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GREGORY H. GOLET*†, DAVID B. IRONS† and JAMES A. ESTES‡

**Department of Biology, University of California Santa Cruz, Santa Cruz, CA 95064, USA; †US Fish and Wildlife Service, 1011 E. Tudor Road, Anchorage, AK 99503, USA; and ‡USGS, Biological Resources Division, University of California Santa Cruz, Santa Cruz, CA 95064, USA*

Summary

1. We tested for costs of chick rearing in the black-legged kittiwake *Rissa tridactyla* (Linnaeus) by removing entire clutches from 149 of 405 randomly selected nests, in which one or both mates was colour-banded. After the manipulation, we monitored adult nest attendance and body condition at unmanipulated and manipulated nests, and measured the survival and fecundity of these adults the following year.

2. Late in the chick-rearing period, adults from unmanipulated nests (i.e. with chicks) went on significantly longer foraging trips, and were significantly lighter for their size, than adults from manipulated nests (i.e. without chicks).

3. Adults from unmanipulated nests also survived to the following nesting season at a significantly lower rate than those from the manipulated nests (0·898 vs. 0·953), suggesting that attempting to raise chicks can reduce life expectancy by 55%.

4. There was a tendency for adults from nests that were unmanipulated in year one to have lower reproductive success in year two, primarily because of reduced fledging success, and a higher incidence of non-breeding.

5. These findings suggest that mass loss in kittiwakes during chick rearing may not be adaptive. Raising chicks can lead to reproductive costs, and the causal mechanism appears to be a reduction in body condition.

6. We compare our results with previous brood (or clutch) size manipulation experiments that have measured adult body condition, survival and/or future fecundity. Although the empirical evidence suggests that long-lived species are more likely to experience survival costs than short-lived species, we believe the opposite may be true. We suggest that shifting the experimental protocol of cost of reproduction studies from brood enlargements (an approach taken in most prior studies) to brood reductions will provide more accurate quantifications of naturally occurring costs.

7. The cost of reproduction is one mechanism proposed to explain the reduced survival rates reported for kittiwake populations in the North Atlantic relative to those in the North Pacific ocean. Oceanographic data, however, suggest that lower food availability may limit survival of kittiwakes in the North Atlantic where a deeper mixed layer and reduced primary production combine to make conditions less favourable for this seabird during the winter months.

Key-words: body condition, clutch-size manipulation, cost of reproduction, life history trade-off, parental investment.

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Introduction

The cost of reproduction is a cornerstone of life history theory (Schaffer 1974; Stearns 1976; Partridge 1989). It predicts trade-offs between current and future reproductive success based on the premise that increased costs arise from increased reproductive effort (Williams 1966; Charnov & Krebs 1974). Despite the central importance of reproductive costs in life history theory, debate remains as to the role such costs play in the short-term maintenance of modern life history strategies (Nur 1990; Wheelwright, Leary, & Fitzgerald 1991; Pettifor 1993).

Reproductive costs may be manifested in one or both of two ways – through elevated mortality, hereafter termed survival costs, or through reduced reproductive success in subsequent breeding efforts, hereafter termed fecundity costs (Williams 1966; Stearns

1976). Although there are notable examples of both for birds, many brood manipulation studies have failed to document reproductive costs, and demonstrations of both survival costs and inter-year fecundity costs are especially rare (Table 1). Part of the challenge in assessing how widespread reproductive costs are stems from the difficulty in determining which studies have large enough sample sizes to conduct tests of sufficient statistical power. As Graves (1991, p. 967) pointed out 'many of the studies that have found no significant effect on adult mortality have sample sizes below that required to have even a reasonable probability of detecting a significant difference . . .'.

Studies of reproductive costs in birds have been of two general kinds – manipulative and correlative (see Lindén & Møller 1989; Partridge 1989; Dijkstra *et al.* 1990; Nur 1990; Lessels 1991, and Stearns 1992 for reviews). Long-term correlative studies of black-legged kittiwakes have revealed striking differences among individuals in lifetime reproductive success (Coulson & Thomas 1985). Some birds consistently rear more young, and live longer than others (Coulson & Porter 1985; Aebischer & Coulson 1990). These individual differences led Thomas & Coulson (1989; p. 261) to propose that 'high-quality birds are able to maintain a high annual reproductive output without apparently reducing their life span'. However, the high survival rate of successful breeders cannot be interpreted as evidence against a cost of reproduction because reproductive output and survival may covary with individual quality. For instance, higher quality adults may have a higher overall rate of energy acquisition, and ultimately this may determine whether the phenotypic correlation between the two traits is positive or negative (Stearns 1992). In addition to quality, age and experience also define reproductive ability (Coulson & White 1958; Pugesek 1981) and shape survival patterns. Through experimental manipulation, however, the effects of confounding factors such as age and experience can be lessened.

In this paper we report the results of a large manipulative experiment to determine the costs of chick-rearing in the black-legged kittiwake. Although numerous brood-manipulation experiments have been carried out to measure reproductive costs in birds, our study is noteworthy because we neither enlarged nor partially reduced brood size. Rather, we compared adults raising their normal broods with adults that had all of their eggs removed. This distinction is important. Previous manipulative experiments that have performed both additions and partial removals may not accurately quantify costs to the parents because compensatory mechanisms may exist whereby adults vary a fixed effort toward parental care on a per-offspring basis. Although such experiments document the existence of reproductive costs, they are most relevant to understanding why clutches other than the modal size are not more common, and thus may best be viewed as investigations into the evolution of clutch size. It is also of interest to measure the cost of raising the modal brood. This is the reproductive cost incurred by the majority of breeding birds and that which the benefits of reproduction are matched against in defining the life history strategy. In this paper, our principal focus is on demographic measures of costs although we also report several behavioural and physiological correlates. Our findings add to the understanding of the selective forces that shape the life history strategy of this long-lived seabird. This study provides clear evidence for a physiologically induced trade-off between longevity and current reproductive success (Bell 1980; Stearns 1992).

Methods

Kittiwakes are long-lived, monogamous seabirds. They are colonial cliff nesters that lay one- to three-egg clutches. Their semi-precocial young require a high degree of parental care and fledge after 5–6 weeks. Because adult kittiwakes have strong nest site and mate fidelity (Coulson & Thomas 1983), it is relatively easy to track their breeding performance and survival. They are therefore ideal subjects for longitudinal demographic studies requiring large sample sizes.

We studied kittiwakes at the Shoup Bay colony in Prince William Sound (PWS), (61°09′N, 146°35′W), a protected embayment in the northern Gulf of Alaska (Fig. 1). Approximately 40 000 black-legged kittiwakes breed at 28 colonies in PWS (Irons 1996). The Shoup Bay colony, which occurs on a small islet about 2 km from the seaward edge of a receding tidewater glacier, was the largest PWS kittiwake colony in 1991 (when our study began) with approximately 5900 breeding pairs.

