

## REPRODUCTIVE COMMITMENT AND SUCCESS OF CASSIN'S AUKLET

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Reproductive commitment is the sum of all efforts put directly into the production of offspring (Cody 1971). These efforts can be discussed for birds in terms of the following factors: clutch size, duration of breeding season, number of broods per season, replacement clutches, nesting success, nestling growth rate, post-fledging survival, age at first breeding, and adult survival.

Because these factors are strongly influenced by natural selection, one should expect differences in the commitment of birds nesting under different environmental circumstances. For seabirds, the most important aspects appear to be timing of breeding, nest-site location, vulnerability to predation, and availability of food. The purpose of this paper is to evaluate the effect of these and other variables on the reproductive commitment and success of a Cassin's Auklet (*Ptychoramphus aleuticus*) population.

Cassin's Auklet is the only plankton-feeding auklet to occupy the southeastern Pacific coast of North America. Normally, it visits colony sites only at night. A permanent pair bond and strong nest-site tenacity are apparently characteristic. Cassin's Auklets have a range of nest-site types, and at most colonies nests are found in both burrows and rock crevices. On the Farallon Islands, for instance, 51% of the auklets nest in rock crevices, whereas 49% nest in burrows excavated in soil. Nesting density varies from 0 to 1.1 nests/m<sup>2</sup> (Manuwal 1974a).

This species lays a single creamy-white unmarked egg that is about 16% of adult body weight (168 g). The mean incubation period is 38 days, and the mean nestling period 41 days. The young are semi-precocial and are brooded by one of the parents for the first five to six days (Manuwal 1974b). The nestling fledges by flying directly to the ocean from the vicinity of the nest.

### STUDY AREA AND METHODS

I conducted my study on Southeast Farallon Island (37°04'N), a 44-ha granitic island located 43 km west of San Francisco, California (for description see Manuwal 1974b, Ainley and Lewis 1974). I spent 42 weeks conducting field work on the island from March 1969 through August 1971 and obtained data from ten 625-m<sup>2</sup> plots varying in topography and auklet breeding density. In 1969, I checked 420

burrows during the breeding season, 386 burrows in 1970, and 352 in 1971. Reproductive data are available for 1970 and 1971 only. Each burrow was marked with a numbered stake placed near the entrance during the pre-egg stage. When nest chambers were not easily accessible from the entrance, I excavated the burrows and fitted them with 20 × 30 cm rectangular masonite covers. Such excavations resulted in little, if any, disturbance to the birds since auklets are absent from burrows during the day early in the reproductive cycle, the time when the excavations were made.

Burrows were checked and some birds banded throughout the breeding cycle. Once an egg was laid, I did not check the burrow again until mid-way through incubation because three or more burrow examinations during this period usually cause the incubating bird to desert the egg. Some of the losses of first eggs, both in 1970 and 1971 resulted from my disturbance, but I do not believe they accounted for more than 5% in either year. Visits were made at 14- to 21-day intervals to check incubation. Nestlings were banded and measured daily after the parents had ceased continuous brooding.

Auklets were captured in a 20 × 5 m fish net (1.25-cm mesh) stretched between two 5-m poles (Ralph and Sibley 1970) during the departure flight, which occurred 1 to 1.5 h before sunrise. They were then banded with regular U.S. Fish and Wildlife Service aluminum bands (sizes 3 and 3A). I used a night vision scope to observe nocturnal behavior and predation.

Auklets carry food to the nestling in a sublingual pouch (Speich and Manuwal 1974). Food samples (n = 22) were collected during the chick-rearing period by methods described by Manuwal (1974b). Growth of nestlings was measured daily by weighing chicks with a Pesola scale and recording linear measurements of culmen, tarsus, and wing.

Thoresen (1964) and Manuwal (1972) reported that iris color can be used to separate adult and subadult Cassin's Auklets. The following criteria were used to evaluate age classes: adults (at least three years old) have a white iris; subadults have white irides with a brown periphery; fledglings have a dark brown iris.

I attempted to measure gull predation in 1970 by systematically collecting all auklet remains in 13 different areas of the island. All remains were collected, but only wings were counted and used to determine the ages of dead young. All were assumed to be the result of gull predation. Auklet burrow density and the number of gulls occupying each area were determined.

I measured soil depth at randomly selected locations in each study plot. A steel rod marked in centimeters was pushed into the ground until it could not be forced any deeper.

In discussing the complex egg-laying characteristics of this population, it is necessary to distinguish four categories of eggs. *First-clutch eggs* are those laid at the beginning of the reproductive cycle and are considered to be the first egg laid by a given auklet pair during the breeding season. *Replacement eggs*

TABLE 1. Egg-laying characteristics during 1970 and 1971.

Category	1970	1971
First-clutch eggs:		
Number observed	362	316
Median egg date	14 April	24 March
Extreme egg dates	6 April–23 May	5 March–10 May
Interval	47 days	65 days
Replacement eggs:		
Number observed	35	56
Median egg date	24 May	12 May
Extreme egg dates	26 April–11 June	3 April–6 July
Interval	46 days	94 days
Percent attempting replacement egg	10	15
Second-clutch eggs:		
Number observed	2	89
Median egg date	—	22 June
Extreme egg dates	—	27 May–19 July
Interval	—	53 days
Percent attempting double brooding	1	30
Total extreme egg dates (earliest first clutch to latest second clutch)	66	134

are those laid by auklets that have either lost or deserted their first clutch egg. *Second-clutch eggs* are those laid by auklets that have already raised a first brood chick during the same breeding season (double broodedness). Finally, *unincubated eggs* are those laid in burrows or on the ground surface but never incubated.

