GULAR POUCH DEVELOPMENT AND POPULATION STRUCTURE OF CASSIN'S AUKLET

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A neck or gular pouch occurs in many species of birds. Among the Alcidae, Gibson (1922) found neck pouches in the Dovekie (Alle alle), and Portenko (1934) reported gular pouches in the Crested Auklet (Aethia cristatella), Least Auklet (A. pusilla), and Parakeet Auklet (Cyclorrhynchus psittacula). Kozlova (1961) noted gular pouches in the Whiskered Auklet (A. pygmaea). In 1968 we found pouches in Cassin's Auklet (Ptychoramphus aleuticus). The alcid pouch is a baglike, single extension of the buccal cavity extending posteriorly alongside the esophagus and trachea (Figures 1 and 2). The structure of the pouch in Cassin's Auklet is to be described elsewhere (Speich, Bédard, and Wolford MS). In this paper we describe the change in pouch length in relation to breeding activity and its use to determine age and population structure.

Cassin's Auklet breeds on coastal east Pacific islands from the Aleutian Islands (Murie 1959) south to San Roque Island, Baja California Sur, Mexico (Friedmann et al. 1950). It is a diurnal nekton-feeder, but is nocturnal in its activities on land. During incubation one adult of each pair remains on the island during the day to tend the single egg. Each parental shift lasts about 24 hours, with nest relief usually occurring in the early evening. The egg normally starts to pip 2 or 3 days before hatching (Thoresen 1964). Vocalizations (peeps) by the chick just before and during pipping probably stimulate adults to bring food to the nestling in the burrow. Hatching is followed by 5 to 6 days of intensive parental care. During this period the adults alternately remain with the nestling in the burrow during the day, and both parents are present for part of each night. After the initial period of intensive parental care both parents are always away during the day, but return each night to feed the nestling.

METHODS

The site of our study was Southeast Farallon Island, 43 km west of San Francisco, California. The island is about 36 ha in area and rises approximately 100 m above sea level with numerous granitic outcrops and steep ridges. Another prominent feature is the marine terrace where about half of the 105,000 breeding Cassin's Auklets nest (Manuwal 1972).

From 1968 to 1971 we spent 58 weeks on the island investigating aspects of the breeding biology of Cassin's Auklet (Speich 1972; Manuwal 1972). With help from employees of Point Reyes Bird Observatory, we banded 8,054 auklets. We used an auklet net trap like that developed by Ralph and Sibley (1970) to ob-

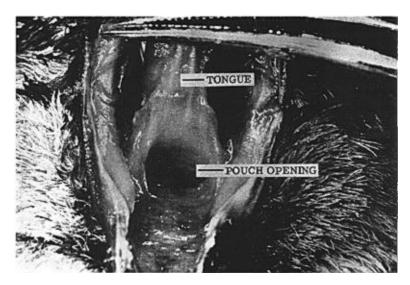


Figure 1. Opening of the gular pouch in Cassin's Auklet, ventral to the base of the tongue.

tain a presumably unbiased sample of the birds on the island. The auklet net was made of ½-inch-mesh fish net strung between two vertical poles so that it formed a J-shaped structure, the bottom of this wall being a trough. The net was placed parallel to the shore and thus across the auklets' flight path when most leave the island in the predawn exodus. Auklets that hit the net fall into the trough and cannot fly out. We then transferred them to holding cages and took a few at a time to the laboratory for measurements. Selective banding was also done by capturing birds in their burrows or by using hand nets on the surface of the island.

The breeding cycle was studied by comparing reproductive data from ten 25×25 m plots at scattered locations on the island. Each burrow in the plot was marked with a numbered stake placed near the entrance. Throughout the breeding cycle study plots were checked, and some birds were banded.

Gular pouches were measured by inserting a plastic rod lubricated with petroleum jelly as far as possible into the pouch. During measuring the neck was always held firmly in an outstretched position: the small amount of pressure exerted on the rod did not tear tissue. The length of the insertion was marked by the thumbnail of the holding hand, and after removal was measured to the nearest millimeter. The measure thus obtained always included the length of the bill and pouch.

