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Cost of reproduction and the evolution of deferred breeding in the western gull

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Survival patterns in a population of western gulls (*Larus occidentalis*) of known age of first breeding, α, indicate a cost of reproduction related to the age of initial breeding. Among both sexes, birds that commenced breeding at the earliest ages (3 years in males and 4 years in females) had higher annual mortality than those that deferred breeding one or more years. In addition, females (but not males) evidenced a cumulative cost of reproduction: holding age constant, females with more annual breeding attempts demonstrated poorer survival. These patterns of α-specific survival were statistically significant after controlling for interannual variation in food availability and are not explained simply by variation in the intrinsic quality of individuals. To assess the effects of these sex-specific costs on fitness, we combined the observed survival patterns with data on prebreeding survivorship and α-specific reproductive success to estimate rates of population growth and lifetime reproductive success for different ages at first reproduction. Males showed a clearly defined fitness optimum at α = 4 years, which coincided with the modal α for males in the population. Females showed no clear optimum, except that breeding at age 4 was suboptimal, hence females benefited from deferring breeding to ages 5–7 years. Observed age of first breeding also showed no clear mode for females, with slight peaks at ages 5 and 7. As a result, in both sexes, the fitness surface for α corresponded well with observed frequencies of α. We suggest that stabilizing selection has acted to shape the phenotypic distribution of α in males but, due to trade-offs between survival and early reproduction, stabilizing selection is weak or absent in females. *Key words:* age, breeding experience, cost of reproduction, deferred breeding, gulls, reproductive success, survivorship. *[Behav Ecol 8:140–147 (1997)]*

Life histories of long-lived organisms often are characterized by substantial intervals between physical maturity and the initiation of breeding (Cody, 1971; Clutton-Brock, 1988; Nelson, 1989; Wooller and Coulson, 1977). For example, Laysan albatrosses (*Diomedea immutabilis*) are full grown at 1 year but do not breed until they are 6–16 years of age (Fisher, 1975). Evolutionary theory, however, predicts that organisms should reproduce as early in life as possible, all else being equal (Charlesworth, 1980; Partridge and Harvey, 1988). Deferred breeding could be adaptive if the reproductive benefits of breeding early in life were outweighed by the costs of early breeding (Lack, 1968). Such costs, in theory, can be expressed as increased adult mortality and/or decreased future fecundity. Although compatible with a large body of theoretical work (Caswell, 1989a, b; Partridge, 1992; Partridge and Harvey, 1988; Reznick, 1992), Lack's hypothesis remains unconfirmed due to a paucity of long-term data and difficulties in measuring trade-offs between current and future reproduction (Bell and Koufopanou, 1986; Lessells, 1993; Nur, 1990; Partridge, 1989; Ricklefs, 1983; Viallefont et al., 1995).

As with many life-history traits, deferred breeding shows considerable intraspecific variation. Among western gulls (*Larus occidentalis*) breeding on Southeast Farallon Island, California, USA, for instance, age of first breeding (α) varies from 3 to 9 years in males (mean ± SD, 4.8 ± 1.17 years) and from 4 to 10 years in females (mean 6.0 ± 1.49 years) (Spear et al., 1995). Such variation in age of first breeding can either be adaptive in nature, reflecting the action of natural selection on α, or nonadaptive, reflecting, for example, the effects of ecological constraints, such as competition for food or limitations on mate and nest-site availability (Lack, 1968; Mills, 1989; Partridge and Harvey, 1988; Reid, 1987; Stearns, 1989; Wooler and Coulson, 1977). Furthermore, observed variation in α may reflect natural selection and ecological constraints acting simultaneously. If the distribution of α in a population is maintained by stabilizing selection (Partridge and Harvey, 1988; Roff, 1992; Stearns, 1992), then the optimal α, defined as the α maximizing fitness, should be most common, and suboptimal phenotypes should be correspondingly less common (Travis, 1989). On the other hand, the lack of a clear optimum in fitness with respect to α implies that selection is relatively neutral, and therefore is not acting to shape the observed phenotypic distribution of α.

Here we use data from a long-term study of western gulls to evaluate Lack's hypothesis that natural selection has shaped the observed distribution of α. First, we examine the evidence that individuals breeding early in life pay a mortality cost compared to those that defer breeding. Second, we ask whether the magnitude of that cost is sufficient to outweigh the benefits of breeding early in life. A similar approach has been applied to the evolution of clutch size (Hochachka, 1992; Nur, 1984), but has rarely been applied to the evolution of other life-history traits.

