THE EFFECTS OF EXPERIENCE AND AGE ON THE BREEDING PEFORMANCE OF WESTERN GULLS

PETER PYLE, LARRY B. SPEAR, WILLIAM J. SYDEMAN, AND DAVID G. AINLEY

Point Reyes Bird Observatory, Stinson Beach California 94970 USA

ABSTRACT.—We examined the independent effects of age and breeding experience on reproductive success in Western Gulls (*Larus occidentalis*) 3–9 years old. Both factors significantly enhanced success after the other factor had been statistically controlled. When the sexes were analyzed separately, previous breeding experience had a significant influence on success of females but not males, whereas among first-time breeders, age was significantly more important to males than to females. The trends with experience were curvilinear, which indicates that the advantages of experience after the first breeding attempt decreased. The linear trends with age implied that increases in success are realized more constantly through 9 years of age. Breeding experience enhanced clutch size of the female as well as hatching success of both sexes, while age enhanced the timing of breeding by both sexes and clutch size, hatching success, and fledging success of the male but not the female. Our results relate to sex-specific roles in reproduction, and we suggest that deferred breeding may be more effective strategy for males than for females. *Received 29 November 1989, accepted 7 July 1990.*

REPRODUCTIVE SUCCESS increases with both age and breeding experience in many species of birds (see summaries in Ryder 1981, Clutton-Brock 1988). Because of small sample sizes of marked individuals of both known-age and known-experience, however, few studies have considered the independent effects of these two factors (see discussions in Davis 1976, Ollason and Dunnet 1978, Ainley et al. 1983, Saether 1990). In several species, reproductive performance of first-time breeders increases with age (Richdale 1949; Hornberger *in* Lack 1966; Davis 1976; Ollason and Dunnet 1978, 1988; Harvey et al. 1988; Wooler et al. 1990), which has prompted speculation that age rather than breeding experience accounts for increased reproductive success (Lack 1968, Ryder 1981; see also Hamann and Cooke 1987). Few studies have examined the contribution of prior breeding experience with statistical controls for age.

Western Gulls (*Larus occidentalis*) that breed on Southeast Farallon Island (SEFI), California, improve reproductive success with age (see Sydeman et al. 1991). In this same population a wide variation in age of first-breeding exists, 4–10 ($\bar{x}$ = 6.0) yr in females and 3–9 ($\bar{x}$ = 4.8) yr in males (Spear 1988, unpubl. data). Thus, birds with varying amounts of breeding experience occur within each age group. Consequently, we examined the relative effects of breeding experience and age in Western Gulls 3–9 years old by determining each effect while statistically controlling the other. We investigated these effects in females and males, and we relate differences to sex-specific roles in reproduction. Our results provide some new perspectives on variation in reproductive performance (Nol and Smith 1987, Wooler et al. 1990) and deferred breeding (Williams 1966).

METHODS

Study area and field methods.—Ainley and Boekelheide (1990) described the breeding ecology of seabirds on SEFI, located 48 km west of San Francisco and within the California eastern boundary current system. Reproductive success in gulls and other seabirds is strongly related to food availability, which in turn shows wide interannual fluctuation. The population of Western Gulls breeding on SEFI (est. 26,000 birds) has been described by Spear et al. (1987) and Penniman et al. (1990). As the result of an annual chick-banding program initiated in 1971, approximately 11% of the breeding population was marked by 1983, when we began our studies of known-age birds. Bands were read at the onset of territory occupation. Clutch initiation date, clutch size, and hatching and fledging success were determined each year for a sample of marked individuals (see Sydeman et al. 1991 for details). Sex of most adults was determined by behavioral observation during courtship and by direct size comparison (Pierotti 1981, Spear 1988).

