

# THE NATURAL HISTORY OF CASSIN'S AUKLET (*PTYCHORAMPHUS ALEUTICUS*)

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Previous knowledge of the natural history of Cassin's Auklet (*Ptychoramphus aleuticus*) (see Thoresen 1964, fig. 2) comes primarily from the early anecdotal accounts of Bent (1919), Bryant (1888), Dawson (1911), Dawson and Bowles (1909), Gruber (1884), Heath (1915), Heerman (1859), Loomis (1896), Smith (1934), and Stephens (1921). More recent work has focused on regional aspects (Gabrielson and Lincoln 1959; Jewett et al. 1953), breeding behavior (Thoresen 1964), molt (Payne 1965), the brood patch (Payne 1966), the gular pouch (Speich 1972; Speich and Manuwal 1974), and population ecology (Manuwal 1972).

The present report embodies information supplementary to these accounts, in the areas of activity cycles, pairing, nest-site selection and micro-climate, egg-laying and incubation, diet, nestling activity, and growth.

The family Alcidae, composed of 14 recent genera and 22 species, is confined to the Northern Hemisphere and its earliest differentiation occurred in the Pacific Basin (Udvardy 1963). There are 18 Pacific alcid species, including 6 species of auklets. *P. aleuticus* has the most extensive breeding distribution of the east Pacific aluids, extending from sub-boreal to subtropic waters. The northern limit is in the Aleutians (Gabrielson and Lincoln 1959) and lies within the Subarctic Zone, as outlined by Ashmole (1971). The southern limit is near Isla San Roque, Baja California (van Rossem 1939) and lies within the Northern Subtropic Zone. The southernmost colonies are of the subspecies *australe* (van Rossem 1939), while the extensive northern populations compose the subspecies *aleuticus*.

This paper is based on 42 weeks of field work conducted on Southeast Farallon Island, California, from March 1969 to late August 1971. It represents part of a more extensive study of the population biology of Cassin's Auklet (Manuwal 1972).

## STUDY AREA

Southeast Farallon Island (37°4' N; 123°) is one of the three rocky islets lying 27 miles west of San Francisco, California. This 40.5-ha granitic island is sparsely vegetated; the most important plants are Farallon weed (*Lasthenia minor*), a succulent sand spurry (*Spergularia* spp.), and two grasses (*Hordeum murinum* and *Polypogon* sp.). The vegetation is green from about January to late May when it begins to dry. Later, dead Farallon weed forms patchy tangles which hold the soil in many areas. Topographical features include numerous rocky peaks, talus slopes, and an extensive relatively flat marine terrace (see map in Bowman 1961).

The climatic environment of the Farallones is typically marine. Average sea-surface temperatures are around 50°F (Thoresen 1964). The monthly average temperature for 10 years (1904–13) was 53°F. The mean maximum temperature was 55.3°F and the mean low, 50.6°F. The maximum temperature recorded between 1904–13 was 81°F in October; the lowest 38°F in January (U.S. Weather Bureau 1913).

Most of the average annual precipitation of 15.3 inches occurs between November and March. May to August are particularly dry months. Between 1951 and 1960, annual precipitation varied from a low of 10.2 inches in 1959 to 23.4 inches in 1952 (U.S. Dept. of Commerce 1964). During much of the year there is fog and high winds may reach 55 knots.

## METHODS

The breeding cycle was studied by comparing reproductive data from eight to ten 25 × 25 m plots varying in topography and auklet breeding density. In 1969, 429 burrows were checked during the latter part of the breeding cycle (May, June, and August). In 1970 and 1971, 386 and 352 burrows, respectively, were checked. Each burrow in the study plots was marked with a numbered stake placed near the burrow entrance. Some burrows which did not allow easy access from the entrance were excavated and then provided with 9 × 12 inch rectangular, masonite burrow covers. Such excavations facilitated easy access with minimum disturbance to the birds inside. Burrows were marked and excavated when necessary during the pre-egg stage. This produced minimal disturbance since no auklets were in burrows during the day at this stage of the reproductive cycle.

Study plots were checked and some birds were banded throughout the breeding cycle. Each time a marked burrow contained a newly laid egg, it was not checked again until midway through incubation as excessive burrow examination caused desertion. Three successive burrow examinations including handling of the incubating bird usually caused desertion of the egg (but not the burrow). Activities which led to desertion were, of course, stopped as

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TABLE 1. Burrow occupancy during February 1970 on Southeast Farallon Island, California.

Location	Date	No. of burrows	% occupied	% pairs
North Landing	5 Feb.	45	No data	29
Exp. Plot No. 2	7 Feb.	25	100	32
Exp. Plot No. 2	9 Feb.	21	80	19
Plot 1	10 Feb.	56	2	0
Plot 1	16 Feb.	56	80	16
Total		203	Mean	24

soon as their effects were recognized. Altogether, less than 5% of the burrows studied were deserted due to effects of this investigation. Nestlings were banded at the age of 5–6 days when the parents had ceased continuous brooding. Auklets were mass-captured using techniques described by Ralph and Sibley (1970).

Selective banding was done by capturing birds in burrows or by using hand nets on the surface of the ground. Regular U.S. Fish and Wildlife Service aluminum bands size 3 and 3A were used. Since 1968, the author and Point Reyes Bird Observatory personnel have banded over 7000 adult and 1000 nestling auklets on the island.