In the first section of this paper, we use a correlative approach to examine survival patterns of free-living gulls of known age at first breeding to determine whether early breeding reduces subsequent survival; an experimental manipulation of α among free-living individuals is not feasible in this population nor in nearly all other vertebrate species. In the second section of the paper, we integrate our results on survival with data on reproductive success (Pyle et al., 1991) to calculate fitness for different α classes using two common metrics: lifetime reproductive success and annual rate of population growth (or equivalently, the Malthusian parameter; Caswell, 1989a). Spear et al. (1995) found that observed values of α in male western gulls on Southeast Farallon Island showed a single mode at α = 4. Under the hypothesis that stabilizing selection accounts for the frequency distribution of α, we predict that fitness measures also will be maximal at α = 4. On the other hand, female western gulls showed a minimum of α = 4 and no clear mode, with the most commonly

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observed values of α being 5 and 7 (Spear et al., 1995). If natural selection has indeed shaped the distribution of α in females, we predict that the fitness of females deferring reproduction to age 5, 6, or 7 will be as great or greater than females that begin breeding at age 4. In addition, we evaluate the hypothesis that the lack of a clear mode among females, in contrast to males, reflects weak or absent stabilizing selection.

METHODS

The breeding population of western gulls on Southeast Farallon Island has remained fairly stable since the 1970s, numbering approximately 23,000 individuals (Ainley and Boekelheide, 1990; Ainley et al., 1994). As the result of an extensive chick-banding program begun by the Point Reyes Bird Observatory (PRBO) in 1971, approximately 12% of this population during the 1980s consisted of individuals of known age. Intensive study of the marked population has demonstrated that (1) this species is socially monogamous; (2) a skewed sex ratio of 1.33 females/male occurred among adults, reflecting sex-specific differences in survival among juveniles and subadults; (3) breeding birds are highly site tenacious, moving nest location at most 10 m between years; and (4) once having bred, nearly all known surviving individuals return every year to attempt reproduction (Pyle et al., 1991; Spear et al., 1987).

Our sample for analyses of survival and reproductive success consisted of 2102 breeding attempts during the 1985 through 1992 seasons by 898 marked gulls of known age, sex, and age at first breeding. Age at first breeding was determined by extensive reading of bands each year within a defined area; birds breeding in the core of this area (at least 10 m from area boundaries) that were not known to have bred during any previous year were assumed to be first-time breeders (see Pyle et al., 1991, for details). We define breeding experience as the number of previous annual breeding attempts, successful or not. In all cases the territories of first-time breeders were marked and thorough searches for returning individuals were conducted each subsequent year, until disappearance or through the 1992 season (see Spear et al., 1995, for details). Because of high site-fidelity in this population (Pyle et al., 1991) and an annual band-loss rate of <1% for bands used on gulls in our sample (Spear and Nur, 1994), we assumed that individuals not encountered during subsequent breeding seasons had died.

Ten gulls skipped 1 or more years (failed to initiate clutches) between breeding attempts, although all birds were present on or near their territories throughout the skipped seasons. Skipping is usually associated with loss of a mate (PRBO, unpublished data). As the costs associated with such skipped breeding attempts were indeterminate, we excluded all 15 breeding attempts (0.7% of our sample) by these 10 individuals subsequent to their skipping. Thus, within our sample,

$$\text{Years previous breeding experience} = \text{current age} - \alpha. \qquad (1)$$

We investigated the effects of α on survival in two ways. First, we examined the effect of α on survival while controlling for breeding experience (through multiple regression models and by stratifying on experience). If α affects subsequent survival of breeders, it should be apparent after the first breeding attempt, but effects of α on survival also may be manifest following subsequent breeding attempts. Second, we examined the effect of α on survival while controlling for age. Note that, as described in Equation 1, with age held constant, increasing breeding experience necessarily implies decreasing age of first breeding (see also Forslund and Pärt, 1995). As a result, statistical analyses of the effect of breeding experience on survival, while controlling for age, are equivalent to analyses of the effect of α on survival while controlling for age. The relationship of breeding experience to survival (holding age constant) not only provides insight about the importance of α, it also can provide evidence regarding long-term, cumulative effects of previous reproduction.

We restricted the data set to individuals 3–9 years of age who had previous breeding experience of 0–4 years because of inadequate samples of older, more experienced gulls. Furthermore, we restricted statistical analyses (but not data summaries) to the five most commonly observed ages of first breeding: males, α = 3–7 years (thus excluding 12 breeding attempts, or 0.9% of the male sample); females, α = 4–8 years (excluding 12 breeding attempts, or 1.6% of the female sample). We analyzed survival of males and females using multiple logistic regression (maximum likelihood method; Cox and Snell, 1989; cf. Sydeman et al., 1991a). Because of interannual variability in food supply that likely affects survival of Farallon seabirds (Ainley and Boekelheide, 1990, Sydeman et al., 1991b), we statistically controlled for "year effects" (i.e., main effects due to calendar year) while estimating the effects of α on survival and reproductive success. Mean values presented have been adjusted for year effects using least-squares adjusted means for regression analyses and an equivalent procedure for logistic regression analysis (described in Sydeman et al., 1991a). We examined linearity of functional relationships by testing for a significant quadratic coefficient in a polynomial logistic regression. We evaluated statistical significance in logistic regression using the likelihood ratio (LR) test, and present the likelihood ratio statistic as LRS_{df} (Cox and Snell, 1989; Lebreton et al., 1992).

