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DETERMINANTS OF REPRODUCTIVE COSTS IN THE LONG-LIVED BLACK-LEGGED KITTIWAKE: A MULTIYEAR EXPERIMENT

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Abstract. We studied reproductive costs of Black-legged Kittiwakes (*Rissa tridactyla*) in Prince William Sound, Alaska (USA) by removing entire clutches from randomly selected nests over four successive years, and then contrasting survival and fecundity of adults from manipulated and unmanipulated nests in each subsequent year. To elucidate mechanisms that lead to the expression of reproductive costs, we simultaneously characterized several behavioral and physiological parameters among adults in the two treatment groups. We also examined naturally nonbreeding adults that previously bred to determine their survival and future nonbreeding probabilities.

Food availability varied during the study, being generally poor at the onset, and improving in later years. Adult nest attendance and body condition (assessed late in the chick-rearing period) varied accordingly among years, and between adults raising chicks and adults that had their eggs removed. Adults from unmanipulated nests incurred significant survival costs in all years, although fecundity costs were strongly expressed in only one of four years. Neither survival nor fecundity costs were strongly influenced by body condition or food availability, and no difference in reproductive costs was detected between the sexes. Although unmanipulated breeders survived at lower rates than manipulated breeders due to costs of reproduction, their survival rates were elevated compared to those of natural nonbreeders, presumably due to differences in individual ability. These findings indicate that models of adult survival must consider not only an organism's reproductive state, but also the factors that lead to that state.

Although body condition appeared to be weakly related to survival, it was insufficient to explain the full magnitude of survival costs observed. We suggest that other parameters that were found to differ between treatment groups (e.g., rates of energy turnover, baseline levels of stress, and patterns of allocating body reserves) may be important mechanistic determinants of reproductive costs in kittiwakes, and potentially other long-lived species. Future efforts should move beyond simple assessments of body condition and toward more integrated measures of physiological condition when attempting to identify factors that influence how long-lived species balance the costs and benefits of reproduction.

Key words: Black-legged Kittiwake; body condition; brood manipulation; corticosterone; cost of reproduction; energy expenditure; life history trade-off; mark–recapture; parental investment; Prince William Sound, Alaska (USA); Rissa tridactyla; *survival.*

Introduction

Ever since Fisher (1930) first recognized that organisms must balance the competing demands of self-maintenance and reproduction over the course of their lives, ecologists have endeavored to identify the mechanisms that shape life history strategies (Roff 1992, Stearns 1992). Williams (1966) postulated that organisms face trade-offs between current and future reproduction, and that these trade-offs, termed ''the costs of reproduction,'' may be important selective agents in the evolution of life histories. Although there is mounting evidence that reproductive costs exist (Stearns 1992, Golet et al. 1998), much remains to be learned regarding the mechanisms that lead to their expression and the role they play in the evolution of life history strategies (Boyce and Perrins 1987, Pettifor 1993, Zera and Harshman 2001).

Studies of long-lived species that demonstrate trade-offs between reproduction and adult survival (hereafter termed survival costs) support the notion that costs of reproduction are important in life history evolution. Because long-lived species typically have low annual reproductive output (relative to their lifetime potential), they have relatively little to gain, and much to lose, in terms of fitness, from investing too heavily in any one reproductive event. Furthermore, because even small increases in mortality rates can lead to large reductions

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in lifetime reproductive success, survival costs are expected to be strongly selected against in species that have the potential for long reproductive life spans. Consequently, long-lived species should (1) take few risks in reproduction (Goodman 1974, Charlesworth 1980, Pugesek 1990, Wooller et al. 1992), and (2) be unwilling to trade their own survival for that of their offspring (Cody 1966, Lindén and Møller 1989, Sæther et al. 1993).

The main emphasis of most experimental studies of the cost of reproduction has been to test for the existence of costs. Statistically significant adult survival costs were detected in three (Reid 1987, Jacobsen et al. 1995, Golet et al. 1998) of four brood size manipulation studies conducted on long-lived birds (Lessells [1986] did not demonstrate such costs). All four studies, however, revealed negative correlations between brood size and adult body condition at the end of the chick-rearing period. These findings suggest that the adults do compromise their own condition for the sake of their chicks, even though such adjustments may decrease postreproductive survival probabilities.

Handicapping studies designed to evaluate reproductive costs provide contrasting results, however. In experiments in which leg weights were added to adult Thin-billed Prions *Pachyptila belcheri* (Duriez et al. 2000), Yellow-nosed Albatross *Diomedea chlororhynchos* (Weimerskirch et al. 2000), Antarctic Petrels *Thalassoica antarctica* (Sæther et al. 1993), and Antarctic Prions *Pachyptila desolata* (Weimerskirch et al. 1999), foraging trip durations increased and chick meal masses were reduced, but adult body condition remained unchanged (except in the albatross study). Furthermore, impacts on adult survival were not found in either of the studies that assessed this parameter (Duriez et al. 2000, Weimerskirch et al. 2000). Also, when wingspan was experimentally reduced in Leach's Storm-Petrels (*Oceanodroma leucorhoa*), no effect was found on adult nutritional condition (assessed by measuring feather growth), although chick growth was depressed (Mauck and Grubb 1995).

Thus the evidence for whether or not long-lived adults incur a reproductive cost for the sake of their chicks is mixed. Brood manipulation studies suggest that long-lived adults accept trade-offs; handicapping studies, in contrast, suggest that experimentally increased costs are shunted to the chicks. That survival costs were detected in studies of larids but not among procellarids or geese also suggests that there may be phylogenetic differences in how birds balance the costs and benefits of reproduction.

Each of these studies provides a legitimate test for the existence of reproductive costs. However, because all were based on single-year experiments, they add little to our understanding of how variability in breeding conditions affects the expression of costs (Weimerskirch et al. 2001). By conducting multiyear manipulative studies, we may better define the mechanisms that generate reproductive costs, information that is needed to understand the degree to which reproductive costs influence the evolution of life histories (Hochachka 1992). More generally, understanding how long-lived species balance reproduction and self-maintenance under variable environmental conditions is critical to population modeling, as the patterns of variance in survival and fecundity (embedded within constant averages) influence the rates at which populations grow or decline (Caswell 2001).

Previously, we reported that survival costs and body condition effects were positively correlated in brood (or clutch) manipulation studies of birds (Golet et al. 1998), thus supporting the notion that survival costs of reproduction arise from differences in body condition (Nur 1984). This idea has intuitive appeal, because adults entering the postbreeding period in poor condition are probably more susceptible to life-threatening, condition-related ailments (e.g., starvation, predation, disease) than are adults in good condition (Pugesek 1987). Our goal in the present study was to identify mechanisms responsible for the expression of reproductive costs in a long-lived seabird, the Black-legged Kittiwake (*Rissa tridactyla*, see Plate 1), and to test the role that body condition, in particular, plays in the expression of these costs. Our experiments were repeated in four successive years that differed in food availability, thus allowing us to test the hypothesis that differences in condition lead to differences in reproductive costs and, more generally, that costs are greater when resources are limited (Tuomi et al. 1983, Bell and Koufopanou 1986, Erikstad et al. 1998). To our knowledge, this is the first multiyear manipulative study of reproductive costs in a long-lived species.

Previously, we reported the reproductive costs arising from a single-year brood manipulation experiment (Golet et al. 1998), and the effects of chick rearing on adult body condition and body composition (Golet and Irons 1999) and energy expenditure (Golet et al. 2000). Here we draw from the results of these studies to ask how behavioral and physiological responses to varying foraging conditions lead to variability in interannual survival and fecundity costs. In addition to data from three additional manipulation experiments and associated information on behavioral and demographic responses to variable foraging conditions, we report the effects of chick rearing on circulating levels of the stress hormone corticosterone. Corticosterone, the primary glucocorticoid released by birds, responds to both unpredictable environmental pertubations, such as food shortages (Kitaysky et al. 1999, Romero and Wikelski 2001), and predictable life history events, such as breeding (Romero et al. 1997). Corticosterone has also been shown to be negatively correlated with body condition (Wingfield et al. 1997*b*, Kitaysky et al. 1999) and survival (Romero and Wikelski 2001).

Our results suggest that adult kittiwakes incur reproductive costs, but only to a point, beyond which the

PLATE 1. (Left) Individually color-banded adult Black-legged Kittiwake (*Rissa tridactyla*) with nestlings at the Shoup Bay colony, Prince William Sound, Alaska. (Right) View of the main nesting area at Shoup Bay. Most of the kittiwakes pictured are on cliff nests. The colony is situated on a rock island that emerged from beneath a receding tidewater glacier. Glaucous-winged Gulls (*Larus glaucescens*), also pictured, nest and roost on the top of the island. Photos by Greg Golet, July 1993. (See Appendices A and B for color versions of these photographs.)

impacts of poor foraging condition are passed on to the chicks. We found significant interannual variability in fecundity costs, but not survival costs. Survival appeared to be influenced to a small degree by adult end-of-season body condition, although differences in condition between the experimental groups failed to explain the full magnitude of differences observed in survival. We suggest that, in addition to body condition, multiple nonexclusive mechanisms contribute to the expression of survival costs in these long-lived birds.