FUNCTION, CONTENTS, AND DEVELOPMENT OF THE POUCH

Cassin's Auklets use the sublingual pouch apparently only to carry food to the nestling, as do Crested, Least, and Parakeet Auklets (Bédard 1969) and Dovekie (Norderhaug 1970). The only Cassin's Auklets that regurgitated food when captured were breeding adults with nestlings,



Figure 2. Relationship of the pouch and esophagus in the throat of Cassin's Auklet. Pouch shown is about 80 mm in length.

pipping eggs, or eggs containing peeping chicks (two instances of the latter).

In 1968 a series of burrows was checked about 19:00 to band and establish the identity of the adults present shortly before nest relief. Of 19 burrows in which adults attended the nestling (period of intensive parental care), four adults regurgitated pouch contents. As nest relief occurs in the early evening and Cassin's Auklet probably does not feed nocturnally, the attending adults must hold food in their pouches for their nestling from 24 to possibly 36 hours. The latter would be a maximum time for birds gathering food in the morning before entering their burrows the following evening. The retained food is presumably given to the nestling in increments throughout the night and day during the

TABLE 1
WEIGHT AND COMPOSITION OF FOOD FROM INDIVIDUAL ADULTS RETURNING
FROM SEA TO THE NESTLING IN THE BURROW

Date of collection	Adult pouch length (mm)	Weight of sample (g)	Contents of pouch sample
14 June 1971	119	13.3	106 Thysanoessa spinifera
"	120	24.7	118 Thysanoessa spinifera, 1 fish
"	126	33.2	149 Thysanoessa spinifera
"	118	21.0	3 fish, unidentified mass
"	115	16.0	Not identified
15 June 1971	124	20.6	" "
"	118	33.6	" "
"	114	35.4	120 Thysanoessa spinifera, unidentified mass
		$\bar{\mathbf{x}} = 24.7$	

period of intensive parental care. Nestlings near fledging are usually fed in the early evening. Eight samples of pouch contents were obtained at dusk 14 and 15 June 1971 from parents arriving at their burrows from the sea. At this time the nestlings were all within 7 to 10 days of fledging. Pouch lengths were measured at the same time (Table 1). The mean weight of food samples was 24.7 g and, as both adults bring food to the nestling each evening, a nestling nearing fledging may receive about 50 g of food each night.

Carrying food in the pouch enables a breeding adult to make one trip each day between the nest and the feeding grounds, and thus to save considerable time and energy relative to that required if food items were carried individually.

Nestlings and fledglings lack a pouch. The mean length of the bill from its tip to the base of the tongue in 12 fledglings captured on the island 3 June 1971 after first leaving their burrows the preceding night was 32 mm (range: 30–34). We interpret the data of Bédard and Sealy (MS, Figure 5) to indicate that nestling and fledgling Crested and Least Auklets also lack pouches.

Cassin's Auklet apparently does not develop a pouch until the first breeding attempt. Six nestlings banded in 1969 were recaptured in 1971 (Table 2). Three of these birds (Nos. 1, 4, and 6) were not breeding. No. 1 was captured with a group of nonbreeders and its plumage was like that of a yearling (see below): all its body feathers were new with light molt lingering on the back and head regions, and its primaries and secondaries were conspiciously worn. Individual No. 6, captured in the auklet net, was in identical plumage. The third bird, No. 4, also

TABLE 2
POUCH LENGTH AND BREEDING STATUS OF 2-YEAR-OLD BIRDS

Bird	Date of recapture	Pouch length (mm)	Status at recapture
1	12 May 1971	35	Nonbreeding
2	16 May 1971	36	Late breeding
3	6 June 1971	36	" "
4	10 June 1971	38	Nonbreeding
5	"	65	Breeding
6	<i>"</i>	38	Nonbreeding

