

Unifying quantitative life-history theory and field endocrinology to assess prudent parenthood in a long-lived seabird

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ABSTRACT

Question: Can field measurements of stress hormones help us to assess the prudent parent hypothesis in a long-lived seabird?

Organism: Black-legged kittiwake, *Rissa tridactyla*.

Location: Duck and Gull Islands, Cook Inlet, Alaska, USA.

Methods: We examined the statistical relationship between the stress hormone corticosterone and mortality in black-legged kittiwakes. We built a demographic model of the kittiwake life cycle to determine whether the mortality rates associated with persisting in a breeding attempt despite high corticosterone caused the birds to sacrifice more lifetime reproductive output than they gain from one year's breeding.

Results: The probability of apparent mortality increased with corticosterone, suggesting some birds incurred increased mortality risk for the sake of breeding. For Duck Island (low reproductive success), it appears birds sacrificed more lifetime reproductive success than a prudent parent would. On Gull Island, it appears most but possibly not all birds were behaving in ways consistent with theory, although definitive statements require larger samples of highly stressed birds.

Keywords: black-legged kittiwake, CORT-fitness hypothesis, corticosterone, endocrinology, life history, prudent parent.

INTRODUCTION

Skipping of reproductive events is frequently observed in long-lived birds (Cam *et al.*, 1998). The 'prudent parent hypothesis' posits that skipping occurs when the costs of breeding reduce expected lifetime reproduction by more than the value of the current brood (Drent and Daan,

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1980; Bokony *et al.*, 2009). However, testing this hypothesis directly is difficult because breeders and non-breeders often differ in intrinsic quality (Cam *et al.*, 1998) so that survival of breeding and non-breeding birds cannot be compared directly to assess the costs of reproduction except through experimental brood manipulations (e.g. Golet *et al.*, 2004), and it is crucial to assess skipping behaviour and concomitant cost–benefit analyses at the individual level. In addition, skipped reproduction is expected to result from the difficulty of reproduction fluctuating through time, so testing the predictions of the prudent parenthood hypothesis require that we identify ways to compare prospects for reproduction in different years.

Recent advances in field endocrinology may provide the key to making this link. The CORT-fitness hypothesis (Bonier *et al.*, 2009) states that increased concentrations of baseline corticosterone (a stress hormone, hereafter CORT) are correlated with decreased individual fitness, either due to direct negative effects of CORT or the correlation between CORT and environmental stressors. Thus CORT may be a good metric of the stress individual birds are experiencing and indicative of their reproductive costs, and indeed elevated baseline CORT has been associated with delayed or skipped reproduction in Florida scrub jays [*Aphelocoma coerulescens* (Schoech *et al.*, 2009)]. However, empirical evaluations of the CORT-fitness hypothesis have yielded mixed results (Bonier *et al.*, 2009) depending on the timing of sampling and the fitness correlates used (usually survival and/or some component of reproductive output), and there are important distinctions between baseline and maximum CORT responses (Bonier *et al.*, 2009) and important interactive effects with other hormones (Angelier *et al.*, 2006). Responses to rising CORT may not be monotonically increasing (Brown *et al.*, 2005), and it is also possible that different individuals have different responses to changes in CORT concentrations, making predictions about the effects of CORT on fitness in mixed populations challenging (Dingenmanse *et al.*, 2010). Thus a simple relationship between CORT and fitness should not be assumed *a priori*, but the CORT-fitness hypothesis posits testable predictions that elevated CORT is an indicator of stress, and thus CORT may inform predictions of fitness (Bonier *et al.*, 2010). Indeed, in periods of prolonged stress (at the scale of the breeding season), links between CORT and fitness components are most apparent (Angelier *et al.*, 2009).

Pacific *Rissa tridactyla* (black-legged kittiwakes) provide an ideal model system for exploring ideas about prudent parent behaviour at the individual level. Pacific kittiwakes are long-lived (Hatch *et al.*, 1993). Skipping behaviour has been observed, with some linkage to broad-scale food availability, suggesting that kittiwakes are able to weigh the costs of a breeding attempt and decide whether and how much to invest into breeding that year (Jodice *et al.*, 2006). In addition, studies of long-lived seabirds at the population level (Kitaysky *et al.*, 2010 and references therein) have demonstrated a link between CORT and food availability, a crucial component of environmentally induced stress. These same studies also established a population-level link between elevated CORT and reduced adult survival. Goutte *et al.* (2010a) demonstrated increased mortality probabilities for individual kittiwakes implanted with supplemental CORT, although pharmacological manipulations of CORT (and resultant biological feedbacks) may have different effects than natural variation. In addition, Goutte *et al.* (2010b) showed that female black-legged kittiwakes with elevated CORT were more likely to skip reproduction. However, directly equating this skipped reproduction to a quantitative change in expected lifetime reproductive success requires that the effects of continuous variation in natural CORT concentrations on mortality be documented at the individual scale for black-legged kittiwakes, as it has been in other species (Blas *et al.*, 2007).

