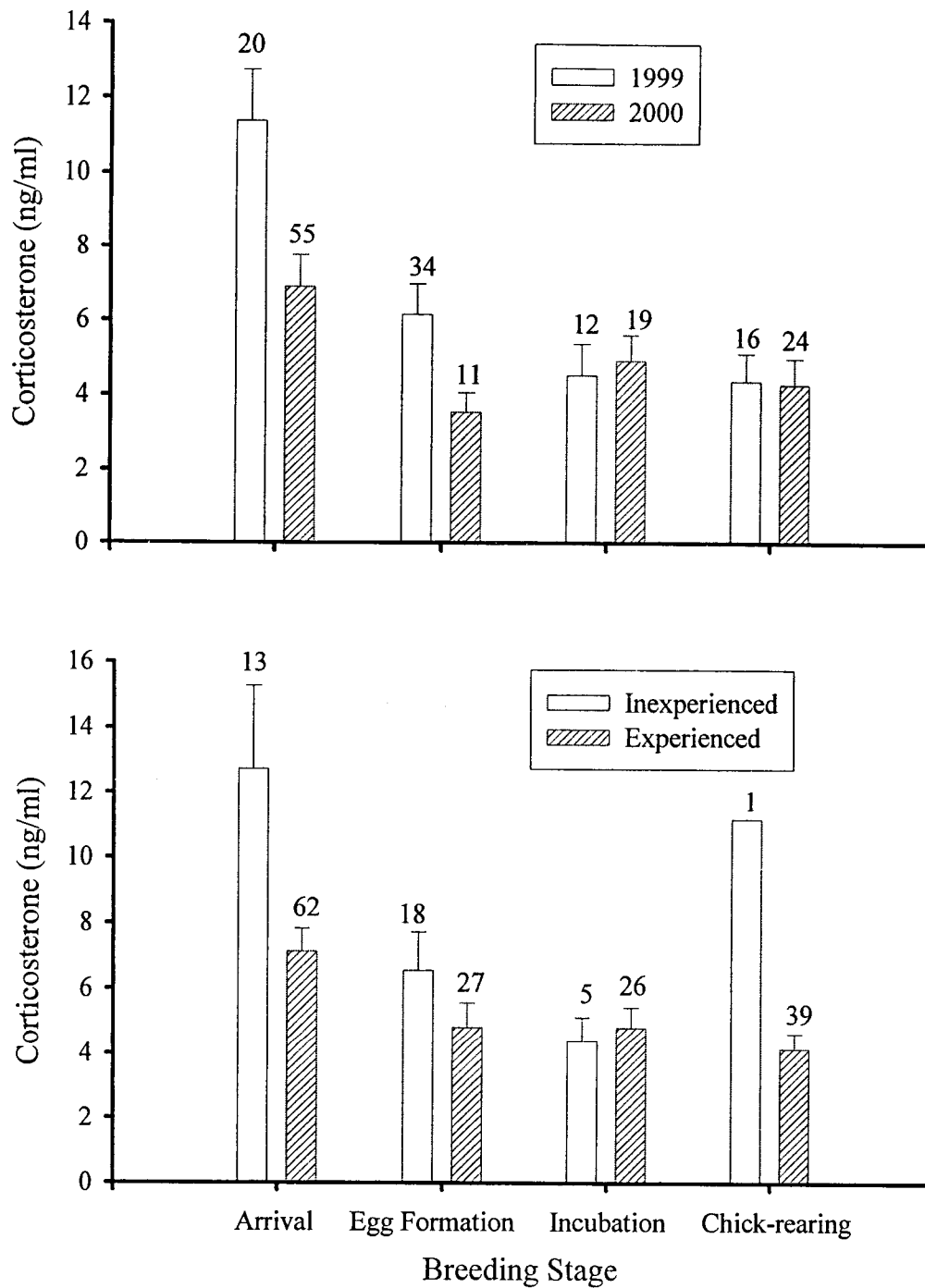


Figure 3. Baseline levels of corticosterone ($\bar{X} \pm \text{SEM}$) in black-legged kittiwake adults sampled during four stages of breeding on Middleton Island in 1999 and 2000 (top panel), and in relation to prior breeding experience (bottom panel; data from 1999 and 2000 are combined). In both cases,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

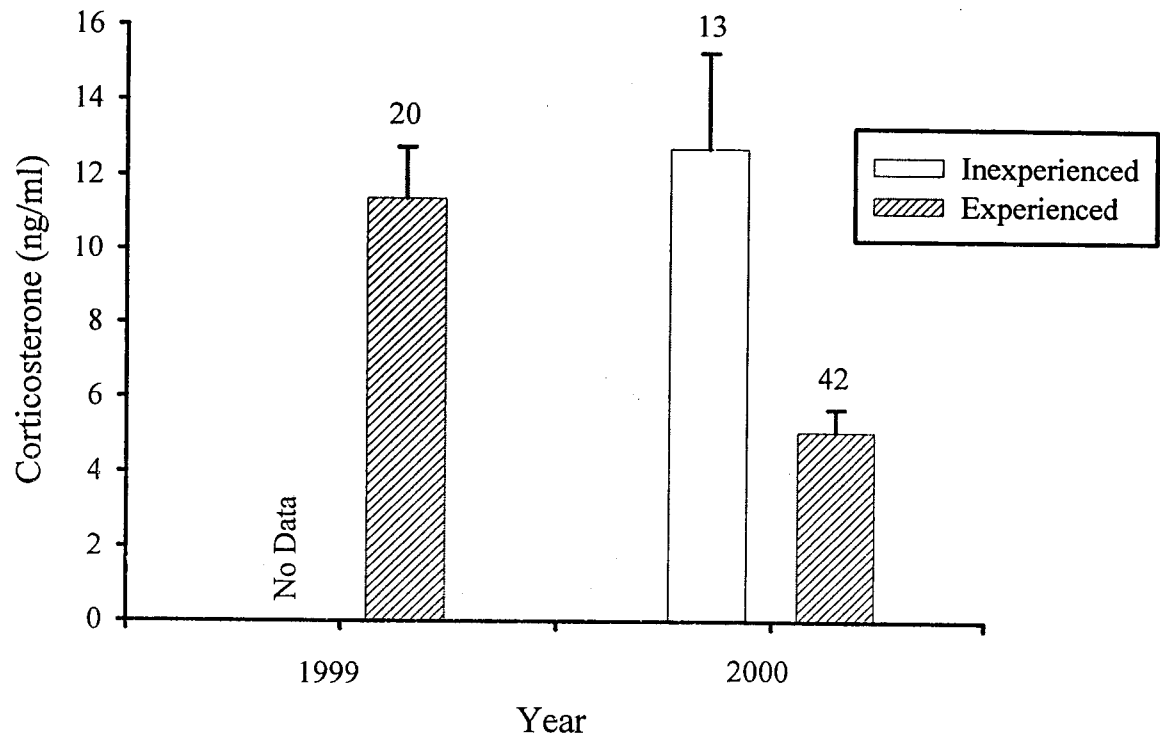


Figure 4. Baseline levels of corticosterone ($\bar{X} \pm \text{SEM}$) in black-legged kittiwake adults sampled shortly after arriving at Middleton Island in 1999 and 2000 in relation to prior breeding experience. Birds were not supplementally fed at the arrival stage.