Studies in Avian Biology No. 10:44–56, 1987.

SURVIVORSHIP AND MORTALITY FACTORS IN A POPULATION OF WESTERN GULLS

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ABSTRACT.—During 1978–1986, we studied survival and mortality in a large, stable (or slowly increasing) colony of Western Gulls (*Larus occidentalis*) breeding on Southeast Farallon Island, California. We monitored breeding adults returning to the colony, and examined 2073 dead birds of all ages at the colony and on the California coast from Monterey to the Oregon border. During the eight years, annual survival rates of adults four to 19 years of age averaged 84% for males and 81% for females. Estimated survival rates of first-, second-, and third-year gulls were 55%, 79%, and 85%, respectively. The sex ratio of young at dispersal was 0.92 M/F, however the sex ratio of fourth-year gulls was 0.68 M/F due to higher starvation rates of first-year males, and higher accident rates (amplified by factors related to food shortage) of second- and third-year males. A tendency for higher mortality rates among breeding females was probably related to competition with the larger males during periods of food shortage.

Knowledge of age- and sex-related survival rates is fundamental to understanding the dynamics of avian populations. Many estimates of survival rates in long-lived species are suspect, however, because of problems associated with band loss and use of samples provided by the public (reviewed by Botkin and Miller 1974, Coulson and Wooller 1976, Anderson et al. 1985). To our knowledge, only four studies provide reliable information on survival rates of adult gulls (Parsons 1971, Coulson and Wooller 1976, Chabryzk and Coulson 1976, Coulson and Butterfield 1986). We know of no estimates of survival rates of gulls in their first year that were not extrapolated from band recoveries, where it was necessary to assume survival rates of subadults (second- and third-year birds) as equal to that of adults (Chabryzk and Coulson 1976, and references therein). Finally, we have found no quantitative estimates of the different mortality factors that affect age or sex composition of gull populations.

The age and sex composition of Western Gull (*Larus occidentalis*) populations are of particular interest because of the apparent excess of adult females in breeding populations (Hunt et al. 1980, Pierotti 1981), and implications that this is a major factor leading to the phenomenon of female-female pairing in this and other larid species (reviewed by Conover and Hunt 1984, Hunt et al. 1984; see also Coulson and Thomas 1985). Sayce and Hunt (1987) hypothesized that the skewed sex ratio was primarily a result of higher mortality rates of males which, because of their larger size, may have more difficulty than females in obtaining enough food, particularly during the first months of independence. We report here the results of a study designed to examine a population of Western Gulls breeding on Southeast Farallon Island (SEFI), 42 km west of San Francisco, California, where female-female pairing has not been found (Pierotti 1981). Our objectives were to determine the sex-ratio at hatching, age- and sex-related survival rates, and mortality factors acting on age/sex groups.

STUDY AREA AND METHODS

COLONY STATUS

The number of Western Gulls breeding on SEFI was much reduced during the early 1900s, increased to an estimated 23,000 by 1959 (Ainley and Lewis 1974), and then to about 26,000 birds by 1986 (Point Reyes Bird Observatory—PRBO, unpubl.). The present population may be the largest ever, as the gulls nest densely over most of the 44 ha island (Coulter 1973, Pierotti 1981), including extensive areas formerly occupied by pinnipeds (Ainley and Lewis 1974). The colony represents approximatey 40% of the world's population of this species (reviewed in Spear et al. 1986).

Over 25,000 Western Gull chicks (approximately 2000 each year) have been banded on SEFI since DGA initiated a gull-banding program in 1971 (several thousand others were banded during the 1960s). It has become apparent that the SEFI population is essentially closed. Although 300–400 Western Gull young were banded at several other northern California colonies from 1975 to 1984, none are known to have immigrated to SEFI. Moreover, all Western Gull colonies within 600 km of SEFI have less than 150 pairs (Sowls et al. 1980), and only four banded Farallon gulls are known to have emigrated to these colonies since 1975 (K. Briggs, R. Lowe, and R. Pierotti, pers. comm.; Spear, pers. obs.).

SEX RATIO AT HATCHING

In 1984, we collected 99 young (one from each nest) immediately after hatching. These included 33 young each from eggs laid first, second, and third in the clutch. All were sexed by gonadal inspection.

SURVIVAL RATES OF FIRST-, SECOND-, AND THIRD-YEAR BIRDS (PREBREEDERS)

Between July 1978 and February 1986, LBS made 41 censuses during which 919 dead Western Gulls were

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found along the Pacific coast from Monterey, California to the Oregon border. Censuses for dead birds were made during January (6), February (5), March (3), April (1), May (1), July (4), August (4), September (4), October (3), November (6), and December (4). No census was made in June. We define the seasons as: summer (Jun–Aug), fall (Sep–Nov), winter (Dec–Feb), and spring (Mar–May). Search effort was standardized by location; each census included all coastal dumps and fishing ports, and about 300 km of beach traversed by foot or automobile. All 919 gulls were fresh enough to be examined as described below (see Methods: Mortality Factors on the California Coast). For dead gulls found on the coast, we considered age classes including adult, third-, second-, and first-year birds. We distinguished age classes by plumage differences (see McCaskie 1983) and arbitrarily set hatching dates at 1 July (see Coulter 1973 for breeding chronology).