In this study, we test predictions arising from the CORT-fitness hypothesis and the prudent parent hypothesis. We test the applicability of the CORT-fitness hypothesis to a specific scenario by examining whether the survival probability of adult individuals decreases with increasing CORT. We then test the prudent parent hypothesis by using the observed relationships between individual CORT and survival along with data on productivity from the same colonies/years to parameterize a life-history model that explicitly quantifies the trade-offs between current and future reproductive output as a function of parent CORT. Finally, we use this model to analyse the CORT–survival link to (1) determine how much survival and potential future reproduction individual kittiwakes are sacrificing for the current year’s breeding, and (2) test the prediction that birds will abandon their chicks rather than tolerate stress levels that reduce their expected lifetime reproductive output by more than the current chicks add to it.

METHODS

Field methods

Field studies were conducted at two major seabird colonies in the Gulf of Alaska [for a detailed description of colonies and methods, see Kitaysky *et al.* (2010)]: Duck Island (also called Chisik, west side of Cook Inlet; 60°09'N, 152°34'W) and Gull Island (east side of Cook Inlet; 59°35'N, 151°19'W). During 1996–1998, incubating and brooding birds were captured from their nests using 9-m long noose poles (6 birds in 1996 on Gull Island only, 27 in 1997, and 114 in 1998). By sampling two islands on multiple occasions, we are able to compare the predictive power of CORT *per se* to potential location and year effects.

For all birds, initial blood samples were taken within 3 min of capture as a baseline measure of circulating CORT (Kitaysky *et al.*, 2010). To determine the maximum CORT concentration attained in response to a standardized stressor, which pertains to recent nutritional history (Kitaysky *et al.*, 2010), a subset of birds (6 in 1996, 20 in 1997, 13 in 1998) were then held in breathable mesh bags and additional blood samples were taken at 10, 30, and 50 min after capture. Because the rate at which CORT concentrations rise can differ among individuals, for each bird we chose the sampling point that yielded the highest concentrations of CORT (hereafter ‘maximum CORT’). Total CORT was measured in blood plasma using a radioimmunoassay (Kitaysky *et al.*, 2010). Inter-assay variation, measured by assaying the 1 ng·ml⁻¹ of corticosterone standard in each assay, was less than 10% and it did not co-vary with differences measured in plasma. For each bird, we recorded the stage of the breeding cycle (incubating eggs or brooding chicks) during which it was sampled. For 96 of 147 birds, we determined sex based on genomic DNA (Kitaysky *et al.*, 2010).

Estimating apparent mortality

To measure survival of birds, we marked individuals with unique combinations of leg bands. In subsequent years (through 2001), we conducted resighting by intense daily searches throughout the colonies for about 6 weeks per year, starting at egg-laying and continuing until resighting curves reached a plateau, indicating that all marked birds present at the site had been encountered (Hatch *et al.*, 1993). We restricted our analysis to birds first sampled in 1998 or earlier, so we had at least 4 years of potential resighting history for every bird analysed. We investigated survival only for the year immediately following the CORT

sample. We considered any record with at least three consecutive failures to resight as an apparent mortality, although we are unable to distinguish actual mortality from permanent emigration. We also identified birds that skipped reproduction in the first year after their CORT sample, but were resighted in subsequent years. Since 27 of 28 birds with two consecutive failures to resight were not resighted a third time, we can be confident that birds with three consecutive failures to resight are unlikely to be seen again. We chose this conservative approach restricted to the first year of individuals with long attempted-recapture histories rather than one built around time-varying estimates of survival and recapture because of our interest in a continuous covariate (CORT) that was measured only once, but likely varied over the capture history of each individual. Since both mortality and detection probability (which is likely more affected by birds skipping breeding than by failure to predict birds that are present) could be affected by CORT, we did not believe it was appropriate to use the full resighting history to attempt to estimate detection probability for the year after CORT was measured. Our approach does suffer from bias introduced by the possibility that a bird with three or more consecutive failures to resight might still be alive the first year it was not detected. Thus we may slightly over-estimate annual mortality. However, such birds very likely did die before returning to the colony to breed again. From a life-history perspective, it is mortality before next breeding that is the crucial parameter to estimate.