Between 1983 and 1988, we monitored 3,069 breeding attempts (defined by the laying of at least one egg) by 1,233 known-age individuals (672 males, 521 females, 40 unknown sex). Within this sample, 826 attempts were made by 476 individuals aged 3-9 yr and of known breeding experience (hereafter "experience"). In these individuals the breeding history, including year of first breeding, was known. We used three different methods to determine year of first breeding. First, 454 of the attempts were by gulls that Spear had marked as chicks in 1978-1980, which were then specifically located through intensive searches of the entire colony during the 1982-1988 breeding seasons. Second, 82 attempts involved 3-yr-old males and 4-yr-old females that were almost certainly breeding for the first time. In observed attempts of >2,000 known-age gulls on SEFI, no 2-yr-olds and only one 3-yr-old female was involved (Point Reyes Bird Observatory [PRBO] unpubl. data; males breed earlier than females in this population because of a skewed sex ratio in breeding birds [Spear et al. 1987]). Finally, 378 attempts resulted from an intensive band-reading effort during the 1986-1988 seasons. Band numbers and nest locations were determined for every marked bird that bred within a defined study area ($\bar{x}$ = 1,164 marked birds per year). Gulls that nested at least 10 m within area boundaries during 1987 or 1988 and that were not recorded the previous year were assumed to be first-time breeders. Nest-site movements between years of up to several meters are not unusual, but relocations >10 m are rare (Spear et al. 1987). We confirmed this by marking nest bowls and measuring relocation distances of 156 banded individuals between the 1987-1988 and 1988-1989 seasons. Only 3 had relocated >10 m, and only one had relocated >14 m (mean [±SE]: 1.5 ± 0.23 m; range: 0.0-21.1 m). In all cases it was also known that birds bred during all interim years. Three individuals of our sample skipped a year (failed to lay eggs) between attempts, although all three maintained territories throughout the skipped season. As it cannot be judged how much experience is gained during skipped years, these three birds were subsequently excluded from the sample.

Data analysis.—We defined *reproductive success* as the number of chicks fledged per breeding attempt. Four components of reproductive success were also examined in sex-specific analyses: timing of breeding (indicated by clutch initiation date), clutch size, hatching success (% of eggs laid that hatch), and fledging success (% of chicks hatched that fledge).

Linear regressions on age- and experience-controlled samples were used for most comparisons. Significance is indicated by P values on the F-statistic. We performed ANOVA and Chi-square analyses, which yielded similar results for all comparisons. We present results of regression analysis because it is a more powerful analysis when the independent variables (age and experience) are quantitative (Breslow and Day 1980, Gaines and Rice 1990). To confirm the results of the regression analyses and to examine the relative contributions of age and experience within the entire sample, we also used a hierarchical log-linear analysis. Partial G-values were calculated for interactions between reproductive success, age, experience, and sex.

Residuals were found to be distributed normally for the independent variables in all comparisons and also for the dependent variables in analyses of reproductive success and timing of breeding (skew was less than 0.02; kurtosis was greater than 2.0 and less than 4.0 where kurtosis of normal equaled 3.0). Residuals were not distributed normally for comparisons of clutch size but because those of the independent variables were normally distributed, no violations of the assumptions of linear regression occurred (Seber 1977: 150). Proportional data (hatching success and fledging success) were also arcsine square-root transformed before further analyses.

To test for curvilinearity we performed polynomial regression of trends with respect to age and experience, to see whether or not quadratic equations significantly improved the fit over linear equations. Analyses of covariance were used to evaluate experience-specific differences in reproductive success with age, and sex-specific differences within all comparisons.

Our sample consisted of age groups 3-9 yr and experience groups 0-4 yr. The effects of age were tested within experience groups 0, 1, and 2 yr. For analyses on the effects of experience, we pooled age groups 6, 7, and 8 yr. Although significant increases in reproductive success occurred between age groups 3 and 6 in our sample, by age 6 this trend had equalized. No significant effects of age were found between ages 6, 7, and 8 for comparisons of reproductive success ($\chi^2 = 0.77$, $P = 0.943$; $F_{1,307} = 0.46$, $P = 0.500$) or of any of its four components ($\chi^2 < 6.3$, $P > 0.3$; $F < 2.7$, $P > 0.1$).

To ensure that our sample was distributed proportionally among years of varying food supply (see Sydeman et al. 1991), we used analyses of covariance to control for year, and we obtained results similar to those presented for all examinations of both age and experience. We also examined the effects of experience within a targeted subsample (135 attempts) of 6-yr-olds breeding in 1988, which controlled for both year and cohort.

In the sample of gulls aged 6-8 yr that were used in the experience analyses, 24% of the attempts involved the same individual in different years. To investigate the effect of dependence among observations, we used a random numbers table to eliminate multiple attempts by the same individual. We again found similar levels of significance between analyses on the full (including multiple attempts) and reduced (one attempt per individual) samples; data from the larger samples are presented. All statistical tests were performed using the SPSSPC+ program; significance is implied when $P < 0.05$.