Several lighted areas near Coast Guard facilities permitted observation of much auklet behavior. A "Starlight" scope (Electro-optical Research Co., Los Angeles) was used from a blind to observe nocturnal behavior, especially where auklets and Western Gulls (*Larus occidentalis*) nested in the same area.

Auklets carry food to the nestling in a sublingual pouch (Speich 1972). Food samples were collected after dark when auklets began returning from the ocean by removing an auklet from its burrow immediately after it had entered. The mandibles were pressed shut so that the bird could not regurgitate the contents of its gular pouch. The bird's head then was forced into a plastic vial into which it regurgitated its pouch contents. It was necessary to press the bird's throat lightly to force out any residual amount of pouch contents. These samples were weighed to the nearest tenth of a gram and contents were subsequently diluted and the components identified. Food specimens were preserved in 10% formalin.

## RESULTS AND DISCUSSION

### OCCURRENCE ON THE FARALLON ISLANDS

Contrary to previous accounts (Bent 1919; Thoresen 1964), Cassin's Auklets are resident on the island the year around. I made visits to the island during all months of the year except October and January and always found auklets present. Extensive auklet banding by the author and the Point Reyes Bird Observatory personnel indicates this population is resident on the island throughout the year. I estimated the breeding population to be 105,000 individuals (Manuwal 1972). Auklets appear to be less numerous in late September and October. It is probable that many auklets remain at sea during the remigial molt (September–October) (Udvardy, Speich, Manuwal, unpubl. data), but still visit the island ir-

TABLE 2. Relative number of Cassin's Auklets present on Southeast Farallon Island from 4–16 February 1970.

Date	Relative no.	Weather
February 4	Good	Partly Cloudy
5	Good	Clear
6	Good	Overcast
7	Poor	Fog
8	Good	Partly Cloudy
9	Fair	Overcast
10	Poor	Clear
11	Poor	Overcast, Windy
12	Poor	Clear, windy
13	Fair	Clear
14	Poor	Clear, ½ moon
15	Poor	Clear, ½ moon
16	Good	Fog

regularly until the beginning of the breeding season (December).

During the winter in Alaska, populations of this species were not present on the islands although some apparently remained near the islands (Gabrielson and Lincoln 1959). More extensive banding would be necessary to determine if the Farallon breeding population is partially displaced in winter by arrivals from more northerly populations.

### PATTERNS OF NOCTURNAL ACTIVITY

Cassin's Auklets usually begin to arrive on the island about 15–30 min after dark. The pattern of the flight varies according to the time of year, stage of the reproductive cycle, and the weather conditions.

During winter, auklet flights are least predictable. On clear moonlit nights, few if any auklets arrive. On foggy nights, there may be 50–90% of the breeding population present. This is based on the frequency of occupied burrows. Table 1 shows the percentage of burrows occupied during 5 nights in early and mid-February 1970. Table 2 shows the relative number of birds present during 13 nights in February 1970. The relative number was a subjective evaluation of the number of auklets observed flying to the island and those on the surface of the ground. The only trend that appears is that auklet flights tend to be sparse on clear nights and greater on overcast or foggy nights. Figure 1 shows the arrival and departure pattern of auklets observed flying over a lighted area of the island during the arrival flights on 7 and 10 February 1970. Counts began when the first flying auklet was observed. I counted all auklets flying to and from the island in the lighted area for 1 min every 6 min. Note that the night of 7 February was clear with a quarter moon. Auklets first arrived at 18:54 compared to 18:41 on

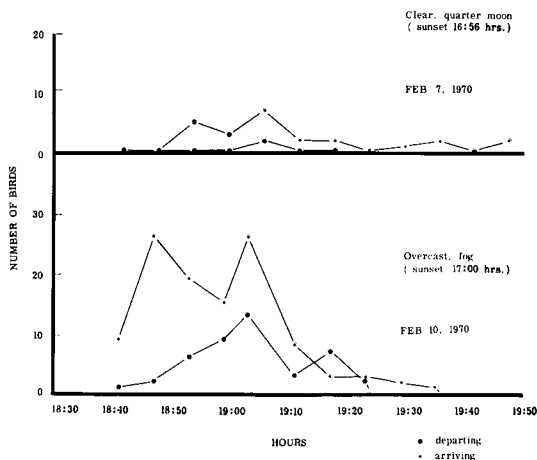


FIGURE 1. Flight pattern of auklets during evening arrival flights in February 1970. Auklets were counted and flight direction was noted as they flew over a brightly illuminated rectangular area of the island. One-minute counts were made every 6 min, beginning with the first flying auklet observed.

10 February which was an overcast night. The number of birds flying on 10 February (155 birds observed) was nearly six times greater than on 7 February (27 birds).

Even though unfavorable conditions (i.e., clear, moonlight nights) may be present at the time auklets would normally begin arriving (i.e., shortly after dark), large numbers of birds may arrive if there is a change to favorable conditions during the night. Such was the case on the night of 15 February 1970. At 23:00 it was clear and there were no auklets occupying 50 burrows checked; only a few auklets were seen elsewhere on the island. This condition continued until about 02:00 16 February at which time the skies became overcast and several auklets were seen around one of the living quarters. By 04:30, thousands of auklets were calling. The majority of birds must have arrived between midnight and 04:00. Also on the same night, I placed toothpicks at the entrance of 50 burrows at 22:30 and all were knocked down by 06:00 on 16 February, indicating that these burrows had been occupied sometime during the early morning.