RESULTS

Survival versus age at first breeding

In both sexes, survival of the youngest α groups (3 years in males, 4 years in females) was lower than that of older α groups (Table 1). Males of α-class 3 showed reduced survival after their first breeding attempt compared to individuals first breeding at all older ages combined (Table 1a; $LRS_1 = 6.26$, $p = .012$). As α increased from 3 to 6, survival after the first attempt increased, followed by a decrease beyond $\alpha = 6$. Thus, the relationship of survival to α was nonlinear (test of quadratic coefficient for α: $LRS_1 = 7.64$, $p = .006$). This increase in survival with α appeared to persist in males into their second breeding attempt as well (Table 1a; test for linear effect of α on survival, $LRS_1 = 4.43$, $p = .037$ for $\alpha = 3$–6). However, among third and fourth-time breeders, the results were not significant (Table 1; $p > .1$, LR tests).

In females (Table 1), survival of first-time breeders increased strongly and linearly throughout the range of α (test of linear α effect, $LRS_1 = 7.05$, $p = .008$; test of quadraticity, $p > .1$). Thus, mortality of 4 year olds breeding for the first time was almost threefold that of 7 year olds breeding for the first time (Table 1). In contrast to males, survival of females was not related to α among second-time breeders (Table 1; $p > .1$, LR test). Survival among third-time or fourth-time breeders was also unrelated to α (Table 1; $p > .1$, LR test). In both sexes, these patterns of survival with α did not reflect simply an increase in age per se: after controlling for α in a multiple logistic regression, survival was not significantly correlated with age in either sex ($p > .1$, LR test).

In the second method of analysis, examining the effect of α on survival while controlling for age (see Methods), we found evidence for a cost of reproduction in females but not in males. There was no significant effect of α on survival for any age class in males (LR tests, $p > .1$ for age classes 4–9) or

Table 1

Annual survival in relation to age and previous breeding experience in male and female western gulls

Years of experience	Age (years) 3	4	5	6	7	8	9	Total
Males								
0	0.67 (47)	0.81 (167)	0.83 (145)	0.84 (85)	0.71 (28)	0.70 (7)	0.99 (1)	0.802 (480)
1	—	0.71 (31)	0.80 (139)	0.82 (115)	0.88 (63)	0.72 (18)	0.52 (4)	0.808 (370)
2	—	—	0.70 (26)	0.86 (109)	0.83 (82)	0.87 (52)	0.62 (10)	0.828 (279)
3	—	—	—	0.88 (18)	0.81 (75)	0.86 (26)	0.83 (27)	0.840 (146)
4	—	—	—	—	0.59 (10)	0.79 (26)	0.99 (17)	0.819 (53)
Total	0.669 (47)	0.797 (198)	0.808 (310)	0.843 (327)	0.828 (258)	0.820 (129)	0.781 (59)	0.814 (1328)
Females								
0	—	0.67 (65)	0.79 (74)	0.76 (79)	0.87 (57)	0.96 (25)	0.92 (12)	0.789 (312)
1	—	—	0.80 (43)	0.79 (57)	0.87 (54)	0.81 (44)	0.94 (12)	0.825 (210)
2	—	—	—	0.72 (34)	0.81 (40)	0.79 (46)	0.85 (27)	0.793 (147)
3	—	—	—	—	0.68 (22)	0.80 (26)	0.72 (16)	0.740 (64)
4	—	—	—	—	—	0.54 (13)	0.98 (10)	0.743 (23)
Total	—	0.669 (65)	0.790 (117)	0.760 (170)	0.833 (173)	0.821 (154)	0.838 (77)	0.794 (756)

Values are the proportion of the sample that survived to return the following year. Values are statistically adjusted for interannual variation (see text), thus explaining fractional numbers of surviving individuals. Sample sizes are in parentheses. Note that, in the absence of birds that skipped years of breeding (see text), age at first breeding classes are represented by successive diagonals, down and to the right. However, this was not strictly a longitudinal study; i.e., each cell was derived from an independent sample combining longitudinal and cross-sectional data.

for all age classes combined using a multiple logistic regression analysis (where age was controlled as a categorical variable; Table 2). In contrast, with age held constant, female survival decreased with increasing years of experience and hence decreased α (Table 1). This pattern was most pronounced for 8-year-old females: survival of those breeding for the fifth time (i.e., α = 4) was reduced by 44% compared to those breeding for the first time (α = 8), with intermediate survival values for those breeding for the second through fourth times (Table 1; test of linear effect of α, $LRS_1 = 10.49$, $p = .001$). We confirmed this relationship by analyzing the effect of α for all females, controlling for age (Table 2; $p = .005$, LR test). This overall relationship of decreasing survival with increased number of breeding attempts was not due simply to low survival of 8 year-old females breeding for the fifth time (see above); the relationship was still significant when excluding this experience group ($p < .05$, LR test).