Between May 11 and 29 1991, prior to egg laying, adult birds were captured using a rocket net. We weighed and marked birds with a unique combination of coloured leg bands, and measured tarsus, culmen, head-plus-bill, and wingcord lengths. In May and June of 1991, 1992 and 1993, marked birds were resighted, and courtship behaviour, mate associations and nest sites were recorded. Although both courtship behaviour and size measurements have been used for sex identification in adult kittiwakes (Coulson *et al.* 1983; Barrett *et al.* 1985; Hatch, Roberts & Fadley 1993; Hamer *et al.* 1993), we used only behaviour to determine sex because errors were found to be less common with this method. The nest location of each marked bird was mapped on colony photographs, and then monitored to determine laying dates and clutch sizes.

Late in the incubation period of 1991 entire clutches were removed from 37% of the nests that contained eggs ($n = 405$). Nest locations of experimental birds were distributed throughout the entire Shoup Bay colony to ensure representation of the colony at large.

Table 1. Results of brood (or clutch) size manipulations that have measured adult body condition, survival, and/or future fecundity. Negative and null effects, indicated by — and 0 respectively, are consequences of adults raising experimentally enlarged broods (unless otherwise noted)

Order/species	Body condition	Adult survival	Adult fecundity	Author(s)
Charadriiformes				
Swallow-tailed gull (*Creagrus furcatus*)	0	0		Harris (1970)
Glaucous-winged gull (*Larus glaucescens*)	—	—	0	Reid (1987)
Black-legged kittiwake (*Rissa tridactyla*)	—	—		Jacobsen *et al.* (1995)
Black-legged kittiwake (*Rissa tridactyla*)	—	—	0	This study†
Pelecaniformes				
South African gannet (*Sula capensis*)	0			Jarvis (1974)
Falconiformes				
European kestrel (*Falco tinnunculus*)	—	—	0	Dijkstra *et al.* (1990), Daan *et al.* (1996), Deerenberg *et al.* (1995)
European kestrel (*Falco tinnunculus*)	0	0	0	Korpimäki & Rita (1996)
Strigiformes				
Tengmalm's owl (*Aegolius funereus*)	0	0	0	Korpimäki (1988)
Anseriformes				
Canada geese (*Branta c. canadensis*)	—	0	—*	Lessels (1986)
Columbiiformes				
Ring dove (*Streptopelia risoria*)	—		—‡	ten Cate & Hilbers (1991)†, ten Cate *et al.* (1993)†
Apodiformes				
Common swift (*Apus apus*)	—			Martins & Wright (1993a, 1993b)
Pallid swift (*Apus pallidus*)	—			Cucco & Malacarne (1995)
Passeriformes				
Pied flycatcher (*Ficedula hypoleuca*)	—	—		Askenmo (1977, 1979)
Pied flycatcher (*Ficedula hypoleuca*)		0		Alatalo & Lundberg (1989)
Collared flycatcher (*Ficedula albicollis*)		0	—*	Gustafsson & Sutherland (1988), Gustafsson (1990)
Collared flycatcher (*Ficedula albicollis*)	0	0		Török & Toth (1990)
House wren (*Troglodytes aedon*)	0		0	Finke, Milinkovich & Thompson (1987)
House wren (*Troglodytes aedon*)			0	Robinson & Rotenberry (1991)
House wren (*Troglodytes aedon*)		0	—*‡	Young (1996)
Tree swallow (*Iridoprocne bicolor*)	0	0		De Steven (1980)
Tree swallow (*Tachycineta bicolor*)		0		Wiggins (1990)
Tree swallow (*Tachycineta bicolor*)		0	0	Wheelwright *et al.* (1991)
Swallow (*Hirundo rustica*)			—‡	Møller (1993)
Blue tit (*Parus caeruleus*)	—	—	—*	Nur (1984, 1988, 1990)
Blue tit (*Parus caeruleus*)		—	0	Pettifor (1993)
Great tit (*Parus major*)			—‡	Slagsvold (1984)
Great tit (*Parus major*)		0	0	Boyce & Perrins (1987), Pettifor *et al.* (1988)
Great tit (*Parus major*)	—		—†	Smith *et al.* (1987), Källander & Smith (1990)
Great tit (*Parus major*)	0	0	—‡	Tinbergen (1987), Tinbergen & Daan (1990)
Great tit (*Parus major*)	0		—‡	Lindén (1988)
Great tit (*Parus major*)			—‡	Verhulst & Hut (1996)†
Willow tit (*Parus montanus*)	0	0§	0	Orell & Koivula (1988, 1990), Orell *et al.* (1996)
Eastern phoebe (*Sayornis phoebe*)	0	0	—‡	Conrad & Robertson (1992)
Snow bunting (*Plectrophenax nivalis*)	—			Hussell (1972)
House sparrow (*Passer domesticus*)	0	0	—‡	Hegner & Wingfield (1987)
European starling (*Sturnus vulgaris*)			—‡	Stouffer (1991)
Rook (*Corvus frugilegus*)		0	—*	Røskaft (1985)
Total number of studies	24	24	26	
Number showing negative effect	11	7	16	(6*, 11‡)
Percentage showing negative effect	46%	29%	58%	(19%*, 42%‡)

* Interyear fecundity costs.

† Effects documented in these studies were demonstrated by comparing adults raising normal broods with adults that had their broods reduced or removed.

‡ Intrayear fecundity costs.

§ But see Orell *et al.* (1994).

The manipulation was performed at random with the exception that equal percentages of nests with original clutch sizes of one (26%) and two (84%) eggs were assigned to each treatment. We controlled for original