Mathematical relationships for estimating survival rates of prebreeders have not been derived for use with data such as ours (see above). Therefore, to estimate the annual survival rates (SR) of first-year gulls (SR^{0-1}) we derived the relationship

$$1 - \left[\frac{(M_a)(N_1)}{(N_a)(P)}\right],$$

where M_a is the annual mortality rate of adults breeding on SEFI, N_1 is the number of first-year gulls in the coastal sample, N_a is the estimated number of adults of breeding status in the coastal sample, and P is the annual productivity rate (no. of young dispersed) of a breeding Farallon adult. Because some adults did not breed, the total coastal sample of adults included both breeding and nonbreeding birds. Therefore, to determine N_a it was necessary to exclude from the coastal sample the percentage of adults that were nonbreeders (see Methods: Number and Sex Ratio of Nonbreeding Adults, and Results: Population Status). We used values of N_a and M_a from adult males only because the population of nonbreeding adult males was more easily estimated than was that of nonbreeding adult females. The relationship above is similar to that derived by Coulson and White (1959), but eliminates possible bias resulting from the assumption that mortality rates of subadults and adults are the same. Survival rates of second-year (SR^{1-2}) and third-year (SR^{2-3}) birds were estimated from the relationships

$$1 - \left(\frac{N_2}{R_2}\right), \quad \text{and} \quad 1 - \left(\frac{N_3}{R_3}\right), \text{ respectively,}$$

where N_2 and N_3 are the respective numbers of second- and third-year birds in the coastal samples, R_2 is the estimated number of gulls surviving their first year and therefore at risk during the second, and R_3 is the estimated number of gulls surviving their second year and therefore at risk during the third. R values were calculated as follows: $R_1 = N_1/1 - SR^{0-1}$, $R_2 = R_1 - N_1$, and $R_3 = R_2 - N_2$.

Because movement patterns of Western Gulls originating from Oregon and Washington populations vary between different age classes (Coulter 1975), we adjusted the coastal sample of dead gulls to exclude these birds. The number of "out-of-state" birds in the study area was estimated from population censuses (Pitman et al. in press, Speich and Wahl in press) together with an analysis of these gulls' movements (Coulter 1975). Assuming that their survival rates were similar to those of resident Western Gulls, this information indicates that Oregon and Washington birds constituted <1.0%, 6.0%, 6.0%, and 18.0%, respectively, of adult, third-, second-, and first-year gulls in our coastal sample. We also assumed that sedentary Western Gulls from southern California colonies (Coulter 1975) constituted an insignificant part of the sample. Finally, we assumed that movement patterns, survival rates and productivity of Western Gulls from other (non-SEFI) northern California colonies, which constituted 15% of the northern California population (Sowls et al. 1980), were not significantly different from that of Farallon gulls (see Coulter 1973, Briggs 1977, Bellrose 1983).

Survival Rates of Breeding Adults

Between 1978 and 1986, we monitored 231 individually marked adults during 611 gull-years as they returned to their breeding territories from year to year. Sexes of breeding adults were determined by observing copulations, courtship feeding of females, or size differences; males are larger than females, there being little overlap in weight between the sexes (Pierotti 1981). We have found no evidence for female-female pairing at SEFI (see Results; Sex-ratios among Independent Birds). Except for 28 birds monitored in 1978–1979 and 1979–1980, ages of each were known and included three- to 19-year-old gulls. All known-age adults had been banded as young with an individually numbered USFWS aluminum, or Lambournes incoloy, band on one leg and a polyvinyl chloride (Warner) color band on the other. A different color or leg combination has been used each year. Because of the high loss rate for aluminum bands after the third year (Spear 1980), birds that had received them were rebanded with highly durable stainless steel or incoloy bands prior to monitoring for survival rates. Each gull also received a new Warner band for which the loss rate is low (Spear 1980). Bands were color-coded with strips of plastic 3M Scotch tape to further facilitate recognition of individuals. In 1986, this tape was still present on nearly all bands.

Farallon gulls rarely skipped a year of breeding after recruiting into the breeeding population; birds that returned to the colony failed to breed in only eight of the 505 gull-years monitored (for reasons given below, 106 birds that failed to return are excluded). Nevertheless, with the exception of one bird, these nonbreeding gulls continued to maintain their territories or to frequent former territory locations. Each year we made band reading surveys throughout the colony in search of birds that no longer occupied their known territories to determine if they had established territories elsewhere. In only four instances did gulls select new nest sites that were more than 10 m from the original site. From 1978 through 1984, LBS also read bands of 2287 different adults at SEFI clubs and along the California, Oregon and Washington coasts. None of the adults that no longer occupied breeding territories was among them. During the course of the study, only one bird that was not seen in the year following a breeding year was seen subsequently in the colony. In view of the above, and

TABLE 1

ESTIMATED SURVIVAL RATES OF THE SEXES OF FIRST-, SECOND-, AND THIRD-YEAR WESTERN GULLS BASED ON COASTAL CENSUSES OF DEAD BIRDS, 1978–1986[a]

	No. of birds found dead on coast (N_i)		No. of birds at risk (R_i)		Survival rates	
Age class	Male	Female	Male	Female	Male	Female
First-year	213	179	426	459	0.50	0.61
Second-year	54	44	213	280	0.75	0.84
Third-year	29	25	159	236	0.82	0.89

[a] For method of calculating survival rates, see Methods: Survival Rates of First-, Second-, and Third-year Birds. For these calculations, N_a, the number of adults of breeding status found dead on the coast was 108 males, i.e., 16% less than the total number found (see Table 8) due to adjustment to exclude nonbreeding adults (see Results: Population Status). The mean annual mortality rate of breeding males (M_a) was 16% (see Table 3). The mean productivity rate (P) for the period 1978–1986 was 0.66 young per breeding adult (PRBO, unpubl.). Because of evidence indicating a female excess among fledglings (see Results: Sex Ratios of Young at Dispersal), the productivity figures used here were 0.630 for males, and 0.685 for females, i.e., 0.92 M/F produced.

the lack of emigration to other colonies, we assumed that all adults disappearing from the colony had died.

Life expectancy after the onset of breeding was estimated from the relationship

$$\frac{\sum_{i}^{n} [(N)(i)]}{\sum_{i}^{n} (N)},$$

where (i) is the number of years that a gull has bred, and (N) is the number of gulls surviving in the respective year of breeding (i). Our formula differs from that used by Lack (1954) because we consider age-related variation in survival rates, whereas Lack assumed a constant rate (see also Coulson and Wooller 1976).

NUMBER AND SEX RATIO AND NONBREEDING ADULTS

Breeding adults rarely attended clubs during the breeding season. During 1978 through 1984, LBS identified 980 breeding adults by reading their bands while they occupied breeding territories on SEFI. During the same period, he read bands of 623 adults at SEFI clubs; these included only 9 (1.4%) of the 980 identified breeders. Therefore, we considered the number of breeding adults at island clubs to be insignificant compared to the number of nonbreeders.