## REPRODUCTIVE EFFORT AND SUCCESS

### EGG-LAYING SYNCHRONY

Courtship behavior during the three years began around December and reached a peak in March and April. In the 1970 and 1971 seasons, egg-laying extended from March or April through June and the nestling period from April to September; a period of heavy molt occurred from June to November (Udvardy, Speich, and Manuwal, unpubl. data).

The general features of the 1969 and 1970 breeding cycles differed from those of 1971. First clutches were laid significantly earlier in 1971 than in 1970 ( $t = 2.80$ ,  $P < 0.05$ ; Table 1, Fig. 1). The number of replacement clutches laid in 1970 and 1971 were similar; however, a major difference between the two years was the large number of second clutches laid in 1971 (Table 1). This had the effect of doubling the spread of egg-laying from 66 days (1970) to 134 days (1971).

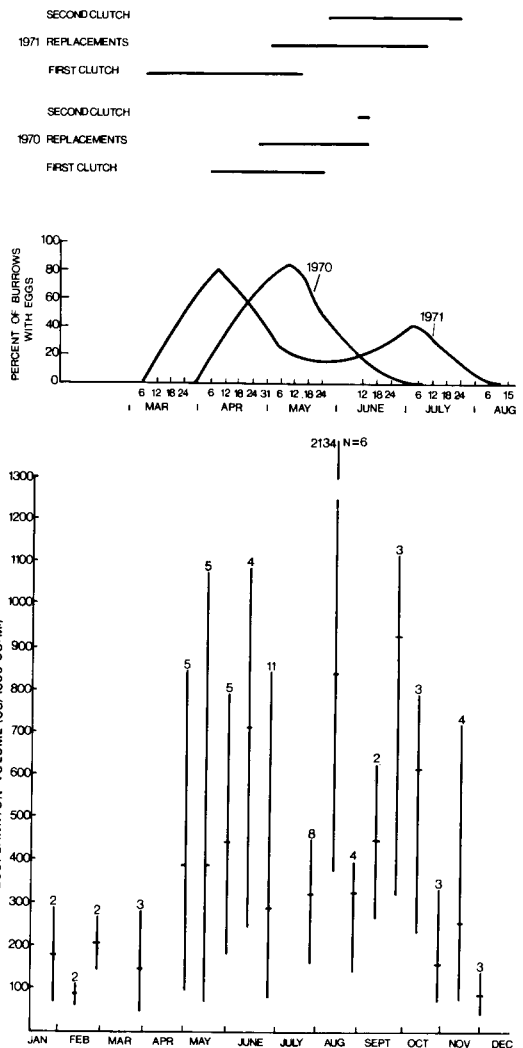


FIGURE 1. Distribution of egg-laying (1970–1971) of Cassin's Auklet and zooplankton volumes (1949–1969) in the vicinity of the Farallon Islands. Vertical lines represent ranges; horizontal lines are mean zooplankton volumes.

TABLE 2. Reproductive status (as percent of total number of burrows checked) of auklets in study plots and randomly selected "control" burrows on 8 June 1971.

Status	Study plots (n = 358)	"Control" burrows (n = 150)
Eggs	15.4	19.4*
Chicks	39.2	37.5
Empty	45.4	43.0

\* Differences are not statistically significant ( $\chi^2 = 1.08$ ,  $P > 0.05$ ).

Synchrony of the first clutch differed among the study plots in 1970 and 1971. The spread in laying dates for the middle 80% of eggs in each plot was used to assess egg-laying synchrony (see Coulson and White 1960). In general, laying was significantly less synchronous in 1971 than in 1970 ( $t = 2.80$ ,  $P < 0.05$ ). In 1970 the mean spread of egg dates was only 17.1 days, while in 1971 it was 23.4 days.

In an attempt to evaluate my effect on the reproductive performance of auklets, I compared data from 358 burrows in study plots with data from 150 randomly selected burrows, which were checked on 8 June 1971. Reproductive performance between birds in the two groups of burrows did not differ significantly (Table 2).

#### REPLACEMENT CLUTCHES

Ability to lay replacement clutches was studied experimentally in 1970. Freshly-laid eggs were removed from nests in two plots ( $n = 20$  and  $21$ ), and the incubating adults were banded. On subsequent checks of each burrow, I learned whether a second egg was laid. Most replacement eggs were laid 15 to 28 days after the first was removed (Table 3), though the exact interval was not determined. In all cases where the burrow remained intact, birds continued occupancy even though I removed their egg.

Under natural conditions, replacement eggs were also documented in 1970 and 1971. In 1970, 8.5% (34 of 399) of the pairs lost first eggs and 10% of these laid a replacement. The interval between egg loss and replacement for 4 pairs was 10, 11, 14, and 24 days.

#### REPRODUCTIVE SUCCESS

Reproductive success is defined here as the percentage of all eggs that result in fledged young. An additional measure of productivity is the reproductive rate. This refers to the number of fledglings produced per occupied burrow and is especially pertinent to Farallon

TABLE 3. Replacement clutch attempts of pairs of auklets subjected to induced desertion.

No. burrows marked	41
No. originally occupied	41
No. replacement attempts	22
No. new pairs	3
No. burrows destroyed	6
Percent replacements	54

auklets, since they lay replacement and second clutches.