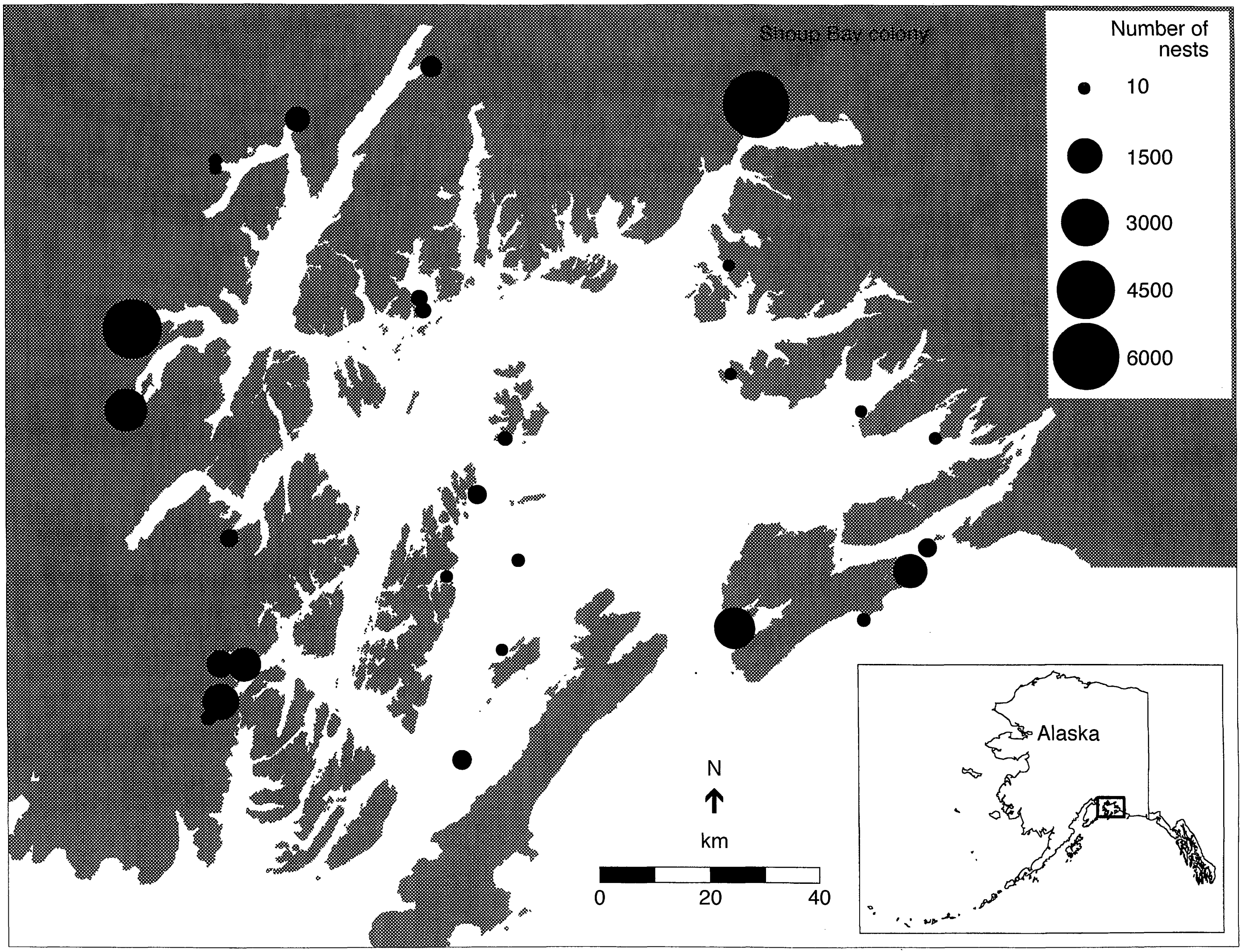

Fig. 1. Map of Prince William Sound (PWS), Alaska, with the location of the Shoup Bay and 27 other kittiwake colonies indicated by the filled circles. The size of the circles corresponds to the numbers of kittiwake nests at each of the colonies in 1991. Inset map of Alaska shows the location of PWS as an open square.

clutch size because differences in this parameter may reflect phenotypic adjustments to body condition (Perrins & Moss 1975; Högstedt 1980), and we wanted to ensure that our experimental groups were composed of adults of equal condition and ability. In fact, a *post hoc* comparison of experimental birds revealed that adults assigned to the two treatment groups had virtually identical 1991 lay dates, clutch sizes and pre-incubation body conditions, thus demonstrating that there was no bias prior to the experiment.

For analyses of reproductive costs one bird was randomly selected from each of the 69 nests that had both mates banded, and added to the pool of birds from the 336 nests that had only one mate banded. Thus, the sample unit used in most of our analyses was the nest. Other studies have used both mates in such analyses (Røskaft 1985; Reid 1987; Dijkstra *et al.* 1990), making the bird the sample unit, but we chose the more conservative alternative to prevent bias that might be caused by a correlation in survival rates between mates. To compare survival estimates from our study with those from other studies of kittiwakes that used the bird as the sample unit, a second set of survival estimates is also presented based on all of the marked birds.

Periodically throughout the 1991 breeding season the entire Shoup Bay colony was searched to determine if any marked adults relocated and bred elsewhere at the colony. Late in the 1991 breeding season, nest attendance and body condition were monitored to determine if behavioural and physiological differences existed between adults from the manipulated and unmanipulated nests. For these investigations, only adults with chicks were included in the unmanipulated group. We excluded adults that had suffered natural chick loss from the unmanipulated group because we were interested in studying the behavioural and physiological manifestations that arise when adult kittiwakes are actively engaged in provisioning their offspring. Attendance patterns of adults were determined at 41 nest sites (9 manipulated and 32 unmanipulated) observed through a spotting scope once every 15 min from 4:00 a.m., 25 July through to midnight, 26 July 1991 (37 h, 1640 nest-hours). Darkness prevented observations from 12:15 a.m. to 4:00 a.m. We compared the average lengths of foraging trips and colony visits of marked adults among unmanipulated nests with chicks and unmanipulated and manipulated nests without chicks. Because activity budgets may differ between day and night, overnight foraging trips were excluded from these analyses. A second survey was conducted the following week (1–5 August) to compare the proportion of adults attending nests with and without chicks. We did this by observing 125 nests (38 manipulated and 87 unmanipulated with chicks), once each day between 8:00 a.m. and 12:00 p.m. for banded birds.

To determine if adults that raised chicks were in a reduced state of body condition at the end of the breeding season relative to those from manipulated nests, 53 birds (15 manipulated, 38 unmanipulated with chicks) were captured with a noose pole or monofilament snare trap and weighed with a spring balance late in the chick-rearing period of 1991. Measured weights of individual birds were subtracted from values predicted from the least squares regression, $Y = 421{\cdot}05 + 21{\cdot}557X$ $(n = 463,\ r^2 = 0{\cdot}25,\ P < 0{\cdot}0001)$, and the differences, or residuals, were compared between treatments. In this regression equation, Y equals pre-incubation body mass (grams), measured during the spring banding period of 1991, and X is an index of body size derived from principle components analysis (PCA). With PCA we assigned weighting coefficients to standardized tarsus, culmen, head-plus-bill and wingcord measurements, which were then combined to form the index of body size, a PCA factor score (SAS 1989). The factor score was a better predictor of body mass than any of the measured variables considered separately. This protocol (Reid 1987; Hamer *et al.* 1993) prevented differences in body size from biasing comparisons of body mass between adults from unmanipulated and manipulated nests. Because we were concerned that disturbances associated with capturing and weighing adults for body condition assessment might cause abandonment, and therefore inaccuracy in our survival estimates, we examined the return rate of these birds. All but one of those adults (from a manipulated nest) returned to breed in 1992, and thus we included these individuals in the survival and fecundity cost analyses.