During the breeding season in all years from 1978 through 1986, counts of Western Gulls attending SEFI clubs were made during evening when numbers were highest. We estimated age-ratios of nonbreeding adults by censusing known-age (color-banded) birds, which composed 8–12% of the Farallon gull population), and adjusting counts of respective age classes for band loss (see Spear 1980). To determine sex ratios of nonbreeding adults, LBS first identified individual gulls at clubs by using a spotting scope to read the numbers on their metal bands. He then sexed 79% of these birds by comparing size differences; this sexing method has an accuracy of 95%, and error is not biased toward either sex (Spear 1981; see also Pierotti 1981, Hand 1986).

MORTALITY FACTORS IN CHICKS

During 1979 through 1986, we collected 658 dead young on SEFI and examined each, noting sex, body condition, and injuries or other ailments. Since the leg muscles of healthy, prefledged young are well developed by 10 d of age (but pectoral muscles are not), we considered a prefledged chick to have starved only if it had atrophied leg muscles, a criterion based on examination of chicks known to have starved. We assumed that young found emaciated as well as seriously pecked (the result of entering territories of non-related adults) had starved before they were pecked (see Fordham 1970, Ward 1973, Hunt and Hunt 1975).

MORTALITY FACTORS ON THE CALIFORNIA COAST

LBS examined 919 Western Gulls found dead along the northern coast of California, noting age, sex, body condition, and injuries or other ailments. Each was skinned and examined subcutaneously for wounds on the head and body. Examination of internal organs included opening and inspection of stomachs and proventriculi. Birds with no visible injuries or disease, but having atrophied pectoral muscles, were considered to have starved. Gulls with ailments that were not readily identified were frozen and later examined by veterinarians. We considered mortality factors of Western Gulls within the study area as representative of Farallon gulls because: (1) 85% of the Western Gulls that bred within this area bred on SEFI (Sowls et al. 1980), and most remain within the area (Coulter 1975); and (2) the number of Western Gulls from outside populations that move into this area is low (see above).

MORTALITY FACTORS IN ADULTS AT SEFI

Between 1978 and 1985, we collected 496 dead adults on SEFI during all seasons and examined each as described above for gulls found dead on the California coast. In 1983 and 1984, 33 adults that had died on SEFI during the breeding season (April through August) were collected at random and sent to the USFWS National Wildlife Laboratory (Madison, Wis.) for examination.

RESULTS

SEX RATIOS OF YOUNG AT HATCHING AND DISPERSAL

The sex ratio of 99 Farallon Western Gulls examined at hatching was 0.98 M/F. We did not

TABLE 2
SEX RATIOS AMONG PREBREEDING WESTERN GULLS FOUND DEAD ON THE NORTHERN CALIFORNIA COAST DURING FALL AND WINTER CENSUSES, 1978–1986

	First-year gulls		Subadults	
	Mean no. found per census	Sex ratio M/F	Mean no. found per census	Sex ratio M/F
1978–1979	26.0	1.17	13.0	1.60
1979–1980	48.5	1.26	12.0	1.18
1980–1981	26.0	1.26	12.5	0.92
1981–1982	27.5	1.20	9.0	1.25
1982–1983	61.0	1.35	14.5	1.07
1983–1984	20.5	0.95	11.0	1.44
1984–1985	23.0	1.09	7.0	1.80
1985–1986	19.5	0.95	8.0	1.00

TABLE 3
THE ANNUAL SURVIVAL RATES OF MALE AND FEMALE WESTERN GULLS BREEDING AT SOUTHEAST FARALLON ISLAND, 1978–1986[a]

At risk from-to	Males	Number monitored	Females	Number monitored
1978–1979	0.84	25	0.83	23
1979–1980	0.85	20	0.74	19
1980–1981	0.89	26	0.86	21
1981–1982	0.82	22	0.83	18
1982–1983	0.80	20	0.72	18
1983–1984	0.83	59	0.77	53
1984–1985	0.85	74	0.89	64
1985–1986	0.86	80	0.85	69
All years	0.84	326	0.81	285

[a] Survival rate estimates based on observations of banded breeding gulls monitored at SEFI (see Methods: Survival Rates of Breeding Adults).

find significant differences in the sex ratio among young hatched from first- (M/F = 0.74), second- (M/F = 1.20) or third-laid eggs (M/F = 1.06) (G test, $P > 0.05$), however, these results should be considered as preliminary because of small sample sizes. The SEFI ratios are similar to those of Western Gulls hatching in a southern California colony (Sayce and Hunt 1987), but opposite to results of Ryder (1983) who found a strong correlation between egg sequence and the sex of Ring-billed Gull (*L. delawarensis*) chicks, in which more males hatched from first eggs while more females hatched from second eggs.

The sex ratio of 658 chicks found dead during all phases of the chick period was 1.08 M/F. Sayce and Hunt (1987) also found evidence for a small excess of male chick mortality (0.89 M/F alive at fledging, n = 1291), apparently due to factors similar to those found during this study (see Results: Mortality Factors of Chicks). Although the M/F ratio in our sample was not statistically different from 1.0 (G test, $P > 0.05$), we assumed that the sex ratio of young dispersing from the Farallons colony was 0.92 M/F.

SURVIVAL RATES AMONG INDEPENDENT BIRDS

Estimates of mean annual survival rates of first-, second-, and third-year birds are given in Table 1. Females had significantly higher survival rates than males (G test; first-year, $P < 0.001$; second- and third-years, $P < 0.01$). The ratio of first-year males to females in coastal samples was highest in years when the greatest numbers of first-year birds were found ($r = 0.777$, df = 6, $P < 0.05$; Table 2). This indicates that when mortality was high it increased faster among males than females. This relationship was not found among second- and third-year gulls (subadults) $r = -0.338$, df = 6).

Annual survival rates of breeding adults are given in Table 3. Males had higher survival rates than females in six of eight years, although the difference was not significant (t test, $P < 0.2$). The regression of annual male survival rate (X) on female survival rate (Y) gives the relationship $Y = 1.354X - 0.330$. If male and female survival rates changed similarly, the slope of the regression should be 1.0, whereas it is 1.35, indicating a tendency (t test $P < 0.1$) for female survival rates to decrease more rapidly in years when survival is low. Thus, in years of greater mortality rates, the effect is proportionally greater among females. The regression indicates that survival rates of the sexes would be equal when the overall survival rate is 0.93.