In both 1970 and 1971, auklets who attempted to breed after their first clutch attempt were generally less successful. Heaviest losses occurred during incubation, 15.8% in 1970 and 35.7% in 1971 (Table 4). The high losses in 1971 can be attributed to the high desertion rate (56.4%) among pairs attempting to raise a second chick. Burrow collapse and infertile or cracked eggs also contributed to nesting failures. Failures due to nestling mortality accounted for only 8.9% in 1970 and 10.3% in 1971. These losses were usually caused by gull predation, starvation, or the death of a parent. I did not witness the actual fledging of chicks, but I assumed fledging was successful if the chick was near the fledging weight of about 115–150 g and age of 41–48 days just prior to its disappearance.

The significant features of the 1971 breeding season are that auklets were more successful in the first breeding attempt than in 1970 and that a large proportion (about one-third) of the population attempted to raise a second brood. Despite the large number of replacement and second clutches attempted in 1971, there is no significant difference ( $P > 0.05$ ) between the number of fledglings per burrow in 1970 (0.57) and in 1971 (0.52). The very high desertion rate and nestling mortality among birds who attempted double brooding in 1971 prevented these attempts from significantly adding to the total reproductive output.

#### FACTORS AFFECTING REPRODUCTIVE SUCCESS

*Food.* The primary prey of auklets during the 1971 chick period were microplanktonic euphausiid crustaceans (Manuwal 1974b). The most common species in 22 food samples was *Thysanoessa spinifera*, followed in relative weight contribution by hyperiid amphipods (*Phromema* sp.), larval squid (identity unknown), a decapod crab (*Cancer* sp.?, megalop stage), and another euphausiid (*T. longipes*). These animals comprise the major portion of the plankton community in Cali-

TABLE 4. Breeding success of Cassin's Auklets on Southeast Farallon Island, California, during 1970 and 1971.

	First clutch		Replacement		Second clutch		Total	
	N	%	N	%	N	%	N	%
Birds attempting								
1970	399		35		2		436	
1971	265		56		95		416	
Lost before incubation								
1970	34	8.5	—	—	0	0	34	7.8
1971	0	0	0	0	0	0	0	0
Lost during incubation								
1970	67	16.8	—	—	2	100	69	15.8
1971	73	27.5	22	39.3	48	50.5	143	34.4
Lost during nestling period								
1970	39	9.8	—	—	—	—	39	8.9
1971	15	5.7	6	10.7	22	23.2	43	10.3
Fates unknown								
1970	37	9.3	10	28.6	0	0	47	10.8
1971	—	—	5	8.9	10	10.5	15	3.6
Number successful								
1970	222	55.6	25	71.4	0	0	247	56.7
1971	177	66.8	23	41.1	15	15.8	215	51.7

formia offshore waters. An analysis of variation in their seasonal and annual abundance may help to explain differences in auklet reproductive effort. Figure 1 shows an index to micronekton biomass (cc/1000 m<sup>3</sup> of water sampled) based on 20 years (1949–1969) of sampling (Thraillkill, pers. comm.) near Southeast Farallon Island (California Cooperative Oceanic Fisheries Investigations [CAL-COFI] Station, 37°N, 123°37'W). Since there was no significant difference between the amount of nekton in the day and night samples ( $t = 1.02$ , d.f. = 19), data were pooled to construct this diagram. Nekton volume increased between April and September, usually consist-

tently from early March to late May but with great fluctuations thereafter.

*Timing of breeding.* First clutches laid before the population's mean laying date were the most successful (Fig. 2). After that date, success decreased rapidly. When birds attempted a second clutch, however, eggs laid up to 20 days before the mean date were unsuccessful. Even auklets laying immediately before the mean date were only 30%–40% successful. Interestingly, all auklets laying at the mean date and later failed to fledge young.

For the first 36 days, the instantaneous growth rate of first-clutch nestlings averaged

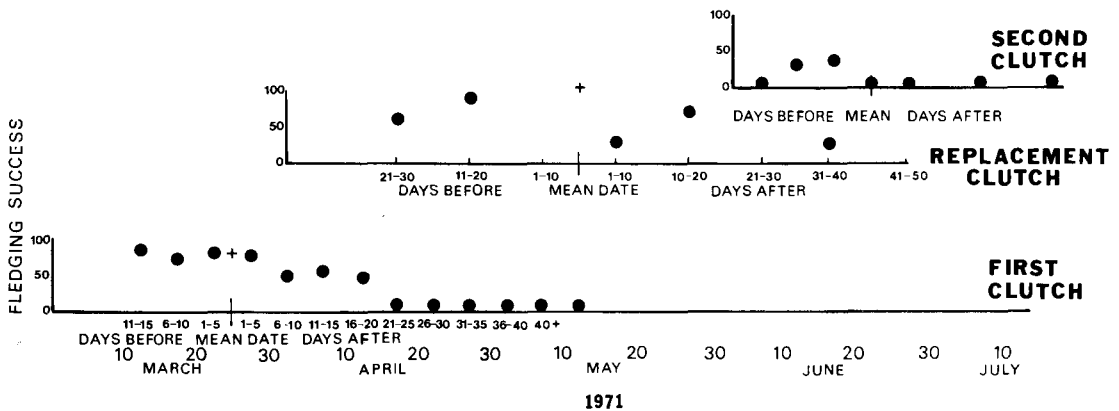


FIGURE 2. Fledging success of auklets attempting first, replacement, and second clutches during 1971.

TABLE 5. Growth and fledging values for first and second broods of Cassin's Auklets on Southeast Farallon Island.

	Brood (sample size)	
	First	Second
Instantaneous growth rate (for first 36 days in percentage)	6.5 (19)	4.9 (10)
Fledging weight (g)*	150.5 (11)	115.0 (10)
Percent of adult weight*	90 (11)	70 (10)
Length of nestling period (days)*	41.1 (11)	48.8 (10)
Mean fledging date	25 May	9 August

\*  $P < 0.01$  between first and second broods.

