THE MOLT OF BREEDING CASSIN AUKLETS

By Robert B. Payne

The breeding and the molt of most land birds living at temperate latitudes take place at different times of the year. Both are critically timed to the seasonal pattern of the abundance of food. The separation of these events of the annual cycle suggests that both breeding and molt are accompanied by increased demands on the energy resources of the birds (Lack, 1954). Similar controls appear to regulate the timing of cycles of sea birds, many of which breed and molt at different times of the year (Ashmole, 1962, 1963; Bent, 1919; Dorward, 1963; Dorward and Ashmole, 1963; Kozlova, 1957; Maher, 1962; Salomonsen, 1944; Storer, 1952; Taylor, 1962; Tuck, 1960; Verwey, 1923). However, compromises between the separate schedules have been reached in others. Some sea birds of tropical latitudes and of high latitudes have overlapping schedules (Dorward and Ashmole, 1963; Johnston, 1961; Maher, 1962; Stejneger, 1885). This study reports that compromises occur at temperate latitudes as well.

Observations of Cassin Auklets (*Ptychoramphus aleutica*) on South Farallon Island, California, were made in summer during the breeding season. Breeding Cassin Auklets had started the postnuptial molt while they were still incubating and feeding young. Birds which were expending the most energy on their breeding activities nevertheless were molting at the slowest rate and had progressed only a short way through the molt.

OBSERVATIONS

Cassin Auklets were observed from July 8 to July 15, 1964, on South Farrallon Island, 27 miles off the coast of San Francisco, California. The auklets spent the days feeding at sea, and at night they flew to the island for courtship and for feeding the young. The first appearance of the auklets on the island was about a half hour after sunset, when thousands of auklets were seen flying low, crashing, stumbling, and running across the cobble- and boulder-strewn sandy flats of the breeding grounds on the southeast end of the island. The auklets sang all night long.

The hourly activity of the auklets at night was recorded on the foggy night of July 14–15. Counts of auklets flying or running across a three-foot wide, lighted walkway through the colony were made during 10-minute walks along the walkway. At 10:00 p.m. Pacific Daylight Time 20 auklets were counted; 33 were counted at 11:00 p.m.; and 9 were counted at midnight. Before midnight most of the breeding adults had arrived at the colony. During the early morning hours most auklets were in the burrows. Four auklets were seen on the walkway at 1:00 a.m., 2 at 2:00 a.m., 3 at 3:00 a.m., and 7 at 4:45 a.m. About an hour before sunrise great numbers of auklets emerged from the burrows and flew off to sea. The first birds left when the rugged outline of the rocky peaks north and west of the breeding colony were barely visible to me. Thirty-six auklets were seen walking or flying across the walkway at 5:00 a.m.; 88 were seen at 5:15 a.m.; none was seen at 5:30 a.m. or later in the morning. Most of the birds flew off to sea before the sky was light enough for notes to be legible. The outgoing flight of the auklets was to the southwest where there was the longest stretch of sea unbroken by high rocks. During the daytime hundreds of old carcasses of auklets were found at the bases of the rocks into which some birds had crashed.

During the first days of observation many burrows with warm eggs and with

TABLE 1

FREQUENCY DISTRIBUTION OF NUMBERS OF OLD PRIMARIES OF BREEDING CASSIN AUKLETS

Breeding state	Numbers of old primaries					
	3	4	5	6	7	Average
Single	1	16	9	2	2	4.6
Paired		13	8	2		4.5
Incubating		3	15	3		5.0
Downy young in burrow		2	3	3	1	5.3
Feathered young in burrow		1	4	8	4	5.9

young of all ages were found in the breeding colony. It was a surprise to find that the adult auklets on the breeding grounds at night were in molt. Further observations of adults caught in the burrows at night showed that the individuals that were molting were at the same time breeding.

The auklets were checked for molt mainly on the nights from July 12 to July 15 between the hours of 2 and 5 a.m. when most birds were in their burrows. The birds were pulled or dug from the burrows and were checked by flashlight and forceps for presence and extent of molt. The adults had very pale, blue-gray eyes and worn plumage, and the young birds had dark brown eyes and fresh plumage. All auklets were then returned unharmed to their burrows, and the disturbed burrows were repaired.