METHODS

Experimental organism and study site

Black-legged Kittiwakes are long-lived, circumpolar, cliff-nesting, colonial seabirds with strong mate and nest site fidelity (Coulson and Thomas 1985), and as such are ideal experimental organisms for longitudinal demographic studies requiring large sample sizes. Males and females share equally at incubating eggs and provisioning the semiprecocial young (Braun and Hunt 1983, Coulson and Wooller 1984). Typically, one adult is constantly present at the nest until the chicks are ~34 days old (Braun and Hunt 1983), although there is considerable variation between both individuals and pairs in guarding and brooding patterns (Coulson and Johnson 1993). If the food supply is poor, chicks may be left unattended at an earlier age while both parents forage at sea (Roberts and Hatch 1993). Kittiwakes lay up to three eggs (typically two), and raise a single brood per breeding season, although widespread reproductive failure, particularly at colonies in the North Pacific Ocean, is common (Hatch et al. 1993). Because nesting kittiwakes that lose their eggs late in the chick-rearing period do not lay again and typically continue to attend the colony during the chick-rearing period (perhaps to guard their nest sites), they offer unique opportunities to study behavioral and physiological effects of chick rearing.

Our study was conducted from 1991 to 1996 at the Shoup Bay kittiwake colony in Prince William Sound (PWS), Alaska, USA (61°09′ N, 146°35′ W) (see Appendix A; see also Plate 1). Of the 29 kittiwake colonies in PWS, Shoup Bay had the highest reproductive success from 1985 to 1997 (Suryan and Irons 2001), and increased in size from ~5900 to ~7800 nesting pairs during the course of our studies. These characteristics made it easier to follow individual birds over multiple seasons; previous work has shown that adult site fidelity among colonies is positively correlated with reproductive success (Danchin et al. 1998). Irons (1998) and Golet et al. (1998, 2000) further describe Shoup Bay and the other 28 kittiwake colonies in PWS (located 19–91 km from Shoup Bay).

Manipulative experiment

Our principle objective was to measure the demographic costs of normal reproductive effort. To this end, we removed entire clutches from randomly selected nests and contrasted subsequent patterns of survival and reproduction of adult birds from these nests and those that were not manipulated. The experiment was repeated in four consecutive years (1991–1994), with manipulated nests being selected anew each year. Some of the birds were included in the experiments in multiple years, but their assignment to treatment groups was always determined at random. We made certain that there were equal percentages of one- and two-egg clutches in the manipulated and unmanipulated groups. The same initial clutch size was imposed on both experimental groups because differences in clutch size may reflect phenotypic adjustments to parental body condition (Perrins and Moss 1975, Högstedt 1980), or general quality, i.e., ability (Thomas and Coulson 1988), and we wanted to ensure that the experimental groups were equal prior to the manipulation. On average, 38.6 ± 3.1% of the nests that we followed were manipulated each year. The manipulation was performed late in the incubation period, and no instances of relaying were observed. Respective sample sizes of manipulated and unmanipulated adults were 174 and 300 in 1991, 270 and 346 in 1992, 162 and 364 in 1993, and 254 and 336 in 1994. We tested for survival costs of reproductive effort during year *t* by comparing the survival of adults of manipulated vs. unmanipulated nests from year *t* to year $t + 1$ (hereafter referred to as year *t* survival). We tested for fecundity costs of year *t* reproduction by contrasting year $t + 1$ fecundity rates between adults from nests that were manipulated and unmanipulated during year *t*.

Resighting

All study animals were individually color-banded (see Appendix B; see also Plate 1). An intensive resighting effort of the marked kittiwakes was begun in early May of each year (1992–1996), the onset of the nest-building period, and continued for an average of 27 days. A less intensive resighting effort continued beyond this period, and lasted until the chicks began fledging in early August. We used binoculars to scan the cliffs of the colony for banded birds, and spotting scopes to identify color combinations when banded individuals were found. Although our resighting efforts were concentrated on the Shoup Bay colony, extensive searches (averaging 15 days per year) were also made during early June and early August of each year at the 28 other colonies in PWS (locations are mapped in Golet et al. 1998). During resighting efforts at the Shoup Bay colony, we marked nest locations on colony photographs. To minimize errors in resighting, we field-checked all observations against records of what birds had been recorded previously at each nest location. Sexes of marked birds were determined through observations of sex-specific behaviors, which included begging, courtship feeding, standing, and copulating (Baird 1994). In total, we determined the sex of 54% of the birds in the study. We did not use morphometrics to assign sex because behaviors have been shown to be more reliable for sex classification in this species (Jodice et al. 2000).

Capture–recapture modeling of survival and fecundity costs of reproduction

Two important costs of reproduction examined in this study were reductions in survival probability and the specific fecundity cost of reduced probability of breeding. Estimating probabilities of survival and breeding both require quantifying rates of return to the colony that control for an imperfect ability to detect (resight) every bird that is alive. Thus, we used capture–recapture methods (program MARK; White and Burnham 1999) that estimated not only survival and breeding probabilities but also resighting probabilities, the latter simply representing the probability that one resights a bird, given that it is alive and available to be seen. Capture–recapture methods for examining hypotheses regarding survival from resighing data have been described in detail by Lebreton et al. (1992) and are generally known as Cormack-Jolly-Seber (CJS) models. Here we used a multistate extension of the CJS models that allows for estimation of survival and resighting probabilites (as in CJS models), as well as probabilities of transitioning to an alternate reproductive state (e.g., becoming a nonbreeder after being a breeder), given that you are alive (Nichols et al. 1994, Nichols and Kendall 1995). A multistate modeling approach was appropriate because all birds in our study did not breed each year (Cam et al. 1998). We distinguished breeders from nonbreeders based on whether or not birds belonged to nests that produced eggs. Because our modeling approach yielded estimates of survival and breeding probability for nonbreeders as well as breeders, it allowed us to test for correlations in demographic components of fitness among subgroups of the population. Heterogeneity within populations is a topic of interest in the study of reproductive costs because it can lead to the masking of costs in natural populations (Partridge and Harvey 1985).

Many possible specific models can be constructed from capture–recapture data, with models differing from one another by the degree to which survival, breeding, or resighting probabilities are constrained to be equal across time (years) or among groups (manipulated breeders, nonmanipulated breeders, and nonbreeders). Inference is made by constructing a limited set of biologically sensible models and comparing the relative ability of each of these models to fit the available data (Burnham and Anderson 1998). We did two separate sets of capture–recapture analyses, one to identify factors influencing survival costs of reproduction and another to elucidate causes of fecundity costs. For each set of analyses, we developed our a priori set of candidate models where the only constraints on parameters where those imposed on the particular reproductive cost of interest. For instance, in modeling survival costs of reproduction, all candidate models contained no constraints on breeding or resighting probabilities among years or groups; thus, differences among models reflected only the hypothesized patterns of survival (e.g., a model with a treatment effect on survival vs. a model with no treatment effect). This modeling strategy minimized bias in parameter estimates (Burnham and Anderson 1992, Lebreton et al.

1992). The only modification to this strategy was that we had to constrain resighting probabilities to be equal between manipulated and nonmanipulated breeders and equal among years for these two groups. This modification was necessary to enable estimation of all parameters by program MARK, and such a resighting constraint seemed logical, based on the ready ease of resighting individuals that returned to the colony to breed (not so for nonbreeders).

For our evaluation of the survival costs of reproduction, we considered eight a priori models. In the most general (fewest constraints) model, survival varied among years and among all groups. Thus, this model contained a treatment effect (survival differed between manipulated and unmanipulated breeders), a time effect (survival varied among years), and a treatment × time interaction (the pattern of annual variation in survival differed between the treatment groups). We also considered models that included an annual measure of the study population's body condition as an explanatory variable for the pattern of survival. Because this was an annual measure for each treatment group, it was used in lieu of time (i.e., to answer the question of whether condition explains variation in survival over time). A model with only body condition as a factor, therefore, implied that any apparent survival difference between treatment groups was not a function of treatment or time, per se, but rather of a correlation of survival with body condition, allowing for differences in condition between treatment groups. The hypothesized pattern of survival represented by each of these eight a priori models is shown in Table 1A.

The first step in our analysis of these eight survival models was to examine the goodness of fit of the most general model, using a likelihood-based test (program MSSURVIV; Brownie et al. 1993). Lack of fit was not detected, so no adjustments to model selection or variance estimation were needed (Buckland et al. 1997). Our inferential statistic for comparing the relative ability of each model to explain the variation in the data was the Akaike Information Criterion (Akaike 1973), adjusted for sample size (AIC_c). The AIC_c balances the competing effects of bias and imprecision (Burnham and Anderson 1992). A model with more estimated parameters is generally less biased (it explains more variation in the data), but yields less precise estimates. The lowest AIC_c value among candidate models reflects the parsimonious model that has found the best balance between bias and imprecision. An additional inferential statistic (AIC_c weight) is useful for interpreting the magnitude of AIC_c differences among models. The model with the lowest AIC_c value always has the highest AIC_c weight, and the sum of AIC_c weights for a set of candidate models equals 1.0. If several competing models have similar AIC_c values, then AIC_c weights allow one to account for the uncertainty of which model is best by providing a means of computing weighted parameter estimates from all of the candidate models. Further, the relative importance of a given factor that appears in several models (e.g., treatment or condition) can be evaluated by summing the AIC_c weights for models including that factor (Burnham and Anderson 1998). If the sum of AIC_c weights for a factor approaches 1.0, then clearly that factor explains significant variation in survival. Following this analysis, we used the estimated survival rates to compute life expectancies as ($[2 - M]/2M$), assuming age-constant mortality, M (Lack 1954).