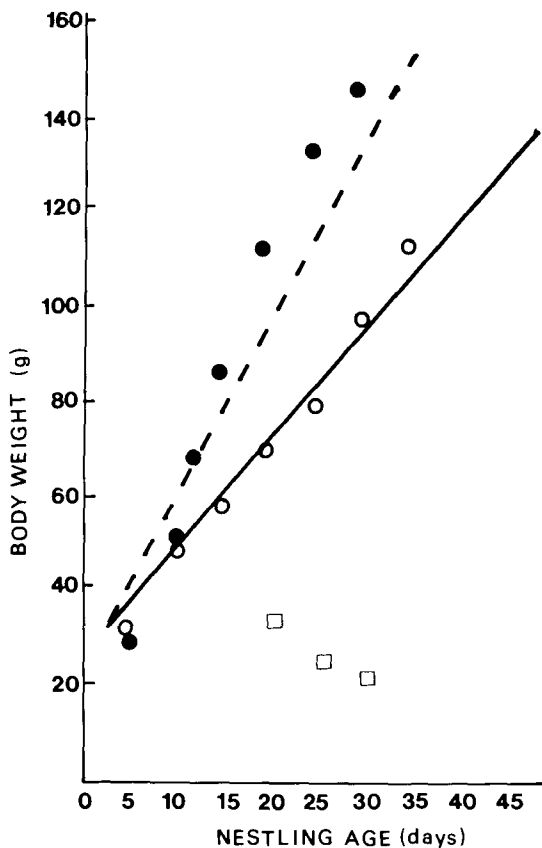


FIGURE 3. Growth rates of nestling Cassin's Auklets during 1971. Lines were fitted by least squares regression analysis. Data for the first brood are represented by the dashed line and solid circles, and the second brood by the solid line and open circles. The open squares resulted from measurements of floater broods.

6.5%/day and for second-clutch young averaged 4.9%/day (Fig. 3 and Table 5). First-brood young were significantly heavier at fledging than were second-brood young ( $t = 5.74, P < 0.01, d.f. = 23$ ). Nestlings of second broods were also significantly older at fledging than those of first broods ( $t = 5.00, P < 0.01, d.f. = 24$ ).

*Annual weight cycle.* Figure 4 shows the long-term annual weight cycle of auklets captured on Southeast Farallon Island from April 1968 to August 1971 (Point Reyes Bird Observatory, unpubl. data). The standard deviations indicate much variability in auklet weights during any particular month (see also Fig. 5). For instance, auklets entered the egg-laying period averaging 181 g in 1968, 169.8 g in 1969 and 173.8 g in 1970. This variation is less among auklets after nestlings have fledged (i.e., late July and August). Adult weights averaged 164.9 g in 1968, 167.6 g in 1970 and 161.6 g in 1971.

Within a single breeding season, auklets

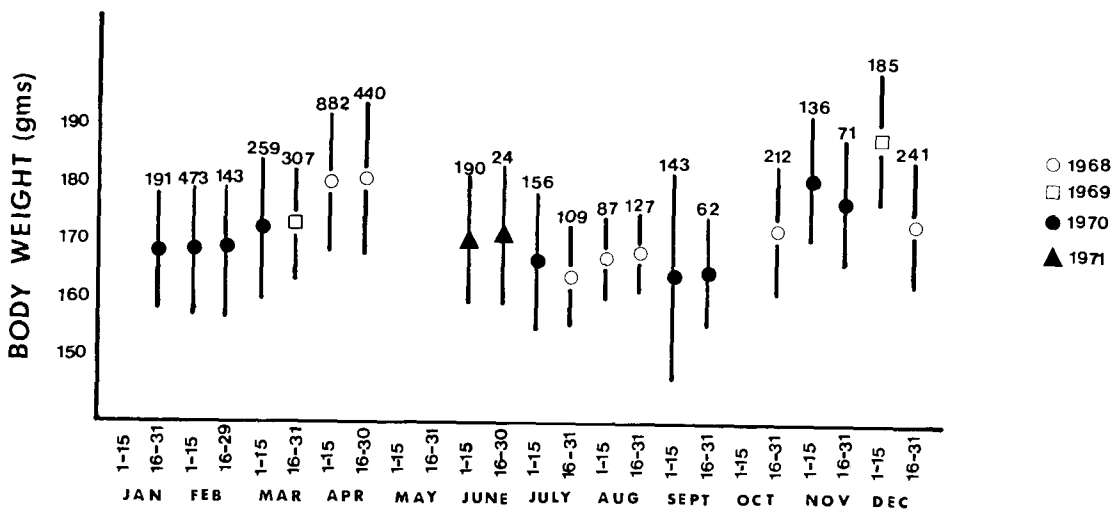


FIGURE 4. Body weights of adult Cassin's Auklets during the period 1968-1971. Vertical lines represent one standard deviation from the mean. Numbers above lines are sample sizes.

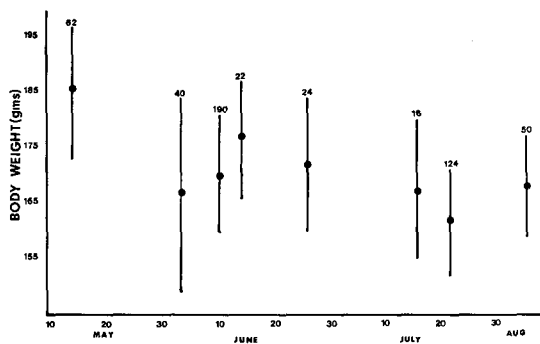


FIGURE 5. Body weights of adult Cassin's Auklets during the nesting season of 1971. Vertical lines represent one standard deviation from the mean. Numbers above lines are sample sizes.

gradually lost weight (Fig. 5), presumably because of the high energy expenditure associated with reproductive activities and molt. Despite this, many auklets made second clutch attempts in 1971 between 27 May and 19 July, a period when they were losing weight most rapidly.