Predictors of mortality

We used model comparison techniques (Burnham and Anderson, 2002) to assess the ability of baseline CORT and maximum CORT to predict adult mortality, along with potential non-monotonic effects (Brown *et al.*, 2005) and potential effects of island, year, sex, and stage at time of CORT measurement (Appendix A). Here we present the best supported model, a logistic regression predicting apparent mortality as a function of baseline CORT for all birds pooled. We performed the logistic regression in R (R Development Core Team, 2009) using the 'glm' function with binomial error and a logit link function to fit the model, the 'confint' function in library 'MASS' to calculate confidence intervals on model parameters, and the 'predict' function to obtain normal approximation confidence intervals on the model predictions of mortality probability as a function of CORT.

Test of prudent parent hypothesis

To test the applicability of the prudent parent hypothesis to kittiwakes from Cook Inlet, we developed a life-history model to quantify the trade-off between raising a chick at varying costs of stress and remaining lifetime reproduction. We aimed to identify the stress level at which mortality risk from raising current chicks causes more future reproductive value to be lost than is gained by raising those chicks. We assumed that near the start of a breeding season, a parent decides whether or not to forfeit current reproduction. This decision is based on a comparison of the expected lifetime reproduction for a bird that keeps versus abandons its current chicks, given that raising chicks this year leads to a stress level as measured by baseline CORT concentration x . This abandonment may have taken place at any time up to and including our measurements in the incubation and brooding stages. Consequently, we observe only birds that have persisted in their breeding attempt despite encountering a stress level as revealed by their CORT measurement. We thus make

a distinction between forfeiting a reproductive event (a choice to not lay eggs at all, or abandon before rearing) and persisting in rearing chicks that later die (a failure rather than a choice).

Specifically, the expected lifetime reproductive output (chicks fledged) of a bird who continues to raise this year's clutch is $c + (1 - m(x))R$, where c is the expected number of chicks surviving to fledging if the parent continues to expend effort feeding them, $m(x)$ is the probability of adult mortality associated with CORT concentration x , and R is expected future reproduction, measured as total chicks fledged in future years, assuming survival until next year but discounting for expected mortality after that. Note that senescence might cause R to be age-dependent, although evidence for senescence in kittiwakes is equivocal (Coulson and Fairweather, 2001). If annual survival probability is not age dependent, the expected remaining lifespan is therefore independent of age.

Conversely, the expected lifetime reproductive output of a bird that abandons this year's chicks is $(1 - m(x_{\text{alone}}))R$, where x_{alone} reflects the lowered stress level achievable by abandoning this year's chicks.

For birds with very low stress, $c + (1 - m(x))R$ will be greater than $(1 - m(x_{\text{alone}}))R$, and indeed it must be if $x \leq x_{\text{alone}}$, but depending on c it may be greater even if $x > x_{\text{alone}}$. We predict birds to give up on their current chicks at some threshold stress level x_{crit} above which $c(x) + (1 - m(x))R$ becomes smaller than $(1 - m(x_{\text{alone}}))R$. Thus at the threshold level x_{crit} ,

$$c + (1 - m(x_{\text{crit}}))R = (1 - m(x_{\text{alone}}))R \quad (1)$$

Rearranging, we determine the expected remaining reproductive output for which any abandonment threshold is optimal, given c , $m(x)$, and x_{alone} :

$$R = \frac{c}{(1 - m(x_{\text{alone}})) - (1 - m(x_{\text{crit}}))} \quad (2)$$

We estimate c , $m(x)$, and x_{alone} from our data and other published literature, and then assess the plausibility of the value of R predicted if x_{crit} as inferred from the distribution of CORT concentrations measured in the field is optimal. In particular, we ask whether the highest CORT concentrations observed would only be optimal for unrealistically low remaining reproductive output R . We discuss our parameterization of $m(x)$ and our choices of c , x_{crit} , and x_{alone} in the Results and Discussion sections.

RESULTS

Baseline CORT concentrations of birds in Cook Inlet ranged from 1.39 to 38.43 ng · ml⁻¹, with a mean of 9.23 ng · ml⁻¹ and a standard deviation of 6.02 ng · ml⁻¹, and a non-normal distribution skewed towards lower values (Fig. 1). Baseline CORT concentrations were similar on Duck (8.82 ± 5.56 ng · ml⁻¹) and Gull (9.39 ± 6.21 ng · ml⁻¹) Islands. Overall, apparent mortality of adult birds from Cook Inlet was 17%. Apparent mortality increased significantly with increasing baseline CORT (Fig. 2, logistic regression $P = 0.018$). In our best-fit model,