MOLT

The wing molt of Cassin Auklets involves the gradual loss and replacement of primaries a few at a time, from the innermost outward, rather than the simultaneous loss and replacement that occurs in the larger flying alcids. This progressive wing molt had started in all 100 adults taken from burrows and in all 22 adults caught around midnight on the ground. No more than three primaries on each wing were in molt at the same time on any birds. The innermost of the growing primaries of each bird was most completely grown, and the outermost of the growing primaries was least completely grown. Primaries are apparently dropped one at a time. Each is generally dropped when its inner neighbor has grown to about half its length. The occurrence of a progressive wing molt in Cassin Auklets was previously suggested in a footnote by Stejneger (1885) on the basis of a single bird with an incompletely grown outer primary.

All the Cassin Auklets examined in the field had replaced some of the inner primaries. The number of remaining, outer, old primaries, however, was directly related to the breeding state of the bird. Auklets feeding young were further behind in their molt than auklets incubating eggs, and auklets incubating were farther behind in their molt than auklets in burrows without eggs or young. The positive correlation between number of old primaries and the breeding state was significant at the 0.05 probability level (Spearman rank correlation coefficient $r_s = 0.92$). The frequency distribution of numbers of old primaries of the breeding auklets is recorded in table 1.

The rate of molt was determined by counting the numbers of growing and missing primaries on each wing. Birds with more molting primaries were thus molting at a faster rate. The auklets which had expended the least energy on their breeding activities were generally molting at a faster rate. Numbers of molting primaries were greatest in auklets in burrows without eggs or young, intermediate in auklets with

TABLE 2

FREQUENCY DISTRIBUTION OF NUMBERS OF GROWING PRIMARIES OF BREEDING CASSIN AUKLETS

Breeding state	Numbers of growing primaries				
	0	1	2	3	Average
Single		11	10	1	1.7
Paired		4	18	1	1.9
Incubating		12	9		1.4
Downy young in burrow		9			1.0
Feathered young in burrow	1	13	3		1.1

eggs, and least in auklets with young. This negative correlation between numbers of molting primaries and breeding state was significant at the 0.05 probability level (Spearman rank correlation coefficient $r_s = 0.93$). The numbers of growing primaries on the 100 adults taken from burrows are recorded in table 2. Birds feeding young had an average of 1.1 growing primaries on each wing and birds without eggs or young had an average of 1.8 growing primaries. The auklets feeding young then were molting, on the average, 40 per cent more slowly than were adult auklets without eggs or young.

One adult had begun and then arrested the annual molt during the period of parental care. This auklet had replaced the inner primaries but had retained the outer five old primaries. No growing feathers or gaps were present between the old and new primaries, and no growing body feathers were present in the tracts examined. In the burrow with this adult was a feathered young auklet nearly ready to fledge. Evidently, some adult Cassin Auklets have an interrupted annual molt with a cessation of loss and replacement of feathers during the period of feeding the young.

Molt of body feathers was checked by lifting the body feathers from behind and shining a light down through the plumage to the base of the shafts. The presence of feathers in sheath was recorded on the back between the scapulae, on the belly by the end of the keel of the sternum, and on the crown. The area of plumage examined in each tract was about one square centimeter. Birds which showed no growing feathers on these areas may have had growing feathers on other parts of the body.

Most adult Cassin Auklets from burrows were in body molt. Two of the 53 adults with no eggs or young showed no molt on the body, while 13 of 47 adults with eggs or young showed no molt on the body. The greater extent of body molt in adults which were not caring for eggs or young was significant at the 0.05 probability level ($\chi^2 = 9.36$, contingency test).