captured in the auklet net, showed intermediate (moderate) plumage wear, its feathers apparently not subjected to the abrasion of a burrow. The other three birds (Nos. 2, 3, and 5) were at various stages of breeding when captured. Nos. 2 and 3 were late nesters. No. 3 was found in a burrow incubating. The second (No. 2) was found mated in a burrow from which the original owners were collected several days earlier. No. 6 was found with a small pouch (65 mm) on 10 June 1971. Its plumage showed wear like that of other breeding birds, and it was probably breeding for the first time. As an inexperienced bird it probably nested later than most of the experienced adults. If it laid its egg on or about 20 May, and its pouch started to elongate at that time and developed at a rate near 1.5 mm per day (see below), then its pouch length would be as observed on 10 June, about 65 mm. The details of the molts and plumages of Cassin's Auklet are in preparation by Udvardy and Speich.

The pouch begins to elongate in breeding Cassin's Auklets at the time of egg-laying. We tried to take a series of pouch measurements in individual breeding birds at this time, but adults in their burrows were easily disturbed and continued handling made birds desert their eggs. The pouch lengths of one bird measured 6 days and two birds 4 days before egg-laying were 25, 28, and 25 mm respectively; 3 (first bird) and 4 (second two birds) days after laying their pouch lengths were 55, 52, and 52 mm respectively. Thus pouch lengths increase markedly near egg-laying.

The pouch continues to elongate and reaches maximal length near fledging time (Tables 1 and 3). Some individual variation occurs, and the data in Table 3 are from both experienced and inexperienced breeding birds. These data and those above show the mean increase in pouch length of a breeding bird to be about 1.5 mm per day. The growth rates are probably greatest just after egg-laying and then diminish progressively as the pouch approaches full development.

 ${\bf TABLE \ 3}$ Rate of Pouch Length Increase of Birds at Various Stages of Nesting

	Pouch length		Change in	Days between	A *******
Bird	Ştart	End	pounch length		Average change
1	51	115	64	25	2.6
2	69	107	38	23	1.1
3	68	125	57	24	2.4
4	91	132	41	26	1.6
5	107	131	24	30	0.8
6	90	131	41	27	1.5
7	77	117	40	22	1.8
8	116	136	20	28	0.7
9	90	134	44	26	1.7
					$\bar{\mathbf{x}} = 1.5$

CHANGES IN POUCH LENGTH IN RELATION TO THE REPRODUCTIVE CYCLE

The auklet population on Southeast Farallon Island was sampled through 1970. Birds captured in the auklet net were measured to determine if a pouch was present (Figure 3). Sample sizes were not uniform, because the times of capture depended on wind, fog, moonlight, rain, and cloud cover conditions and on presence of enough workers to complete the operation.

The samples from February, March, and April each contained two groups of birds (Figure 3). One group included birds lacking pouches and those showing slight development (less than 50 mm), and the other group contained birds with small pouches (between 50 and 105 mm). The two groups were nonoverlapping in February and April, but in March were indistinct, possibly because the sample was small (n=36). The 11 July sample contained two distinct groups: one including birds lacking pouches and those showing slight pouch development. The other July group exhibited a continuous distribution from small to large and thus contained birds whose pouches were intermediate.

The 10 and 11 September 1970 sample included three distinct groups of birds (Figure 3). One contained birds that lacked pouches or whose pouches showed slight enlargement (less than 70 mm). The second group birds had small pouches, and the third group birds had large ones. The November sample resembled those of February, March, and April, with two groups of birds present (Figure 3). One group included birds lacking pouches or having slightly enlarged pouches, while the second group had small pouches.