Both sexes of first-year birds had significantly lower survival rates than respective sexes of second-year birds (G test, $P < 0.001$, Table 1). Survival rates of second-year males was significantly lower than that of adult males, and third-year females had significantly higher survival rates than adult females (G test, $P < 0.01$; see Table 3 for SR values of adults). Survival rates of younger breeding adults (3–8 years old) averaged higher than that of older breeders (9–19 years old), but the difference was not significant (t test; $P < 0.2$, Table 4). The tendency among different age classes of breeding birds is similar to that found in Kittiwakes (*Rissa tridactyla*), in which younger birds had significantly higher survival rates than older birds (Coulson and Wooller 1976).

SEX-RATIOS AMONG INDEPENDENT BIRDS

The age/sex-related survival rates indicate a female bias in sex ratios of each age class from one to 14-year-old birds (Table 5). The greatest female bias in sex ratios is expected for three- and four-year-old cohorts. Assuming that survival rates of gulls older than 19 years are similar to those of 9–19-year-olds, we estimated the sex

TABLE 4

THE ANNUAL SURVIVAL RATES OF "YOUNG" AND "OLD" WESTERN GULLS BREEDING ON SOUTHEAST FARALLON ISLAND, 1978–1986[a]

Years of age	Males	Gull yrs. monitored	Females	Gull yrs. monitored
Young (3–8 years)[b]	0.85	118	0.84	129
Old (9–19 years)	0.83	138	0.79	126

[a] Survival rate estimates based on observations of banded breeding gulls monitored at SEFI (see Methods: Survival Rates of Breeding Adults).

[b] These data include 6 gull-years of males that bred in their third year.

TABLE 5

SEX RATIOS AMONG DIFFERENT AGE CLASSES OF FARALLON WESTERN GULLS ESTIMATED FROM SURVIVAL RATES OF RESPECTIVE GROUPS (1978–1986)[a]

	Percent surviving		Sex ratio
Age	Males	Females	M/F
1	50.0	61.0	0.82
2	37.5	51.2	0.73
3	30.8	45.6	0.68
4	26.2	38.3	0.68
5	22.3	32.2	0.69
6	19.0	27.0	0.70
8	13.8	19.1	0.72
10	9.5	11.9	0.80
12	6.6	7.4	0.89
14	4.6	4.6	1.00
16	3.2	2.8	1.14
18	2.2	1.7	1.29
20	1.5	1.0	1.50
22	1.0	0.6	1.67
24	0.7	0.4	1.75

[a] Survival rates are calculated from coastal censuses of dead birds for age classes 1–3, and from observations of banded breeding adults for all remaining age classes (see Methods: Survival Rates of First-, Second-, and Third-year Birds, and Survival Rates of Breeding Adults).

ratio among the adult population at 0.77 M/F. This is similar to the female bias (0.67 M/F) observed among adults in another population of Western Gulls (Hunt et al. 1980).

In spite of a large excess of females in the adult population, we found no evidence of a bias in the sex ratio of breeding birds and no evidence of female-female pairing. Only one of the many thousands of nests examined over nine years contained a supernormal clutch (4 eggs), and we have not seen pairs of two female-sized birds. We assumed, therefore, that the sex ratio among breeding birds was unity, and expected to find a female excess among nonbreeders. Because the age that male Farallon gulls breed for the first time averages younger than that of females (M = 4.7 years, F = 5.6 years; Spear, unpubl.), we expected a sex ratio in the population of nonbreeding adults of 0.32 M/F. Within SEFI clubs, however, we found a female bias of lesser magnitude (0.48 M/F). This included 0.63 M/F for four-year-olds, and 0.35 M/F for birds >4 years. The discrepancy between predicted and observed values may have resulted from a greater tendency for nonbreeding females to remain away from SEFI compared to nonbreeding males (Spear 1981).

POPULATION STATUS

The evidence suggests that the number of gulls that attain breeding age should nearly equal that of adults that die, i.e., that the population status is relatively stable (Table 6). This conclusion is corroborated by the low incidence of emigration and stability in the breeding population. Limitations imposed by a shortage of unused breeding space could also be responsible for stability, however, in which case the status of the nonbreeding adult population should be the best indication of the population status as a whole. The censuses of nonbreeding adults in clubs show a gradual increase from 1978 through 1983, an abrupt decline in 1985, and partial recovery in 1986 (Fig. 1). The decline in 1985 apparently resulted from heavy recruitment of nonbreeders into the breeding population following two years of higher-than-average mortality among breeders (Table 3). These data indicate that the nonbreeding population has been only slightly greater than that required to replace breeding adults that have died (approx. 4550 per annum), and that on a long-term basis the nonbreeding population is relatively stable.

Based on the above, and coastal censuses showing small numbers of adults more than one foraging range (85 km; Hunt et al. 1979) from SEFI during the breeding season (LBS and DGA, ms), we estimate that the nonbreeding adult population averaged approximately 7500 birds per annum (1978–1986); i.e., composed 22% of the

TABLE 6

EXPECTED RATES OF REPLACEMENT OF BREEDING ADULT WESTERN GULLS AT SOUTHEAST FARALLON ISLAND

	Survival rate: fledging to recruitment[a]	Subsequent no. breeding years expected	Young dispersed/breeding adult/year[b]	No. progeny surviving to breeding age/adult dying
Males	0.24	6.2	0.630	0.94
Females	0.29	5.2	0.685	1.03

[a] The mean age of recruitment of males is approximately 4.7 years, and of females, 5.6 years (Spear, unpubl.).

[b] This value is the mean for the period of 1978–1986 (PRBO; unpubl., this study).