We conducted two other capture–recapture analyses regarding survival costs of reproduction. We contrasted the best model from the earlier analysis of eight models with three additional models representing the effects of food availability on survival, as represented by a yearly food index. The structure of the food effect in these models is similar to that of body condition in the previous analysis. For example, $S_{\mathrm{trt+food}}$ represents a model in which survival varies in relation to both treatment and food availability, whereas S_{food} represents a model in which survival varies only in relation to food availability. However, unlike the condition index, which was measured separately for manipulated and unmanipulated birds, food availability was presumed to be the same within a year for the two treatment groups.

We also examined whether sexes differed in their survival response to the treatment effect. This analysis was limited to the subset of birds for which sex was determined by behavioral observation (54%). Determination of sex occurred some time subsequent to marking; thus, we analyzed these birds as if they had been marked at the time when sex was determined. This analytical process excludes bias that would arise from undocumented sex-specific mortality occurring prior to determination of sex (Buckland 1982). We contrasted the best model from the initial analysis (S_{trt}) with two other models: $S_{\mathrm{trt+sex}}$, representing both a treatment and a sex effect on survival, and $S_{\mathrm{trt\times sex}}$, representing an interaction between sex and treatment, meaning that the survival response to the treatment effect was stronger for one sex than the other.

Our modeling approach for evaluating whether future breeding probability was affected by reproduction (raising chicks) was similar to that just described for survival. We began with exactly the same general model as shown in the first row of Table 1A. We then followed the same series of parameter constraints, except that we constrained breeding rather than survival probabilities to arrive at a set of eight candidate models. To clarify definitions of parameters, we note that there were three reproductive states in our multistate model: manipulated breeder, nonmanipulated breeder, and natural nonbreeder. For each time interval, it was possible to derive up to nine possible transition probabilities representing the probability that an individual in state a, b, or c at time t would be in state a, b, or c at time $t + 1$. We were only interested in three of these nine

TABLE 1. Models compared to evaluate effects of various parameters (treatment [trt], time, body condition [cond], sex, and food availability [food]) on adult survival (*S*) and nonbreeding (NB) probabilities. For all models, natural nonbreeders had time-varying survival and nonbreeding probabilities that were allowed to vary independently of the two treatment groups. Analyses were performed with program MARK.

Model	Hypothesized pattern of variation	$\Delta\mathrm{AIC}_c$	AIC_c weight	No. parameters†
A) Test of effects of time, treatment, and body condition on survival probability				
S_{trt}	Survival varies only in relation to treatment.	0.00‡	0.55	22
$S_{\mathrm{trt+cond}}$	Survival varies by treatment group and annually by body condition, with the same magnitude of body condition effect among treatment groups. Body condition is an annual mean measured for each treatment group.	2.04	0.20	23
S_{cond}	Survival varies among years only in relation to body condition.	2.87	0.13	22
$S_{\mathrm{trt}\times\mathrm{cond}}$	Survival varies by treatment group and body condition, with a different magnitude of body condition effect between treatment groups.	3.39	0.10	24
$S_{\mathrm{trt+time}}$	Survival varies between treatment groups and among years.	7.81	0.01	26
$S_{\mathrm{trt}\times\mathrm{time}}$	Survival varies between treatment groups, among years, and with a different yearly pattern of survival between treatment groups.	11.21	0.002	29
S	Survival does not vary.	12.58	0.001	21
S_{time}	Survival varies among years (but not by treatment).	20.47	<0.001	25
B) Test of effect of food availability on survival probability				
S_{trt}	Survival varies only in relation to treatment.	0.00‡	0.84	29
$S_{\mathrm{trt+food}}$	Survival varies between treatment groups and in relation to an annual index of food availability.	4.08	0.11	31
$S_{\mathrm{trt}\times\mathrm{food}}$	Survival varies in relation to food availability, and the magnitude of this variation differs between treatment groups.	5.76	0.05	32
S_{food}	Survival varies in relation to an annual index of food availability.	16.64	<0.001	30
C) Test of effect of sex on survival probability				
S_{trt}	Survival varies only in relation to treatment.	0.00§	0.56	32
$S_{\mathrm{trt+sex}}$	Survival varies relative to treatment and sex.	1.13	0.32	33
$S_{\mathrm{trt}\times\mathrm{sex}}$	Survival varies between sexes, and the magnitude of this variation differs between treatment groups.	3.18	0.11	34
D) Test of effects of time, treatment, and body condition on nonbreeding probability				
$\mathrm{NB}_{\mathrm{trt}\times\mathrm{time}}$	Nonbreeding varies between treatment groups, among years, and with a different yearly pattern of survival between treatment groups.	0.00‡	0.62	29
$\mathrm{NB}_{\mathrm{time}}$	Nonbreeding varies among years, but not between treatment groups.	1.93	0.23	26
$\mathrm{NB}_{\mathrm{trt+time}}$	Nonbreeding varies between treatment groups and among years.	2.83	0.15	27
$\mathrm{NB}_{\mathrm{trt}\times\mathrm{cond}}$	Nonbreeding varies by treatment group and annually in relation to body condition, with a different magnitude of body condition effect between treatment groups.	15.74	<0.001	27
$\mathrm{NB}_{\mathrm{trt+cond}}$	Nonbreeding varies by treatment group and body condition, with the same magnitude of body condition effect between treatment groups.	17.37	<0.001	26
$\mathrm{NB}_{\mathrm{cond}}$	Nonbreeding varies by year only in relation to body condition.	47.49	<0.001	25
NB	Nonbreeding does not vary.	48.55	<0.001	24
$\mathrm{NB}_{\mathrm{trt}}$	Nonbreeding varies only in relation to treatment.	50.47	<0.001	25
E) Test of effect of food availability on nonbreeding probability				
$\mathrm{NB}_{\mathrm{trt}\times\mathrm{time}}$	Nonbreeding varies among years, with a different yearly pattern for each treatment group.	0.00‡	1.00	29
$\mathrm{NB}_{\mathrm{food}}$	Nonbreeding varies in relation to an annual index of food availability.	33.13	0.00	25
$\mathrm{NB}_{\mathrm{trt+food}}$	Nonbreeding varies between treatment groups and in relation to food availability.	34.90	0.00	26
$\mathrm{NB}_{\mathrm{trt}\times\mathrm{food}}$	Nonbreeding varies in relation to food availability, and the magnitude of this variation differs between treatment groups.	35.99	0.00	27
F) Test of effect of sex on nonbreeding probability				
$\mathrm{NB}_{\mathrm{trt}\times\mathrm{time+sex}}$	Nonbreeding varies among years, with a different yearly pattern for each treatment group, and with a constant difference between sexes.	0.00‖	0.45	48

TABLE 1. Continued.

Model	Hypothesized pattern of variation	$\Delta\mathrm{AIC}_c$	AIC_c weight	No. parameters†
$\mathrm{NB}_{\mathrm{trt}\times\mathrm{time}}$	Nonbreeding varies among years, with a different yearly pattern for each treatment group.	0.93	0.28	47
$\mathrm{NB}_{\mathrm{trt}\times\mathrm{time}\times\mathrm{sex}}$	Nonbreeding varies among years and sexes, with a different pattern of variation between treatment groups.	0.99	0.27	49

† The number of unique parameters that are estimated from the model, given its specified structure.

‡ The AIC_c value of the best fitting model in this comparison is 5614.72.

§ The AIC_c value of the best fitting model in this comparison is 3002.05. The value differs from that presented for the same model in 1B because models in 1C are constructed only from those birds of known sex.

‖ The AIC_c value of the best fitting model in this comparison is 3010.38.

transitions: the probabilities that individuals in each of the three reproductive states at time t would be in a nonbreeding state at time $t + 1$. Testing of food and sex effects on breeding probabilities was similar to that described previously for survival probabilities.

We used individual birds as sample units when testing for survival costs (as did Røskaft 1985, Reid 1987, and Dijkstra et al. 1990) and the fecundity cost of nonbreeding. Some nests contained two marked birds, and thus survival and nonbreeding probabilities likely were not completely independent among some birds. However, we felt it justified to include both mates in these analyses because (1) these specific costs of reproduction are exacted upon individuals, not pairs per se, (2) we wanted to capture the full range of response to the manipulations, and (3) the statistical consequences of lack of independence, if significant, should be detectable by the goodness-of-fit test described previously and countered with a variance inflation factor (Burnham and Anderson 1998). No lack of fit was detected. We note that the percentage of nests that contained two marked birds was similar among manipulated (41%) and unmanipulated (37%) subsets of the study population.

Other fecundity costs

To determine if raising chicks affected subsequent reproductive success, we contrasted additional components of future fecundity between adults from nests that were manipulated and unmanipulated in the previous year. We used only one bird per nest in these analyses because the additional components were the same for both mates at each nest. We checked the nests of all marked adults that laid eggs at least once every four days (more frequently around the time of hatch and at fledging) to calculate lay date, clutch size, incubation period, hatching success (the percentage of eggs laid that hatched), fledging success (the percentage of chicks hatched that fledged), and nesting success (the percentage of nests that fledged at least one chick).

Body condition

Using methods described by Golet and Irons (1999), we measured adult body condition in the later third of the chick-rearing period for each of the four experimental years (1991–1994) and in 1995 (although no manipulation was performed in this year). Briefly, this involved (1) establishing an index of body size through a principle components analysis (PCA, SYSTAT 1997) of tarsus, head-plus-bill, and wing cord lengths of captured adults, (2) developing regression equations between the index of body size and body mass for the study population at large, and (3) applying measurements of our study animals to these equations and using residuals to generate individual body condition estimates. This method of estimating body condition is recommended over other techniques because it yields a metric that is independent of an individual's linear size (Piersma 1984, Jakob et al. 1996).