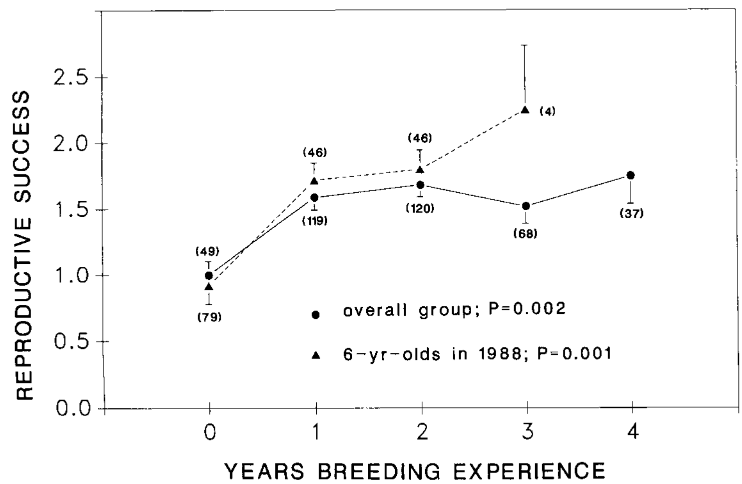

Fig. 1. The effects of breeding experience on reproductive success in 6–8 yr olds (overall) and 6-yr-olds breeding in 1988 ($\bar{x} \pm 1$ SE). Reproductive success is defined as chicks fledged per breeding attempt. Sample sizes are in parentheses. Significance is determined with linear regression. See text for results of analyses of curvilinearity.

Results

Breeding experience and reproductive success; age controlled.—Among individuals aged 6–8 yr, reproductive success increased significantly with experience (Fig. 1). Most of the increase occurred between the first and second breeding attempt. This resulted in a significant curvilinear trend ($P = 0.002$). A significant correlation also existed in the 1988 subsample of 6-yr-olds, although this trend was not curvilinear ($P = 0.08$), perhaps because of smaller sample sizes. The increase in success with experience is present when cohort and year, as well as age, are controlled.

The positive influence of experience proved significant with females but not with males (Fig. 2), although analysis of covariance showed no difference between the sexes ($F_{1,415} = 2.49$, $P = 0.116$). In females, reproductive success in-

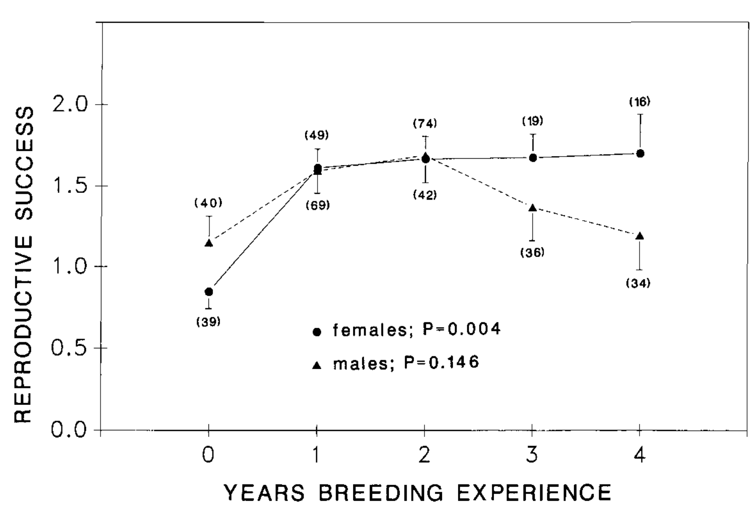

Fig. 2. The effects of breeding experience on reproductive success of males and females 6–8 yr old ($\bar{x} \pm 1$ SE). Reproductive success is defined as chicks fledged per breeding attempt. Sample sizes are in parentheses. Significance is determined with linear regression. See text for results of analyses of covariance and curvilinearity.

TABLE 1. Log-linear analyses on number of chicks fledged. Interactions of reproductive success with age and experience are given for the entire population and separately for each sex. Interactions with age and experience by sex are also given for the entire sample, to confirm the results of analyses of covariance. Twenty-seven cases (16 male, 11 female) were rejected because of missing data points.

	df	Partial G	P
All birds (799)			
Age	10	47.984	0.001
Experience	6	37.413	0.001
Age by sex	6	76.169	0.001
Experience by sex	6	16.544	0.198
Females (297)			
Age	9	15.984	0.594
Experience	6	27.746	0.006
Males (502)			
Age	10	44.329	0.001
Experience	6	18.918	0.090

creased through 4 yr of experience, but especially between the first and second breeding attempts. This trend was significantly curvilinear ($P = 0.008$). In males success actually declined after two years of experience, although this decline was not significant ($P = 0.146$). The log-linear analysis on the entire sample confirmed the results of linear regression with the sexes grouped and separated, and it confirmed that the relationship of success with experience did not significantly vary with sex (Table 1).

Timing of breeding and fledging success were not significantly related to previous breeding experience in either sex, although a tendency for later breeding and poorer fledging success by less-experienced females was evident (Table 2). Clutch size increased significantly with experience in females but not in males, and the sex-specific difference in this trend was significant. As with overall reproductive success, the largest increase in clutch size of females occurred between the first and second breeding attempts. Hatching success increased significantly with breeding experience of both sexes, with the largest increases again occurring between the first and second attempts. Thus, the overall increase in reproductive success resulted primarily from increased clutch size of experienced females and improved hatching success with experience of both sexes.