Groups in each sample presumably have different breeding histories. Birds lacking a pouch or with only a slight pouch enlargement probably

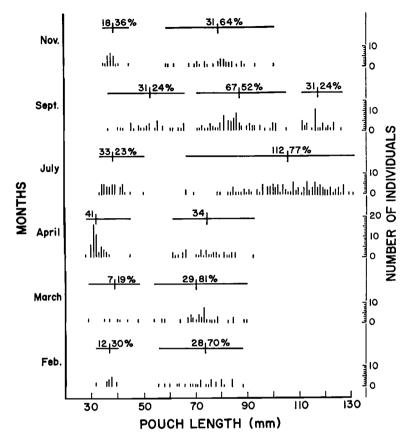


Figure 3. Frequency distributions of pouch lengths in 1970. Auklet net samples were from 14 February, 6 March, 11 July, 10 and 11 September, and 26 and 28 November. The 23, 25, 26, and 27 April sample contained birds collected from their burrows. Sample size, range, and mean are given for each group. The percentage of each group within each sample is given, except for the biased April sample.

had never bred. Such birds occurred in each sample. Also always present were birds with small pouches that had bred some time previously. Individuals with large pouches occurred only in July and September and represented breeders feeding young or birds that recently finished nesting. Birds with intermediate pouches in the July sample presumably had laid a replacement clutch (a second egg) after the first was lost earlier in the same season; their pouches were thus enlarging. The intermediate pouches of birds in September were regressing and were from birds that had fledged their young.

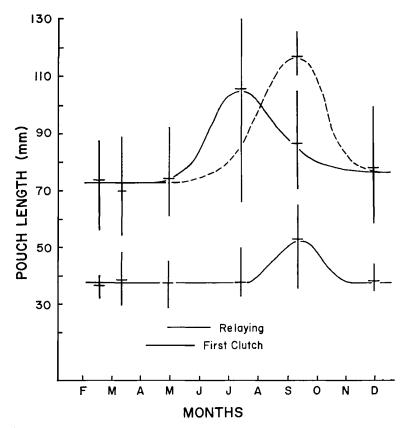


Figure 4. Changes in the pouch length. Curves fitted by inspection connecting means of pouch class groups. Lower curve is that of nonbreeding inexperienced birds and upper curves those of breeding birds (first clutch solid line; relaying broken line). Data from Figure 3.

In 1970 egg-laying started on 6 April and continued through 23 May (n = 330). Relaying commenced 26 April and ended on 11 June (n = 24; Figure 4). As the incubation period is 38 days and the fledging period 41 to 50 days (Manuwal 1972), the July sample birds were at varied stages of breeding (Figure 4). The mean pouch length for the July sample, excluding pouches less than 50 mm, was 104.6 mm (n = 112). This is smaller than expected for birds that were fledging young or had recently fledged young and whose pouches were beginning to regress. As the sample contained few birds with small inactive pouches, the mean pouch length was not lowered appreciably by nonbreeders, but instead apparently mainly by birds that lost their egg or nestling and whose pouches were not continuing to lengthen. Birds with large

pouches (mean = 116 mm; n = 31) in September had laid replacement clutches and comprised 24% of all birds captured in September. Indeed, auklet chicks were still being fed in mid-September. The birds with intermediate pouches (mean = 84.8 mm; n = 67) in the September sample probably were those that (1) successfully fledged a nestling and whose pouches were regressing, or (2) lost their egg or nestling, did not relay and whose pouches were continuing to regress. As Figure 4 shows, the pouch takes about 4 months after the end of chick-rearing to regress from around 120 mm to 65 mm.

The November auklet net sample showed breeding activity to be essentially completed. Only two groups were present, one lacked pouches or had pouches that showed slight development, and the other contained birds with small pouches. No birds with large pouches were present, and only a few had intermediate pouches.

Birds that bred in past years but not in the current year were always present, and it was impossible to separate them from the unsuccessful breeders of the same season. Also problematical was distinguishing individuals relaying after a nesting failure earlier the same season from those nesting late in the season but having bred successfully in a prior year. We believe that once a bird develops a small pouch it will always retain at least a small pouch. The sequence of pouch size changes in individuals that breed, fail, and then relay is unknown and remains to be clarified.

As mentioned before, one group in each sample lacked pouches or showed slight pouch enlargement. The pouch measurements of the birds in this group were less than 50 mm. This group showed greater pouch lengths in September than in other months (Figures 3 and 4), possibly the result of lessened territorial pressures. Night observations in 1970 and 1971 revealed a social structure in the colony. Cassin's Auklet occupies the island throughout the year. In February 1970, 2 months prior to egg-laying, some birds had completed burrows while others were digging. Nocturnal studies in June and July 1970 showed that at least half the birds on the surface were continually exploring the island and the burrows. Nonbreeders trying to acquire burrows, all of which were held by breeders, apparently produced considerable territorial pressure, for the burrow occupants were constantly repelling surface birds.