Corticosterone

We measured circulating levels of corticosterone (a stress hormone) to determine if these differed between adults raising chicks and adults that had their eggs removed. Samples were obtained from 11 adults raising chicks (seven with one chick, and four with two chicks) and 13 adults from manipulated nests. One mate was sampled at each nest. These birds were captured at their nests with a noose pole or a monofilament snare trap between 1330 and 2030 hours in the later third of the chick-rearing period (19–27 July) in 1994. Sex was known for all but one of the 24 adults (see Appendix C). We collected the blood samples in 70-μL heparinized microhematocrit tubes following a prick of the brachial vein with a 26-gauge (0.45-mm) needle. All samples were collected within 3 minutes of capture and are thus assumed to reflect baseline levels of corticosterone (Kitaysky et al. 1999). Within 2 hours of collection, the blood samples were centrifuged in microhematocrit tubes and the plasma was aspirated with a 50-μL Hamilton glass syringe. Plasma was injected into 500-μL cryotubes, immediately frozen at −20°C, and transported to the University of Washington for radioimmunoassay analyses. Steroid concentrations were measured after extraction in 4 mL dichloromethane. Recovery values (84 ± 0.8%, mean ± 1 SE) following extraction were used to adjust assayed concentrations of steroids. For further details on methods followed in the radioimmunoassays, see Wingfield and Farner (1975) and Wingfield et al. (1992). All birds that had their corticosterone measured were subjected to the rigorous resighting protocol previously described.

Nest attendance patterns

We contrasted nest attendance patterns between adults raising chicks and adults from manipulated nests late in the chick-rearing period (25 July–3 August), 1991–1994. We selected this period of the nesting cycle because it is when nestling demand and adult energy expenditure peak (Walsberg 1983, Bryant and Tatner 1988, Masman et al. 1988). Each year, we observed an average of 22.8 ± 3.7 adults from manipulated nests and 26.8 ± 2.6 adults from unmanipulated nests. All birds included in the surveys were individually marked, and both mates were included in the analyses where possible. Surveys were conducted continuously during daylight hours for an average of 40.8 ± 4.5 h (1619 nest-hours). Darkness prevented observations between midnight and 0500 hours. From data collected in each survey, we determined the durations of adult absences from the nest, durations of adult stays at the colony, and percentages of adult birds attending their nests. Overnight trips were not included in the analyses.

Foraging conditions

We interpreted behavioral and demographic data of this study in light of variation in food availability, information that is relatively uncommon in studies of widely foraging pelagic seabirds. The food availability index (1991–1994) was calculated from pre-fishery biomass estimates of Pacific herring (*Clupea pallasii*) in northeastern Prince William Sound, the main foraging area of kittiwakes from our study colony (Irons 1998). Kittiwakes at the Shoup colony appear to preferentially select 1-yr-old herring, and their percentage occurrence in the chick's diet is positively correlated with reproductive success (Suryan et al. 2000, 2002). Herring biomass estimates were derived from aerial flights conducted by the Division of Commercial Fisheries, Alaska Department of Fish and Game (ADF and G). We estimated the strength of the 1-yr-old herring cohort from 4-yr-old biomass estimates three years later. Biomass of 1-yr-old herring could not be estimated directly because herring do not recruit into the adult schools until they are 3–4 years old (E. Brown, *personal communication*). A year-class strength index was calculated for year t by multiplying the total herring biomass estimate in year $t + 3$ by the proportion of 4-yr-old fish in that year's run. Age class composition of adult herring was determined from samples of fish collected in nets (data provided by John Wilcock, ADF and G).

Foraging conditions were further assessed (indirectly) from chick growth rates, brood size at fledging, number of chicks fledged per pair, adult foraging trip durations, durations of colony stay by adults, and adult body condition. Food quality and abundance potentially influence all of these parameters. Growth rate was calculated as the slope of the regression of mass on age for chicks 6–22 days old, the linear phase of the growth cycle (Barrett and Runde 1980). Masses were determined by placing chicks in an open-ended cone suspended from a spring balance. We recognized alpha (the first to hatch or the larger chick in two-chick nests), beta (the second to hatch or smaller chick in two-chick nests), and single chicks in our growth rate calculations, and entered chick type as an independent random variable in multiway ANOVAs to test for differences in chick growth rates among years. We define brood size at fledging as the mean number of chicks present in those unmanipulated nests that still contained chicks at 27–30 days post-hatch (kittiwake chicks typically fledge 5–6 weeks after hatching). Fecundity, attendance, and body condition measures are as previously defined.

Statistics

We used multistate models to test for effects of reproduction on adult survival costs and nonbreeding probability (a fecundity cost). Additional components of fecundity were compared between manipulated and unmanipulated kittiwakes by constructing multiple logistic regression (logit) models to analyze binomial (e.g., fledging success) or multinomial (e.g., chicks per pair) categorical response variables (Agresti 1990). Statistical significance of individual parameters in the logistic regression models was evaluated by comparing fully saturated models with models lacking particular parameters (SYSTAT 1997). The deviance in the models was expressed as a G statistic, and significance was determined with the log-likelihood ratio test (SYSTAT 1996). Because life history theory makes a clear prediction regarding the directionality of fecundity costs, we present significance values derived from one-tailed tests, as did Smith et al. (1987), Dijkstra et al. (1990), ten Cate and Hilbers (1991), Jacobsen et al. (1995), and Young (1996) in their cost of reproduction studies. Lilliefor's test was used to assess normality for variables having continuous frequency distributions. Variables identified as nonparametric (foraging trip duration, duration of colony stay) were square-root transformed (all resulting distributions were normal) and then contrasted with multiway ANOVAs. Values are presented as means or proportions and standard errors. Corticosterone concentrations were compared between treatment groups with a Kruskal-Wallis one-way ANOVA.

RESULTS

Survival costs

Our findings provide clear evidence for survival costs of reproduction in Black-legged Kittiwakes. The best fitting model suggested that differences in survival were ascribed to the experimental treatment, egg re-

TABLE 2. Parameter estimates (mean ± 1 SE) computed by program MARK from weighted averages of models.

Group	Year *i*					Mean % difference
	1991	1992	1993	1994	1995	
A) Survival probabilities (the probability of a bird in year *i* surviving to year *i* + 1)						
Manipulated breeders	0.968 ± 0.008	0.968 ± 0.007	0.969 ± 0.006	0.969 ± 0.007	†	+4.0
Unmanipulated breeders	0.930 ± 0.009	0.930 ± 0.008	0.931 ± 0.007	0.934 ± 0.010	0.941 ± 0.027	
Natural nonbreeders	‡	0.670 ± 0.055	0.875 ± 0.028	0.837 ± 0.044	0.841 ± 0.059	−13.7
B) Transition probabilities (the probability of a bird in year *i* becoming a nonbreeder in year *i* + 1)						
Manipulated breeders	0.193 ± 0.028	0.251 ± 0.025	0.056 ± 0.027	0.0§	†	−12.5
Unmanipulated breeders	0.202 ± 0.024	0.251 ± 0.023	0.103 ± 0.019	0.0§	‖	
Natural nonbreeders	‡	0.540 ± 0.076	0.378 ± 0.052	0.988 ± 0.012	‖	+191¶
C) Resighting probabilities (the probability of a bird being resighted in year *i* + 1)						
Manipulated breeders	0.997 ± 0.001	0.997 ± 0.001	0.997 ± 0.001	0.997 ± 0.001	†	0.0
Unmanipulated breeders	0.997 ± 0.001	0.997 ± 0.001	0.997 ± 0.001	0.997 ± 0.001	0.945 ± 0.032	
Natural nonbreeders	0.740 ± 0.054	0.886 ± 0.026	0.844 ± 0.040	0.866 ± 0.042	0.945 ± 0.032	−16.3

Notes: Survival and resighting parameters were derived from models in Table 1A, and the probabilities of transitioning to nonbreeder status were derived from models in Table 1D. Mean percentage differences were calculated by computing the average of the percentages by which the manipulated breeders and the natural nonbreeders differed from adults at the unmanipulated nests.

† These values could not be estimated because there was no manipulation in 1995.

‡ Survival and transition probabilities for group C were not estimable for first year of the study (year *i* = 1991) because all birds were in either groups A or B at the start of the experiment.

§ Because there were no documented occurrences of this transition, program MARK estimates these probabilities as zero and does not associate any variance with them.

‖ This parameter could not be estimated because the breeding status of the birds that returned in 1996 was not determined.

¶ Calculated by averaging the percentage differences for 1992 and 1993 only. Calculating the percentage difference between natural nonbreeders and birds from unmanipulated nests could not be done in 1994 because this requires dividing by zero.

moval (Table 1A). The mean annual difference in survival between treatment groups was 0.037 ± 0.011 (Table 2), and the sum of $\mathrm{AIC_c}$ weights for models including a treatment effect was 0.87. We calculated the breeding life expectancy of individual kittiwakes based on modeled estimates of adult survival (Table 2), after noting that the general model fit the data adequately ($G^2 = 93.6$, df = 116, $P = 0.901$). Our calculations suggest that chick rearing may cause a 55% reduction in life expectancy, a value that closely matches an earlier estimate based on simple enumeration (Golet et al. 1998). Life expectancy estimates were calculated as 31.2 yr for adults from manipulated nests, 14.5 yr for adults from unmanipulated nests, and 4.6 yr for natural nonbreeders.