Age and reproductive success; breeding experience controlled.—We tested the effects of age on reproductive success within experience groups of 0, 1, and 2 yr (sexes grouped; Fig. 3). Age correlated significantly with reproductive success during the first breeding attempt; most of the difference occurred between the ages of 3 and

TABLE 2. The effects of previous breeding experience on components of reproductive success of males and females ($\bar{x} \pm$ SE). Significance was determined with linear regression (P_1). P_2 compares the regression of males and females using analysis of covariance. Experience groups 3–4 are lumped in the table although regressions were performed without pooling. Proportional data (hatching and fledging success) were arcsine square-root transformed before analyses were performed. Sample sizes (in parentheses) for each mean are ±2 because of missing data points.

	Years Breeding Experience						
	0 (39♀, 40♂)	1 (48♀, 69♂)	2 (44♀, 74♂)	3–4 (35♀, 72♂)	β	P_1	P_2
Timing[a]							
Females	133.1 ± 1.3	132.0 ± 0.9	130.1 ± 0.8	130.2 ± 1.0	−0.93	0.069	0.157
Males	132.3 ± 1.3	130.0 ± 0.7	129.6 ± 0.6	130.1 ± 0.8	−0.01	0.986	
Clutch size							
Females	2.56 ± 0.10	2.83 ± 0.06	2.89 ± 0.05	2.89 ± 0.06	0.11	0.004	0.011
Males	2.75 ± 0.08	2.91 ± 0.05	2.77 ± 0.06	2.83 ± 0.05	−0.01	0.724	
Hatching success							
Females	0.598 ± 0.06	0.885 ± 0.03	0.837 ± 0.04	0.919 ± 0.04	0.12	0.001	0.415
Males	0.738 ± 0.06	0.797 ± 0.04	0.836 ± 0.03	0.890 ± 0.03	0.08	0.004	
Fledging success							
Females	0.575 ± 0.07	0.653 ± 0.06	0.724 ± 0.06	0.677 ± 0.06	0.04	0.220	0.354
Males	0.581 ± 0.07	0.672 ± 0.04	0.721 ± 0.04	0.647 ± 0.05	0.00	0.923	

[a] Timing is represented as the Julian date of clutch initiation.

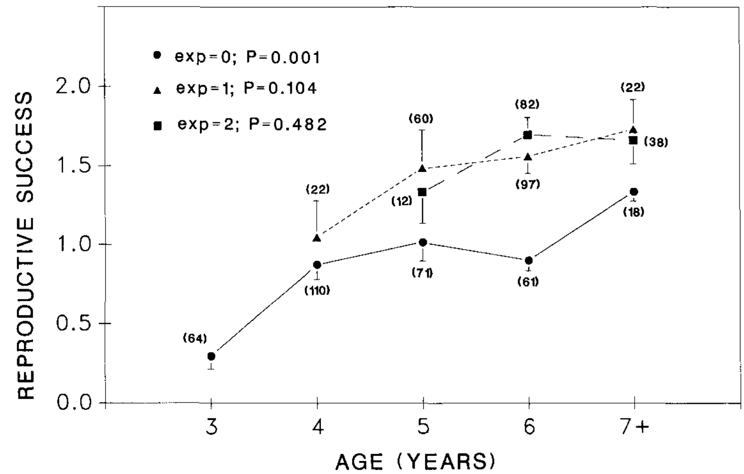

Fig. 3. The effects of age on reproductive success in three experience groups ($\bar{x} \pm 1$ SE). Reproductive success is defined as chicks fledged per breeding attempt. Sample sizes are in parentheses. Significance is determined with linear regression. See text for results of analyses of covariance and curvilinearity.

4 yr. The effect of age on reproductive success was not significant in the 1-yr and 2-yr experience groups (Fig. 3), although analysis of covariance showed no differences between the trends of the three groups ($F_{2,665} = 0.43$; $P = 0.651$). The trend in first-time breeders was significantly curvilinear ($P = 0.035$). We suspect that this resulted from the combination of the separate, noncurvilinear trends observed when the sexes were separated (see Fig. 4).