During the breeding season, arrival and departure patterns were more consistent. On very windy or clear moonlit nights during incubation and the nestling period, auklets arrive somewhat later than on cloudy nights. It appeared that all the birds were arriving within 2 hr after dark, but I noticed stragglers most of the night. To determine the exact pattern of arriving and departing auklets, I set up a large net at 24:00 on the night of

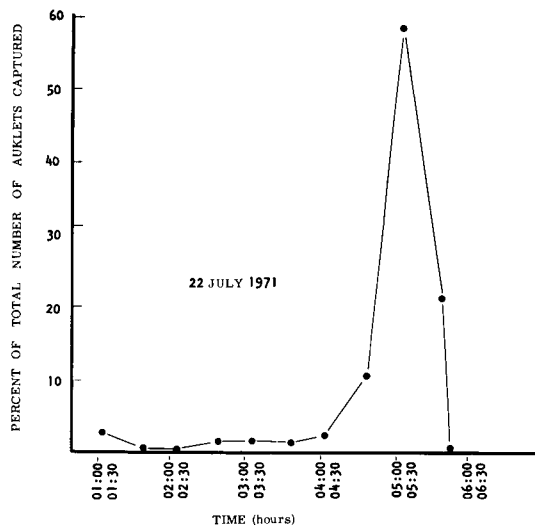


FIGURE 2. Numbers of auklets captured in a large net from 01:00–06:00, 22 July 1971.

22 July 1971 and recorded the number of auklets captured every half hour until dawn. Figure 2 shows the percentage of all captured auklets departing at half-hour intervals. A total of 186 departing and 2 arriving birds were captured. There was a relatively consistent but small number of auklets departing from 24:00 to 04:30. However, at 04:30 the rate of departure increased, reaching a peak between 05:00–05:30 when 108 (58%) of the birds departed. Auklets normally leave in pairs during courtship (about 70%) but tend to leave singly at other times of the breeding cycle. This was determined by observing auklets depart just prior to sunrise.

The departure pattern described above may be characteristic only when the majority of birds are feeding chicks, the condition prevailing at the time of the experiment. I have no data on the hour-by-hour departure flight pattern at other times of the year.

Cody (1973) discusses the evolution of nocturnality in Cassin's Auklet and other alcids as a response to intense predator pressure. While there is supportive evidence for this, other evidence contradicts it. For example, there is intense predator pressure on some breeding alcid colonies in the Arctic where there is continuous daylight during the summer (Larson 1960; Salomensen 1951; Tuck 1960; and others). Furthermore, Kittlitz's Murrelet (*Brachyramphus brevirostris*) is nocturnal at the southern limit of its distribution, and yet it maintains this schedule in the Bering Strait under conditions of continuous light (Bedard and Sealy, pers. comm.). Other factors such as availability of food, method of

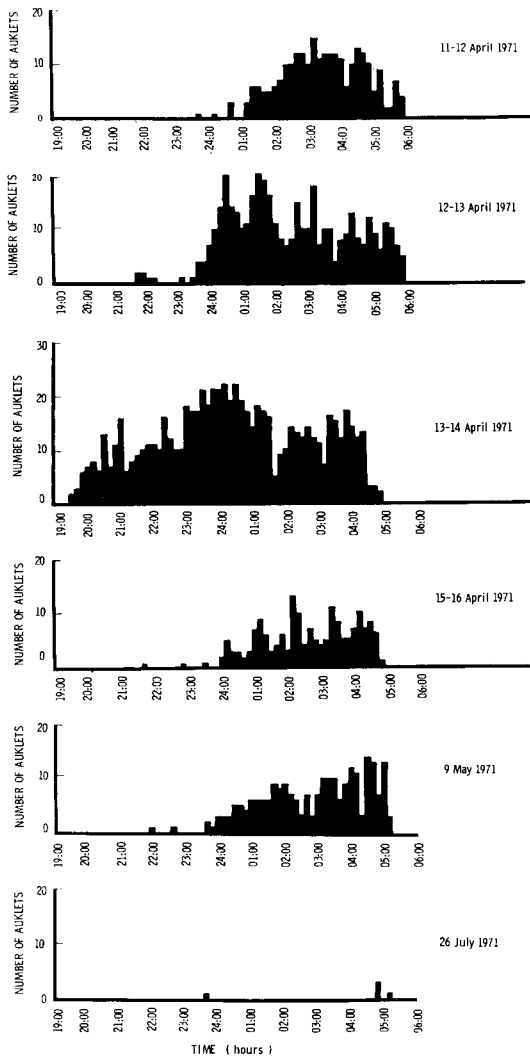


FIGURE 3. Numbers of auklets present on a rectangular grid at 10-min intervals, throughout the nights of 11, 12, 13 and 15 April, 9 May, and 26 July 1971.

capturing prey, or the energetics of feeding young may contribute to the evolution of nocturnality, especially in the small alcids such as Cassin's Auklet.