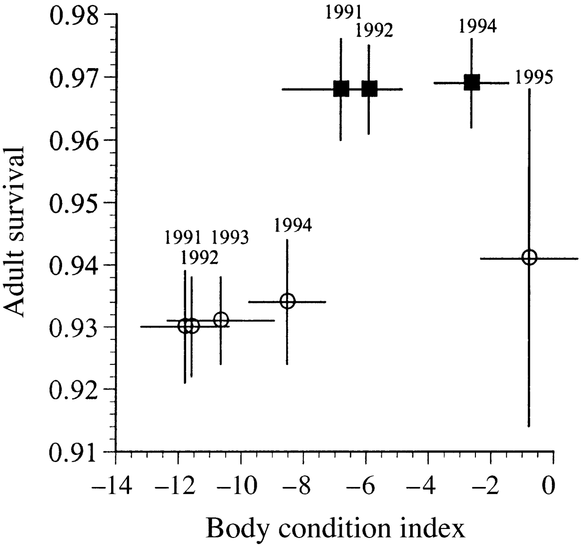

FIG. 1. Relationship between survival (mean ± 1 SE) and body condition (assessed late in the chick-rearing period) in adult Black-legged Kittiwakes at Shoup Bay, Prince William Sound, Alaska, 1991–1995. Individual points represent yearly mean values for birds from manipulated (solid squares) and unmanipulated (open circles) nests. Nests were selected for egg removal at random, and anew, each year.

Adult body condition appeared to have some influence on survival (sum of $\mathrm{AIC_c}$ weights for models with a condition effect = 0.43), although body condition alone was insufficient to explain the difference in survival between treatment groups. This is illustrated by treatment differences in the functional relationships between survival (generated from $\mathrm{AIC_c}$-weighted averages of the models presented in Table 1A) and body condition (values from Golet and Irons 1999); see Fig. 1. Although these functions have similar slopes, they have different intercepts, suggesting that raising chicks brings with it a survival cost above that resulting from reduced body condition. These results are robust to uncertainties due to model selection, because the plotted estimates were derived using weighted estimates of all models shown in Table 1A.

We found no direct evidence of an effect of food availability on survival (Table 1B), although food availability and body condition did vary in a consistent manner across years (Fig. 2). We found no sex-specific effect on the survival cost of chick rearing (model 3,

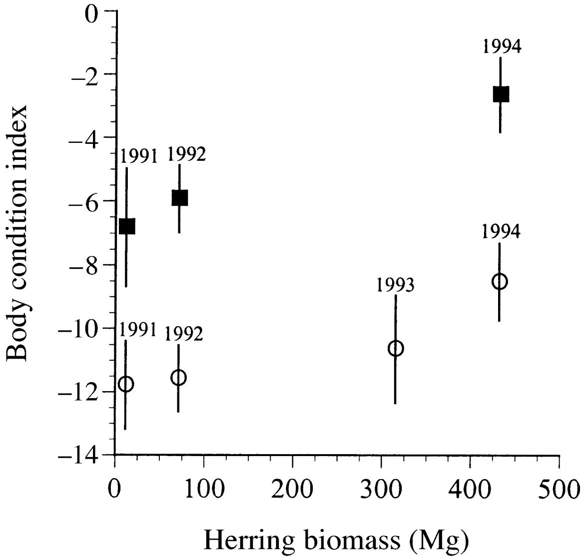

FIG. 2. Relationship between body condition (mean ± 1 SE, assessed late in the chick-rearing period) and herring biomass (a prey availability index) for adult Black-legged Kittiwakes from manipulated (solid squares) and unmanipulated (open circles) nests at Shoup Bay, Prince William Sound, Alaska, 1991–1994. No point is plotted for the manipulated group in 1993 because body condition data were not collected for this group in this year.

Table 1C), nor did we find any overall difference in survival rates between the sexes (model 2, Table 1C). Mean annual survival rates (across the four study years) of known-sex individuals were similar for males and females in the two treatment groups (unmanipulated males, 0.927 ± 0.011; unmanipulated females, 0.920 ± 0.013; manipulated males, 0.968 ± 0.009; manipulated females, 0.966 ± 0.010; estimates derived from AIC_c-weighted averages of the models are presented in Table 1C).

Adult survival was calculated based on capture histories of experimental birds ($n = 829$; see Supplement for complete histories) derived from 20 190 individual resightings. Experimental birds were resighted for a minimum of two and up to five years after each experiment. Surviving birds were observed an average of 8.7 times/year, and toward the end of each year's resighting period, very few observations of color-marked birds were first sightings (Fig. 3). These findings indicate that the number of surviving experimental birds present at the colony but missed by our observations was virtually nil. Furthermore, none of the marked birds that disappeared from the Shoup Bay colony were subsequently observed elsewhere in PWS during our larger scale surveys.

Fecundity costs

The best fitting model, treatment × time, demonstrates that raising chicks affected future breeding probability, but that the magnitude of this effect varied considerably among years (Table 1D). The highest fecundity cost of chick rearing was observed in 1994, when unmanipulated adults from 1993 transitioned to the nonbreeding state at significantly higher rates than did adults that had their eggs removed. The probability of birds transitioning from the breeding to nonbreeding state varied widely among years, with the lowest transition probabilities for both treatment groups occurring in the last two years. Variability in nonbreeding probability did not appear to be related to either condition (Table 1D) or food availability (Table 1E), nor was there any compelling evidence of a difference in this fecundity cost between the sexes (model 3, Table 1F). However, nonbreeding probabilities in both treatment groups were consistently higher for females than for males (Table 1F, Fig. 4).

When considering the reproductive performance of birds that did breed, no overall difference was observed, although birds from manipulated nests tended to have higher fledging success than birds from un-

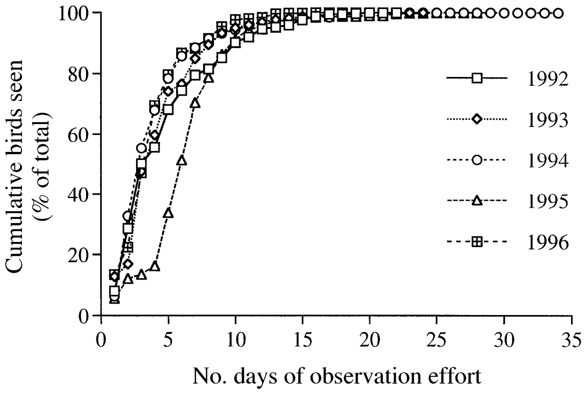

FIG. 3. Cumulative number of experimental adult kittiwakes resighted (expressed as a percentage of the yearly total) in relation to the number of days of observation effort. All birds were individually color-banded. Observations took place in May and June.

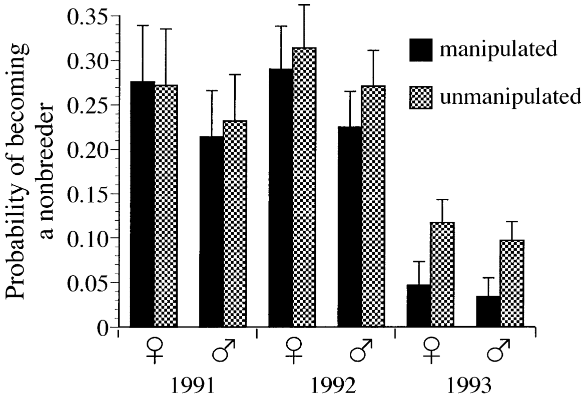

FIG. 4. Nonbreeding probabilities (mean + 1 SE, a fecundity cost of reproduction) of male and female adult kittiwakes from manipulated and unmanipulated nests at the Shoup Bay colony in the years following the manipulations.

TABLE 3. Fecundity parameter values (mean ± 1 SE, additional to those presented for nonbreeding probability in Table 2) for kittewakes from manipulated and unmanipulated nests at Shoup Bay, Alaska.

Breeder group	Year *i* 1991	1992	1993	1994	Mean % difference
Nesting success					
Manipulated	0.150 ± 0.03 (108)	0.39 ± 0.04 (153)	0.75 ± 0.05 (76)	0.64 ± 0.03 (196)	+16.6
Unmanipulated	0.096 ± 0.02 (178)	0.42 ± 0.04 (174)	0.63 ± 0.04 (156)	0.64 ± 0.03 (256)	
Fledging success					
Manipulated	0.60 ± 0.09 (20)	0.53 ± 0.04 (80)	0.73 ± 0.04 (66)	0.81 ± 0.03 (136)	+11.5
Unmanipulated	0.43 ± 0.08 (30)	0.58 ± 0.04 (102)	0.65 ± 0.03 (121)	0.79 ± 0.02 (184)	
Hatching success					
Manipulated	0.25 ± 0.05 (66)	0.65 ± 0.04 (111)	0.78 ± 0.04 (71)	0.64 ± 0.03 (190)	+1.2
Unmanipulated	0.24 ± 0.04 (101)	0.66 ± 0.04 (137)	0.72 ± 0.03 (147)	0.70 ± 0.03 (239)	
Clutch size					
Manipulated	1.8 ± 0.03 (132)	1.8 ± 0.03 (155)	1.9 ± 0.03 (127)	1.8 ± 0.03 (190)	+1.5
Unmanipulated	1.8 ± 0.03 (202)	1.7 ± 0.03 (201)	1.9 ± 0.02 (254)	1.7 ± 0.03 (240)	

Notes: Values were determined by tracking the reproductive performance of birds from each group in the year subsequent to the experiments; see *Methods*. Mean percentage difference was calculated by computing the 4-yr average of the percentages by which the manipulated nests differed from the unmanipulated nests. Sample sizes are provided in parentheses.

manipulated nests (Tables 3 and 4). Considering the four years separately, 1991 and 1993 stand out as the only years that led to fecundity costs. We observed a pronounced difference in nesting success between adults from manipulated and unmanipulated nests following the 1993 breeding season ($G = 3.17$, df = 1, $n = 232$ adults, $P = 0.037$; Table 3), resulting from the additive effects of significantly lower hatching success ($G = 5.8$, df = 2, $n = 218$, $P = 0.028$; Table 3) and a nonsignificant difference in fledging success ($G = 2.8$, df = 2, $n = 187$, $P = 0.12$; Table 3), a pattern similar to what was observed in 1991 (Table 3; Golet et al. 1998).