In contrast to the effects of breeding experience, age and reproductive success related significantly in males but not females during the first breeding attempt (Fig. 4). This sex-specific difference was significant both overall (analysis of covariance, $F_{1,315} = 10.15$, $P = 0.002$), and when 3-yr-old males were excluded ($F_{1,252} = 4.52$; $P = 0.034$). The latter analysis ensured that the overall effect was not solely due to the fact that males but not females breed at age 3. In males, most of the increase occurred between 3- and 5-yr-olds, but interestingly this trend was not sig-

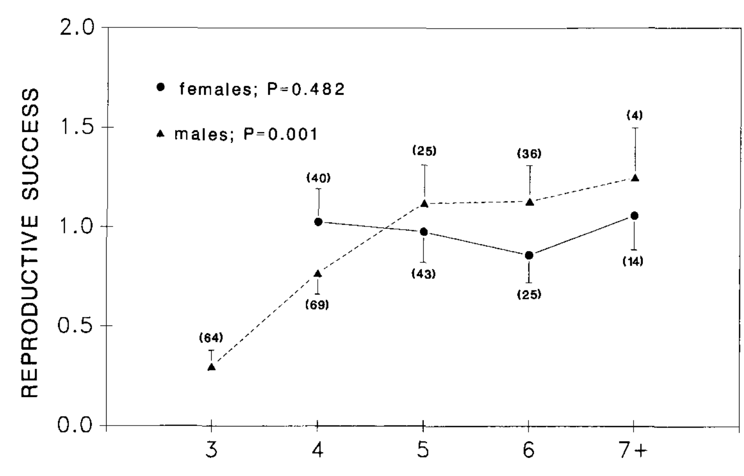

Fig. 4. The effects of age on reproductive success in first-time breeding females and males ($\bar{x} \pm 1$ SE). Reproductive success is defined as chicks fledged per breeding attempt. Sample sizes are in parentheses. Significance is determined with linear regression. See text for results of analyses of covariance and curvilinearity.

TABLE 3. The effects of age during the first breeding attempt on components of reproductive success of males and females ($\bar{x} \pm$ SE). Significance was determined with linear regression (P_1). P_2 compares the regressions of males and females using analysis of covariance. Age groups 6–9 are lumped in the table, although regressions were performed without pooling. Proportional data (hatching and fledging success) were arcsine square-root transformed before analyses were performed. Sample sizes (in parentheses) for each mean are ±4 because of missing data points.

	Age (yr)						
	3 (56♂)	4 (39♀, 68♂)	5 (42♀, 24♂)	6–9 (39♀, 40♂)	β	P_1	P_2
Timing[a]							
Females	—	137.3 ± 1.2	133.7 ± 0.1	133.1 ± 1.3	−1.92	0.009	0.127
Males	142.9 ± 1.3	134.9 ± 1.1	133.1 ± 1.5	132.3 ± 1.3	−3.48	0.001	
Clutch size							
Females	—	2.44 ± 0.10	2.57 ± 0.09	2.56 ± 0.10	0.06	0.257	0.033
Males	2.04 ± 0.08	2.44 ± 0.07	2.54 ± 0.13	2.75 ± 0.08	0.21	0.001	
Hatching success							
Females	—	0.645 ± 0.06	0.746 ± 0.05	0.598 ± 0.06	0.04	0.306	0.467
Males	0.467 ± 0.06	0.615 ± 0.05	0.750 ± 0.06	0.738 ± 0.06	0.07	0.011	
Fledging success							
Females	—	0.583 ± 0.08	0.447 ± 0.06	0.575 ± 0.07	0.04	0.348	0.039
Males	0.278 ± 0.07	0.490 ± 0.06	0.561 ± 0.09	0.581 ± 0.07	0.09	0.001	

[a] Timing is represented as the Julian date of clutch initiation.

nificantly curvilinear ($P = 0.084$). The sex-specific differences and age effects on reproductive success were confirmed by the log-linear analysis using the entire sample (Table 1).

All four components of reproductive success contributed to the age-related increase found in males, but only timing of breeding related significantly to age in first-breeding females (Table 3). The differences between the sexes in trends of clutch size and fledging success were significant. Hence the increase in reproductive success with age of first-time breeders results primarily from increased clutch size, hatching success, and fledging success with age of the male. Earlier breeding by older individuals of both sexes may also contribute to increased success.