In summary, both sexes showed diminished survival for earliest ages of α: for males the difference was between α = 3 and all greater α combined; for females, survival continuously increased across the whole range of α. Even at ages 7 and 8, females who started breeding early in life had lower survival than those who deferred breeding.

Estimating fitness in relation to α

The above results imply a benefit to deferred breeding among younger western gulls. To address whether this benefit outweighed the cost of not rearing offspring at an early age, we next evaluated α in relation to two measures of fitness. First, we calculated cumulative reproductive success (CRS) after each year of life for the four most common α classes of each sex. Specifically,

$$\text{CRS to age } w = \sum_{x=t}^{x=w} l_x m_x ,$$

where $t = 3$ (males) or $t = 4$ (females), l_x = survivorship from age t to age x, and m_x = reproductive success (chicks fledged) at age x. When w = maximum age, CRS is equal to lifetime fledgling production (LFP). To determine CRS, we collated data on l_x and m_x in relation to α from this population.

Prebreeding survivorship for ages 3–7 years could not be determined from direct observation. Instead, we used two approaches based on values for gulls aged 0–3 years, obtained by Spear et al. (1987) and Spear and Nur (1994). For both males and females, annual survival increased substantially and nonlinearly as age increased from 0 to 3 years (Table 3). In the first approach, we used these data to extrapolate to ages 3 to 7, inferring that prebreeding annual survival continued to increase beyond the third year, by 1.6% to 0.3% per year, in a decelerating fashion (statistical details in Table 3). In the second approach, we assumed that prebreeding annual survival of gulls aged 3–7 remained constant at the values attained by 3-year-old males and females (0.82 and 0.89, respectively; Table 3). The second approach provides a minimum value for prebreeder survival, and the extrapolated values provide a reasonable upper bound. In the results presented below, we use both sets of prebreeder survival values to provide upper and lower bounds for expected LFP and λ. Note that

Table 2

Multiple logistic regression analyses of effect of α on male and female survival in western gulls

Effect of	Deviance explained	df	p
Males (ages 4–9, 3–7)[a]			
α (= effect of breeding experience)	0.11	1	>.7
Year	33.64	6	.0001
Age	2.01	5	>.7
Females (ages 5–9, α 4–8)[b]			
α (= effect of breeding experience)	7.76	1	.005
Year	16.53	6	.011
Age	2.92	4	>.5

Three-year-old males and 4-year-old females were excluded from the analysis because α does not vary within either age class (e.g., all 3-year-old males began breeding at age 3). Deviance explained likelihood ratio statistic (LRS) compares the full model (with the term in question) and reduced model (without the identified term but with all other listed terms). The deviances explained do not add up to the total deviance due to correlation among terms.

[a] For males, overall model is $LRS_{12} = 35.45$, $p = .0004$, $n = 1272$.

[b] For females, overall model is $LRS_{11} = 28.04$, $p = .0032$, $n = 679$.

prebreeding survivorship depended on sex and age but was assumed to be independent of future α.

Reproductive success was estimated as mean number of chicks fledged (see Sydeman et al., 1991b, for methods) in relation to age and previous breeding experience (hence, α), adjusted for effects of year, among a subsample of the gulls used in the survival analysis (Table 4; 1572 breeding attempts where m_x was determined; see Pyle et al., 1991, for methodology). When sample size for a combination of age and breeding experience was 0–10 (10 of 48 values), we substituted predicted values derived from statistical models of reproductive success for each sex, in which age and breeding experience were covariates and year was a categorical variable (statistical details in Table 4).

For survivorship of breeders (i.e., l_x where $x > \alpha$), we used survival values from Table 1. The exception to this was that, where sample sizes were 0–15 (11 of 48 values; a larger minimum sample size was needed because survival, unlike reproductive success, is binary), we used predicted values for survival derived from a multiple logistic regression model. The statistical equations, controlling for year effects, were logit(survival) = p = constant + year-effect + $0.268x - 0.208y$ for males and p = constant + year-effect + $0.311x - 0.302y$ for females, where x = age and y = years of breeding experience. The effects of age and experience were significant in each model ($p < .05$ in all cases; $p < .001$ for the overall model, LR tests) for each sex.