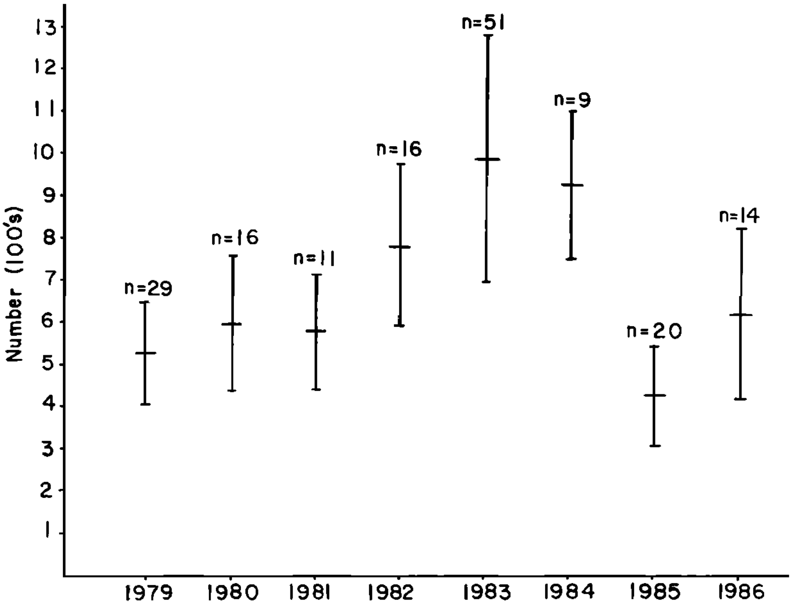

FIGURE 1: Evening counts of nonbreeding adult Western Gulls at clubs on Southeast Farallon Island, 1979–1986; "n" denotes the number of counts, central bar shows the mean, and bars above and below the mean show one standard deviation on each side of the mean.

adult population. Based on a sex ratio of 0.48 M/F in the population of nonbreeding adults (see preceding section), the adult male population (including an estimated 13,000 breeders) would include approximately 2440 (16%) nonbreeders (i.e., just enough males to replace breeders that die), and the adult female population, 5060 (28%) nonbreeders.

Mortality Factors among Chicks

The relative importance of mortality factors among chicks varied significantly during different months (G test, $P < 0.001$, Table 7; gulls dying from unknown causes were excluded from this analysis). In June, when most young hatched (Coulter 1973), starvation caused at least 50% of the deaths. In July, when young were highly mobile and beginning to fly, 54% of the deaths were due to pecking by adults. During the dispersal period of August and September, 91% of the dead young had starved. More male chicks starved when compared to females, while more females died from being pecked by adults (G tests, $P < 0.05$).

Conspecific predation is not usually common on SEFI, but appeared to be an important mortality factor during the El Niño year of 1983 when natural food was scarce and many chicks from one to 10 d old were eaten. We could not examine these chicks and assumed that predators were not sexually selective.

Mortality Factors on the California Coast

Starvation was a more important mortality factor among first-year gulls than among subadults (G test, $P < 0.001$, Table 8); 59% of the mortality of first-year birds was caused by this factor. The relative importance of different mortality factors did not vary significantly between subadults and adults (G test, $P > 0.05$, sexes were grouped and variables tested were starvation, disease, and combined accidents); most were accidental, with gunshot wounds ranking first. Broken wings, many of which probably resulted from gunshot, were also a major factor.

Starvation was a more important mortality factor among first-year males than among first-year females (G test, $P < 0.001$; Table 8). In contrast, there was a higher incidence of starvation among subadult and adult females (grouped) than respective age classes of males (G test, $P < 0.05$). During a given year, the percent of first-year males dying from starvation increased significantly as the number of first-year gulls found dead increased ($r = 0.727$, $df = 6$, $P < 0.05$; Fig. 2), and a similar relationship existed among subadult and adult females (grouped) $r = 0.792$, $df = 6$, $P < 0.02$; Fig. 3). A similar tendency among subadult and adult males was not significant ($r = 0.544$, $df = 6$, $P < 0.2$).

The number of subadults and adults (grouped) that died from accidental causes was highest in

TABLE 7
MORTALITY FACTORS IN 658 WESTERN GULL CHICKS ON SOUTHEAST FARALLON ISLAND, 1978–1986

		Starvation					
	N	Starved only (%)	Starved & pecked (%)	Total (%)	Pecked only (%)	Other (%)[a]	Unknown (%)
June							
Males	42	36	17	53	28	2	17
Females	36	35	11	46	31	6	17
July							
Males	133	14	22	36	53	0	11
Females	135	10	22	32	56	2	10
August							
Males	124	19	46	65	12	10	13
Females	120	21	36	57	23	5	15
September							
Males	43	93	0	93	0	7	0
Females	25	88	0	88	0	12	0
Overall							
Males	342	29	27	56	29	4	11
Females	316	23	25	48	36	4	12

[a] "Other" causes of mortality were broken wings, deformities, and entrapment within or between rocks, vegetation, debris and buildings.

years when the number dying from starvation was highest (males; $r = 0.816$, $df = 6$, $P < 0.02$, and females; $r = 0.793$, $df = 6$, $P < 0.02$, Fig. 4). Other evidence suggesting that starvation and accident rates were interrelated was the significant correlation of annual survival rates of adults (mortality due mostly to accidents) with that of first-year gulls (mortality due mostly to starvation) ($r = 0.924$, $df = 6$, $P < 0.002$, Table 9).

MORTALITY FACTORS IN ADULTS AT SEFI

The relative importance of mortality factors in adults found dead at SEFI varied significantly between seasons (G test, $P < 0.001$; sexes were grouped and variables tested were starvation, disease and combined accidents, Table 10). Lower rates of starvation occurred during spring, and lower accident rates during summer. The relative importance of mortality factors did not vary significantly between the sexes (G test, $P > 0.05$; seasons grouped with variables same as above). We could determine the cause of death, however, in only 36% of the cases. The cause of many undiagnosed deaths was probably Botulism C toxin. During all years we noticed that a large proportion of the gulls dying on SEFI during the

TABLE 8
MORTALITY FACTORS IN 919 WESTERN GULLS FOUND DEAD DURING ALL SEASONS ON THE COAST OF NORTHERN CALIFORNIA, 1978–1986, AND THEIR PERCENT VALUES

				Accidents					
	N	Starved	Diseased[a]	Broken wing	Fishing gear	Shot	Other[b]	Accidents combined	Unknown
First-year									
Males	260	68	0	13	3	4	8	28	4
Females	218	49	0	19	3	10	11	43	8
Subadults									
Males	88	23	3	17	8	29	17	71	3
Females	73	30	0	20	6	24	14	64	6
Adults									
Males	128	14	7	15	8	30	22	75	4
Females	153	27	6	24	1	24	14	63	4

[a] Diseases included gout, tuberculosis, and sinusitis. The incidence of aspergilosis was 70%, 68%, and 76%, respectively, among emaciated adults, subadults, and first-year gulls. Because this disease is a secondary infectant we did not consider it a mortality factor.