The nocturnal activity pattern of Cassin's Auklet was quantified by marking a rectangular grid on the ground and counting the number of auklets present at 10-min intervals throughout the night. All counts began at the same time each night. Six counts were made in 1971 during the nights of 11, 12, 13, and 15 April, 9 May, and 26 July.

Table 3 gives the weather conditions and the total number of auklets counted during each nightly census. There are some major trends evident from table 3, figure 3, and supplementary observations. First, there is a general reduction in auklet activity from court-

TABLE 3. Number of auklets counted and weather conditions during six censuses of nocturnal activity.

Date	Auklet count	Weather
April 11	252	Clear, full moon, wind 5-10 knots.
12	408	Overcast but cleared at 24:40; wind calm.
13	694	Overcast but cleared at 04:25; wind calm.
15	175	Clear, moon, wind 25-35 knots.
May 9	242	Clear, full moon, overcast-04:10.
July 26	4	Overcast, foggy, wind 10-20 knots.

ship period to chick-rearing. Weather conditions may strongly influence the amount of behavior occurring outside burrows. In general, auklets are most active during foggy or cloudy nights (12 and 13 April). Very little activity occurs on moonlight nights (11 and 15 April); however, if it becomes overcast during the night, auklet activity may increase (9 May). Strong winds may reduce auklet behavior on nights otherwise suitable for much activity (26 July). The peak activity times varied from one night to the next. If there is a definite pattern to nightly activity, more censuses would be needed to detect it.

The activity of other auklets is variable. The Rhinoceros Auklet (*Cerorhinca monocerata*) is unusual in its degree of nocturnality. It is totally nocturnal on Protection Island (Richardson 1961) and Smith Island (pers. observ.) in the Straits of Juan de Fuca, Washington, but it is crepuscular at Destruction Island on the Olympic Peninsula (Cody 1973). Most surprisingly, this auklet is mostly diurnal on South Farallon Island (Ainley and Lewis, pers. comm.).

Both the Least and Crested Auklets (*Aethia pusilla* and *A. cristatella*) on St. Lawrence Island, Alaska, have two peaks of activity on the colony sites during daylight hours (Sealy and Bedard, pers. comm.).

#### PAIRING AND NESTING

*Pairing.* Many auklets remain paired throughout the year, but those that lose mates and first breeders acquire mates during the courtship period from about January to April. An average of 24% of 203 burrows checked from 2-16 February 1970 contained "paired" birds. Lost mates may be replaced anytime during the reproductive cycle. The pair bond may last at least 3 years (four instances) and might possibly be permanent. This is apparently also true for Least and Crested Auklets on St. Lawrence Island (Sealy 1968).

*Nest-Site Selection.* Cassin's Auklet apparently avoids nest-site competition because

it is relatively smaller in size than its normal acid nesting associates (Cody 1973). This species prefers burrows to rock crevices. The large population and resulting social pressure for nest sites (Manuwal 1972) have probably forced a large portion of the Farallon population to utilize rock crevices for nesting. In other parts of its range, it normally excavates burrows (Jewett et al. 1953; Gabrielson and Lincoln 1959; Drent and Guiget 1961).

Nesting success is low for auklets nesting in rock crevices that are large enough for the Western Gull to reach the nest chamber or to capture a nestling near the crevice opening. Predation is also severe for auklets with burrows in loose, shallow soil. Such burrows often cave in or erode near the entrance. Furthermore, auklet burrows located away from gulls were more successful than those closer (Manuwal, pers. observ.). Nettleship (1972) found that breeding success of the Common Puffin (*Fratercula arctica*) was higher where there were fewer Herring Gulls (*Larus argentatus*).

In general, auklet nests are found in two major habitats: (1) burrows excavated in soil (see Bent 1919, Plate 24); and (2) in rock piles and crevices. Fifty-one percent ( $N = 5, 693$ ) of the auklets breeding on Southeast Farallon Island nest in rocky sites. Forty-nine percent excavate burrows in soil. Those burrows constructed in rocky areas (talus slopes) are generally very durable and last for many years. Burrows excavated in soil, however, are subject to trampling by humans, water, and wind erosion due to winter rains and summer winds.

On Southeast Farallon Island, the greatest burrow concentration occurs on the marine terrace on the southwest side of the island. There, burrow densities may be as high as one burrow per square meter in soil 100 mm deep. These areas are easily distinguishable by the dense cover of Farallon weed. There are few auklet burrows in the large Western Gull colonies on the marine terrace but this is primarily due to the shallow, rocky soil prevalent there. An extensive study of the population ecology is reported elsewhere (Manuwal 1972).

Cassin's Auklets excavate burrows by digging with their sharp claws and pecking with their bills. Burrow excavations are repeatedly interrupted by courtship and other social behavior and, consequently, auklets may require several weeks to complete burrow construction. Both birds of a pair take part in the excavation. The claws are extremely sharp during February but by April when burrow

excavation is nearly completed, most birds have dull nails. The configuration of the burrow is generally determined by underground objects such as rocks. As a result, there is no uniformity to the shapes and lengths of auklet burrows. A typical auklet burrow in sod is about 0.75–1.0 m long ( $N = 288$ ). Most burrow excavation occurs from December to the middle of April. Old established burrows are cleaned and sometimes lengthened during this period. New burrows are often initiated in areas where there is a high destruction rate (shallow soil) and are usually never completed.