Table 3

Prebreeding survival in western gulls

Age (years)	Males	Females
1	0.555	0.610
2	0.750	0.840
3	0.820	0.890
4	0.8364	0.9076
5	0.8474	0.9206
6	0.8537	0.9214
7	—	0.9240

Values represent survival probability for the year (spring to spring) preceding each age. Proportions for ages 1–3 were estimated by Spear et al. (1987) and Spear and Nur (1994). Derived proportions for ages 4–7 were based on an extrapolation of these data using an inverse function of the form, logit (survival) = $b_0 + b_1 * (\text{age} + 1)^{-2}$, where logit ($q$) = $\ln[q/(1 - g)]$; in this case, q = survival probability. Separate equations were fit for each sex ($R^2 = .995$, $p = .044$ in males; $R^2 = 1.00$, $p = .003$ in females). The form of the age transformation was chosen, among all standard transformations, so as to maximize R^2 for each sex.

These procedures allowed us to calculate CRS through age 10 for each α class, for each sex. Beyond age 10 we had inadequate data on individuals of known age and known α class; here we assumed survival and reproductive success depended only on age and sex, but not on α. For survival and reproductive success for ages 11–22 years (22 years being the maximum observed age of breeding in our study; $n = 1$), we used observations on 1798 reproductive attempts by 482 known-age (but unknown α) gulls in our study population. For each sex, we determined separate survival and reproductive success values for ages 11–17 years (males, 0.809 and 1.272; females, 0.806 and 1.369, respectively) and 18–22 years (males, 0.681 and 1.026; females, 0.741 and 1.234), the reduced values of the latter group reflecting the onset of senescence effects at approximately age 17–18 years (Sydeman WJ et al., unpublished data). Only a small proportion of CRS depended on the contributions of gulls aged 17 and older (see Figure 1). We assumed no gulls survived beyond age 22, thus CRS for age 22 = LFP.

Whereas lifetime reproductive success has been commonly used as a surrogate of fitness (e.g., Clutton-Brock, 1988; Newton, 1989) such use has been criticized because it provides a valid index of fitness only in stable populations that are not undergoing changes in age structure (Caswell, 1989a; cf. Mertz, 1971; Schaffer, 1983). Therefore, we examined a second fitness measure, λ (equivalent to e^r, where r = realized rate of population increase), that incorporates the effect of growing or shrinking populations. Lambda, the finite (annual) rate of growth of a subpopulation of specified composition (in this case an α class), has the additional advantage of providing an absolute scale by which to judge fitness. We calculated λ in relation to α using the same survival, reproductive success, and prebreeding survivorship data (ages 1–7; Table 3) used to calculate LFP. Lambda was calculated as the dominant eigenvalue of the Leslie matrix containing age-specific survival and fecundity (Caswell, 1989b).

Table 4

Reproductive success (number of chicks fledged) in relation to age and breeding experience in male and female western gulls

Years of experience	Age (years)							
	3	4	5	6	7	8	9	10
Males								
0	0.03 (46)	0.45 (106)	0.69 (89)	0.67 (57)	—	—	—	—
1	—	0.74 (29)	1.10 (107)	1.07 (116)	1.28 (43)	—	—	—
2	—	—	1.03 (20)	1.19 (10)	1.38 (67)	1.26 (34)	—	—
3	—	—	—	1.79 (20)	1.37 (73)	1.27 (39)	1.38 (28)	—
4	—	—	—	—	1.80 (12)	1.52 (36)	1.12 (23)	1.49 (20)
5	—	—	—	—	—	1.69 (1)	1.61 (7)	1.51 (6)
6	—	—	—	—	—	—	1.67 (0)	1.56 (6)
7	—	—	—	—	—	—	—	1.58 (0)
Females								
0	—	0.61 (58)	0.61 (64)	0.43 (52)	0.99 (12)	—	—	—
1	—	—	0.79 (37)	1.21 (56)	1.44 (32)	1.90 (19)	—	—
2	—	—	—	1.30 (33)	1.13 (33)	1.03 (27)	1.21 (18)	—
3	—	—	—	—	1.50 (14)	1.34 (32)	1.78 (22)	1.61 (8)
4	—	—	—	—	—	1.58 (10)	1.74 (20)	1.44 (10)
5	—	—	—	—	—	—	1.41 (5)	1.50 (8)
6	—	—	—	—	—	—	—	1.36 (6)

Sample sizes are in parentheses. Values for males first breeding at ages 3, 4, 5, or 6 and for females first breeding at ages 4, 5, 6, or 7 are least-square means, adjusted for effects of interannual variation on success (see text). Values with sample sizes < 10 are predicted by regression models, one for each sex. Regression equations for these values are, for males, predicted reproductive success (PRS) = constant + $1.073x - 0.118x^2 + .0040x^3 + 0.279y - 0.200y^2$, and for females, PRS = constant + $0.089x + 0.381y - 0.078y^2 + 0.0038y^3$; where x = age and y = years of breeding experience. There were significant ($p < .05$) cubic age and quadratic experience terms for males, and significant linear age and cubic experience terms for females, but no other higher order terms were significant; the interaction age*experience was not significant for either sex. Note that, because of the absence of skipping (see text), age at first breeding classes are represented by the diagonals, down and to the right.