Corticosterone and chick rearing

Late in the chick-rearing period in 1994, baseline corticosterone levels were significantly higher among adults raising chicks than among adults that had their eggs removed (unmanipulated, 15.4 ± 3.2, $n = 11$ birds; manipulated, 9.2 ± 1.2, $n = 13$ birds; $U = 28.5$, $P = 0.013$; Fig. 5). Although the survival of adults from manipulated and unmanipulated nests differed significantly in 1994 (Table 2), this was not observed in the small subset of birds that had their corticosterone measured. In fact, corticosterone concentration did not appear to be related to survival, body condition, or sex (Appendix C), although the power to detect such effects was low, given the small sample size.

TABLE 4. Results of analyses testing for fecundity costs of chick rearing in kittiwakes at Shoup Bay, Prince William Sound, Alaska (1991–1994).

Parameter	*G*	*F*	df	*n*	*P*
Lay date		0.03	1	1498	0.42
Clutch size	1.36		1	1501	0.12
Incubation period		3.5	1	687	0.44
Hatching success	0.63		2	1062	0.49
Fledging success	4.1		2	739	0.064
Nesting success	1.41		1	1297	0.12

Notes: To derive test statistics for clutch size, hatching success, and fledging success, multiple logistic regression models of the following type were constructed: parameter = treatment (manipulated or unmanipulated) + year (1991–1994) + (treatment × year). The *G* statistic is a measure of deviance between the fully saturated model and the model lacking the treatment effect. Test statistics for lay date and incubation period were calculated from general linear model analyses. Significant year effects were detected for all parameters, although these are not reported here.

Nest attendance

Nest attendance patterns differed significantly between adults from manipulated nests and unmanipulated nests with chicks. Overall, the percentage of nests with attending adults was significantly greater in un-

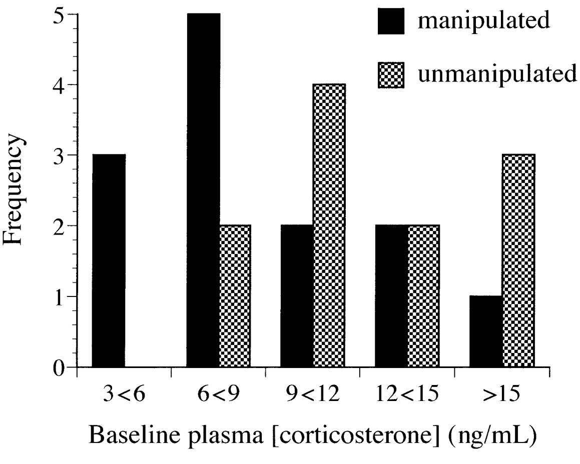

FIG. 5. Baseline plasma corticosterone concentrations of adult kittiwakes from manipulated and unmanipulated nests at the Shoup Bay colony, late in the chick-rearing period in 1994. All samples were taken within three minutes of capture.

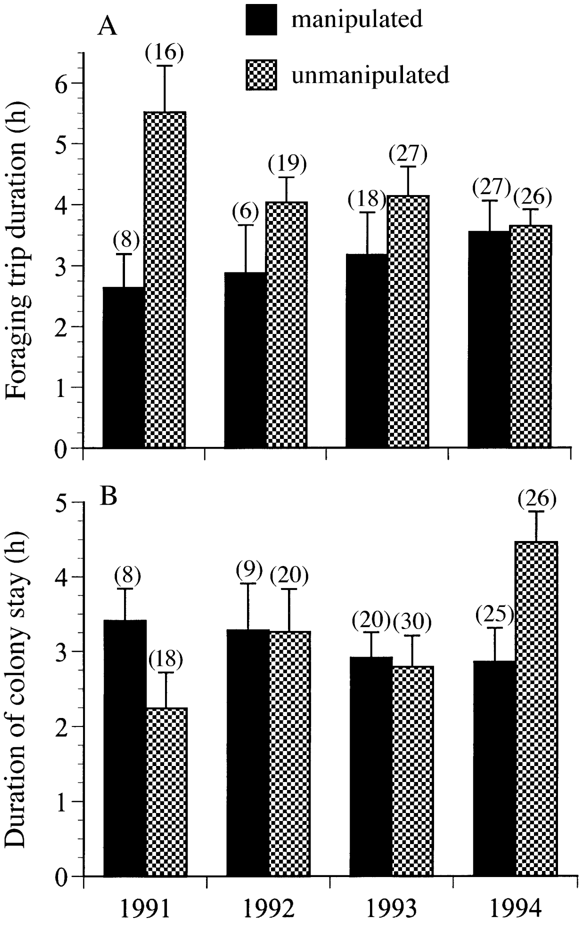

FIG. 6. Comparison of (A) foraging trip duration and (B) duration of colony stay of adult kittiwakes from manipulated and unmanipulated nests late in the chick-rearing period at Shoup Bay, Prince William Sound, Alaska, 1991–1994. All adults from unmanipulated nests had chick(s) during the survey. Data are presented as mean + 1 SE. Sample sizes are indicated in parentheses.

manipulated than manipulated nests (four-year means: unmanipulated, 98.4 ± 1.6%; manipulated, 78.3 ± 12.8%; $G = 21.2$, df = 1, $n = 225$, $P < 0.001$). Adults with chicks had significantly longer foraging trip durations (two-way ANOVA controlling for year, $F_{1,145} = 10.7$, $P = 0.001$; Fig. 6A), this difference being most pronounced during the early years of the study when foraging conditions were worst. The durations of colony stay observed also differed significantly between the two groups among years (significant year × treatment interaction), being longer for adults from unmanipulated nests with chicks in the later years of the study, when foraging conditions were better (two-way ANOVA, $F_{3,152} = 3.04$, $P = 0.031$; Fig. 6B).

Interannual variation in foraging conditions

Biomass estimates of Pacific herring increased steadily from 1991 to 1994 (Fig. 2), and similar improvements were observed in kittiwake reproductive performance. Chick growth rate (two-way ANOVA controlling for chick type [see Methods], $F_{3,217} = 14.4$, $P < 0.001$; Tukey multiple comparisons, 1991 < 1992, 1993, and 1994 [$P < 0.001$ for all]; Fig. 7A), brood size at fledging ($G = 38.8$, df = 3, $n = 568$, $P < 0.001$; Fig. 7B), and the fecundity parameters listed in Table 3 all differed significantly among years. The durations of colony stay by adults from unmanipulated nests also varied significantly among years (ANOVA $F_{3,92} = 5.7$, $P = 0.001$; Tukey multiple comparisons, 1991 < 1994 [$P = 0.002$], 1993 < 1994 [$P = 0.005$]; Fig. 6B), although there was no significant annual variation in the foraging trip durations of these same individuals (ANOVA $F_{3,84} = 1.8$, $P = 0.15$; Fig. 6A). In addition, adult kittiwake end-of-season body condition varied significantly among years (Fig. 2). The consistent pattern of covariation between food availability, body condition, nest attendance, and reproductive performance strongly suggests that foraging conditions consistently improved during the study.

DISCUSSION

Our findings provide clear evidence for survival and future fecundity costs of reproduction, and insight into

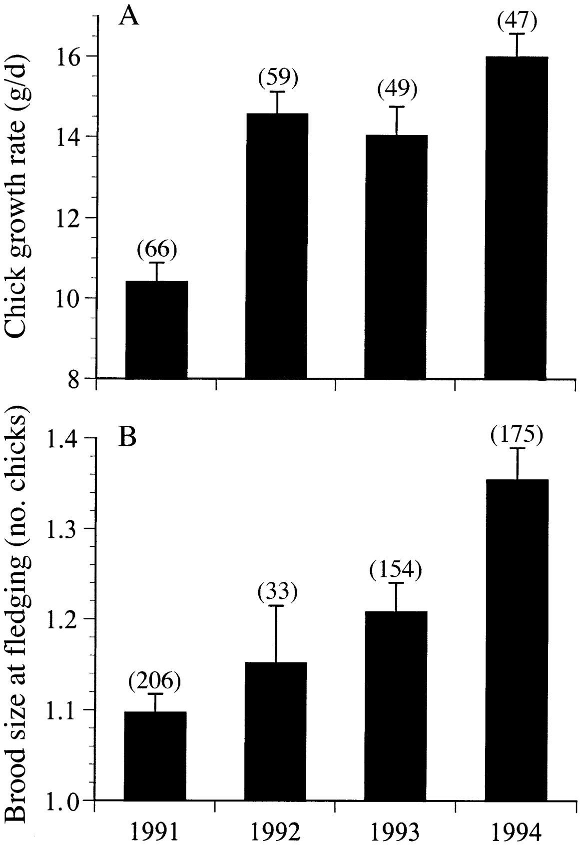

FIG. 7. Comparison of (A) chick growth rate and (B) brood size at fledging of kittiwakes at Shoup Bay, Prince William Sound, Alaska, 1991–1994. Sample sizes are indicated in parentheses.

their mechanisms of expression in Black-legged Kittiwakes. Although food availability differed greatly among years, the magnitude of survival costs observed was remarkably consistent. Fecundity costs, in contrast, varied widely, but not in a manner simply linked to either food availability or body condition. Our findings contribute to a growing body of evidence linking patterns of reproductive investment to foraging conditions, body condition, and individual ability. More generally, they confirm the importance of state-dependent processes (Caraco et al. 1980, Mangle and Clark 1988, McNamara and Houston 1992) in the evolution of life history strategies for long-lived species.