An experiment was conducted in February 1970 to study the effect of burrow destruction on the distribution and density of burrows subsequently constructed. A  $10 \times 10$  m plot was set up and all 45 burrows in the plot were marked with 350-mm steel reinforcing rods placed just to the right of the burrow entrance. A  $2 \times 2$  m grid was used to map the original burrow locations, and auklets occupying these burrows were banded. All burrows were then crushed. By June 1970, 74 new auklet burrows had been excavated by many of the same birds in the area formerly occupied by 45 burrows. All of these new burrows were used. This represents an increase of 60% over the original number of burrows.

Elsewhere (Manuwal 1972), I present evidence of a surplus auklet population that is capable of breeding if nest sites become available. These "floaters" (as outlined by Brown 1969) are probably responsible for the increased burrow density discussed above. The experiment was conducted during a time when "floaters" were very common on the island. Aggressive territorial behavior acted as a limitation on the excavation of additional burrows by nonbreeders.

*Nest Microclimate.* Birds nesting in burrows or rock crevices are presumably subjected to less environmental extremes than those birds constructing ground-surface nests exposed to direct sunlight, rain, and other environmental factors.

Temperature of the nest site is very important to the reproductive success of birds for two reasons: (1) stable, relatively warm temperatures minimize the amount of energy required of the incubating bird for its own temperature regulation; and (2) these conditions minimize the amount of heat lost between the incubating bird's body (via brood patch) and the egg.

Nest temperatures of 25 burrows were obtained by installing a telethermometer probe on the nest floor of auklet burrows, while

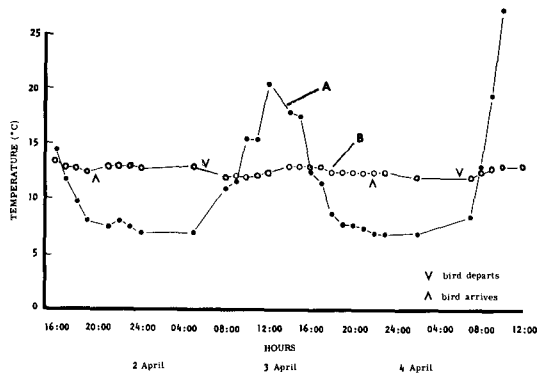


FIGURE 4. Air temperatures recorded in an auklet burrow excavated in deep sod. "A" is the ambient temperature; "B" is the burrow air temperature.

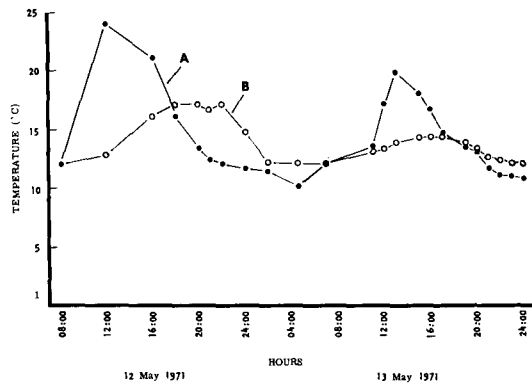


FIGURE 5. Air temperatures recorded outside a rock crevice (A) and inside the crevice (B).

coincident ambient temperatures were obtained by placing a probe immediately outside the burrow entrance. Figure 4 shows ambient and burrow temperatures taken on 2-4 April 1971 from a burrow excavated in firm soil in Plot 1. There are two noticeable characteristics: (1) burrow temperatures remain stable despite large fluctuations in outside ambient temperature; and (2) burrow temperatures are never lower than ambient temperature means. Average burrow temperature was 12.7°C for the warm, partly sunny days of 2-4 April. Similar burrow temperature trends were also found in this burrow from 9-11 May 1971. However, the temperature pattern of large rock crevices differed from the above pattern. Temperatures were recorded on 12-13 May 1971 (fig. 5) and show that the burrow temperature fluctuates as much as 5°C on warm, sunny days. Mean burrow temperature for the rock crevice was 13.3°C. Sealy (1968) found a mean crevice temperature for a nest of *Aethia pusilla* was 11.3°C. Even though mean low burrow temperatures are never lower than ambient lows, they do fluctuate in proportion to the changes in ambient temperature. Temperatures of the rock crevices varied from 12-17°C, while those of the burrow in deep sod varied only 12-13°C.

Even though the temperature in rock crevices fluctuates more than in sod, the brooding of adults insures the survival of the nestling during the development of thermoregulation. Once thermoregulation is established, altricial nestlings are able to maintain body temperature (Kaftanowski 1951; Rolnik 1948). However, interruptions in brooding caused by harassment by Western Gulls or deterioration of burrows in loose soils may cause the death of a nestling prior to development of thermoregulation. Thus, one might expect some losses of nestlings in auklet burrows or rock

crevices located near high density of nesting gulls.

It appears, then, that nest temperatures in burrows excavated in soil are much more stable than in nests located in rock crevices. Undoubtedly, the amount of temperature fluctuation is strongly dependent on the substrate and perhaps the shape of the nest chamber. Consequently, some rock crevices may show stable temperature conditions.