As the young start to fledge, the situation changes. Of 247 burrows checked on 6 July 1971 during the fledging period, 42% were empty. The social pressures from overcrowding apparently decrease as more and more burrows are vacated. Surface birds, whose numbers on the island have also decreased, can then explore and occupy burrows previously unavailable. Physiological changes following the easing of territorial pressures

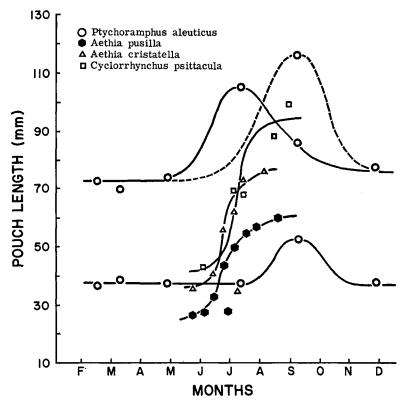


Figure 5. Pouch cycles in plankton feeding auklets. Curves for A. cristatella, A. pusilla, and Cyclorrhynchus psittacula adapted from Bédard and Sealy (MS). Curves for Ptychoramphus aleuticus as in Figure 4.

may produce a small transient enlargement of pouches in inexperienced birds.

Surface birds are generally inexperienced nonbreeders, and are scattered throughout the colony, but they tend to concentrate at certain sites. We tried three times to sample one such site beside an electrical generating plant in May and June 1971, with hand nets and a portable auklet net trap. Unfortunately our activities disturbed breeding birds on the slope above, and some breeders were captured inadvertently. In spite of this, 76% (n = 58) of the birds captured lacked a pouch. Others captured were in various breeding stages, except for three nonbreeding experienced birds.

A basic difference exists between the pouch length of Cassin's Auklet and the other auklets (Crested, Least, and Parakeet). In the latter species (Figure 5) the fledglings, individuals that have never bred, and

the prebreeding experienced birds seemingly all lack a pouch. In contrast, in Cassin's Auklet, as already mentioned, once an individual has bred it apparently never lacks a pouch.

The growth curves for pouches of all auklets are similar (Figure 5). The curves for the three northern species are based on data from St. Lawrence Island, Alaska (Bédard and Sealy MS). The birds arrive there in late May and lay eggs in late June and early July, with variations according to species and years (Sealy 1968). The pouch growth curves of the northern auklets appear to be steeper and to start ascending before eggs are laid. This might be adaptive to the shortened nesting period available to these species.

The differences between the St. Lawrence Island species and Cassin's Auklet appear to correlate directly with environmental conditions. On Southeast Farallon Island, Cassin's Auklet occurs through the year, while on St. Lawrence Island the birds do not appear on the colonies until the end of May and leave by the end of September. Wind, snow, and cold make it impossible for birds to occupy the northern island any earlier or much later, and egg-laying extends over only 2 weeks (Sealy 1968). On Southeast Farallon Island Cassin's Auklet normally starts laying in early March or April and continues to mid-July, a period of nearly 4 months.

Age Classes

In some alcids 1-year-old birds are easily distinguished from older birds: Crested and Least Auklets (Bédard and Sealy MS), Common Murre (*Uria aalge*, Tuck 1961), Common Puffin (*Fratercula arctica*, Lockley 1953), and Pigeon Guillemot (*Cepphus columba*, Drent 1965). The plumage of yearling Cassin's Auklets in June is distinct, the feather coat being new except for worn primaries and secondaries, as compared to the uniformly worn plumage of older birds. Also, iris color changes from dark brown in fledglings to white in adults (Manuwal 1972). Cassin's Auklets are not sexually dimorphic.