Survival costs

Our findings are particularly noteworthy because they demonstrate unequivocally that raising chicks compromises the future reproductive potential of adult birds while simultaneously revealing a positive phenotypic correlation between reproduction and survival in the unmanipulated segment of the study population. Numerous correlative studies have reported positive relationships between these components of fitness (Thomas and Coulson 1988, Mills 1989, Harris and Wanless 1995, Cam et al. 1998), raising uncertainty as to whether or not the state of nonbreeding presents a mechanism whereby residual reproductive value may be conserved. We combined manipulative experiments and multistate modeling to affirm that reproduction entails a cost (by demonstrating lower survival among birds raising chicks compared to birds that had their eggs removed), while simultaneously showing that some individuals are able to both succeed as parents and have a high likelihood of survival. Although the per-year reduction in survival that normally results from chick rearing appears to be small, it is clearly nontrivial (55%) when projected over the lifetime of an individual kittiwake. Our findings clearly demonstrate that it can be wrong to interpret positive phenotypic correlations between reproduction and survival as evidence that the allocation of resources to reproduction does not entail a cost. Instead, these results may just as well indicate that some individuals have greater abilities to acquire resources than others. Our study supports the idea that positive correlations between components of fitness may be expected in populations where differences in the ability of individuals to acquire resources are greater than differences among individuals in how those resources are allocated (Van Noordwijk and de Jong 1986, de Jong and Van Noordwijk 1992, Reznick et al. 2000).

Our findings are also relevant to demography and population analysis by suggesting that models of adult survival should consider not only an organism's reproductive state, but also the factors that dictate that state. Whereas breeding adults may often have higher survival than natural nonbreeders due to differences in individual ability (Thomas and Coulson 1988, Cam et al. 1998, Cam and Monnat 2000), their survival may be lower than that of adults that attempt to breed but are unsuccessful because of random events (e.g., the manipulation in the current study, or a flood as noted by Pugesek and Diem 1990), due to the incursion of reproduction costs.

A survival cost threshold

Long-lived birds are expected to allocate available resources to body maintenance rather than to reproduction when resources are limiting (Cody 1966, Lindén and Møller 1989). Sæther et al. (1993) extended this argument to suggest that long-lived birds should restrict their reproductive investment so that their breeding-season body condition does not drop below a threshold at which adult survival is reduced. Our study does not support the prediction of Sæther et al. because we found that chick rearing lowered body condition (Golet and Irons 1999), in turn apparently contributing to a reduction in survival. However, our findings do provide support for a recent model that suggests that long-lived birds breeding in stochastic environments seek an optimal balance between reproductive effort and survival based on varying costs and benefits of reproduction (Erikstad et al. 1998). This model suggests that, under poor breeding conditions, parents will invest less heavily in reproduction to avoid facing reduced survival. The kittiwakes in our study apparently did just that. Although adults attempted to buffer their chicks from adverse foraging conditions (e.g., they spent less time at the colony between foraging trips), ultimately the price of poor conditions was paid by the chicks (growth rates and reproductive success were lower) and not the adults (survival costs did not increase). Thus, although reproductive costs did not disappear when conditions improved, they also did not rise beyond a threshold when conditions were bad. Reproductive costs probably were expressed in all years of our study because breeding conditions were never good enough for adults to obtain sufficient resources to maximize their survival probability while simultaneously raising offspring. In fact, our studies were conducted in relatively poor years; reproductive success of kittiwakes at Shoup Bay was higher during the years preceding (1985–1990) and following (1995–2001) our experiments (see Suryan and Irons 2001: Fig. 5A).

Mechanisms of expression for survival costs

Body condition.—Our study provides some evidence in support of the hypothesis that body condition influences survival costs; adults raising chicks had both lower end-of-season body condition and reduced survival compared to adults that had their eggs removed. However, the relationship between these two parameters differed greatly among groups (Fig. 1), such that for a given level of condition, adults raising chicks had markedly lower survival than adults that had their eggs removed. Thus only a portion of the experimentally induced increase in survival can be accounted for by improved body condition. We hypothesize that multiple processes operating in parallel contributed to the reduced survival of adults raising chicks in our study. Just as aging (lifetime survivorship) is influenced by many different factors (Jazwinski 1996), there probably are multiple mechanisms contributing to the manifestation of survival costs of reproduction in kittiwakes (and other long-lived organisms). Below we discuss those mechanisms that our studies suggest may be important in this species. Other mechanisms (e.g., parasitism; Møller 1993, Norris et al. 1994) are not discussed because we did not collect data to assess their importance to kittiwakes.

Body composition.—Differences in body composition may cause survival costs to vary beyond what is explainable by our metric of body condition alone. Golet and Irons (1999) used TOBEC (Keim et al. 1988, Walsberg 1988) to predict lean mass content and found that adult kittiwakes raising chicks had a significantly lower percentage of body fat (by 28%) than adults that had their eggs removed. The difference was apparent at all levels of condition, thus suggesting that chick-rearing adults apportion their reserves differently than adults that must only meet their own needs. This finding makes intuitive sense, because birds raising chicks probably need stores of lean mass (i.e., protein) for muscle repair following periods of high exercise (Evans et al. 1992), as when foraging for chicks. Because fat has roughly twice the energy content of lean mass on a per gram basis (Schmidt-Nielsen 1990), it may make evolutionary sense for birds that are not foraging for chicks to store more of their reserves as fat and thus maximize their survival probabilities (Blem 1990). Differences in body composition may therefore compound differences in body condition, thus leading to an exacerbation of costs.

Energy turnover.—Increased rates of energy turnover also may have contributed to the lower survival of adults raising chicks. Previous studies on a variety of taxa (including insects, mammals, and birds) have demonstrated that high rates of energy turnover can negatively impact survival (Daan et al. 1996, Hurlbert and Else 2000, Rogina et al. 2000). The favored mechanistic explanation for this observation is that high levels of caloric intake, needed to fuel increased energy expenditure, lead to elevated production of free radicals, causing degradation of proteolytic enzymes, and ultimately cellular dysfunction and premature death (Harman 1968, Perez-Campo et al. 1998). These biochemical processes may contribute to elevated mortality in kittiwakes, because adults raising chicks had 21% higher rates of energy expenditure (assessed with the doubly labeled water method, Lifson and McClintock 1966, Nagy 1980) than did kittiwakes that had their eggs removed (Golet et al. 2000).

Higher energy expenditure among unmanipulated birds probably resulted from additional time spent foraging, because adults raising chick(s) had to capture twice as many prey, on average, as adults that were feeding only themselves (Golet et al. 2000). That foraging activities (especially plunge diving) are energetically expensive for Black-legged Kittiwakes was recently demonstrated by Jodice et al. (2003). Although chick-rearing adults also expressed lower body condition, there was no relationship between energy expenditure and body condition at the individual level, perhaps due to differences in foraging efficiency (Golet et al. 2000). The decoupling of energy expenditure and body condition at the individual level may, in part, explain why the full magnitude of survival costs was not captured by modeling condition alone; however, we were unable to specifically model effects of energy expenditure on survival because this parameter was assessed in only one year.

Although field metabolic rate may vary with local conditions, such as temperature, wind speed (Montevecchi et al. 1992), and food availability (Kitaysky et al. 2000, Jodice et al. 2002), there also must be ceilings to energy expenditure. This supposition is supported by a recent study of Great Tits (*Parus major*) in which energy expenditure of females rose, but then reached an asymptote with increasing latitude, suggesting a physiological constraint on energy budgets when activities were not limited by daylight (Sanz et al. 2000). Adult kittiwakes also appeared to reach a threshold of parental investment (perhaps a situation-dependent energetic ceiling) beyond which the costs of poor foraging conditions were passed on to the chicks. Whether this constraint was imposed by hormonal regulation or other mechanisms is presently unknown. In either case, however, field metabolic rates may serve as another mechanism enabling individuals to balance current and future reproduction.

Physiological stress.—Increased physiological or psychological stress, exhibited by elevated corticosterone concentrations, also may have contributed to the lower survival of adults raising chicks. A negative correlation between survival and baseline levels of corticosterone was recently demonstrated in Galapagos marine iguanas *Amblyrhynchus cristatus* (Romero and Wikelski 2001), and corticosterone is known to have profound deleterious effects (including immune suppression, muscle wasting, and neuronal cell death) when present over extended time periods (Sapolsky et al. 1986, Abraham et al. 2001). Gustafsson et al. (1994) suggested that adult birds investing heavily in reproduction might have increased susceptibility to disease due to suppression of the immune system, although they did not explicitly link corticosterone to the process.