*Deposition of eggs.* The Cassin's Auklet lays a single, creamy-white, unmarked egg. Weights of 110 eggs averaged 27.4 g, while average length-width dimensions were 46.2 × 33.5 mm for 75 eggs. Eggs are normally laid 50-100 mm from the back end of the burrow. Upon disturbance, incubation may be terminated and the egg subsequently forced out of the burrow. Auklets may replace a lost egg, at which time they frequently extend the burrow or excavate a side branch where the new egg is usually laid. I found two burrows in which three eggs were deposited during the period 6 April-4 June 1970. In both cases the first egg was deserted due to disturbance. A second egg was laid shortly after desertion, but may have come from foreign birds since they were never incubated. Both eggs were forced out of the burrow and a third egg was laid in each of the two burrows. The egg in one burrow was incubated to completion, but the egg in the other was never incubated.

TABLE 4. Fate of first clutch eggs that were not incubated immediately after being laid.

Fate	Study plots								Total	%
	1	2	3	4	5	6	7	8		
Eventually incubated	1	1	2	2	2				8	26.5
Replacement egg laid	1	1	1	3	1	5	2		14	47.0
No replacement		2	1	4	1				8	26.5
Total	2	3	2	6	2	7	6	2	30	

TABLE 5. Gular pouch contents of adults feeding chicks, 1971.

Date	Weight of contents	No. of:				Total organisms
		Euphausiids	Squid	Amphipods	Other	
June 14	24.8	118			1 Fish	119
	35.2	149				149
	21.0	-			3 Fish	3+
June 15	20.6	106				106
	35.4	240				240
	33.6	120				120
Aug. 8	8.6	136		38		174
	16.7	45	38			83
Aug. 13	31.9	38			4	42
	24.9	79				79
	30.5	11	26	2		39
Aug. 15	31.3	4		2041		2045
	36.7	50				50
	18.1	14	2	34	6	56
	33.2	261	8	490	52	811
	31.5	-		1350		1350
	27.6	24	25	22	1	72
	12.5	10		281		291
	39.5	17		1735	6	1758
	45.6	14	81	2	2	99
	37.6	100	15	4		119
14.3	269	8	1		278	
Total	X = 27.78 SD = 9.69 SE = 2.07					

In 386 burrows in 1970, 30 eggs (8% of 386) were laid but not immediately incubated. Table 4 shows the fate of these eggs. More than 73% of these eggs were never incubated. A similar phenomenon was observed in 1969 and 1971. Other than the possible effect of my disturbance, I cannot offer a satisfactory explanation.

*Incubation.* Cassin's Auklet, as well as other auklets, has two well-developed lateral incubation patches (contrary to Payne 1966). De-feathering occurs rapidly just prior to egg-laying, but the patches re-feather midway through incubation (Manuwal 1974).

The incubation period will be considered the time between the first day the egg is incubated (not necessarily the day the egg was laid) and the day the chick hatches. An egg laid and incubated on 10 April and found hatched on the morning of 19 May would have an incubation period of 38 days. This includes the day the egg is laid but not the day the egg is found hatched. The average incubation period of 86 eggs was calculated to be 37.8 days, with a range of 37-42 days. This differs markedly from the incubation period of 21 days previously reported by Bent (1919) and is consistent with the estimate by Thoresen (1964) of "at least 37 days."

Members of an incubating pair alternate incubation duties every 24 hr. Some birds may continue incubation for a time after the mate

is lost. One marked female auklet lost its mate during the last week of May 1970. This bird continued incubation for 10 days. The bird was found incubating the egg every other day. The egg was finally deserted, possibly because of my intrusions.

#### DIET

Cassin's Auklets feed on micronekton which is present in varying amounts on shoals in the vicinity of the nesting colony (Payne 1965). Capture is facilitated by the use of the wings for underwater propulsion. With the exception of the auklets, Dovekie (*Alle alle*), and Ancient Murrelet (*Synthliboramphus antiquus*) (Sealy 1972), all other alcids feed primarily on fish. Once captured, the prey is stored in the gular pouch if the auklet is feeding a nestling. The function of this sublingual gular pouch is the transportation of food to the nestling (Speich and Manuwal 1974).

In the manner previously described, I obtained food samples by forcing auklets to regurgitate. Auklets excessively frightened invariably regurgitated even though they were not actually captured. The regurgitant is usually light pink in color when the diet consists primarily of euphausiids (Crustacea: Euphausiacea), but may be gray to dark pink when the birds are feeding heavily on squid and amphipods. The consistency of the regur-

gitant reminds one of catsup and has a strong "fishy" odor. Major prey were the euphausiid (*Thysanoessa spinifera*), amphipods (*Phronema*), and unidentified immature squid. In mid-August, there were proportionately more amphipods in the diet than euphausiids (table 5). Thoresen (1964) found euphausiids but also reported small lanceolate fishes in the diet.