**Burrow destruction.** In 1970, I attempted to calculate the exact percentage of burrows that were destroyed by natural and man-made causes. By examining marked burrows in several plots, I determined that by 15 August, 20% of 385 burrows had been destroyed, including 5.0% resulting from trampling by humans.

During May and early June, the nesting activities of the Western Gull (*Larus occidentalis*) often resulted in the crushing or closing of burrow entrances where the soil was loose, particularly where auklets and gulls nested in the same area. However, far more damage was done by Brandt's Cormorants (*Phalacrocorax penicillatus*) that moved through areas in flocks of 5 to 300 birds and totally uprooted annual vegetation for use as nest material. Three auklet plots were particularly damaged by such activity. For example, from 1-11 June 1969, cormorants denuded one plot and in so doing caved in or shut the entrances to 48 of the 80 marked

burrows. This resulted in the deaths of 24 young and 5 adult auklets. Most chicks were killed inside their burrow; other chicks and the adults were killed by gulls as the auklets tried to leave the burrow. On the same plot between 20 May and 1 June 1971, another cormorant flock destroyed 11 of 40 marked auklet burrows, resulting in the loss of at least 6 chicks and 5 eggs. Auklet remains were found in the plot but the exact number of deaths could not be determined. In another plot in 1971, 8 of 20 burrows containing at least 6 eggs and 2 chicks were destroyed by a combination of cormorants and gulls.

**Position in colony and age.** Study plots were chosen to represent differences in topography, in auklet breeding density, and in proximity to the chief predator, the Western Gull. There was a significant correlation ( $r = 0.71$  for 1970;  $r = 0.66$  for 1971; both  $P < 0.05$ ) between soil depth and the number of chicks produced per pair. This indicates that auklets nesting in burrows excavated in firm deep soil were more successful than birds nesting in shallow soil. No comparison could be made between birds nesting in deep soil and those in rocky talus slopes. Since firm, deep soil also allowed a greater density of burrows, a significant positive correlation ( $r = 0.50$  for 1970;  $r = 0.56$  for 1971; both  $P < 0.05$ ) also existed between burrow density and number of chicks fledged per pair. I have no evidence that certain areas of the island were colonized predominately by specific age groups as was found for the Black-legged Kittiwake (*Rissa tridactyla*; Coulson and White 1958).

**Predation.** Gull predation occurs primarily where gulls and auklets nest in the same areas (Fig. 6), based on the fact that more dead auklets were found where the ratio between auklet and gull territories (pairs or nesting birds) was closest to unity (Tables 6 and 7). Gulls frequently capture adult auklets who are incubating eggs in shallow burrows. During the day they actually look into burrows for unwary or easily accessible adult and nestling auklets. Most of this activity occurs

TABLE 6. Auklet mortality at different locations on Southeast Farallon Island during June and July 1970.

	No. birds in all plots		Live auklets: live gulls	No. dead auklets		Dead auklets: live gulls
	Auklets	Gulls		Adults	Nestlings	
Study plots	4766 <sup>a</sup>	190+ <sup>b</sup>	25:1	65	55	1:1.6
Gull colony	16	84	1:5	9	1	1:8.4
Gull roosts	154	700	1:5	5	7	1:58.0

<sup>a</sup> 0.95 burrows/m<sup>2</sup> for auklets.

<sup>b</sup> 0.04 gulls/m<sup>2</sup>.

TABLE 7. Nesting densities of Western Gulls and Cassin's Auklets in the study plots.

Study plot	Gull nest density <sup>a</sup>	Auklet burrow density <sup>a</sup>	Auklet breeding success <sup>b</sup>	
			1970	1971
6	0.05	0.68	50	33
4	0.05	0.33	64	58
9	0.03	0.06	—	41
5	0.03	0.04	36	48
3	0.03	0.07	36	59
10	0.02	0.06	—	52
2	0	0.16	74	43
1	0	0.30	68	52
7	0	1.06	59	37
8	0	1.18	80	55

<sup>a</sup> No. nests or burrows/m<sup>2</sup>.

<sup>b</sup> Percent of all eggs that were successful to fledging.

when the majority of burrows contain growing chicks. On seven occasions I saw Western Gulls pull auklet chicks from burrows. Once an auklet is killed, it is either eaten there or carried back to the gull's territory.

I found a significantly higher proportion of dead nestlings at gull roost areas than in the gull colony ( $\chi^2 = 2.86$ ,  $P < 0.05$ ; Table 6). This may be due to the presence of specialist

gulls that came from other areas of the island to "search" for young auklets in burrows. Upon killing a young auklet, such a gull would eat it at the roost site early in the day when few other gulls were there. At least two of five gulls responsible for the piles of dead auklets found in the vicinity of the roost hunted in this manner.

Adult auklets were more vulnerable to gull predation in early June than were nestlings; however, by mid-July both adults and young were equally vulnerable (Table 8). Nestlings near fledging (36–43 days old) comprised 86.9% of all dead auklets (Table 9). No chicks younger than 16 days were found in the gull kills but this may have been because such chicks can be swallowed whole, making any remains difficult to identify. Gulls took approximately 7%–8% of the nestlings in burrows.