Apparently, this species usually does not breed until 3 years old, but of about 1,025 nestling Cassin's Auklets banded in 1969 and 1970, one bird attemtped to breed when 1-year-old in 1970. A small percentage of 2-year-old Least Auklets probably breed on St. Lawrence Island, Alaska (Bédard and Sealy MS). Drent (1965) noted that 2-year-old Pigeon Guillemots occurred in a colony and engaged in displays, but probably did not breed. Two-year-old Common Murres sometimes return to the colony and look for nesting sites, but probably do not breed until they are 3 years old (Tuck 1961). Lockley (1953) indicates that the Common Puffin does not breed until at least 3 years old. A few

Cassin's Auklets breed when 2 years old. Of about 700 young banded in 1969, 3 were found breeding in 1971; 3 others, in nonbreeding condition, were also captured.

One-year-olds are scarce in the colony, as most remain at sea. A few, with numbers varying nightly, are present among groups of older inexperienced birds. The nonbreeders (surface birds) concentrate mainly in traditional gathering sites on the surface of the island, but many are dispersed through the colony. The 1-year-old birds at the gathering sites are generally less active than are older birds, and sometimes spend a half hour or more sitting in one place just idly looking about the colony.

Discussion

If the auklet net trap samples of the population are unbiased, as we believe, then through measurement of the pouches of captured birds, we can determine what proportion of birds on the island have never bred. Similarly, the proportion of the population that has bred or is breeding can also be determined. Through 1970 the proportion of Lirds with no pouches or slight pouch enlargement (birds that had never bred) varied from 19-36% (Figure 3). A test for the significance of difference between two percentages (Sokal and Rohlf 1969) reveals no significant difference (0.05 < P < 0.65) between any two samples. Therefore, all samples are combined (n = 399), giving a mean percentage of birds without breeding experience on Southeast Farallon Island in 1970 as approximately 27%, or 40,000 birds (Figure 6). Consequently, birds breeding in or prior to 1970 comprised 73% of the birds (105,000 birds; Figure 6). Included in the 105,000 birds are those that had bred previously but not in 1970. At present it is impossible to distinguish them from experienced birds at most stages of the reproductive cycle, but the rate (R₁, Figure 6) at which they stop breeding is probably low. Also, it is impossible to determine the rate (R₂) at which they resume breeding. Apparently few birds stop breeding; most seem to continue to breed annually.

The proportion of inexperienced nonbreeders (i.e. those without pouches and those with slight development) might be expected to decrease significantly during the year with their incorporation into the breeding population (I_1 , I_2 , and I_3 refer to incorporation rates of 1 year, 2 year, and 3 year and older birds respectively; Figure 6). The proportion is also supplemented by increased visitation (Figure 6) of 1-year-old (V_1), 2-year-old (V_2), and older inexperienced birds (V_3) as the season progresses, at least until most young have fledged (July-August). Most 1-year-old and 2-year-old birds apparently remain at sea, but few 3-year-olds seem to remain entirely at sea. We have too few data to

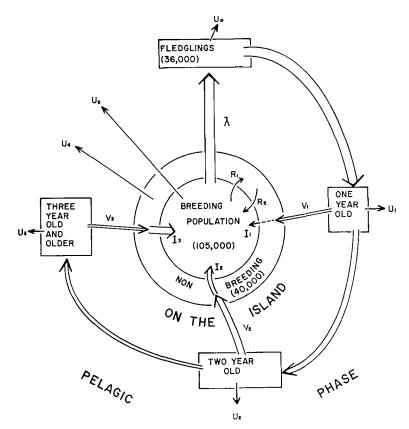


Figure 6. Population dynamics of Cassin's Auklet on Southeast Farallon Island, California. Mortality rates are shown by U's; rates of visitation of inexperienced birds to the island, V's; rates of incorporation of inexperienced birds into the breeding population, I's; rate at which experienced birds leave and re-enter the breeding population, R's; and the mean rate of chicks fledged per burrow per year is λ . See text for complete explanation.

estimate accurately the numbers in the age classes at sea. Increased visitation of young with greater age occurs in the Common Murre (Tuck 1961), Common Puffin (Lockley 1953), and Pigeon Guillemot (Drent 1965). In the last, 1- and 2-year-olds form up to 30% of the birds in the colony studied. In the Crested and Least Auklet populations, presumed second-year birds may compose 25–30% of the colony (Bédard and Sealy MS). As only part of the nonbreeding inexperienced birds are in the colony at any one time, all the percentages given for young are presumably underestimates for each species as a whole.