Identifying the role played by corticosterone in the expression of reproductive costs is complicated by its known multiplicity of body functions (Sapolsky et al. 2000). For example, changes in circulating levels can facilitate foraging behavior, trigger irruptive migration, and mobilize stored energy to fuel increased locomotor activities (Astheimer et al. 1992). Further difficulties arise from the apparently paradoxical concentration-dependent actions of this hormone. For instance, corticosterone is involved in both the survival and death of neurons (Abraham et al. 2001), and although high circulating levels can suppress reproduction, field studies often reveal a positive relationship between corticosterone and reproductive activity (Wilson and Wingfield 1994).

Despite these challenges, recent studies suggest that corticosterone may play an important role in the expression of reproductive costs. Baseline corticosterone secretion in Black-legged Kittiwakes was found to increase during the breeding season coincident with a decline in body condition, with this increase being more pronounced at a food-stressed colony (Kitaysky et al. 1999). Corticosterone level is also negatively related to body condition in marine iguanas, but only below a condition threshold (Romero and Wikelski 2001). Detailed studies of Emperor Penguins (*Aptenodytes forsteri*) offer some of the most compelling evidence that corticosterone plays an important role in regulating how individual birds balance the costs and benefits of current reproduction (Patrice et al. 1998, Groscolas and Patrice 2001). The authors of these studies found that below a critical body mass threshold (but above the point at which all fat stores were depleted), circulating baseline levels of corticosterone increased, leading adult penguins to abandon their eggs and initiate refeeding, presumably to maximize their own chances of survival. When corticosterone concentrations were experimentally increased in adult kittiwakes during a year of high food availability, similar behavioral changes occurred as time spent foraging by the parents increased, thus leaving their chicks unattended at the colony (Kitaysky et al. 2001). Interestingly, this result seems consistent with our finding that unmanipulated birds displayed higher baseline levels of corticosterone and significantly longer foraging trip durations than adults that had their eggs removed. Collectively, these findings provide strong evidence that secretion of corticosterone influences the behavior of birds (Wingfield et al. 1997*a*, 1998), and moreover that it plays an important role in how organisms balance the costs and benefits of current reproduction (Silverin 1986, Wingfield and Silverin 1986, Zera and Harshman 2001), based on intrinsic physiological cues (Patrice et al. 1998, Groscolas and Patrice 2001).

Further study is needed to determine whether the levels to which corticosterone is naturally elevated during breeding are sufficient to reduce survival. However, empirical evidence for this idea was recently provided by Kitaysky et al. (2001), who contrasted survival between corticosterone-implanted and sham-implanted kittiwakes and found the former to be significantly lower. Interestingly, the concentration to which circulating levels of baseline corticosterone were elevated was similar to that observed naturally in food-stressed kittiwakes (Kitaysky et al. 1999), although it was slightly lower than the mean level observed for unmanipulated kittiwakes in our study.

Predation.—Adult Black-legged Kittiwakes raising chicks must capture more than twice as many fish as adults from manipulated nests to meet the added needs of their chicks (Golet et al. 2000). If these activities expose adults to increased mortality risks, through predation or injury (Lima and Dill 1990), then a reduction in survival, below that explained by decreased body condition, might be expected (Magnhagen 1991). This scenario predicts that survival costs would be exacted during the breeding season, yet a 34-year study of survival of Black-legged Kittiwakes at another colony reported virtually no mortality of breeding adults during the reproductive period (Aebischer and Coulson 1990). Mechanisms other than increased rates of predation are more consistent with the observation that survival costs of reproduction are manifested in the nonbreeding period.

Fecundity costs

Although fecundity costs may more often be expressed when intervals between successive reproductive attempts are short, as with species that have multiple broods in one season (Verhulst et al. 1997), our study and others (Røskaft 1985, Lessells 1986, Gustafsson and Sutherland 1988, Nur 1988, Young 1996) demonstrate that interannual fecundity costs sometimes occur. We found fecundity costs expressed strongly following one experimental year (1993), weakly in another (1991), and not at all in the remaining two. Yet in the years when fecundity costs were expressed, they were observed in multiple additive ways. That is, in years when adults from unmanipulated nests had higher probabilities of nonbreeding (Table 2), they also tended to have lower hatching and especially fledging success (Table 3), suggesting that the influence of the previous year's reproductive effort was felt throughout the subsequent breeding season.

The probability of nonbreeding appeared to be influenced more by year-to-year variation in some unspecified parameter(s) than by the experimental treatment. In other words, whereas the best-fit model suggests that there was a treatment effect on nonbreeding probability, there was an even larger effect caused by other factors. We cannot presently identify what these factors were because the parameters that we modeled (e.g., body condition, food availability) did not appear to exert a strong influence on nonbreeding probability. Other studies similarly found large variation in breeding proportions among years and attributed these differences to variability in current-year food abundance (Coulson 1984, Aebischer and Wanless 1992, Chastel et al. 1993). In general, strong interannual variation in reproductive success is a typical feature of long-lived seabirds (Murphy et al. 1991, Chastel et al. 1993).

In long-lived species that breed only once per year, fecundity costs may be less tightly linked to food availability or body condition than survival costs because there is a greater time span between the period of parental investment and when fecundity costs are expressed (the subsequent breeding season) than when survival costs are typically manifested (the winter immediately following; Daan et al. 1996). More time may provide a greater opportunity for adults to recover lost reserves and thus avoid costs. If, however, there are carry-over effects of reduced condition or other physiological impairments from the previous season, then impacts on future fecundity would be expected. This was demonstrated in Antarctic Petrels (*Thalassoica antartica*): adult body condition at the time of hatch was positively related to meal delivery rates and chick growth rates, two factors known to influence reproductive success (Lorentsen 1996). Foraging conditions in the subsequent spring may play a role in determining whether or not fecundity costs are expressed.

Interestingly, an effect of chick rearing on nonbreeding probability was observed only when both experimental groups had relatively low rates of becoming nonbreeders. Thus, we were only able to detect a treatment effect when environmental conditions were fairly benign. It could be that in 1993, when food and body condition were greater than in either of the previous two years, the negative effects of food or condition on future fecundity were sufficiently reduced to allow a treatment effect to stand out. Cam and Monnat (2000) drew a similar conclusion in noting that the effects of age on breeding probability (and survival) only occurred under benign conditions (at higher quality breeding habitats), where the effects of extrinsic factors were the weakest.

Comparisons of males and females

We detected no differences in survival costs of reproduction between the sexes. This differs from the findings of Jacobsen et al. (1995) for Black-legged Kittiwakes in Norway, where only females experienced costs. Because the Norwegian study had a relatively small sample size ($n = 82$ individuals partitioned into six treatment groups), however, additional investigations are needed to confirm the results (see also Boulinier et al. 1997). Alternatively, the reproductive tactics of kittiwakes might differ fundamentally between our study sites. More generally, we found no difference in survival between males and females. This agrees with analyses by Cam et al. (1998) of kittiwakes in Brittany, France, but differs from findings at North Shields, United Kingdom, where male survival was consistently lower than that of females over a 34-year period (Aebischer and Coulson 1990).

Although we detected no difference in fecundity costs between males and females, our results do suggest that females had higher probabilities of becoming nonbreeders than did males (Fig. 4). Cam and Monnat (2000) reported a similar finding for kittiwakes in Brittany. This phenomenon was also observed at North Shields, but only among young females (Coulson and Thomas 1985). One possible explanation for these observations is that females more often skip breeding in an attempt to recover reserves lost through egg production.

Identifying the forces that shape life histories

Life history theory seeks to identify those factors that most strongly influence observed patterns of reproductive investment. Current theoretical models of state-dependent reproductive strategies suggest that investment patterns should vary depending upon the condition of the individual and the predictability of the environment (McNamara and Houston 1996, Morris 1996). Based on the findings of our studies, we would add to this that patterns of reproductive investment are also shaped by past levels of reproductive effort. Moreover, our studies suggest that effort put into reproduction leads to a multitude of responses (including reductions in body condition, increased allocation of reserves to lean mass, elevated energy expenditure, and higher levels of baseline stress), all of which have the potential to affect not only patterns of future reproduction, but also patterns of future survival. Determining the relative importance of these responses, and finding ways to integrate them into predictive models, remains a central challenge in our efforts to better identify the forces that shape the evolution of the complex life histories observed among species.

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APPENDIX A

A color photograph of the main nesting area at the Shoup Bay Black-legged Kittiwake (*Rissa tridactyla*) colony at Prince William Sound, Alaska, is available in ESA’s Electronic Data Archive: *Ecological Archives* M074-009-A1.

APPENDIX B

A color photograph of an individually color-banded adult Black-legged Kittiwake (*Rissa tridactyla*), with nestlings, at the Shoup Bay colony, Prince William Sound, Alaska, is available in ESA’s Electronic Data Archive: *Ecological Archives* M074-009-A2.

APPENDIX C

A table comparing baseline levels of circulating corticosterone and other parameters (sex, mass, body size, body condition, etc.) for adult kittiwakes from manipulated nests (eggs removed) and unmanipulated nests (adults raising chicks) at Shoup Bay, Alaska, late in the 1994 chick-rearing period, is available in ESA’s Electronic Data Archive: *Ecological Archives* M074-009-A3.

SUPPLEMENT

Resighting histories for 829 individually color-banded Black-legged Kittiwakes observed from 1991 to 1996 at Shoup Bay, Alaska, are available in ESA’s Electronic Data Archive: *Ecological Archives* M074-009-S1.