I saw no gulls attack adult auklets at night even though some auklets were within one meter of a gull ( $n = 220$  auklet arrivals). If gull predation on auklets occurs at night, it is not during the evening arrival or the morning departure flight. The only auklets I observed

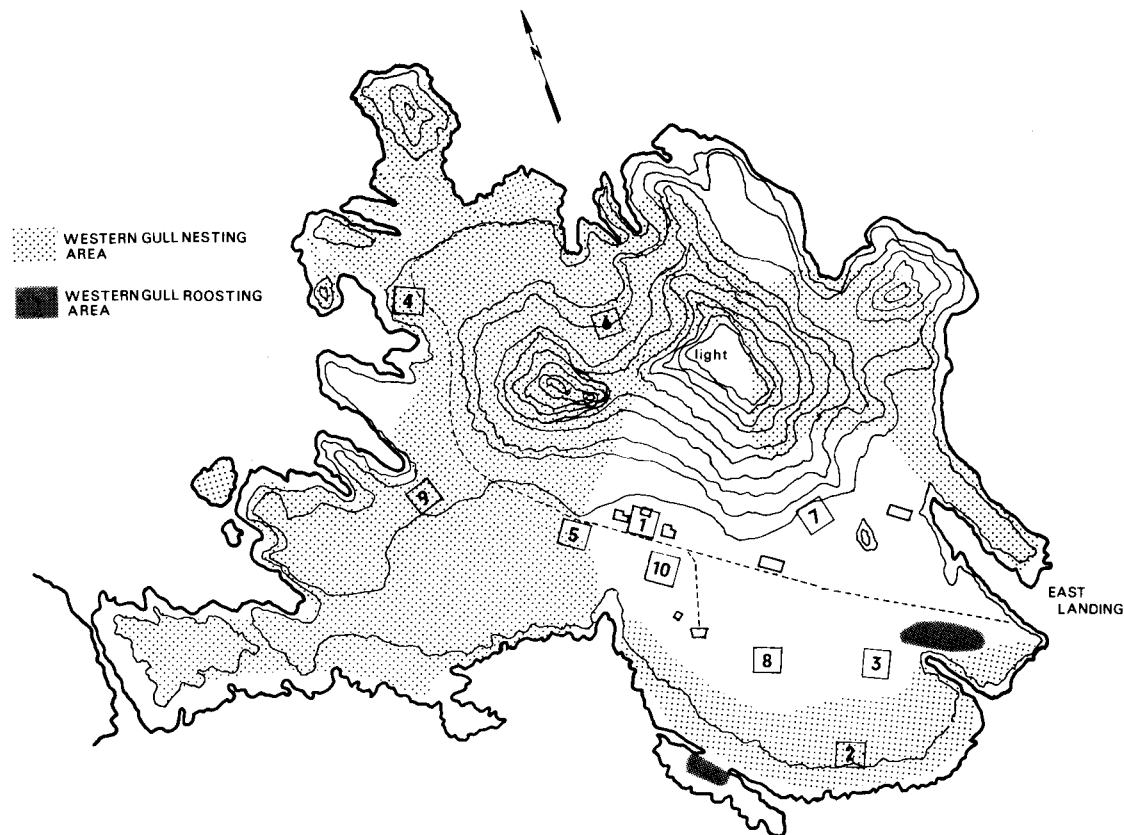


FIGURE 6. Map of Southeast Farallon Island showing location of the 10 Cassin's Auklet study plots in relation to Western Gull nesting and roosting areas.

TABLE 8. Numbers of adult and young Cassin's Auklets found dead on Southeast Farallon Island during June and July 1970 and 1971.

Date	Adults	Young	Total	Adult: young
5 June 1970	18	8	26	2.2:1.0
11 July 1970	71	60	131	1.2:1.0
25 June 1971	44	44	88	1.0:1.0
1 July 1971	61	80	141	1.0:1.3
16 July 1971	60	71	131	1.0:1.2
TOTAL	254	263	517	1.0:1.0

being killed at night by gulls were fledglings. The short trial flights of fledglings make them particularly vulnerable. Some gulls have learned to watch for young auklets on the brightly illuminated Coast Guard helicopter landing pad. At 02:30 h on 17 July 1970, I saw a young auklet killed by a gull as it was making trial flights near there.

In general, it appeared that gulls preyed with equal frequency on both adults and young auklets. Adults were killed most often by gulls who removed them from shallow burrows while the parent was incubating. Young auklets were vulnerable under three major circumstances: (1) in shallow burrows near gull concentrations; (2) in most burrows during the late nesting period when nestlings tended to be near the burrow entrance; and (3) during the process of fledging.

## DISCUSSION

Compared with other intensively studied alcids, Cassin's Auklets in the Farallon population have an unusually large reproductive commitment, with extended egg-laying including a large number of replacement and second clutches. Replacement clutches have been reported in only a few alcids (Tuck 1961, Drent 1965, Sealy 1968, 1972), but the Farallon auklets are unusual in attempting to raise second broods during the same breeding season. While double broodedness occurs among many avian species, I know of only two other documented cases in seabirds. Nicholls (1974) reported that the Silver Gull (*Larus novae-hollandiae*) is double brooded on Carnac Island in western Australia, although it is apparently single brooded elsewhere in Australia and New Zealand. Reilly and Balmford (1974) reported double broodedness in the Little Penguin (*Eudyptula minor*) on Philip Island, Victoria, Australia. Finally, Murphy (1936) gave circumstantial evidence for the

TABLE 9. Differential mortality of auklet chicks during 1971.