Because kittiwakes exhibit strong mate and nest site fidelity, the proportion of birds returning to their nest sites in subsequent years can be used to measure survival (Coulson & Wooller 1976; Aebischer & Coulson 1990; Hatch *et al.* 1993; Jacobsen, Erikstad & Sæther 1995). We employed simple enumeration to estimate survival because our resighting probabilities were sufficiently high to obviate the use of Jolly Seber or related models. Throughout the 1992 and 1993 breeding seasons, the entire Shoup Bay colony and 27 other black-legged kittiwake colonies (located 19–91 km from Shoup Bay) were searched for birds banded in 1991. We concentrated our resighting effort at Shoup Bay during May and early June, and spent 10 days in mid-June, and seven days in early August looking for banded birds at the other colonies. We assumed that adults not seen in either year had died, and those seen in 1993 but not 1992 had skipped the 1992 breeding season. All birds that were associated with nest sites were monitored throughout the breeding seasons, regardless of whether or not they produced a clutch. Three classes of skipping were recognized based on the phenological stage at which the adults abandoned their 1992 breeding effort – 'skipped attending' includes birds that were not seen at all in 1992; 'skipped nesting' applies to birds that returned to the colony but failed to build nests; and 'skipped laying' refers to birds that returned, built nests, but never produced eggs. In addition, we combined these three groups, hereafter termed 'skipped total', to provide a cumulative measure of skipping.

To see if there were differences in the abilities of individual kittiwakes to raise young, survive and return to the colony to reproduce in the subsequent year, we monitored all 1991 experimental nests at least once every fourth day from the egg-laying stage through the fledging period, and then compared survival and skipping rates between adults that were successful fledging their chicks and adults that failed to fledge their chicks.

To determine if fecundity costs were expressed in females at the egg stage, laying dates, the proportion of clutches containing two eggs and egg volumes were measured in 1992. Eggs were categorized as A, B (the larger and smaller, respectively, in two-egg nests) or S (singles), and egg volumes were compared [volume (ml) = length (mm) × breadth^2 (mm^2) × 4·866 × 10^{-4} (Thomas 1983)] for each category between the nests that were manipulated and unmanipulated in 1991. We also monitored hatching success (expressed as a percentage of the number of eggs laid) and fledging success (expressed as a percentage of the number of eggs hatched) as potential fecundity costs in 1992, comparing birds from the 1991 unmanipulated and manipulated nests for both measures. Two measures of cumulative fecundity costs were calculated: (i) the number of chicks fledged per nest (this combines 1992 hatching and fledging success), and (ii) the number of chicks fledged per pair. To calculate this second measure all living birds from the 1991 sample were included regardless of whether or not they built a nest in 1992. Chicks fledged per pair is a better measure of fecundity cost than chicks fledged per nest because it accounts for adults that skipped breeding in 1992. A more comprehensive assessment of fecundity costs could be made by measuring the recruitment of offspring into the breeding population, but because kittiwakes at the Shoup colony do not attempt to breed until age 4 on average (R. Suryan, unpublished data), and because natal dispersal may be significant, this parameter was not addressed in the present study.

THE EXPERIMENTAL YEAR

Reproductive costs were tested for following the 1991 breeding season, a year in which kittiwakes at the Shoup Bay colony were moderately successful raising and fledging chicks. The 1991 clutch size of experimental birds averaged 1·83 ± 0·019 eggs nest^{-1} ($n = 405$ nests), and the reproductive success of adults at unmanipulated nests averaged 0·883 ± 0·027 chicks nest^{-1} ($n = 256$ nests), although only 9·7% of the successful nests fledged two chicks.

STATISTICS

For contingency table analyses, log-linear models (LOGIN command, SYSTAT 1996), and log-likelihood ratio tests (*G*-tests) (Fienberg 1970; Bishop, Fienberg & Holland 1975) were used. For *G*-tests involving only two classes, the Williams correction was applied to reduce the likelihood of type 1 errors (Sokal & Rohlf 1995). To compare binomial proportions that had ⩾25% of the cells with expected frequencies of ⩽5, the conditional binomial exact test (CBET) was used (Rice 1988).

Lilliefors test was used to assess normality with variables having continuous frequency distributions. Variables identified as non-parametric were compared between treatment groups with the Mann–Whitney *U*-test, while the remainder were contrasted with ANOVAs or *t*-tests assuming equal or unequal variance as appropriate. Mean values are presented ± standard error, while proportions are reported ± standard deviation.

Because life history theory makes a clear prediction regarding the directionality of many of the results in this study, we often present significance values derived from one-tailed tests, as did Smith, Kallander & Nilsson (1987), Dijkstra *et al.* (1990), ten Cate & Hilbers (1991), Jacobsen *et al.* (1995) and Young (1996) in their cost of reproduction studies. All two-tailed tests are identified as such.

Results

ADULT SURVIVAL

Adults from unmanipulated nests survived at a significantly lower rate than adults that had their eggs removed (Table 2). The treatment effect was the only significant main effect documented in the survival analyses. Differences were not found in survival according to sex or clutch size. There were no significant interaction effects documented: the survival cost of females was not significantly different from that of males, nor was the survival cost for adults from one-egg nests significantly different than that of adults from two-egg nests. In addition the survival of adults from unmanipulated nests that were successful fledging chicks in 1991 was not significantly different from that of adults that failed to fledge their chicks (fledged: 89·9 ± 2·3%, $n = 179$; failed: 89·5 ± 3·5%, $n = 77$; $G = 0{\cdot}013$, $P = 0{\cdot}910$, two-tailed test).

For the last four days of the resighting period in 1992 (Fig. 2), and the last five days in 1993, none of the birds observed were first-time sightings, suggesting that virtually all of the colour-banded kittiwakes that returned to the colony were observed. For this reason, and because we found no evidence of emigration to neighbouring colonies, we believe that our survival estimates are accurate.

FECUNDITY MEASURES AND SKIPPING

Kittiwakes from unmanipulated nests in 1991 tended to fledge fewer chicks in 1992 than did those from manipulated nests (Fig. 3) (unmanipulated: 0·20 ± 0·043 chicks pair^{-1}, $n = 96$ pairs; manipulated: 0·34 ± 0·082 chicks pair^{-1}, $n = 56$ pairs; $U = 2971$, $P = 0{\cdot}068$). To distinguish which parts of the breeding cycle contributed most to this trend, we can consider the subset of fecundity measures that collectively determined the 1992 reproductive success of 1991 experimental birds. To successfully fledge chicks 1991 experimental birds had to return to breed in 1992, lay eggs, hatch their eggs and fledge their chicks.