$$m(x) = \frac{e^{-2.399 + 0.0803x}}{1 + e^{-2.399 + 0.0803x}} \quad (3)$$

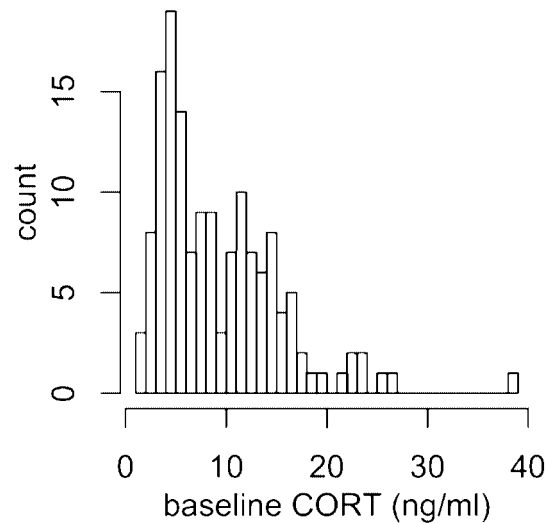


Fig. 1. Baseline CORT concentrations ($\text{ng} \cdot \text{ml}^{-1}$) of Cook Inlet adult birds.

where $m(x)$ is the probability of mortality when baseline CORT in $\text{ng} \cdot \text{ml}^{-1}$ is x . The 95% confidence interval on the constant term in equation (3) was -3.31 to -1.60 and the confidence interval for the regression coefficient was 0.014 to 0.15 .

Test of prudent parent hypothesis

To determine whether parent kittiwakes take on more mortality risk for the sake of one year's chicks than predicted if they were maximizing lifetime reproductive success, we bracketed plausible ranges on parameter values for the life-history model as follows. We solved equation (2) using equation (3) and giving-up thresholds (x_{crit}) of $16 \text{ ng} \cdot \text{ml}^{-1}$ (90th percentile of observed distribution) or $26 \text{ ng} \cdot \text{ml}^{-1}$ (99th percentile) baseline CORT for both islands combined. Although the means and standard deviations for CORT concentrations on the two islands were similar, the overall range was less on Duck Island, possibly due to small sample size. Nonetheless, $16 \text{ ng} \cdot \text{ml}^{-1}$ was the 90th percentile for just Duck Island CORT concentrations as well. We then calculated the expected remaining lifetime reproductive success (R , measured as chicks fledged) for which each of these thresholds would be optimal over a range of plausible values for expected chicks fledged this year (c) and stress level of a bird without chicks (x_{alone}).

We estimated an upper bound on x_{alone} of 10, choosing a value near the most stressed birds found on a nearby island with higher survival [Middleton Island (Kitaysky *et al.*, 2010)]. In contrast, we selected a lower bound on x_{alone} of 1 if once freed from frequent returns to a central place to feed their chicks birds are able to seek out optimal feeding habitats regardless of their distance from the colony. Intermediate values of x_{alone} are also plausible. Furthermore, the exact value of x_{alone} chosen is not crucial, since as Fig. 3 demonstrates R is more sensitive to changes in c than x_{alone} and the range of x_{alone} explored only allows the maximum likelihood estimate of $m(x_{\text{alone}})$ to range between 0.08 and 0.17 , a much smaller range than the plausible variation in c and thus of less impact on the R value calculated.