[b] Most common "other" accidents included plastic six-pack wrappers over head, poisoning, collision with automobiles and wires, entrapment in fish bins, oiling, and entanglement in machinery.

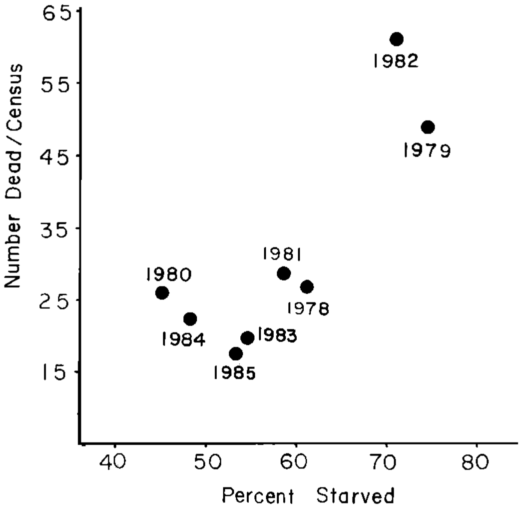

FIGURE 2. Percent of first-year males dying from starvation as a function of the number found dead during coastal surveys, 1978–1986.

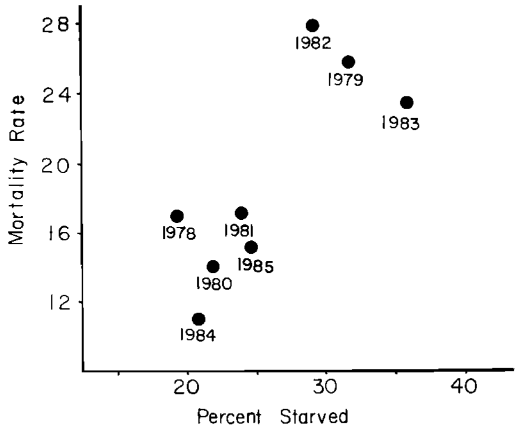

FIGURE 3. Percent of subadult and adult females (grouped) that died on the mainland coast from starvation as a function of the mortality rates of breeding females monitored on Southeast Farallon Island, 1978–1986.

breeding season developed symptoms of botulism. Tests on 33 gulls by the USFWS confirmed this; at least 42% of the gulls examined died from Botulism C toxin.

Mortality during the breeding season was not severe, however. Among 65 breeding adults that died while being studied during the five years including 1978–1980 and 1982–1985 (see Table 3), only 13%, 0%, 33%, 9%, and 0% ($\bar{x} = 11 \pm 12.1\%$), respectively, died during the spring and summer. Of the deaths that occured per annum, the proportion occurring during the breeding season varied significantly between years (G test, $P < 0.05$), being highest in years (1978, 1983) when food was apparently least abundant, i.e., in years when productivity of gulls and other seabirds breeding on SEFI was lowest (PRBO, unpubl.). Years of exceptionally low food availability are infrequent, however, as only three such years have occurred during the last 16.

Chronology of Coastal Mortality

Recovery rates of dead Western Gulls on the northern California coast peaked during winter in all age classes, although that of first-year gulls and adults was bimodal, with smaller peaks occurring in the fall (Fig. 5).

Additional evidence suggests that these patterns are realistic: This includes: (1) close agreement between the percent of dead adults we found on the coast during the breeding season and the percent of annual deaths in that same period among known adults monitored for survival on SEFI; 12% on the coast vs. 11% on SEFI; and (2) a significant correlation in numbers of dead adults found per annum during coastal searches with that of mortality rates among known adults monitored on SEFI ($r = 0.735$, $df = 6$, $P < 0.05$, Table 9).

The mortality patterns in Figure 3 are different from ones derived from band recoveries, which show peak recoveries in late summer (Coulter 1975). These differences may have resulted from several factors. First, the general public is most active during spring and summer, especially at

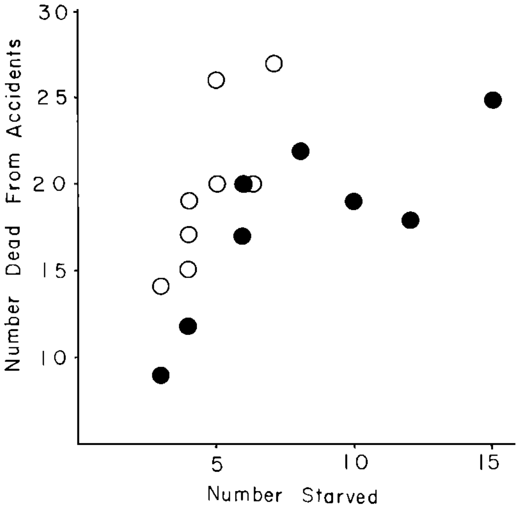

FIGURE 4. Mortality on the mainland coast: number of subadult and adult Western Gulls (grouped) that died from accidents as a function of the number dying from starvation, 1978–1986. Solid circle = females, open circle = males.