Some 1991 experimental birds that did not return to breed in 1992 died, but others simply skipped breeding that year. For all three skipping categories a larger percentage of the adults from unmanipulated nests skipped breeding in 1992 than adults that had their eggs removed, but these differences were neither separately nor cumulatively significant (Fig. 4) ('skipped attending' unmanipulated: 5·65 ± 1·53%, $n = 230$; manipulated: 3·52 ± 1·6%, $n = 142$, $G = 0{\cdot}95$, $P = 0{\cdot}17$; 'skipped nesting' unmanipulated: 7·87 ± 1·8%, $n = 216$; manipulated: 7·30 ± 2·2%, $n = 137$, $G = 0{\cdot}20$, $P = 0{\cdot}42$; 'skipped laying' unmanipulated: 5·53 ± 1·6%, $n = 199$; manipulated: 3·94 ± 1·7%, $n = 127$, $G = 0{\cdot}66$, $P = 0{\cdot}26$; 'skipped total' unmanipulated: 17·83 ± 2·5%, $n = 230$; manipulated: 14·08 ± 2·9%, $n = 142$, $G = 0{\cdot}95$, $P = 0{\cdot}17$). Within the unmanipulated group, there were no significant differences between adults that were successful fledging chicks and those that failed to fledge chicks in the proportions of birds to 'skip laying' or 'skip nesting', however, significantly more of the adults from the failed nests 'skipped attending' in 1992 (failed: 11·76 ± 3·9%, $n = 68$; fledged: 3·11 ± 1·4%, $n = 161$, $G = 6{\cdot}01$, $P = 0{\cdot}014$, two-tailed test).

There were no differences during the 1992 breeding season between adults from nests that were unmanipulated and manipulated in 1991 in mean laying date

Table 2. Comparison of adult survival rates ± standard error for birds from unmanipulated (adults attempted to raise chicks) and manipulated (adults did not raise chicks) nests at Shoup Bay, Prince William Sound, Alaska 1991 to 1992

	Unmanipulated	Manipulated
All nests*	89.8 ± 1.9	95.3 ± 1.7
n	256	149
All birds†	90.7 ± 1.7	96.0 ± 1.5
n	300	174
Two-egg nests*	89.7 ± 2.3	96.8 ± 1.5
n	184	124
One-egg nests*	91.9 ± 4.6	88.0 ± 6.6
n	37	25
Males*	86.2 ± 4.6	96.9 ± 3.1
n	58	32
Females*	81.3 ± 7.0	100 ± 0·1
n	32	19

	G	*P* value
Treatment × status*	4.05	0.022
Treatment × status†	4.95	0.013
Treatment × sex × status*	1.18	0.28‡
Treatment × clutch size × status*	2.63	0.10‡
Sex × status*	0.42	0.52‡
Clutch size × status*	0.33	0.56‡

* Analysis conducted using nests as sample units, therefore only one bird per nest was included.

† Analysis conducted using birds as sample units, therefore all banded birds were used. There were 336 nests with one bird banded, and 69 nests with two banded birds.

‡ Two-tailed tests.

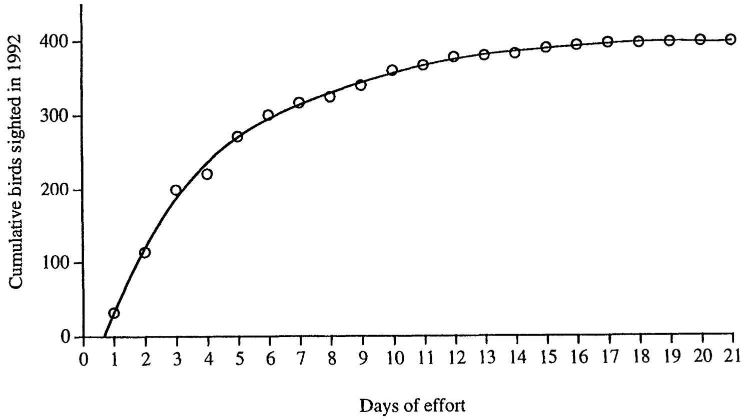

Fig. 2. Cumulative number of colour-banded black-legged kittiwakes resighted in relation to days of observation effort. Respective days of first and last observations were 19 May 1992, and 17 June 1992.

(unmanipulated: 6·85 ± 0·31 June, $n = 224$; manipulated: 7·15 ± 0·38 June, $n = 144$, $t_{367(1)} = 0{\cdot}53$, $P = 0{\cdot}30$), proportion of clutches containing two eggs (unmanipulated: 83·33 ± 0·031%, $n = 225$ manipulated: 82·67 ± 0·025, $n = 144$, $G = 0{\cdot}0008$, $P = 0{\cdot}49$), or average egg volume (class A – unmanipulated: 48·55 ± 0·44 cm^3, $n = 175$; manipulated: 48·17 ± 0·29 cm^3, $n = 55$; $t_{228(1)} = 0{\cdot}68$, $P = 0{\cdot}25$; class B – unmanipulated: 45·85 ± 0·53 cm^3, $n = 178$; manipulated: 45·68 ± 0·29 cm^3, $n = 54$, $t_{230(1)} = 0{\cdot}30$, $P = 0{\cdot}38$; class S – unmanipulated: 46·74 ± 0·90 cm^3, $n = 108$; manipulated: 46·30 ± 0·39 cm^3, $n = 20$, $t_{126(1)} = 0{\cdot}45$, $P = 0{\cdot}33$).

A non-significant difference in hatching success between the treatments (unmanipulated: 43·56 ± 5·0%, $n = 101$; manipulated: 49·25 ± 6·2%, $n = 67$, $G = 0{\cdot}23$, $P = 0{\cdot}24$) contributed to the overall fecundity cost, as did a trend in fledging success (unmanipulated nests: 43·18 ± 7·5%, $n = 44$; manipulated nests: 57·58 ± 8·7%, $n = 33$, $G = 0{\cdot}11$, $P = 0{\cdot}11$) (Fig. 5). The combined effect of these two measures was a trend in fewer chicks being fledged in 1992 from

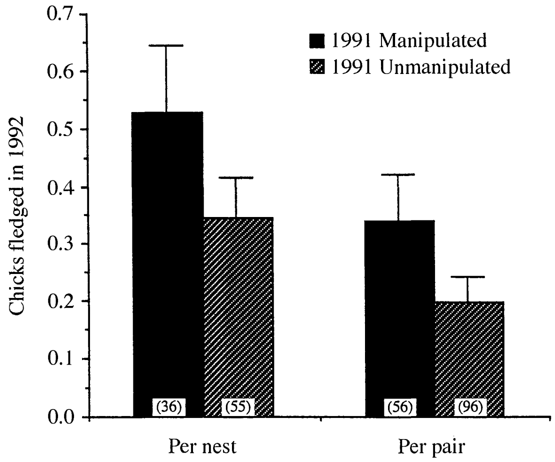

Fig. 3. Chicks fledged in 1992 by adults from 1991 manipulated and unmanipulated nests. Two cumulative measures of 1992 reproductive success are shown, the number of chicks fledged per nest, and the number of chicks fledged per pair. The latter measure accounts for living birds that skipped breeding in 1992 (Fig. 5). Sample sizes are indicated in parentheses.

unmanipulated nests compared to manipulated nests (unmanipulated nests: 0·35 ± 0·07 chicks nest^{-1}, n = 55 nests; manipulated nests: 0·53 ± 0·12 chicks nest^{-1}, n = 36 nests; U = 1125, P = 0·098)(Fig. 3).