The members of pairs of adults in burrows tended to be alike in the extent and rate of molt. However, the tendency was not statistically significant. Pairs of adults were found together at night in burrows with no eggs or young, in burrows with eggs, and in burrows with young. Pairs at two other burrows with eggs were determined by examining the burrows on successive days both before and after one bird relieved the incubating partner of incubation duties for a few days. For each of these three groups of pairs of breeding birds a corresponding group of the same number of pairs was constructed at random. Random pairs were formed by coupling birds drawn from the total sample of the corresponding stage of breeding by a table of random numbers. The mean difference in numbers of old primaries in the two members of each of the 11 burrowing pairs was 0.54, whereas the mean difference in 11 random burrowing pairs was 0.94. Similarly, the mean difference within burrowing pairs in

numbers of growing primaries was slightly less (0.27) than the mean difference within the random pairs (0.45). The probability that these differences could have been due to chance alone was just greater than 0.10 (t-test), and the differences were not considered to be statistically significant. Differences in extent and rate of molt within five incubating pairs and also within six pairs of adults feeding young were about the same in real and random pairs. The degree of correspondence in molt within real pairs was about the same for adults in all three stages of breeding.

MOLTING SEASON

The timing of annual molt of Cassin Auklets was determined in detail from museum study skins collected off the coast of California. Specimens were examined in the collections of the Museum of Vertebrate Zoology and the California Academy of Sciences. I am grateful to the curators of these collections for permission to study the skins.

The total series of 147 auklets showed a prolonged period of postnuptial molt during summer and autumn. Adults were aged by the presence of worn feathers. The body molt begins some time before the molt of the primaries. Most of the 30 adults taken in June had started replacing many worn feathers on the head, neck, back, and undersides. One adult taken in the last week of June had started replacing the inner primaries. All eleven adults in July and August were molting body feathers, and all but one of these were molting the primaries progressively. That one, an adult taken in the last week of August, had completed replacing the primaries. All adults had replaced all the primaries by the middle of September, but all remained in body molt through the end of September. Half the sample from October and half from November and one bird from December showed a continuation of the body molt. The fresh plumages of adults and of young were similar after completion of the wing molt of the adults, and the ages of birds molting in late autumn were not determined. No molt was seen in 37 other birds from December through April. Four of seven adults taken in May were in body molt, and some of these may merely have been replacing feathers lost by abrasion in the burrows.

Alcids generally have two molts each year (Coues, 1868; Kozlova, 1957). Cassin Auklets, in contrast to most alcids, have no distinct seasonal changes of plumage. No prenuptial molt has been described in Cassin Auklets. Until molting birds from October and November are aged, the significance of this late molt remains obscure.

BREEDING SEASON

Cassin Auklets breed on the Farallon Islands most of the year. The excavation of burrows begins as early as January (Thoresen, 1964). Eggs have been found from April through July (Bent, 1919; Bowman, 1961; Thoresen, 1964; the present study). Young auklets fully grown and ready to fly to sea have been seen in May, June, and July (Dawson, 1911; Loomis, 1896; Thoresen, 1964; the present study). The incubation period is over a month and the young remain in the burrow for six more weeks (Thoresen, 1964), so the May fledglings represent eggs laid by March.

The auklets also breed through late summer and early autumn. In the present study 17 warm eggs were found in burrows, and the one egg accidentally broken contained a small embryo about as far developed as a five-day chicken embryo. These July eggs would probably hatch in July and August, and the successful young would fledge in August and September. Smith (1934) found fresh eggs in the middle of August, and the parents at these burrows, if successful in hatching the young, would

continue feeding young through October. Bryant (1888) reported that eggs had been found in November, but he did not note their condition. These late eggs may have been laid and abandoned in burrows in spring or summer.

The presence of unpaired and paired auklets in burrows at night with no eggs or young further indicates that egg laying had not been completed by early July. One pair was found alone in a burrow at 3:45 p.m., and another single adult was found in a burrow at midday. One adult was caught at night in a collapsible aluminum live trap set out to catch small mammals. The entrance to the trap was about the same size as the entrance to auklet burrows. The bird may have mistaken the trap for an unoccupied burrow. Most burrows in the colony were unoccupied during the second week of July, however. In one study plot, 64 burrows were found in an area 30 by 30 feet. Nine of these burrows were occupied by adults without eggs or young, and another eight burrows had either eggs or young. Another plot (fig. 1), 35 by 20 feet below Farallon Cave, had 46 burrows; five had adults only while nine others had eggs or young. A third concentration of 84 burrows in an area 40 by 30 feet north of the only pine tree on the island had only adults in 12 burrows and eggs or young in 15 other burrows.