Comparison of fitness values and observed frequencies of α

Values of CRS in relation to α and age are shown in Figure 1, and comparisons of LFP and λ with observed distributions of α are shown in Figure 2. For males, breeding at age 3 was a suboptimal strategy; e.g., by age 14 α = 3 years had become the least optimal strategy, and by age 16 cumulative success was 34% greater for α = 4 versus α = 3 years (Figure 1A). Already by age 6, CRS for α = 4 is greater than all other α groups (Figure 1A). According to both LFP and λ models, optimal α for males was 4 years (Figure 2A), and an α of 5 years is second best by both criteria. Hence, males should have deferred breeding to at least age 4, assuming they were acting optimally. Deferring breeding to age 6 years was also a suboptimal strategy, as both λ and LFP were reduced compared to α classes 4 and 5. The results of both fitness metrics coincided remarkably with the observed distribution of α in this population in males, the rank orders of each being identical (Figure 2A; r_s = 1.0 comparing frequency distribution with both upper and lower bounds of each fitness measure).

Due to reduced survival of females first breeding at age 4, CRS for these individuals begins to level off after age 8, and from age 11 on, α = 4 yields the lowest cumulative fledgling production (Figure 1B). In females, expected LFP and λ generally increased as α increased from 4 to 7 years, although our estimated values for α = 6 were less than those for α = 5 years (Figure 2B). Thus, optimal α among the four classes was 7, with a secondary optimum at 5; the same pattern applied to both fitness measures. It is possible that fitness of α = 8 is even greater, but sample sizes were insufficient to examine this α class. For α classes 4–7, the rank order of fitness measures broadly agreed with that of observed frequencies of α (Figure 2B; r_s = .8 for both upper and lower bounds of each fitness measure), but the concordance was not as great as in males. For females, α class 7 showed the highest fitness, whereas α = 5 was the most frequently observed.

The fitness patterns revealed in Figure 2 provide an explanation for greater mean α in females versus males: in males, optimal α was 4 (cf. mode = 4, mean = 4.8), whereas in females the optimum was at least 5, and possibly 7 (cf. mode = 5, mean = 6.0). The shape of the fitness functions correlated well with sex-specific differences in the frequency distributions: for males, fitness was sharply defined around α = 4

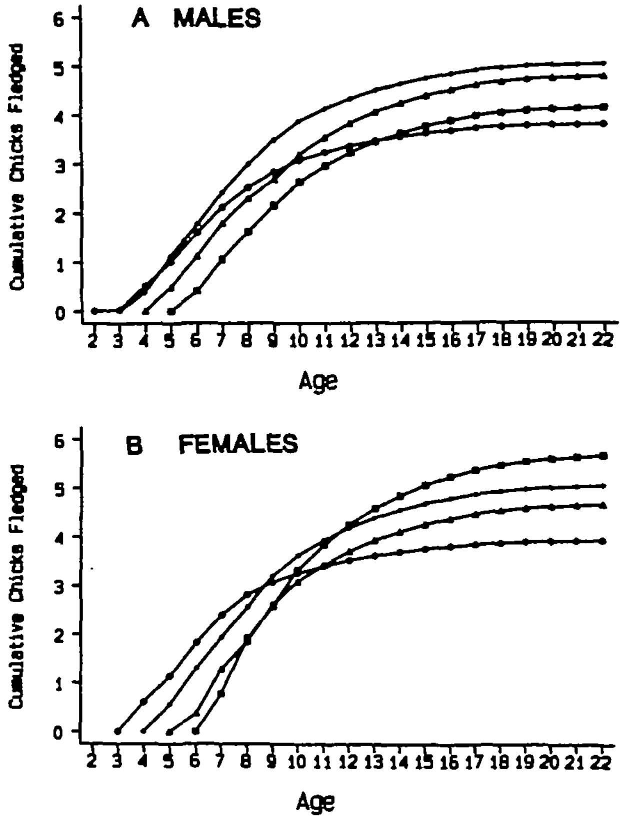

Figure 1
Expected cumulative reproductive success (CRS) after each year of life for different ages of first breeding in (A) males and (B) females. Males (○) $\alpha = 3$; (●) $\alpha = 4$; (△) $\alpha = 5$; (□) $\alpha = 6$; females (○) $\alpha = 4$; (●) $\alpha = 5$; (△) $\alpha = 6$; (□) $\alpha = 7$. Note that CRS = 0 whenever age $< \alpha$, but only one symbol is shown for sake of clarity (e.g., at age 4, CRS = 0 for $\alpha = 5$, 6 or 7). See text for methods of calculation. Note that, for the sake of clarity, we only show results using extrapolated prebreeding survivorship (upper bound) values (see Table 3). Lifetime fledging production values are those of CRS at age 22 years.

and the frequency distribution showed a clear peak, whereas, for females, there was no clear optimum and the frequency distribution showed no clear mode.