ATTENDANCE PATTERNS

During the July 25–27 attendance survey, adults from unmanipulated nests with chicks went on significantly longer foraging trips than adults from manipulated nests (Table 3). However, neither the average length of colony visit nor the percentage of time spent on nests differed significantly between adults from unmanipulated and manipulated nests. There was a tendency for more adults from unmanipulated nests with chicks to be seen during the survey than adults from manipulated nests, although this difference was not statistically significant. A similar result was found during the second attendance survey, conducted on 1–5 August, in which more adults from unmanipulated nests tended to be seen (43·8 ± 8·9%, n = 32) than adults from manipulated nests (21·4 ± 7·9%, n = 28, G = 3·43, P = 0·064, two-tailed test).

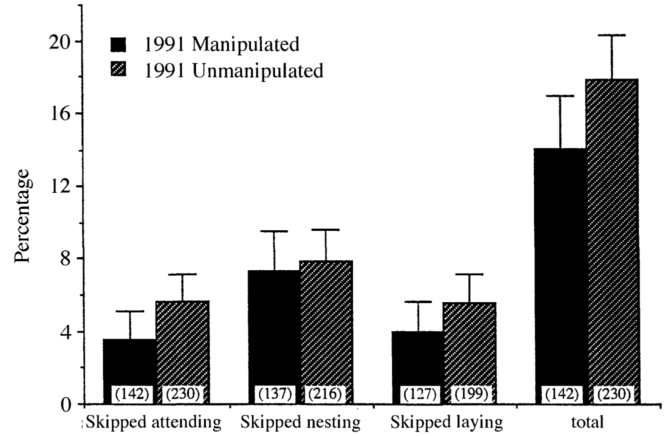

Fig. 4. Percentage of adults from 1991 manipulated and unmanipulated nests to skip breeding in 1992. Birds that 'skipped attending' did not return to the colony until 1993; 'skipped nesting' birds returned in 1992, but never established nest sites; 'skipped laying' birds returned, established nests, but never laid eggs. Sample sizes are indicated in parentheses.

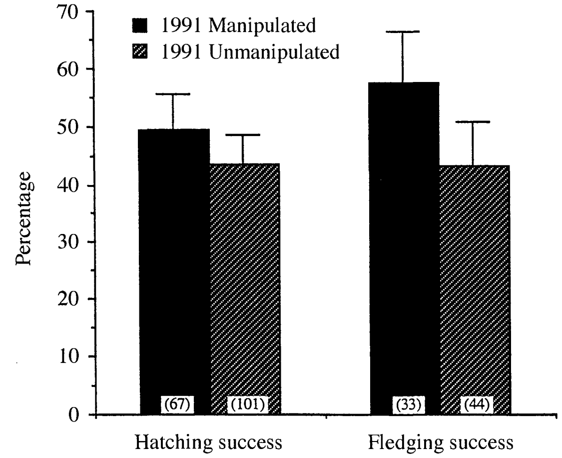

Fig. 5. Hatching and fledging success in 1992 of adults from 1991 manipulated and unmanipulated nests. Sample sizes are indicated in parentheses.

BODY CONDITION

Despite considerable variation in body mass among individuals, adults from unmanipulated nests with chicks were significantly lighter for their size (11·7 ± 1·3% lighter than predicted, n = 38) than adults from manipulated nests (7·1 ± 1·6% lighter than predicted, n = 15, $t_{51(1)}$ = 1·86, P = 0·025) nests. This result suggests that on average, adults from unmanipulated nests lost 39% more mass than adults from manipulated nests (Fig. 6). Mass loss appeared to be equivalent among all size classes, as indicated by the common slope of the regressions ($F_{(14,33)}$ = 0·00, P = 0·99) in Fig. 6. This equality indicates that small birds lost proportionately more mass than larger ones.

Table 3. Attendance patterns of adults from unmanipulated and manipulated nests late in the chick-rearing period 1991. All adults from unmanipulated nests had chicks during the survey. All tests are two-tailed

	Unmanipulated (w/chicks)	Manipulated (w/o chicks)	Test statistic	P value
Average trip length (h)	5.51	2.64	$U = 26.0$	0.020
n	16	8		
SE	0.77	0.55		
Average colony visit (h)	2.24	3.41	$U = 82.0$	0.58
n	18	8		
SE	0.48	0.43		
Percentage of time present	25.68	31.98	$U = 101.0$	0.60
n	18	10		
SE	5.03	8.22		
Percentage of time absent	74.32	68.74	$U = 80.0$	0.63
n	18	10		
SE	5.03	7.81		
Percentage of adults seen	100	80	*CBET*	0.099
n	18	10		
SD	<0·01	0.13		

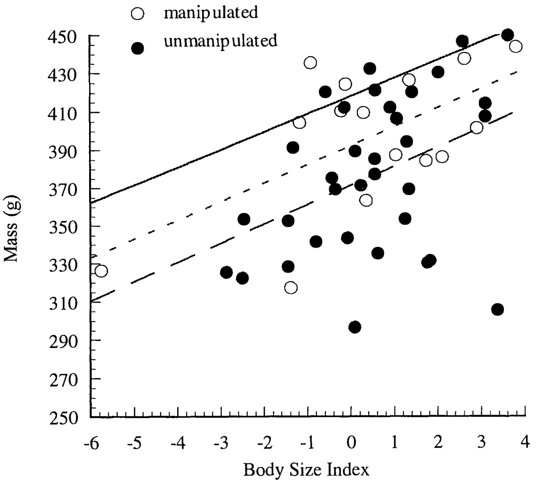

Fig. 6. Adult kittiwake body condition at manipulated and unmanipulated nests late in the chick rearing period. All adults from unmanipulated nests had chicks. Note that adults from unmanipulated nests (long-dashed regression, $n = 38$, $r^2 = 0.39$, $P < 0.001$) were significantly lighter than adults from manipulated nests (short-dashed regression, $n = 15$, $r^2 = 0.57$, $P = 0.001$). For clarity, the points that generated the preincubation level (solid regression line, $n = 463$, $r^2 = 0.25$, $P < 0.0001$) have been omitted.