TABLE 9
THE ESTIMATED ANNUAL SURVIVAL RATES OF FIRST-YEAR WESTERN GULLS FROM SOUTHEAST FARALLON ISLAND, 1978–1986[a]

Year	No. of 1st-yr. gulls found dead (N_1)	No. of breeding adults found dead (N_a)	Young dispersed/ breeding adult/year[b] (P)	Survival rate of adults[c] ($1 - M_a$)	Est. survival rate of 1st-yr. gulls (SR^{0-1})
1978–1979	22	16	0.52	0.83	0.55
1979–1980	79	31	0.81	0.79	0.34
1980–1981	42	28	0.72	0.87	0.73
1981–1982	45	27	0.54	0.83	0.48
1982–1983	100	39	0.90	0.76	0.32
1983–1984	34	33	0.33	0.80	0.38
1984–1985	38	20	0.67	0.87	0.63
1985–1986	32	23	0.76	0.85	0.73

[a] See Methods: Survival Rates of First-, Second-, and Third-year Birds, for method of calculating survival rates.
[b] PRBO (unpubl. data).
[c] Survival rate values ($SR = 1 - M_a$) represent the mean between males and females (Table 8).

beaches where, during those respective seasons, we found the majority of dead gulls (see also Kadlec and Drury 1968). Moreover, during fall and winter, when the public is less active, we found the majority of dead gulls at dumps. Even if search efforts by the public were consistent over time, people are less likely to examine a dead gull in a dump than a dead gull on the beach. Another bias for adult gulls may have resulted from using band recoveries from SEFI, especially those from August and September when biologists regain access to the entire island. (Activities are restricted near to paths during the breeding season.) Many birds that died throughout the breeding season are then inspected, and this may have biased band recovery rates towards late summer. For example, we found nearly twice as many dead adults on SEFI during the breeding season than we found on the coast during all seasons, although only 11% of the mortality of known breeding adults occurred during the breeding season. Third, the temporal pattern of mortality may have changed since the period (1933–1971) when the band recovery information used by Coulter (1975) was accumulated.

DISCUSSION

When production of one sex is more costly than another, selection should favor the production of unequal sex ratios (reviewed by Meyers 1978). In applying this hypothesis to species of birds which are sexually dimorphic in size (such as Western Gulls; Pierotti 1981) and that breed in food-limited environments, Meyers predicted that the larger sex should have lower survival rates due to starvation in the nestling stage. This

TABLE 10
MORTALITY FACTORS AMONG 496 ADULTS FOUND DEAD AT SOUTHEAST FARALLON ISLAND, 1978–1985, AND THEIR PERCENT VALUES

				Accidents				
	Gulls examined (N)	Starved	Diseased[a]	Broken wing	Shot	Other[b]	Accidents combined	Unknown
Fall–winter								
Male	55	24	9	0	0	16	16	51
Female	57	37	5	5	2	9	16	42
Spring								
Male	40	17	5	3	2	10	15	63
Female	68	7	3	1.5	3	1.5	6	84
Summer								
Male	135	25	4	0	0	1	1	70
Female	141	30	5	0	1	1	2	63
Total								
Male	230	23	5	<1	<1	6	<8	64
Female	266	26	4	1	2	3	6	64

[a] Diseases included gout, tuberculosis, and sinusitis.
[b] "Other accidents" included oiling, broken beak, and entanglement with fishing tackle and six-pack wrappers.

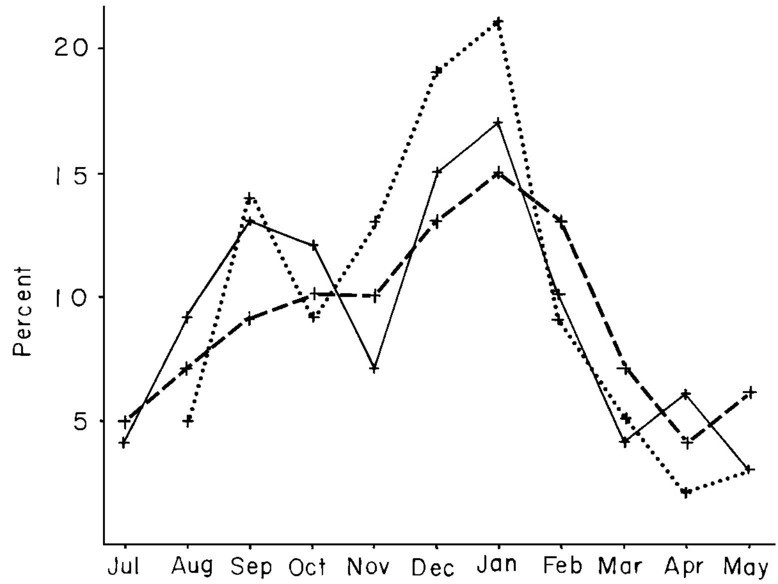

FIGURE 5. Chronology (by month) of mortality in three age classes of Western Gulls on the northern California coast, 1978–1986. Solid line = adults (4 yrs and older), dashed line = subadults (second- and third-year birds), and dotted line = first-year birds. Values are given as the mean number of birds found per monthly census expressed as the percent of the mean annual total (no coastal searches in June).

was demonstrated in icterids and corvids (reviewed by Meyers 1978, Roskaft and Slagsvold 1985) but was not found for other species (reviewed by Sayce and Hunt, 1987). Nevertheless, before assessing the importance of selective factors operating differentially upon the sexes, survival rates and mortality factors among all age groups must be studied (Meyers 1978). Our study is the first to attempt this in an avian species. We have found additional support for Meyers' prediction, as well as evidence that other selective factors act differentially on sexes of all age groups. In the following discussion these various factors are evaluated.