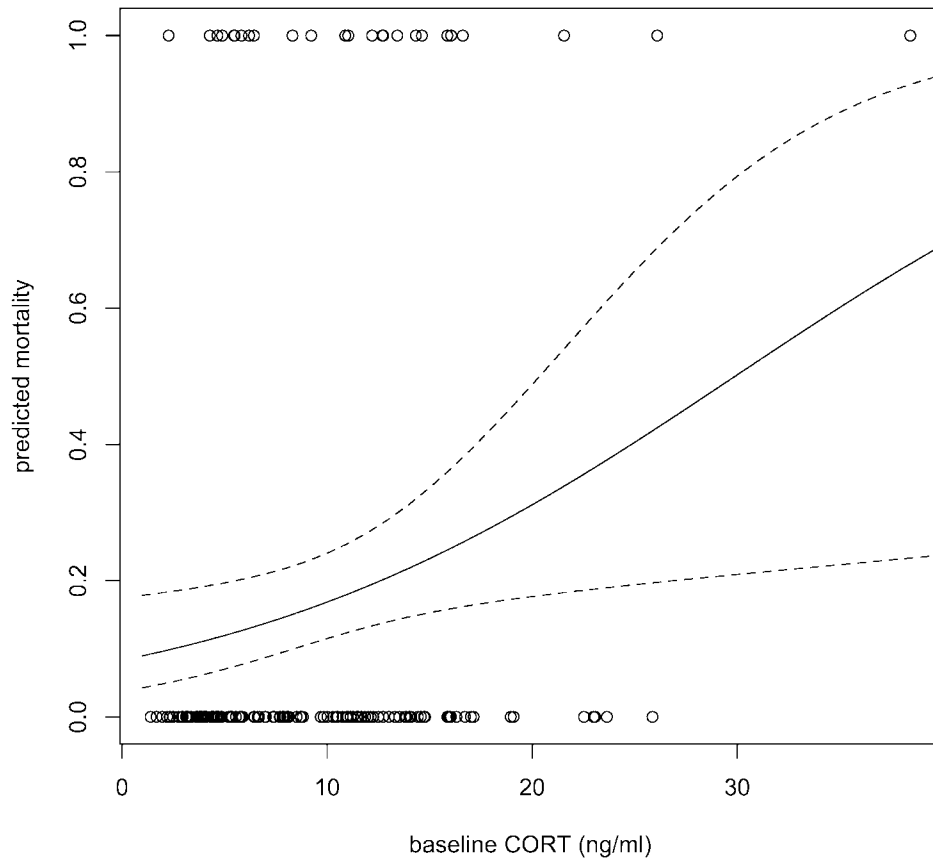


Fig. 2. Apparent mortality of adult birds from Cook Inlet versus baseline CORT concentration. Solid line is best-fit logistic regression, dashed lines are 95% prediction intervals, and circles are individual data points.

Previous literature suggests that the mean number of chicks fledged (c) may vary between islands, and through time (Kitaysky *et al.*, 2010). Mean fledging success was consistently low on Duck Island from 1996 to 2000, ranging from 0.00 to 0.036 chicks fledged per chick hatched (Kitaysky *et al.*, 2010). Even assuming two eggs in every nest and 100% hatching success, this implies $c \leq 0.072$. For c this small, solving equation (2) based on the maximum likelihood estimates for predicted mortality risk reveals the high abandonment threshold would only be optimal for expected remaining lifetime chick production < 0.28 chicks fledged (even less if $x_{\text{alone}} < 10$), while the low abandonment threshold would only be optimal for expected remaining lifetime chick production < 0.92 .

The lower bound on the 95% confidence interval for predicted mortality does show slower increase than the maximum likelihood estimate, suggesting the possibility of reduced costs of high CORT. However, the lower bound on mortality still rises from 0.115 at x_{alone} to 0.159 at the lower proposed threshold and 0.197 at the higher proposed threshold. These correspond to optimal behaviour given expected remaining chick production of < 1.65 (low threshold) or 0.88 (high threshold).

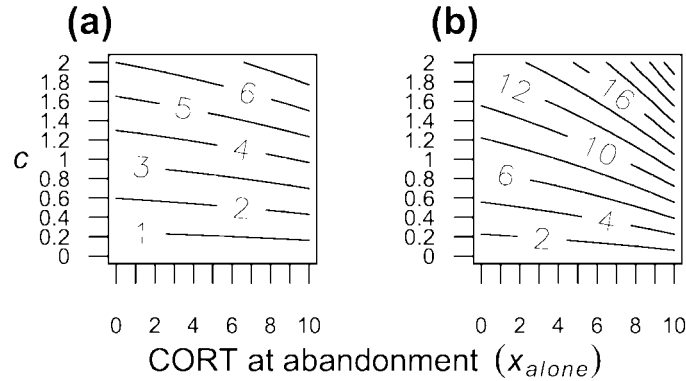


Fig. 3. Contour lines for remaining expected lifetime reproductive output (chicks fledged) corresponding to the optimal abandonment threshold CORT concentration (x_{crit}) of $26 \text{ ng} \cdot \text{ml}^{-1}$ (a) or $16 \text{ ng} \cdot \text{ml}^{-1}$ (b), for various combinations of CORT concentration achievable upon chick abandonment (x_{alone} , x axis) and expected number of chicks fledged in the year of potential abandonment (c , y axis). For example, a high abandonment threshold (a) would be optimal given expected fledging success $c = 1$ and stress corresponding to abandonment $x_{alone} = 4$ would be optimal if the expected remaining lifetime chicks fledged (R) was ≤ 3 chicks. For higher R , persisting in the face of this much stress sacrifices more residual reproductive value than is optimal.