Because male kittiwakes are generally larger than females, this finding suggests that females lost proportionally more mass than males.

ABANDONMENT AND RELOCATION

Kittiwakes that fail to fledge chicks may have lower nest site fidelity than those that are successful (Coulson 1966; Danchin & Monnat 1992). In our study, this effect could have been manifested if birds that had their eggs removed abandoned their original nests and either relocated within the colony or emigrated to another colony. Despite exhaustive searches throughout the chick-rearing period we found no evidence of adults from manipulated nests relocating and breeding elsewhere at the Shoup Bay colony. Furthermore there were no instances of manipulated birds relaying after their clutches were removed. Therefore we are virtually certain that adults from manipulated nests did not raise chicks in 1991. As well, we found no evidence of any adults (from either manipulated or unmanipulated nests) emigrating to other colonies to breed in 1992 or 1993. Moreover even if adults did emigrate because of the manipulation, and were falsely tabulated as dead, this could not explain the difference in survival that we found between manipulated and unmanipulated nests. This is because the observed return rate of adults from manipulated nests (the group that would be expected to have a higher emigration rate) was significantly higher than that of adults from unmanipulated nests. Thus it is unlikely that the return rates observed in this study represent differential dispersal patterns instead of differential survival rates, although this interpretation merits consideration in other cost of reproduction experiments with different experimental designs (see Boulinier *et al.* 1997).

Discussion

If reproduction did not incur a cost, all species would be expected to reproduce early and often, which they do not. A number of studies (Table 1) provide conclusive evidence for costs incurred by birds that are forced to raise experimentally enlarged clutches. However, it is less clear whether future reproductive success is significantly compromised by the effort required to raise clutches of normal or natural size. Such costs to reproductive success can be manifested in two general ways – reduced survival and/or reduced future fecundity (Williams 1966; Stearns 1976, 1992). Our study provides conclusive evidence for survival costs, and suggests that fecundity costs may also occur.

Pugesek & Diem (1990) found that California gulls *Larus californicus* (Lawrence), whose nests were flooded and eggs were lost during incubation, survived at a significantly higher rate than did adults from nests that were not flooded. Our experimental results demonstrate that raising natural-sized clutches reduces survival in another larid species. These findings are important because they run counter to the predictions that long-lived birds: (i) do not trade their own survival for that of their offspring (Linden & Møller 1989), and (ii) delay breeding until the risk of increased mortality has been eliminated (Weimerskirch 1992).

Although the per-year survival cost of chick-rearing seems small, the effect is substantial when projected over the lifetime of an individual black-legged kittiwake. If the annual probability of mortality (M) is assumed to be constant with age, life expectancy can be computed as $(2 - M)/2M$ (Gill 1990), and the difference in life expectancy between birds that rear chicks and those that do not is a measure of the lifetime survival cost of chick rearing. In our four years of manipulative experiments (the first of which is detailed in this paper), in which nests were randomly selected for egg removal anew each year, M averaged $0{\cdot}078 \pm 0{\cdot}0063$ for adults that attempted to raise chicks and $0{\cdot}036 \pm 0{\cdot}0058$ for those that did not. Therefore, life expectancy for birds that reproduce each year is 12·3 years whereas it is 27·3 years for those that never reproduce. Thus, chick rearing reduces longevity in black-legged kittiwakes at our study site by an estimated 55%. This calculation suggests that an individuals decision of whether or not to breed can greatly influence its life span. The ability of an individual to extend its life span by not breeding in poor food years may be highly adaptive for marine birds in the North Pacific ocean, where interannual foraging conditions are highly variable and can be poor for several years in succession (Murphy, Springer & Roseneau 1991; Springer 1991).

In general, studies of intermediate- to long-lived adults raising experimentally altered broods have more often demonstrated survival costs than have studies of short-lived species (Table 1). We caution, however, that the paucity of significant effects from studies of short-lived species should not be interpreted as evidence that such species do not incur survival costs associated with chick rearing. Life history theory predicts that because short-lived species have a relatively low chance of surviving to the next breeding season they should invest as much as possible in the current reproductive event (Charlesworth 1980; Kozlowski & Uchmanski 1987; Stearns 1992). Therefore short-lived species should be more likely than long-lived species to trade their own survival for that of their progeny (Lindén & Møller 1989). Why then have the majority of studies of passerines failed to document survival costs? Lindén & Møller (1989) and Nur (1990) pointed out several potential problems associated with previous studies that may in part explain the experimental record, but in addition, we suspect that the explanation in large measure results from the fact that the majority of these experiments involved brood enlargements. If short-lived species normally operate at or near their maximum reproductive rates, then brood enlargements may have little or no effect in altering reproductive effort. Brood reductions may alter reproductive investment more effectively, particularly in short-lived species.

Our study provides the first suggestion of fecundity costs in a seabird, expressed through the combined probabilities of building nests, laying eggs, incubating eggs and fledging nestlings. Although in isolation none of these probabilities differed significantly between manipulated and unmanipulated nests they all varied in the expected direction. These results are also noteworthy because although many studies have demonstrated intra-year fecundity costs, there are fewer records of inter-year effects (Table 1).

Contrary to the findings from many studies of passerines (Slagsvold 1984; Røskaft 1985; Hegner & Wingfield 1987; Smith *et al.* 1987, 1989; Lindén 1988; Pettifor, Perrins & McCleery 1988) and Canada geese *Branta canadensis* (Linnaeus) (Lessels 1986), our results provided no indication of fecundity costs at the egg-laying stage (i.e. there were no differences between unmanipulated and manipulated nests the following year in laying dates, clutch size or egg volume). Perhaps birds which raise multiple or large broods each year are more likely to incur fecundity costs at the egg-laying stage than species that raise only one small brood per year.

MECHANISMS OF EXPRESSING REPRODUCTIVE COSTS

Although the most important manifestations of reproductive costs on fitness are expressed in demographic terms (survival and future fecundity), the mechanisms by which these costs are incurred most likely involve behavioural and physiological processes. Comparisons of attendance patterns and weight loss for birds from manipulated and unmanipulated nests indicate that both behavioural and physiological adjustments took place in association with chick rearing.