The evidence indicates that food available to Farallon gull chicks was often in limited supply. During this study at least 29% of all young hatched, died before dispersing (PRBO, unpubl.). Since 52% of the dead chicks had starved (Table 7), it follows that at least 15% of all young hatched died from this factor. Similarly, data from Coulter (1977) indicated that 19% of the Western Gulls hatched on SEFI during 1969–1970 died as a result of "food limitation." The higher rate of starvation among male chicks does support Meyers' (1978) prediction, but interestingly, did not result in a significantly biased sex ratio prior to dispersal because of higher mortality rates among females from attacks by adults. Death from pecking (by unrelated adults) was most frequent in July when recently fledged young (with poor flight control) frequently landed on territories other than their own. Fledgling females average smaller in size than males (Sayce and Hunt 1987), and thus their greater mortality during fledging may have resulted from being less able to withstand adult attacks as they returned to their territories. In colonies of low density this may not be an important mortality factor because, with larger territories, young have a better chance of landing on their own territory. This could explain a smaller female bias in the sex ratio of Farallon young at dispersal (0.92 M/F) compared to that of Western Gull young on Santa Barbara Island, California (0.89 M/F; Sayce and Hunt 1987), where territories average 15 times larger than territories on SEFI (Hunt and Hunt 1975, Pierotti 1981). Nevertheless, the higher starvation rate among male chicks on SEFI suggests that many may have been in poorer physical condition than females when they dispersed, and this could, in part, explain the higher mortality rates of first-year males after dispersal. Possible advantages gained by females during the chick period, however, probably diminish by fall. When mortality peaked during the winter, survival was probably most dependent on foraging skills. It is likely, therefore, that lower survival rates of first-year males resulted primarily from their need to meet higher energy demands (due to larger body size) before foraging skills were sufficiently developed (see also Sayce and Hunt

1987). (For review of age-related foraging success, see Briggs 1977, Verbeek 1977, Searcy 1978, Burger 1981.) In some sexually diomorphic species the larger sex also fledges at a lower percent of the adult weight (Ricklefs 1968, Bancroft 1984). As a result, independent young of the larger sex are at a disadvantage; besides meeting higher energy demands for maintenance they must grow more, proportionally, to attain adult size.

Although nearly 50% of the deaths of independent males less than four years old occurred during the first year as the result of starvation, the greatest biasing of the sex ratio occurred during the second and third years due to accidents involving humans. It is important to note, therefore, that accident and starvation rates were correlated. This suggests that food limitation was a more important factor than indicated by starvation rates alone; gulls are probably bolder when hungry. But why would subadult males be more prone to death from starvation and accidents than females if foraging skills were improved and, because of larger size, they held an advantage over females when competing for stationary food sources (i.e., human refuse; see Briggs 1977, Monaghan 1980)? One possibility is that males may be bolder than females and thus more prone to accidents. Another possibility is that this could be related to the tendency for subadult females to remain farther away from SEFI than subadult males (Spear 1981). The majority of subadult males remain within foraging range of adults and may, therefore, be more prone to higher stress related to competition for food.

The tendency for a higher survival rate of breeding males compared to breeding females (Table 3) is interesting. Coulson and Wooller (1976) found higher survival rates among female Kittiwakes and suggested that greater mortality among males resulted from stress associated with territory establishment. Although territory establishment is also primarily the responsibility of male Western Gulls (Pierotti 1981, Hand 1986), the tendency for lower survival rates of Farallon females was probably due to differences in ability to make use of local foraging opportunities. Pierotti (1981) found that females caring for young take longer than males to complete foraging trips and return with lighter food loads. The reason is not known, but this suggests that females would be at a disadvantage during times of food shortage. Competition for food among adults did, in fact, appear severe during late fall and winter of some years when many foraged up to 70 km from SEFI at San Francisco Bay Area (SFBA) dumps (Spear 1979). At this time, most adults forage in the vicinity of SEFI to maintain territories (males) and mates (females). During these period, females from SEFI had to compete for a stationary food source not only with male Western Gulls, but also with even larger Glaucous-winged Gulls (*L. glaucescens*) which compose up to 50% of the large larids foraging in the SFBA during winter (Cogswell 1969, Spear unpubl.). Moreover, competition in the SFBA has probably increased between 1979 and 1986 due to the closure of three of the six dumps most important to large larids. The high winter mortality of adults and sharper decrease in survival rates with increases in the incidence of starvation of SEFI females suggests that the above discussion is applicable. It is interesting that in British populations of Herring Gulls that were increasing at 12% per annum (i.e., little evidence of food shortage), no difference was found between survival rates of the sexes (Chabrzyk and Coulson 1976, but see Coulson and Butterfield 1986). These gulls were experiencing a survival rate of 0.93, equal to the projected value for Farallon gulls when survival rates of the sexes should be equal.

In conclusion, it appears that sexual differences in the survival rates of Farallon gulls are determined primarily by three factors: higher rates of starvation among first-year males, higher incidence of accidents among subadult males (amplified by factors related to food shortage), and a tendency for higher rates of starvation in breeding females. If larid populations are, in fact, often limited in size by food (see Lack 1954, Ashmole 1971, Furness and Birkhead 1984, Coulson and Thomas 1985), our results suggest that a shortage of males can be expected in many populations and that this may not be a recent phenomenon. This could explain instances of female-female pairing and polygamy in these otherwise monogamous species (Conover and Hunt 1984, Coulson and Thomas 1985), although other factors may affect sex-ratios in some populations (see Fry and Toone 1981; Fry et al., 1987). In the case of the SEFI population, the absence of female-female pairs may result from high density nesting where the smaller females cannot compete with males for breeding territories (Hand 1980, Conover and Hunt 1984).

ACKNOWLEDGMENTS

We thank the San Francisco chapter of the Oceanic Society for transporation to and from SEFI. The USFWS allowed our research on the Farallon National Wildlife Refuge and provide invaluable assistance in examining mortality factors; we especially thank R. Lowe and R. K. Stroud, D.V.M. Other persons who advised on mortality factors or examined gulls include D. M. Fry, L. Lowenstein, D.V.M. (University of California, Davis), and P. Quinn (Monterey County SPCA). Dr. J. Martin (Moss Landing Marine Laboratories) and M. R. Graybill, (Oregon Institute of Marine Biology) provided LBS with facilities for examining dead gulls he found on the coast. We are grateful to them, and to R. J. Boekelheide, R. P. Henderson and the many Farallon volunteers who collected carcasses on SEFI. Logistical support for coastal work was provided by J. C. and E. B. Spear, and S. Goldhaber kindly typed the final draft. This paper was much improved by the comments of M. C. Coulter, D. M. Fry, J. L. Hand, G. L. Hunt, Jr., and C. A. Ribic. Spear was funded in part by a Packard Foundation grant administered through Moss Landing Marine Laboratories. This is PRBO contribution no. 330.

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