DISCUSSION

Age versus experience.—On the basis of studies that find improvement with age in the success of first-time breeders, Lack (1968) and Ryder (1981) speculated that previous breeding experience does not enhance reproductive performance. Rather, observed increases in reproductive success are strictly age-related or at least related to experience not associated with nesting. Nelson (1966) suggested further that increased reproductive success with age in Northern Gannets (*Morus bassanus*) probably resulted from a maturation of innate qualities with age as opposed to a learning process through increased breeding experience. Wooler et al. (1990) concluded that age rather than breeding experience enhanced reproductive success in Short-tailed Shearwaters (*Puffinus tenuirostris*). It was suggested that "environmental" experience, or age, rather than breeding experience accounted for increases in clutch size with age of female Adélie Penguins (*Pygoscelis adeliae*; Ainley et al. 1983), Snow Geese (*Chen caerulescens*; Hamann and Cooke 1987), and Brandt's Cormorants (*Phalacrocorax penicillatus*; Boekelheide and Ainley 1989). In Western Gulls, on the other hand, we have shown that both age and breeding experience separately enhance reproductive success. Furthermore we found that clutch size increased with breeding experience rather than age of female Western Gulls, which suggests that in this species reproductive experience has a greater influence than age on the reproductive condition of the female (see Ainley et al. 1983). We believe that hatching success is influenced by learning through experience, while timing and fledging success are more affected by age. The curvilinear relationships of success with experience further imply that the advantages of this learning process become smaller with each additional year after first breeding, whereas the linear trends with age indicate that age-related factors continue to influence success, at least through 9 yr of age.

Breeding failure of individual Western Gulls has been ascribed largely to egg neglect, infertility, and intraspecific predation on eggs and young chicks (Coulter 1973, Spear et al. 1987, Penniman et al. 1990). These components of reproductive success may, in general, be reduced by increased experience, whereas timing and foraging efficiency seem to improve more with age. In other species, such as those mentioned above, reproductive success could be more dependent on timing and food acquisition than on egg loss and predation, which might account for the implicit higher correlation with age than with experience in these species. Unlike the penguins and cormorants, Western Gulls on SEFI also have a high rate of mate fidelity (PRBO unpubl. data), which may amplify the effect of previous breeding experience (see Coulson 1966). In situations where adult survivorship and mate fidelity are lower, breeding experience may have less effect on reproductive success.

Females versus males.—We found that increased breeding experience significantly enhances the reproductive success of females but not males, whereas age is significantly more important to males. Other studies (Davis 1976, Thomas and Coulson 1988, Sydeman et al. 1991) that did not differentiate between age and experience found no differences between females and males when correlating either of these factors with reproductive success. In our study, it was only after age and experience were alternately controlled that the difference between the sexes became apparent.

We believe that this sex-specific effect results primarily from differences in parental roles in reproduction. Pierotti (1981) found that female Western Gulls on SEFI typically spend more time incubating and directly protecting the eggs and small chicks, while males spend more time in territorial defense and feed the young larger amounts of food than the females. It follows that hatching success, which is strongly influenced by nest-site breeding skills (Nelson 1966, Ollason and Dunnet 1986), increases significantly with experience of the female and to a lesser degree the male, while the increase in fledging success observed for older males results in part from an increase in foraging skills with age (Nur 1984; see also Searcy 1978, Greig et al. 1983, MacLean 1986). The significant increase in clutch size with age of male Western Gulls may also result from the amount of food fed to the female during courtship. Again this relates to increased foraging efficiency. In contrast to the female's nest-site skills, the male's foraging experience increases continually with age, but would not be influenced as much by increased breeding experience.

Life-history strategy.—Four hypotheses have been proposed recently to explain increases in reproductive success with age in birds (Nol and Smith 1987, Wooler et al. 1990). In addition to higher success due to increases in reproductive efficiency with (1) breeding experience and with (2) chronological age per se, it has also been suggested that (3) older birds increase reproductive effort to offset decreased survival (residual reproductive value) with age, and that (4) apparent increases with age are simply an artifact of increased survival of higher-quality individuals, which have higher rates of reproductive performance irrespective of age or experience. Our results are consistent with the first two hypotheses. Although in the present analysis we lack the data on older birds needed to fully test the third hypothesis, the experience-, age-, and sex-related variation in the effects of the four components of reproductive success implies that the increase in reproductive success in Western Gulls results primarily from a combination of increase in foraging skills with age, and improvement of other nesting skills through increased breeding experience (Nur 1984, Reid 1988), rather than through a general increase in reproductive effort (Pugasek 1981, 1984). As for the fourth hypothesis, the curvilinear effect of breeding experience when age was controlled suggests that the effect of breeding experience is real rather than an artifact of differential survival rates. However, a cost of reproduction (if it exists in this species) would complicate this relationship. The linear increase in success with age in first-time breeders and the sex-specific differences also imply that the effect of age in males is real. We suspect that quality of individual and differential survival may partially account for observed increases after the first breeding attempt, perhaps more influentially with females. We are currently collecting the data to examine older age groups of Western Gulls, and in a separate analysis, we will consider the effects of age and experience on survivorship.