On Gull Island from 1996 to 2000, mean fledging success was 0.69 chicks fledged per chick hatched (Kitaysky *et al.*, 2010), equating to 1.38 chicks per nest assuming all nests have two eggs and all eggs hatch. However, at least at the population scale, fledging success decreased with increasing CORT (Kitaysky *et al.*, 2010, their Figure 4B). Thus a more appropriate estimate of chick production under stressful conditions would likely be the lowest observed population mean of 0.50 chicks fledged per chick hatched, for a total production of 1.00 chicks per nest at most. In addition, rather than two eggs per nest with 100% hatching success, nests on Gull Island averaged 1.67 eggs per nest with eggs and 58% of eggs hatched, resulting in 0.48 chicks per nest [raw data from Kitaysky *et al.* (2010), data collection described therein]. Thus it appears that c should be assumed to be below 1.0 for Gull Island, possibly well below. For $c = 1.0$, solving equation (2) reveals the high abandonment threshold would be optimal for expected remaining lifetime chick production < 3.93 chicks fledged, while the low abandonment threshold would be optimal for expected remaining lifetime chick production < 12.7 . For $c = 0.48$, the high abandonment threshold implies 1.89 expected remaining chicks fledged and the low abandonment threshold implies 6.10 expected remaining chicks fledged.

Figure 3 summarizes the remaining expected reproductive value (chicks fledged) for which each of the putative abandonment thresholds x_{crit} are optimal for plausible values of c and x_{alone} . As c increases (making current reproduction more valuable), a larger amount of lifetime reproduction R can be sacrificed (moving along y axis of figures). As x_{alone} decreases (meaning there is a larger survival advantage to abandoning reproduction), less lifetime reproduction can be sacrificed (moving along x axis of figures). A high abandonment threshold (x_{crit}) is optimal for smaller amounts of remaining lifetime reproduction than a low x_{crit} (overall elevation of Fig. 3a vs. Fig 3b).

DISCUSSION

Our results shed light on the promises and pitfalls in using stress hormones to assess the question of prudent parenthood. We have confirmed that stress hormones are useful in quantifying mortality risk for breeding birds, an essential component of this and many other life-history trade-offs. At the same time, we have shown that the precision needed to make definitive statements may at times require much larger sample sizes than can easily be collected, especially of the most stressed birds.

Our results confirm that natural variation in baseline CORT during the breeding season can predict apparent adult mortality probability at the individual level. This likely represents a hypothesized mechanistic link between baseline CORT and actual adult mortality (Kitaysky *et al.*, 2010). The link between CORT and relative mortality risk would only be suspect in the unlikely case that CORT also affects the probability of permanent emigration (Brown *et al.*, 2005), and only relative mortality risk needs to be estimated for our life-history model. Nevertheless, our apparent mortality estimates likely reflect actual mortality since relocation between colonies is unlikely for kittiwakes in the absence of major disturbances (Coulson and Fairweather, 2001). Furthermore, we only observed two out of several hundred banded birds move temporarily across Cook Inlet from one colony to the other in 6 years of study. Thus our results provide support for the CORT-fitness hypothesis (Bonier *et al.*, 2009) as applied to Pacific black-legged kittiwakes during the breeding season, and extend previous results to allow modelling of individual mortality probability as a continuous function of CORT.

We demonstrated the CORT-survival relationship only during the breeding season, a time of high stress. The weak support for including interaction terms in our models (Appendix A) suggests that CORT is a useful predictor of mortality risk across years, locations, and sexes, but these and other aspects must be considered when extrapolating from context-specific survival estimates (cf. Angelier *et al.*, 2009).

We therefore conclude that some birds subject themselves to substantial stress over the course of rearing their chicks, so much so that they sacrifice substantial long-term survival. This is perhaps unexpected for a long-lived bird (Drent and Daan, 1980; Bokony *et al.*, 2009), although willingness to bear some cost of reproduction in kittiwakes has been previously demonstrated (Golet *et al.*, 1998, 2004). In addition, rigorously quantifying how much survival birds are sacrificing is a challenging task due to the paucity of data for birds breeding at the highest stress levels (which may itself be suggestive of prudent behaviour on the part of most birds).

Over the full range of c and x_{alone} explored, the apparent threshold CORT levels for abandonment would imply remaining reproductive value on the order of 2–20 chicks fledged (Fig. 3), and an even higher range when accounting for uncertainties in survival. The higher end of this range (corresponding to $c \geq 1$ and a low abandonment threshold) seems plausible. However, even taking the lower bounds of estimated mortality risk, the Duck Island birds would only be predicted to persist in rearing chicks at the high end of the observed CORT distribution for expected remaining lifetime chick production < 1.65 . Such a population could not possibly sustain itself after accounting for sex ratios and survival from fledging to first reproduction. Thus it appears the Duck Island birds are not behaving as prudent parents. It is true that low c might likewise imply low R , and this colony has been in recent decline (Piatt, 2004), but the fact that this population still exists suggests that over the long term there must be periods of higher reproductive success. It is also possible that c for birds exerting the most effort in raising chicks may be above the population mean, but it is unlikely that any such effect could be strong enough to compensate for the very low

fledging success on Duck Island. Furthermore, the trend in decreasing productivity with increasing CORT demonstrated at the population level for Gull Island suggests, though it cannot prove, that fledging success decreases with CORT at the individual level as well.