Approximate age (days)	Mean wing length (mm)	Range	Mortality (% of total)	No. of dead auklets found
1-5	18.8	15.7-21.3	0	0
6-10	29.5	26.0-31.7	0	0
11-15	37.3	28.5-43.3	0	0
16-20	46.5	35.9-51.9	1.0	1
21-25	64.8	57.6-72.2	4.2	7
26-30	77.6	72.1-82.3	2.6	5
31-35	90.2	84.1-95.3	5.3	11
36-40	99.7	95.7-102.1	16.3	31
41-43	104.6	103.0-120.0	70.6	152

existence of double broodedness in the Guanay Cormorant (*Phalacrocorax bougainvillii*).

The effect of food on the reproductive cycle of seabirds is extremely difficult to assess because little is known about the availability of prey. In this study, we must rely on circumstantial evidence. First, I obtained samples of food brought to nestlings in order to determine diet composition, but only during mid-June and August (Manuwal 1974b). Second, the CAL-COFI data (Fig. 1) provide a general picture of micronekton abundance which can be qualitatively compared with the breeding cycle of Cassin's Auklet. Based on these kinds of data, some speculation is necessary to explain various aspects of the Farallon auklet breeding cycle.

Extensive surface shoals of *Thysanoessa spinifera*, one of the principal prey species for Farallon auklets, occur from about July to September off central California (Brinton 1962), but occurrence is seasonally quite variable (Fig. 1). Seasonal variability in the abundance of these and other crustaceans causes unpredictability and the potential for food shortages at crucial times during the auklets' reproductive cycle. This may partly account for the lowered reproductive success among late-laying auklets. It is not the whole answer, however, as shown by the data presented in Figure 2. For example, auklets laying replacement clutches in mid- to late April are quite successful (62% to 92%) whereas those laying their first egg of the season at this same time are totally unsuccessful. A similar phenomenon is evident between late replacement clutches and early second clutches. Clearly, other factors must be involved.

Age, food supply, and nest-site quality operating singly or in combination with other factors, may explain the trends in Figure 2. Coulson and White (1958) have shown that older, more experienced Black-legged Kittiw



wakes breed earlier and are more successful than inexperienced birds. A similar phenomenon may occur with auklets. The fact that breeding success is higher for replacement clutches in late April and early May than for first clutches at the same time suggests that auklets attempting replacement clutches are more experienced breeders than those laying first clutches so late in the season. The same situation probably exists with "floaters" (Manual 1974a). Late in the season these birds initiate egg-laying that is largely unsuccessful. The poor success of second broods may be due to parents' poor physiological condition, which is revealed by declining body weights (Fig. 4; see below).

Yearly and long-term fluctuations in breeding success of Farallon seabirds have been convincingly linked with changes in the California Current (Ainley and Lewis 1974). In some years the current weakens and warm waters move unusually far north along the California coast. During such periods the breeding success of auklets decreases (Ainley and Lewis 1974). Possibly this could account for within-year variation in breeding success, as California waters annually become quite warm during late summer (Ainley and Lewis 1974). If waters warmed early, resulting in lessened food availability, then late eggs (whether of first, second, or replacement clutches) would have less chance of success.

The seasonal differences in growth rate, fledging weight and fledging age are most likely due to a decrease in food availability for foraging parents. Such a conclusion has been made by other authors regarding decreased breeding success in later stages of the breeding season (Coulson and White 1958, Perrins 1965, Lack 1966, and Nettleship 1972). Underweight fledglings undoubtedly have a lower survival rate than healthy ones. Other factors, however, cannot be disregarded until more information is available. For instance, lower growth rates of second brood nestlings may reflect parental "reproductive fatigue" accrued as a result of the energy demands of courtship, egg formation, feeding of young, and molt. Whether the fall in body weight of adult auklets between mid-May and August is due to such stresses or to a reduced food supply, or both, cannot be accurately determined with available data. However, since micronekton tends to increase from April to August (Fig. 1), and adults regain weight beginning in August (end of breeding), it seems likely that the weight loss is due to high energy expenditure.

I suggest that an unusually early "bloom"

of micronekton enabled auklets to initiate egg-laying one month earlier in 1971 than in 1970. This seems reasonable because of the large year-to-year fluctuations in micronekton numbers netted from 1949-1969. Further, nekton was presumably available for a long period of time because a significant percentage of the auklet population attempted to produce a second brood. The sharp decrease in breeding success of second clutch attempts (Fig. 2) indicates that food may suddenly have become less available soon after the later attempts at second-brooding. However, the shoals on the continental shelf near the Farallon Islands must produce a relatively consistent minimum amount of available micronekton throughout the year since Cassin's Auklets are resident and active on the island.

Investigating the relationship between nest site (habitat) and breeding success in seabirds, Coulson (1968), Tenaza (1971), and Nettleship (1972) found differences in reproductive success and other factors according to nest-site location. Most nest losses noted by both Nettleship and Tenaza were due either to predation and/or kleptoparasitism. Birds that breed among predators may show differential success, depending on their vulnerability.

Researchers working with larids have found that breeding success increases with density of breeding pairs, which Darling (1938) attributed to social facilitation and Coulson and White (1960) to the result of older and more experienced birds occupying the best available habitat. Cassin's Auklets in peripheral burrows may have little or no previous breeding experience. These burrows are in areas where gull predation is high and in shallow loose soil where burrows often collapse. Consequently, the high turnover in burrow occupants allows more opportunities for surplus breeders to start nesting there.