DISCUSSION

Evidence for a cost of reproduction

We interpret the observed patterns of survival with α as evidence that, by initiating breeding at young ages, western gulls trade-off potential fecundity early in life for reduced subsequent survival. We recognize the potential pitfalls of inferring reproductive costs from correlative data (Bailey, 1992; Linden and Møller, 1989; Nur, 1988b; Partridge and Harvey, 1988; Reznick, 1985); however, our results cannot be explained simply by confounding factors. The analysis controlled for annual variability in environmental conditions and for the potential increase in survival with age per se. We also maintain that the diminished survival of gulls breeding early in life cannot be explained by variation in the intrinsic quality of individuals, assuming that individuals of higher quality show increased survival (Coulson and Porter, 1985; Nur, 1988b; Partridge, 1989). If differences in α are due to low-quality individuals being prevented or constrained from breeding early in life, this would not explain the low survival of those breeding early. Alternatively, reproductive effort may be optimized with respect to individual quality. However, an optimality model developed by Nur (1988a) demonstrated that reproductive effort of low-quality individuals should be lower than that of high-quality individuals, thus low-quality individuals are expected to begin breeding late in life, relative to other individuals.

Thus, we would expect that the effect of quality on α would result in high-quality individuals breeding earlier in life, on average. That western gulls breeding early in life show poor survival is therefore evidence of a cost of reproduction, one that has not been swamped by a quality effect. In females and males of α 3–5, a quality effect may be operating, but it does not offset the effects of a cost of reproduction. For males with $\alpha = 6$ or greater, however, survival decreased with α. This result may indicate that, for males beginning to breed late in life, differences in individual quality are sufficient to outweigh differences associated with a cost of breeding (i.e., males of $\alpha \geq 6$ may be of low intrinsic quality).

These differences in the effects of quality may also explain the sex-specific differences in survival patterns. As noted above, a quality effect might be evident in males of α classes 6–8, swamping the cost of early breeding (Table 1). No suggestion of such an effect was observed among females (Table 1). Due to the skewed sex ratio among adult birds in this population (adult females outnumber adult males), the lowest-quality females (but not males) might be excluded from breeding altogether and hence excluded from our sample. A smaller range in individual quality would thus be expected among breeding females than among breeding males (see Spear et al., 1995).

Results of this study indicate that female western gulls may also incur a cumulative, or long-term, cost of reproduction. The significance of long-term costs of reproduction has not been generally appreciated; prevalent views in the past have been that a cost of reproduction is expressed quickly. For example, Ricklefs (1977) and Hogstedt (1981) assumed that a cost of reproduction would be expressed simultaneously with breeding, or soon after. Some other studies have demonstrated cumulative or long-term costs of reproduction. Gustafsson and Pärt (1990) found that clutch size in collared flycatchers (*Ficedula terminickii*) was reduced for several years subsequent to high reproductive effort in one year. Nur (1988a) found that, in blue tits (*Parus caeruleus*), artificial brood enlargement one year caused decreased fledgling production the following year.

Cost of reproduction and fitness in western gulls

Within our study population, lifetime reproductive success was quite similar for the two sexes, but λ was consistently higher for females than for males (Figure 2). The proximal reason for the difference in λ values was the lower prebreeding survivorship in males (Table 3). Additionally, individuals breeding at late α were not included in these calculations and, among females but not males, a sizeable fraction probably never bred at all; for these females, α was undefined but fitness was essentially zero.

Our analyses of LFP and λ indicate a benefit to deferring breeding beyond the smallest possible values of α (earliest breeding). Other studies of lifetime reproductive success versus α in shorter-lived birds, Eurasian sparrowhawks (*Accipiter nisus*) and collared flycatchers, found that earlier breeding resulted in more young produced over a lifetime, and this was explained as a quality effect (Gustafsson and Pärt, 1990; Newton, 1985). In contrast, our results on western gulls indicate a clear advantage to deferring breeding to at least age 4 years