At Gull Island our best estimate of $c = 1.0$ implies expected remaining lifetime reproductive output of 4–13 chicks. We can approximate reproductive lifespan as the inverse of adult mortality rate (Bokony *et al.*, 2009), or 5.8 years based on 17% annual mortality. Other studies of Pacific black-legged kittiwakes have typically reported lower mortality [e.g. 6–9% on Middleton Island (Hatch *et al.*, 1993); 10.2% with chicks or 4.7% without in Shoup Bay (Golet *et al.*, 1998)], corresponding to reproductive lifespans as long as 20 years. Since kittiwakes typically lay two eggs per clutch and can usually raise at least one chick under good conditions, this would imply a lifetime reproductive output on the order of at least 6–20 chicks fledged. Thus while it is possible that most Gull Island birds are behaving as prudent parents, the birds with the highest stress levels (CORT above the 90th percentile) appear to be persisting in their breeding attempts in the face of more risk than theory would predict. However, broad confidence intervals on predicted mortality risk at the highest CORT levels make definitive statements about the prudence of Gull Island birds difficult. Although some increase in mortality risk with increased CORT appears well supported, precisely quantifying the mortality risks of high CORT requires a large sample of highly stressed birds, a logistically challenging endeavour.

Thus in the case of Gull Island birds we are limited to suggesting that most birds are behaving in a manner consistent with prudent parenthood, but the most stressed birds may not. On Duck Island, it is clear that many birds are persisting in their breeding attempts despite elevated mortality risks that are not balanced by the small chance of reproductive success observed in recent years. There are several potential explanations for this apparent mismatch (in addition to parameter uncertainty). It may be that some Cook Inlet kittiwakes (and particularly those on Duck Island) are not behaving as prudent parents. Indeed, Oro and Furness (2002) found that kittiwakes in Shetland, UK did not follow the predictions of prudent parent theory, although this might reflect lower survival of Atlantic versus Pacific kittiwakes. A lack of prudent parent behaviour might reflect a recent deterioration in conditions that natural selection has not kept up with, such that birds in declining colonies are following a strategy that may have been selected for in a more favourable past environment where the mortality costs of high stress were lower or greater fledging success might be expected. Alternatively, the decision to attempt reproduction in a given year may be essentially fixed by the decision to establish a nest, with the assessment of likely success made based on information available at that time. If so, birds may simply do a poor job of predicting their chances of success later in the year (cf. Shultz *et al.*, 2009).

There are, however, possible mechanisms that would generate apparently imprudent behaviour even in birds obeying prudent parent life-history theory predictions. First, abandonment thresholds might be age dependent, with older birds having less remaining residual reproductive value and thus willing to persist in the face of more stress. Studies of other long-lived birds have reported results consistent with (Angelier *et al.*, 2007) and contrary to (Angelier *et al.*, 2006) this hypothesis. It is also possible that rather than tolerating higher CORT, older individuals would produce less CORT in response to the same stress (Heidinger *et al.*, 2006), which would not explain the pattern observed in our study. Similarly, low-quality individuals might have higher abandonment thresholds. Second, generation time effects might penalize delayed reproduction even if total expected lifetime output remained similar. Third, abandonment probability may be a continuous rather than stepped response to risk.

Fourth, kittiwakes might be constrained, either in their ability to assess survival risks at different stress levels or because holding onto a nest site has an as-yet-unquantified value in ensuring future reproductive opportunities. Finally, serial autocorrelation in environmental quality might promote higher than expected persistence in reproductive effort, so that repeated abandonment does not eliminate any chance of an individual's successful reproduction.

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APPENDIX A: SURVIVAL ANALYSES AND MODEL COMPARISONS

Methods

Individual- vs. population-level predictors of mortality

Our first step in describing the mortality patterns among our sampled birds was to compare shared population-level (year and island) and individual-level effects. The analysis was based on the initial CORT measurement and only considering apparent mortalities where the first failure to resight came the next year. Since baseline CORT was the only individual-level metric collected on every bird, we used it as our metric of individual stress. We will show below that baseline CORT better predicted mortality than maximum CORT or responsiveness (see Results). We used generalized linear models (GLMs) with a logit link function and Akaike's information criterion, corrected for sample size [AICc (Burnham and Anderson, 2002)], to compare models of apparent mortality based on only baseline CORT, only island, only year of first sighting, and all possible combinations of additive effects, along with potential CORT \times year and CORT \times island interactions (together with a null model

of constant mortality probability). We used R (R Development Core Team, 2009) for all statistical analyses.