Cassin's Auklets at the Farallons thus demonstrate the complexities involved in a species' reproductive effort. These birds are capable of producing second broods during some years and only single broods during others. What is gained, though, in producing second chicks that fledge late at a reduced weight? In 1971, despite the large reproductive effort expended, productivity did not increase significantly over the previous year when only single broods were produced. The most plausible explanation for second or replacement broods is that the ability to produce them provides a buffer for long-term periods of warm water intrusions and reduced food availability. Ainley and Lewis

(1974) have shown that such intrusions have occurred in the vicinity of the Farallon Islands. Double brooding in some years of food abundance may help offset losses in periods of warm water.

## SUMMARY

Cassin's Auklets at the Farallon Islands show plasticity in their breeding activities by responses to changes in the marine environment. Major features of the reproductive cycle, including a relatively slow growth rate, long nestling period, prolonged egg-laying, widespread replacement clutches, and presence of extensive double brooding indicate responses to a marine environment where food may be available for a longer time. The extreme variation in the dates of clutch initiation and extent of double brooding show that this species is capable of responding rapidly to changes in some proximate environmental factor, probably the food supply. Although the evidence is indirect, the food supply of Cassin's Auklet appears to vary both from one year to the next and within a single breeding season. The evidence for its effect on auklets is revealed here by variation in the timing and synchrony of egg-laying, the number of clutches per year, the growth rates of nestlings raised during various times of the reproductive cycle, and finally, the general annual trends in weight of auklets captured from 1968 to 1971. Reproductive success was lower among auklets that laid eggs later in the breeding season. Furthermore, growth rates and fledgling weights were higher, and nestling periods shorter among young hatched early in the season. Gull predation is heavy where both auklets and gulls nest together, particularly where the soil is shallow. Gulls exert a strong selective influence on the population.

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## RECENT PUBLICATIONS

**Chemical Zoology, Volume X. Aves.**—Edited by Alan H. Brush. 1978. Academic Press, New York. 436 p. \$53.50. The physiology and biochemistry of birds comprise some mechanisms that are common to vertebrates as well as others that are uniquely avian. This volume (in the series edited by Marcel Florkin and Bradley T. Scheer) is intended to present the chemical aspects of avian biology to both ornithologists and researchers from other fields. For the latter, it opens with a chapter by Donald S. Farmer that sketches the relevant structural and behavioral attributes of birds. The succeeding chapters treat recent advances in the knowledge of avian plasma and egg white proteins, chemical embryology, keratins, pigmentation, uropygial gland secretions, endocrinology, calcium metabolism, energy, and respiratory proteins. The 14 contributors, including Brush himself, represent several nationalities, an indication that they were chosen carefully and are authorities in their specialties. This book deserves to be read by more than biochemists because it helps to explain many of the physiological requirements and environmental interactions of birds.

**The Evolutionary Ecology of Animal Migration.**—R. Robin Baker. 1978. Holmes & Meier Publishers, Inc., New York. 1012 p. \$85.00. Many kinds of animals migrate, yet researchers of this phenomenon in different groups have scarcely paid attention to each other's work. Indeed, as the author of this work notes, entomologists and ornithologists have each defined "migration" in mutually contradictory ways! Baker has now taken an ambitiously comprehensive approach to the subject, analyzing and comparing migratory behavior throughout the animal kingdom. He attempts to (1) rationalize the use of the term "migration," (2) construct and evaluate an evolutionary model of migration, and (3) review the great variety of migration patterns shown by invertebrates and vertebrates. The well-organized text is a synthesis of material, not merely a compilation. Generously illustrated with maps, diagrams, drawings, and photographs. List of references and four indexes. Students of avian migration will gain perspective from this treatise.

**Parrots of the World. Second Revised Edition.**—Joseph M. Forshaw and William Cooper. 1978. Eastview Editions, International Scholarly Book Services, Inc., Forest Grove, Oregon. 616 p. \$39.50. The first

edition of this monograph was produced in a deluxe version in 1973. An unabridged edition with minor improvements was published in a lower-priced version in 1977. We now have a completely revised edition with updated information, much hitherto unpublished. As before, every known species and subspecies of parrot, including those now extinct, is treated. Species accounts give description, distribution, general habits, call, and nesting habits. A distribution map and a fine color painting are given for each species. By adopting a smaller format (8½" × 12") and other economies in printing, it has been possible to produce this edition at a much lower cost than the original. Ornithologists who want a reference work on parrots, not a show-piece, will find it a good value.

**A Bibliography of the Birds of Rhodesia 1873-1977.**—Michael P. Stuart Irwin. 1978. Rhodesian Ornithological Society, Salisbury. 241 p. Paper cover. Rhod. \$5.00. Available: Secretary, R.O.S., P.O. Box 8382, Causeway, Salisbury, Rhodesia. This bibliography is arranged taxonomically. Under each species are listed references, first to important faunal works and check-lists, and then to articles about the species itself. Often-repeated citations are keyed to a list and the rest are given in full. The introduction explains the organization and limits of the work. This will be a most useful reference tool for anyone doing research on species which occur in Rhodesia, even if the study is not focused on that country.

**Working Bibliography of Owls of the World.**—Richard J. Clark, Dwight G. Smith, and Leon H. Kelso. 1978. Scientific/Technical Series No. 1, Raptor Information Center, National Wildlife Federation, Washington, D.C. 336 p. Paper cover. \$9.00. Available: N.W.F., 1412 16th Street, N.W., Washington, D.C. 20036. Collaboration among three owl researchers has produced this exceptionally comprehensive and well-prepared bibliography. Introductory chapters (1) explain the nature of the work, (2) summarize the taxonomy and distribution of owls, and (3) give some common names of owls in foreign languages. The major part of the book, a master list of over 6,500 citations, is followed by three computer-generated indexes. It is fortunate that the volume is sturdily bound because it will doubtless be much used by those who seek access to the scientific literature on owls.