To determine what proportion of the birds (first brood) are breeding

for the first time, one measures pouches of breeding birds captured in their burrows immediately before the start of pouch enlargement or during its early phases at the time of egg-laying. Inexperienced birds then lack a pouch or have only a slightly developed one. Thus, new inexperienced birds totaled approximately 17% (n = 74; calculated 17,850) of the breeding population in 1970 and 1971. This figure combines the numbers for 1-year-old (I_1 ; Figure 6), 2-year-old (I_2), 3-year and older birds (I_3) initially entering the breeding population. Assuming the population is in stable equilibrium with its resources, this percentage probably roughly equals the turnover rate and also the approximate mortality rate (U_5) of experienced breeding birds in the population. This approximate mortality rate is heterogeneous in that it represents the sum of the mortalities of all age classes of experienced birds.

The mean reproductive rate (λ ; Figure 6) of Cassin's Auklet for 1970 and 1971 was 0.69 chicks fledged per burrow (0.66–0.71, n = 459; Manuwal MS). This indicates that on the average about 36,000 fledglings leave the island annually. If annually 17% of experienced birds die, then presumably an equal number of inexperienced birds enter the breeding population (I_1 , I_2 , and I_3). If we assume the population to be stable, the remainder of the inexperienced birds must die. Thus, the combined mortality rates of fledglings (U_0), 1-year-old (U_1), 2-year-old (U_2), and 3-year and older (U_3) inexperienced birds at sea and the inexperienced birds on the island (U_4) must approximate 50%, i.e. about 18,150 inexperienced birds die each year. This also is a composite rate. Presumably the probability of death is greater than 0.5 during a bird's first year of life but less in later years.

The mortality rates given here for inexperienced nonbreeding birds (50%) and experienced birds (17%) are only approximations. Obviously these values fluctuate from year to year and are perhaps different in other Cassin's Auklet colonies, but the calculated rates for Cassin's Auklet are similar to mortality rates obtained for seabirds in other studies (see Ashmole 1971). In Cassin's Auklet measurements of pouches reveal much about population structure. Ordinarily only an intensive, long-term banding program could yield equivalent data for an avian species.

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SUMMARY

The cyclic development of the gular pouch of Cassin's Auklet was studied on Southeast Farallon Island, California. Nestlings, fledglings, and older auklets with no previous breeding experience lack pouches. In birds breeding for the first time, the pouch begins to elongate at the time of egg-laying and reaches a maximum length of about 130 mm near the time the chick fledges. After the breeding season, the pouch regresses to about 65 mm and remains at this length until the next breeding season. Consequently birds with previous breeding experience can be identified by the presence of the pouch.

An individual auklet carries as much as 24.7 g of zooplankton to its nestling nearing fledging each night.

The pouch length of auklets captured at various times of the year was used to indicate stage of the reproductive cycle. The population always contains a nonbreeding segment and most of these birds have no pouch, indicating they never have bred. The mean percentage of auklets with no previous breeding experience was 27%. Most Cassin's Auklets first breed at the age of 3 years. One- and 2-year-olds comprise about 30% of the population. The rate at which new inexperienced auklets are incorporated into the breeding population was calculated to be 17% per year. This is presumably also the annual adult mortality rate. The annual combined mortality rate of fledglings, 1-, 2-, and 3-year-old inexperienced birds was estimated to be 50%.

The gular pouch length of Cassin's Auklet was found to be an accurate tool for determining the proportion of inexperienced breeders, state of the reproductive cycle of birds, and helpful in describing the dynamics of the population.

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