The mean wet weight of 22 food samples obtained from 14 June to 15 August 1971 was 27.78 g (SD = 9.69, range = 8.6–45.6). Since both parents feed the chick each night, the chick may potentially receive an average of about 55 g of food per night. Nestlings less than 2 weeks old probably cannot consume this amount of food per night. The largest number of individual euphausiids found in a single sample was 269, while the largest number of amphipods was 2045 (table 5). The Dovekie, also a nekton-feeder, feeds its nestling 8.5 times per 24 hr. Each feeding weighs about 3.5 g, thus the nestling receives 29.8 g of food every day (Norderhaug 1970). This represents combined feeding by both parents, and is only slightly more than half the amount of food given to *P. aleuticus* chicks during a day's feeding. *A. alle* chicks fledge in 27 days and are 71% of the adult weight. Cassin's Auklets fledge in 41 days but are 90% of adult weight. On St. Lawrence Island, Parakeet, Crested, and Least Auklets fledge at 79, 80, and 88% of adult body weight, respectively (Sealy 1968).

#### NESTLING PERIOD

The nestling period is the time between the hatching and fledging of the chick. The average length of the nestling period was 41.1 days ( $n = 16$ ; range = 35–46). Thoresen (1964) calculated the nestling period to be 44.7 days for this species. Sealy (1968) found that nestling period lengths for the Parakeet (*Cyclorhynchus psittacula*), Crested, and Least Auklets on St. Lawrence Island were 35.3, 33.5, and 29.2 days, respectively. These shorter periods are presumably an adaptation to the short season of food availability or perhaps greater food abundance during a restricted period in the Arctic.

*Growth and development.* With the exception of the first 5–6 days when the parents alternate brooding, the chick is alone in the burrow. Both parents were consistently found in the burrow feeding the chick each night until a few days just before fledging.

Growth rates were calculated for development of the tarsus, culmen, and wing, in addition to general body growth as revealed

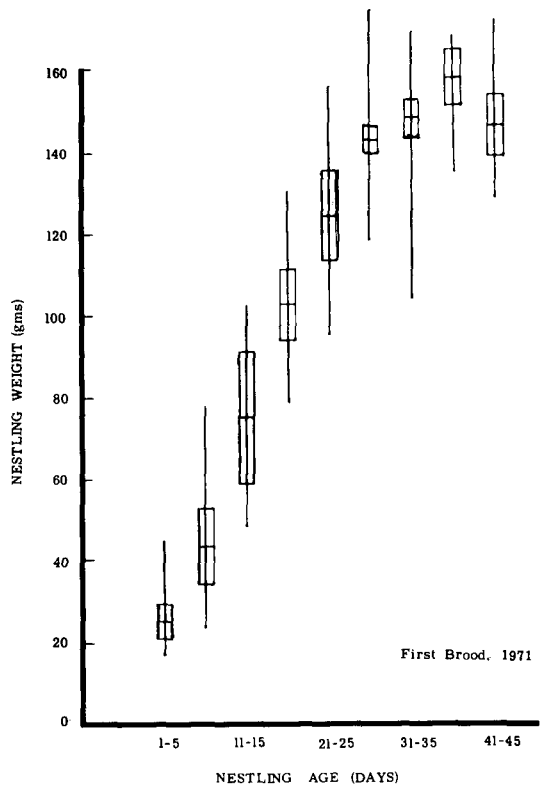


FIGURE 6. Weight gain of Cassin's Auklet nestlings of the first brood in 1971. Rectangles are one standard deviation above and below the mean (horizontal line). Vertical lines represent the range.

through weight gain. Table 6 summarizes growth rates in the extremities and body weight. The instantaneous growth rate ( $R$ ) calculated by the Brody Formula (Brody 1945: 508) modified by Banks (1959:103) is one of the most accurate measures of growth. The formula is:

$$R = (2.3 \log W_2 - \log W_1) / (t_2 - t_1)$$

where 2.3 is a factor used to convert logs base 10 to natural logs. Instantaneous growth rates were determined in the following manner for both the author's data for 1971 and Thoresen's (1964) for the 1959 breeding season.  $R$  of weight was calculated for each day of the nestling period. Since the time interval was only one day,  $t_2 - t_1$  equals 1 and the formula becomes  $R = 2.3 \log W_2 - \log W_1$ . To smooth out irregularities caused by sampling error, growth rates were determined for 5-day intervals, thus they merely represent the mean growth rate for each of the 5-day intervals. Standard deviation (SD) and standard error (SE) were also calculated. The values in table 6 can be converted to percent by multiplying each rate by 100. Finally, the mean  $R$  was obtained by calculating the mean rate for each day of the nestling period. Since



the weight reaches a peak and then decreases, there are two  $R$ 's involved. The first represents the rate of increase up to the peak weight; and the second rate (Manuwal 1972) is negative and measures the rate at which chicks lose weight after the peak until they fledge.

One-day-old chicks weigh about 21 g. The mean instantaneous growth rate for the first 36 days of age is 6.49% for the first brood in 1971. Thoresen (1964) also obtained growth data for Farallon Island auklets. Using his weight data, I calculated the mean  $R$  to be 4.61% during the first 36 days. The difference in growth rate between 1971 and 1959 might be due to a change in the California Current, thus influencing the abundance of the food supply (Ainley and Lewis, pers. comm.). At age 37–38 days, chicks begin to lose weight at the rate of 2.5%. This weight loss prior to fledging is common among burrowing alcids. Figure 6 shows that the daily average gain in weight per day was 3.9 g until the peak weight was reached on about day 37. At this time the nestling lost 2.3 g per day until fledging on day 41.