Deferred breeding.—To explain deferred maturation and low-intensity breeding in seabirds, Williams (1966; see also Nur 1988) suggested that the cost of reproductive effort jeopardizes future reproductive output by increasing the parental risk of mortality. Other researchers (Lack 1968, Goodman 1974, Chabrzyk and Coulson 1976, Ainley et al. 1983, Hamann and Cooke 1987, Ainley et al. 1990) have further suggested that breeding at a young age is disadvantageous, as the costs in terms of reduced survivorship do not justify the low reproductive output of younger birds. Assuming these strategies are adaptive, we suggest that deferred breeding in Western Gulls is more advantageous to males than to females. By gaining more foraging experience before attempting to breed, males enhance their chances of reproductive success without incurring the costs of potentially unsuccessful breeding.

For females, by contrast, initial low-intensity breeding may be more adaptative, as females more than males gain from the experience of earlier reproductive attempts. In contrast to foraging skills, competence in incubating eggs and caring for newly hatched chicks is gained through breeding experience, regardless of age (see Curio 1983). The improvements in reproductive success gained through deferred breeding in females were negligible. The fact that first-breeding females but not males had smaller clutches indicates that initial costs are minimized by females through a low-intensity effort.

ACKNOWLEDGMENTS

Our work on SEFI has been enthusiastically supported by the Farallon Patrol of Ocean Alliance, the U.S. Coast Guard, and especially the U.S. Fish and Wildlife Service, which administers the Farallon National Wildlife Refuge. Former and present Farallon biologists were instrumental in initiating and developing the Western Gull project; we especially thank R. Boekelheide, J. Penniman, T. Penniman, H. Carter, and S. Emslie. Much of the fieldwork was carried out by Farallon volunteers; we would like to especially acknowledge the efforts of C. Askew, L. de Forrest, K. Donaghue, S. Johnston, K. Lee, M. Lerdau, J. Lyons, M. Rossi, and C. Valle. Significant help with statistics was offered by N. Nur and L. Stenzel, and the comments of S. Emslie, N. Nur, R. Pierotti, and an anonymous reviewer improved the manuscript. This is Contribution No. 448 of the Point Reyes Bird Observatory.

LITERATURE CITED

AINLEY, D. G., R. E. LERESCHE, & W. J. L. SLADEN. 1983. Breeding biology of the Adélie Penguin. Berkeley, Univ. California Press.

———, & R. J. BOEKELHEIDE (EDS.). 1990. Seabirds of the Farallon Islands: ecology, structure and dynamics in an upwelling system. Palo Alto, Stanford Univ. Press.

———, C. A. RIBIC, & R. C. WOOD. 1990. A demographic study of the South Polar Skua *Catharacta maccormicki* at Cape Crozier. J. Animal Ecol. 59: 1-20.

BOEKELHEIDE, R. J., & D. G. AINLEY. 1989. Breeding biology of the Brandt's Cormorant: interaction between age and resource availability. Auk 106: 389-401.

BRESLOW, N. E., & N. E. DAY. 1980. Statistical methods in cancer research. Vol. 1, the analysis of case-control studies. Lyon, France, Int. Agency Res. Cancer.

CHABRZYK, G., & J. C. COULSON. 1976. Survival and recruitment in the Herring Gull *Larus argentatus*. J. Animal Ecol. 45: 187-203.

CLUTTON-BROCK, T. H. (ED.). 1988. Reproductive success: studies of individual variation in contrasting breeding systems. Chicago, Univ. Chicago Press.

COULSON, J. C. 1966. The influence of pair bond and age on the breeding biology of the kittiwake gull, *Rissa tridactyla*. J. Animal Ecol. 35: 269-279.

COULTER, M. C. 1973. The breeding biology of the Western Gull (*Larus occidentalis*). M. S. thesis, Oxford, Oxford Univ.

CURIO, E. 1983. Why do young birds reproduce less well? Ibis 125: 400-404.

DAVIS, J. W. F. 1976. Breeding success and experience in the Arctic Skua, *Stercorarius parasiticus* (L.). J. Animal Ecol. 45: 531-536.

GAINES, S. D., & W. R. RICE. 1990. Analysis of biological data when there are ordered expectations. Am. Nat. 135: 310-317.

GOODMAN, D. 1974. Natural selection and a cost ceiling on reproductive effort. Am. Nat. 108: 247-268.

GREIG, S. A., J. C. COULSON, & P. MONAGHAN. 1983. Age-related differences in foraging success in the Herring Gull. Animal Behav. 31: 1237-1243.

HAMANN, J., & F. COOKE. 1987. Age effects on clutch size and laying dates of individual female Lesser Snow Geese *Anser caerulescens*. Ibis 129: 527-532.

HARVEY, P. H., M. J. STENNING, & B. CAMPBELL. 1988. Factors influencing reproductive success in Pied Flycatcher. Pp. 189-200 *in* Reproductive success: studies of individual variation in contrasting breeding systems (T. H. Clutton-Brock, Ed.). Chicago, Univ. Chicago Press.