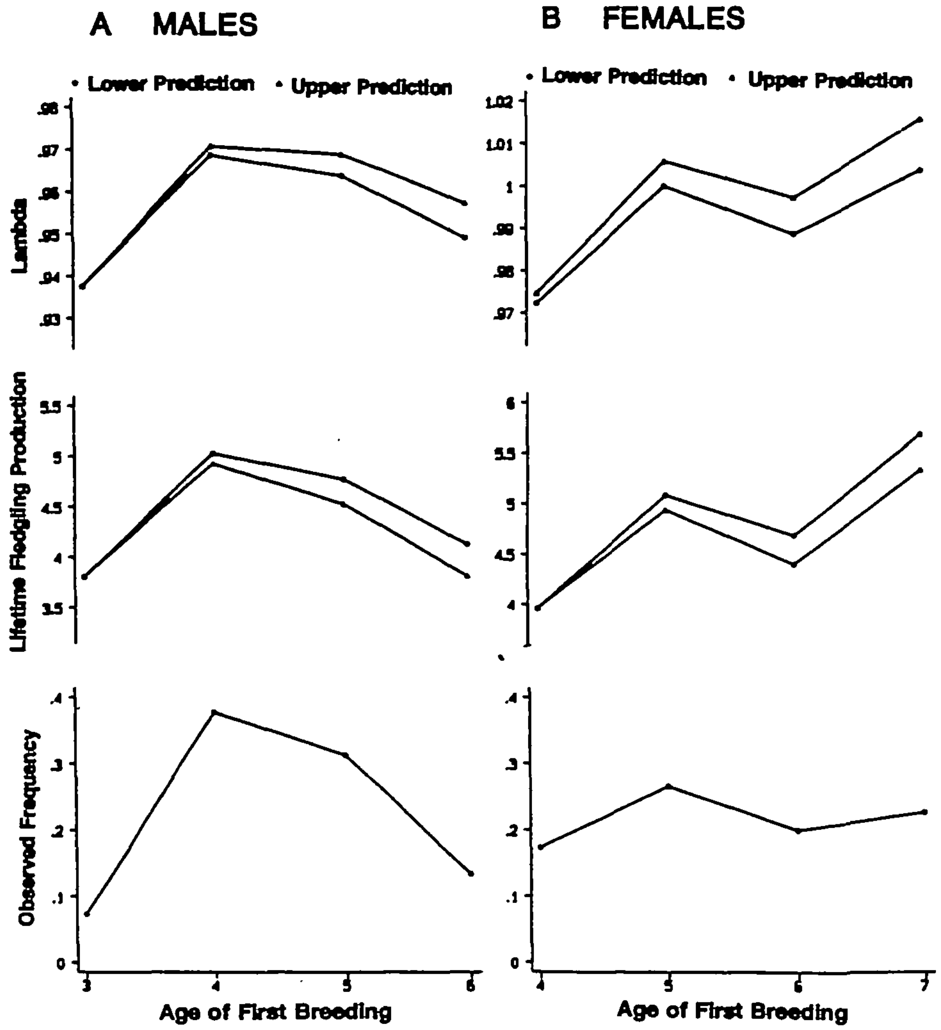

Figure 2
Observed frequencies of α (Spear et al., 1995), predicted lifetime fledgling production in relation to α (see Figure 1), and estimates of λ (see text) in relation to α, among (A) male western gulls, α 3–6 and (B) females, α 4–7. Observed frequencies depicted in the figure do not sum to 100% because males with α > 6 and females with α > 7 are not shown. Upper and lower predictions with regard to fitness measures refer to estimates differing according to the method of extrapolating prebreeder survivorship (see Table 3).

in males and 5–7 years in females. Similarly, Viallefont et al. (1995) found that in lesser snow geese (*Anser caerulescens caerulescens*), females who bred at the earliest age, 2 years, did not achieve higher lifetime reproductive success than those who deferred breeding to age 3 years due to a reproductive cost incurred by 2 year olds. We suggest that the benefits of deferred breeding may increase with the mean life span of an organism, all else being equal.

Our results also suggest that in males, natural selection has moved age of first breeding toward its fitness optimum, consistent with the action of stabilizing selection. In females, fitness was similar among α classes 5, 6, and 7, presumably because of the trade-off between early breeding and subsequent survival. The resulting lack of a clear optimum in females, in contrast to males, implies little or no stabilizing selection, except for selection against α = 4. The sex-specific difference in optimal and observed α reflects sex-specific variation in reproductive costs and benefits. This variation in costs and benefits, in turn, likely relates to differences in roles of parental care during breeding (Pierotti, 1981; cf. Pyle et al., 1991; Spear et al., 1995), differences in foraging behavior away from the breeding grounds (Spear, 1988), and the skewed sex ratio (cf. Michener and Locklear, 1990).

As with other life-history traits (Stearns, 1989), age at first breeding is likely to be the joint outcome of adaptation and constraint. The distribution of actual age at first breeding among Farallon western gulls likely fluctuates from year to year, reflecting changes in both optimal α (a result of interannual variation in the costs and benefits of reproduction) and changes in food, mate, and/or nest-site availability. In this study we calculated optimal α based on a synthesis of demographic data collected at the population level. In future years we hope to evaluate these results further, using fitness measures obtained from observations at the individual level.

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