Intraspecific variation in growth rate may be as much as 20% for some birds with respect to geographic location and time of breeding season (Ricklefs 1968). Among alcids, Cody (1973) found that in-shore feeders such as the Pigeon Guillemot (*Cepphus columba*) have higher growth rates than distant feeders (Cassin's Auklets). This is a result of greater energy expended in flight between the food source and the nest site.

*Nestling activity and fledging.* After the chick has been brooded by its parents for the first 6 days, it becomes somewhat active inside the burrow until it fledges at 41 days. Continuous tape recordings of burrows containing chicks 35–49 days old indicate considerable activity inside the burrow 1–3 hr prior to the evening arrival of the food-laden parents. Another peak of chick activity occurs in the early morning hours (06:00–09:00) when I observed, on numerous occasions, chicks near the entrance of the burrow. This is probably due to the necessity for feces elimination. Burrows occupied by auklet chicks often have pinkish deposits of feces around the burrow entrance. Chicks inhabiting deep, curved burrows often deposit feces at some corner or the rear end of the burrow. Feces are always deposited at one or two locations, not all over the nest chamber.

As the time of fledging grows closer, chicks spend proportionately more time near the burrow entrance. This behavior often pre-

TABLE 6. Instantaneous mean growth rates of the weight, wing, culmen, and tarsus for Cassin's Auklet nestlings in 1971 and 1959.

	1971		1959	
	mean	SE	mean	SE
Weight	0.050	—	0.046	—
Wing	0.077	0.012	0.040	0.005
Culmen	0.042	0.006	0.016	0.002
Tarsus	0.017	0.003	0.012	0.002

disposes those chicks living in shallow burrows to predation by Western Gulls. A similar phenomenon for the Common Puffin was observed by Nettleship (1972). Some chicks emerge from the burrow for a short time at least 2–3 days prior to actual fledging. During this time, birds make short walks and flap their wings. This behavior was observed in auklets on St. Lawrence Island by Sealy (1968). A typical fledging may be described as follows:

One fledgling that I observed from 02:10–02:20 on the night of 17 July 1970 made three short flights (two—5 m, one—10 m) around the north side of the powerhouse. After each flight, the bird hesitated a minute or so, looked around, and then made another short flight. Each flight ended in a somewhat clumsy landing; however, on the fourth flight, the bird left the island on a seemingly strong, steady flight west out over the helipad at a height of about 7 m. Weather conditions at this time were overcast with a 15–20 knot north wind.

Some adults may feed the nestling up to fledging, while others may continue to return with a pouch full of food to their burrow after the nestling has departed. I recorded the number of occasions adults were present before and after fledging in 22 burrows. On 10 occasions, I found at least one adult present at 23:00–01:00 in the burrow 1–2 days prior to chick fledging. On six occasions, birds were found 1–2 days after the chick fledged. It was apparent that either the arrival of both members of the pair became very asynchronous just prior to fledging or one or both members of the pair lost the drive to feed the chick. On several occasions, only one parent was consistently found in the burrow with the chick. The pair bond remained intact in most cases since many birds were eventually found back in their burrow several days after the chick had fledged.

#### SUMMARY

The natural history of Cassin's Auklet was studied for 42 weeks from March 1969 to late

August 1971 on Southeast Farallon Island, California. The climatic environment of the Farallon Island is typically marine and consequently, there is little variability in the mean monthly air and sea temperatures. Precipitation usually occurs in the winter months when auklets are not breeding.

Cassin's Auklet has the most diverse breeding distribution of any alcid. There are an estimated 105,000 breeding auklets on Southeast Farallon Island. Over 7000 adults and 1000 nesting auklets have been banded on the island since 1968. The population is resident and auklets continue to visit the nesting burrows throughout the year. Occupancy is irregular during winter months when few birds arrive on moonlit nights. Occupancy becomes regular in about February. Courtship extends from December through May, with the peak usually in March or April. The pair bond may last at least 3 years and might possibly be permanent.

Fifty-one percent of the auklet population nests in rock crevices, but highest densities occur in deep sod areas where the birds excavate burrows. Nest-site temperatures are more stable in sod burrows than rocky sites.

Cassin's Auklets lay a single, creamy white egg which is 16% of the adult body weight. The mean incubation period is 37.8 days and members of a pair alternate incubation duties every evening. Auklets have a sublingual pouch which is used for transporting food to the nestling from distant foraging areas (Speich and Manuwal 1974).

Major prey species of auklets in 1970 were the euphausiid (*Thysanoessa spinifera*), amphipods (*Phromema*), and unidentified immature squid, which are primarily components of micronekton. Mean wet weight of 22 pouch contents was 27.8 g.

The mean length of the nestling period for first brood chicks was 41 days. The Brody formula was used to obtain instantaneous growth rates. Mean rates for the entire nestling period were 5.0% gain in weight, 7.7% for the wing, 4.2% for the culmen, and 1.7% increase in tarsus length. Young nestlings were relatively inactive inside the burrow until just prior to the nightly return of the parents. Nestlings near fledging spend much of the time near the burrow entrance and may actually leave the burrow to make short walks or test flights. Fledging involves a series of short test flights just before extended flight.

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