Comparing metrics of stress

Among just the subset of birds with baseline and maximum CORT measurements, we used logistic regression to explore the relationship between baseline, maximum, or responsiveness (maximum – baseline) in CORT and probability of apparent mortality for birds from both islands and all years combined. We also looked for non-monotonic effects of CORT on survival by comparing models based on CORT, CORT², and CORT + CORT², which allows for lowest mortality at intermediate CORT.

Context dependence of stress measures and their predictive power

We analysed models of survival based on CORT, sex, and/or stage (incubating eggs vs. brooding chicks) at which an individual was sampled. *A priori*, we hypothesized that sex could have either additive or interactive effects with respect to CORT. However, stage could only have an additive effect if the sampling event itself posed a significant mortality risk, otherwise stage could only have an interactive effect with CORT if stress and CORT scaled differently across stages. Furthermore, we ruled out the possibility of a stage × sex interaction, since sex does not vary through time. Thus we used AICc to compare support for a null model and all possible combinations of baseline CORT, sex, and stage except for models with an additive effect of stage or an interaction between sex and stage.

Results

Individual- vs. population-level predictors of mortality

The best supported model contained only CORT, with 77% AIC weight for all models combined containing CORT, compared with 53% support for all models including a year effect and 50% support for all models including an island effect based on AIC weights (Table A1). There was little support for a CORT × island (8%) or CORT × year (7%) interaction, suggesting that the effects of CORT are consistent across ecological scenarios. Results were qualitatively similar with 1996 (small sample size, only one island sampled) excluded. There was little support for the null model (3%), indicating that the various models explained substantial variation in mortality. Because CORT may vary by year and across islands, there was some redundant information in the various independent variables and one model formulation did not dominate, but overall CORT received the strongest support and so was the best predictor of mortality.

Comparing metrics of stress

Among birds with both baseline and maximum CORT measures, baseline CORT is a substantially better predictor of adult mortality than maximum CORT ($\Delta\text{AIC} = +5.19$) or responsiveness (maximum – baseline, $\Delta\text{AIC} = +6.18$). Adding a squared term to the CORT-survival model to account for non-monotonic effects did not result in a better supported model ($\Delta\text{AICc} = +0.18$ for replacing with a squared term, $\Delta\text{AICc} = +1.99$ for adding a squared term). Thus the most parsimonious model of post-breeding mortality is a monotonically increasing function of baseline CORT.

Table A1. Model comparison of individual versus population-level approaches to predicting apparent mortality of adult birds from Cook Inlet

Model	Deviance	k	AICc	Weight
CORT	128.40	2	132.48	0.231
CORT + year	125.30	4	133.58	0.133
CORT + island	127.44	3	133.61	0.132
CORT + island + year	123.71	5	134.14	0.101
year	128.00	3	134.17	0.100
Island + year	126.65	4	134.93	0.068
CORT*island	127.32	4	135.60	0.049
CORT*year + island	121.12	7	135.93	0.041
(null)	134.06	1	136.09	0.038
CORT*island + year	123.67	6	136.27	0.035
CORT*year	123.83	6	136.43	0.032
island	132.91	2	136.99	0.024
CORT*year + CORT*island	120.83	8	137.87	0.016

Note: A plus sign denotes additive effects, an asterisk denotes interactive effects, while k is the number of fitted parameters. CORT refers to baseline corticosterone concentration.

Table A2. Model comparison of various individual-level traits in predicting apparent mortality of adult birds from Cook Inlet

Model	Deviance	k	AICc	Weight
CORT + sex	102.13	3	108.39	0.289
CORT	104.49	2	108.62	0.258
CORT*sex*stage	92.06	8	109.72	0.149
CORT*sex	101.78	4	110.22	0.116
sex	106.95	2	111.08	0.075
(null)	110.11	1	112.15	0.044
CORT*stage + sex	101.79	5	112.46	0.038
CORT*stage	104.38	4	112.82	0.032

Note: A plus sign denotes additive effects, an asterisk denotes interactive effects, while k is the number of fitted parameters. CORT refers to baseline corticosterone concentration. This analysis uses the subset of birds with sex data, thus a lower AICc for the null model than in Table A1.

Context dependence of stress measures and their predictive power

All four of the best supported models of mortality risk with $\Delta\text{AICc} < 2$ included baseline CORT (Table A2). Baseline CORT received 88% support across all models, compared with 67% support for sex and 22% support for stage. Although sex effects may have some importance, there was only 27% combined support for models including a CORT \times sex interaction. Again there was little support for the null model (4%), indicating that the various metrics explained substantial variation in survival, and CORT explained it best. Therefore, it is reasonable to analyse our life-history model based on the overall best-fit model of survival as a function of baseline CORT.