Behavioural costs

Most adults from manipulated nests continued to attend the colony throughout the chick-rearing period, however, some did not. This implies both benefits and costs associated with this behaviour. By regularly attending the colony, adults without chicks may reinforce their pair bond, defend their nest site, and entrain long-distance foraging patterns, all of which may help them successfully fledge chicks in subsequent years. However, it is likely that these activities are energetically more costly than simply remaining on the foraging grounds, which may explain why some kittiwakes from manipulated nests were absent from the attendance surveys.

Activity budgets late in the chick-rearing period revealed that adults from unmanipulated nests with chicks spent more time foraging than adults from manipulated and unmanipulated nests without chicks (Table 3). Foraging trips of adults with chicks were significantly longer (109%, on average) than those of adults without chicks, but the length of colony stays did not differ significantly between these groups. Because kittiwakes expend more energy when foraging than when on the nest (Gabrielsen, Mehlum & Nagy 1987), these findings suggest increased energetic expenditure by kittiwakes raising chicks. Higher energetic expenditures may lead to greater mass loss in birds with chicks.

Physiological costs

If chick-rearing results in parental mass loss, and if the probability of survival to the next breeding season is related to body condition as individuals enter the fall and winter seasons (Norberg 1981), then the cost of reproduction may be physiologically manifested as an increased probability of death by a host of condition-related challenges that kittiwakes face after the breeding season (e.g. migration, resistance to disease, starvation and predation) (Pugesek 1987). Our findings support this interpretation. Kittiwakes from unmanipulated nests were in poorer body condition at the end of the breeding season and had lower survival rates to the beginning of the next breeding season than those from manipulated nests (Fig. 6). Similar results have been obtained for other bird species from brood manipulation experiments (Table 1). In 16 studies reporting both adult body condition and survival following brood enlargement, significantly more of the studies that demonstrated negative body condition documented a negative survival effect ($85 \cdot 71 \pm 14 \cdot 3\%$, $n = 7$) than did studies which found null effects on condition ($0 \cdot 0\%$, $n = 9$, $P = 0 \cdot 0004$, two-tailed CBET). These findings suggest that reproductive costs in birds are often expressed via a physiological mechanism in which the demands of reproduction cause a loss of body mass, thereby reducing survival.

Mass loss during the breeding season has been reported in many species of birds, and a proposed benefit of this phenomenon is reduced wing loading, which may increase foraging efficiency (Blem 1976; Freed 1981; Norberg 1981; Croll, Gaston & Nobel 1991; Gaston & Perrin 1993). However, our findings demonstrate that, for kittiwakes at least, the net result of this mass loss may be reduced survival.

DIFFERENCES IN INDIVIDUAL ABILITY WITHIN THE STUDY POPULATION

Comparing the survival and skipping rates of adults from unmanipulated nests that were successful fledging chicks in 1991 with those that were unsuccessful in their chick-rearing attempt demonstrates that there were differences in the ability levels of kittiwakes within the study population. Despite having their chicks for a shorter period of time, unsuccessful adults did not have higher survival, and in fact they 'skipped attending' at a significantly higher rate than adults that successfully fledged their chicks. Whether these unsuccessful birds failed to fledge their chicks because they were of lower quality (Thomas & Coulson 1989), or were simply younger and/or less experienced is unclear.

DEMOGRAPHIC VARIATION AMONG KITTIWAKE COLONIES

There is considerable life history variation among individuals at different black-legged kittiwake colonies. One striking example is a difference in demographic parameters between kittiwake populations in the North Pacific and North Atlantic oceans (Hatch *et al.* 1993; Hatch, Kondratyev & Kondratyev 1994). Black-legged kittiwake populations in the North Pacific ocean have had significantly higher survival rates (Table 4, $U = 0 \cdot 0$, $P = 0 \cdot 014$) and lower fecundities than those in the North-east Atlantic ocean. This difference could occur if kittiwakes in the North Pacific allocate fewer resources to reproduction and more to maintenance and growth. The survival costs of reproduction demonstrated in our study and by Jacobsen *et al.* (1995) make this mechanism plausible, especially when viewed in the context of ecological differences between the North Pacific and Atlantic oceans. Oceanographic data suggest that the reduced over-winter survival of kittiwakes in the North Atlantic may be a response to reduced food availability in that region. In winter, when the majority of kittiwake mortality occurs (e.g. >99% at North Shields; Aebischer & Coulson 1990) there are fundamental differences in the near-surface ecology of the two oceans. In the subarctic Pacific the mixed layer extends to only about 100 m while in the North Atlantic it reaches >200 m, the result being that productivity is substantially reduced in the North Atlantic (Parsons & Lalli 1988). The degree of mixing affects productivity by limiting photosynthetic radiation which is below the compensation light intensity for an estimated 5 months out of the year in the North Atlantic vs. 2 months in the North Pacific where large zooplankton stocks remain in the upper 150 m even during winter (Parsons & Lalli 1988). Kittiwakes are dependent upon prey (predominantly small schooling fish and large zooplankton) whose distribution and abundance may be greatly affected by physical processes such as

Table 4. Adult survival of black-legged kittiwakes at colonies in the North Pacific and North Atlantic oceans. Survival was studied from the year(s) listed to the year(s) subsequent

	Adult survival	Range of yearly sample size	Year(s)	Authors
Pacific colonies:				
Middleton Island, Alaska	92.6	178–298	1988–1991	Hatch *et al.* 1993
Talan Island, Sea of Okhotsk	92.0	254–313	1993–1994	S. A. Hatch, unpublished data
St. George Island, Alaska	93.0	15	1994	Dragoo & Dragoo 1996
Shoup Bay, Alaska	92.2*	474–616	1991–1994	This study; Golet, unpublished data
Pacific mean	92.5 ± 0.22			
Atlantic colonies:				
North Shields, England	80.1	?†	1954–1984	Aebischer & Coulson 1990
North Shields, England	79.0	133–173	1987–1992	Fairweather & Coulson 1995
Brittany, France	80.8	59–144	1980–1985	Danchin & Monnat 1992
Isle of May, Scotland	89.0	161–176	1986–1991	Harris & Calladine 1993
Hornøy, Norway	84.8	33	1990	Jacobsen *et al.* 1995
Atlantic mean‡	82.7 ± 1.8			

* Adults from unmanipulated nests only.

† Yearly sample sizes not reported. Survival estimations from 1954 through 1984 were based on data from 1102 adult kittiwakes.

‡ Calculation of Atlantic ocean mean incorporated a single value for the North Shields colony (79.9) derived by weighting the survival values reported above by the number of years they represent.

winter mixing. It is plausible therefore that the reduced survival of kittiwakes in the North Atlantic is a response to more harsh winter environments in that region. Favourable conditions during the breeding season may explain the relatively high productivity at North Atlantic colonies, or alternatively, given a reduced chance of breeding in subsequent seasons due to difficult winters, kittiwakes in this region may be investing more in current reproduction.

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