LACK, D. 1966. Population studies of birds. Oxford, Clarendon Press.

———. 1968. Ecological adaptions for breeding in birds. London, Methuen & Co.

MacLean, A. A. E. 1986. Age-specific foraging ability and the evolution of deferred breeding in three species of birds. Wilson Bull. 98: 267–279.

Nelson, J. B. 1966. The breeding biology of the Gannet *Sula bassana* on the Bass Rock, Scotland. Ibis 108: 584–626.

Nol, E., & J. N. M. Smith. 1987. Effects of age and breeding experience on seasonal reproductive success in the Song Sparrow. J. Animal Ecol. 56: 301–313.

Nur, N. 1984. Increased reproductive success with age in the California Gull: due to increased effort or improvement of skill? Oikos 43: 407–408.

———. 1988. The cost of reproduction in birds: an examination of the evidence. Ardea 76: 155–168.

Ollason, J. C., & G. M. Dunnet. 1978. Age, experience, and other factors affecting the breeding success of the Fulmar, *Fulmarus glacialis*, in Orkney. J. Animal Ecol. 47: 961–976.

———, & ———. 1986. Relative effects of parental performance and egg quality on breeding success of Fulmars *Fulmarus glacialis*. Ibis 128: 290–296.

———, & ———. 1988. Variation in breeding success in Fulmars. Pp. 268–278 *in* Reproductive success: studies of individual variation in contrasting breeding systems (T. H. Clutton-Brock, Ed.). Chicago, Univ. Chicago Press.

Penniman, T. M., M. C. Coulter, L. B. Spear, & R. J. Boekelheide. 1990. Western Gull. Pp. 218–244 *in* Seabirds of the Farallon Islands: ecology, structure and dynamics of an upwelling system community (D. G. Ainley and R. J. Boekelheide, Eds.). Palo Alto, Stanford Univ. Press.

Pierotti, R. 1981. Male and female parental roles in the Western Gull under different environment conditions. Auk 98: 532–549.

Pugasek, B. H. 1981. Increased reproductive effort with age in the California Gull (*Larus californicus*). Science 212: 822–823.

———. 1984. Age-specific reproductive tactics in the California Gull. Oikos 43: 409–410.

Reid, W. V. 1988. Age-specific patterns of reproduction in the Glaucous-winged Gull: increased effort with age? Ecology 69: 1454–1465.

Richdale, L. E. 1949. A study of a group of penguins of known-age. Dunedin, New Zealand, Biol. Monogr. No. 1.

Ryder, J. P. 1981. The influence of age on the breeding biology of colonial nesting seabirds. Pp. 153–164 *in* Behavior of marine animals. Vol. 4, marine birds (J. Burger, B. L. Ollan, and H. E. Winn, Eds.). New York, Plenum Publ. Co.

Saether, B. 1990. Age-specific variation in reproductive performance of birds. Pp. 251–283 *in* Current Ornithology, vol. 7 (D. Power, Ed.). New York, Plenum Publ. Co.

Searcy, W. A. 1978. Foraging success in three age classes of Glaucous-winged Gulls. Auk 95: 586–588.

Seber, G. A. F. 1977. Linear regression analysis. New York, John Wiley & Sons.

Spear, L. B. 1988. Dispersal patterns of Western Gulls from Southeast Farallon Island. Auk 105: 128–141.

———, H. R. Carter, T. M. Penniman, J. P. Penniman, & D. G. Ainley. 1987. Survivorship and mortality factors in a population of Western Gulls. Pp. 44–56 *in* Studies in Avian Biology, vol. 10 (J. L. Hand, W. E. Southern, & K. Vermeer, Eds.). Lawrence, Kansas, Allen Press.

Sydeman, W. J., J. F. Penniman, T. M. Penniman, P. Pyle, & D. G. Ainley. 1991. Breeding performance of the Western Gull: effects of parental age, timing of breeding, and year in relation to food availability. J. Animal Ecol. In press.

Thomas, C. S., & J. C. Coulson. 1988. Reproductive success of kittiwake gulls, *Rissa tridactyla*. Pp. 251–262 *in* Reproductive success: studies of individual variation in contrasting breeding systems (T. H. Clutton-Brock, Ed.). Chicago, Univ. Chicago Press.

Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. Am. Nat. 100: 687–690.

Wooler, R. D., J. S. Bradley, I. J. Skira, & D. L. Serventy. 1990. Reproductive success of Short-tailed Shearwaters *Puffinus tenuirostris* in relation to their age and breeding experience. J. Animal Ecol. 59: 161–170.