FOOD

Parental care of eggs and young is thought to raise the food requirements of adult birds during the breeding season. Breeding adults must catch enough extra food for the growth of the young as well as for their own increased activity. Molt also is thought to raise the metabolic level of birds.

Cassin Auklets feed at sea several miles from the coast and dive for plankton. On the afternoon of July 15, on the United States Coast Guard Cutter "Magnolia," I watched Cassin Auklets at sea. Two miles southeast of Farallon Island scattered groups of three to six auklets were on the water. Auklets occurred in thousands between four miles southwest and ten miles northwest of the island. North and east of North Farallon Island no auklets were seen.

Adult auklets on the island at night often regurgitated food when they were handled before they entered the burrows. This food consisted mainly of a pink, soupy mass of small crustaceans. The regurgitation was partly digested, and the food could not be identified. Thoresen (1964) records euphausids as the main food of the auklets on the Farallones. *Thysanoessa spinifera* is the only euphausid near the Farallon Islands which is abundant during the daytime near the surface of the sea. This species does not migrate to depths during the day. Vertical sampling of plankton has shown that most of these euphausids are found in the upper 100 meters, and the density in the upper four meters of water is high. Extensive surface shoals of breeding *T. spinifera* have been seen from July to September off central California, and spent females have also been found in June (Brinton, 1962). This euphausid is also the main food of king salmon (*Oncorhynchus tshawytscha*) off the Farallon Islands in spring and summer (Merkel, 1957). *Thysanoessa spinifera* is the main food of breeding Cassin Auklets on islands off Vancouver Island, British Columbia (Carl, Guiguet, and Hardy, 1951). Probably most of the euphausids taken by auklets near the Farallon Islands are of the same species. Other euphausids migrate down below 300 meters during the daytime (Brinton, 1962) and so are not available to the Cassin Auklets during their feeding hours. Shoals of another euphausid, *Euphausia pacifica*, also occur irregularly from March to August off California (Brinton, personal communication) and may provide food for auklets attracted to the shoals.

Fig. 1. Burrows of Cassin Auklets on South Farallon Island. Burrows were dug in sandy soil under granite rocks or weeded turf. At night several of these burrows held nesting adults in molt. Photograph taken July 13, 1964; enlarged by Gene M. Christman.

Studies on the seasonal abundance of euphausids of the coastal waters of California are still in progress (Brinton, personal communication). Seasonal changes of the standing crop of all zooplankton have been studied, however, and the abundance of zooplankton in general probably parallels the abundance of auklet food. Figure 2 summarizes the seasonal abundance of small organisms sampled within 25 miles of South Farallon Island, a distance which includes much of the feeding area of Cassin Auklets. The data are taken from a series of annual reports on the plankton volumes collected by the California Cooperative Oceanic Fisheries Investigations (Staff, South Pacific Fishery Investigations, 1952, 1953, 1954, 1955, 1956; Thrailkill, 1957, 1959, 1961, 1963). In most years zooplankton is particularly abundant from May through July and is least abundant during the winter. Food appears to be most abundant during the months the auklets are feeding the most young and are beginning the postnuptial molt.

DISCUSSION

The breeding season and molting season of most alcids do not overlap. The larger alcids shed all the remiges at sea after the breeding season. They generally drop the inner primaries first but also drop all the outer primaries before the inner ones have grown out. All the primaries grow out at the same time. The birds are able to swim or to "fly" under water with their reduced wings even when the flight feathers have been dropped, but they cannot fly until the remiges have grown (Storer, 1960).

Cassin Auklets, like the smallest auklets, *Aethia pygmaea* (Stejneger, 1885) and *A. pusilla* (Storer, 1960), retain the outer primaries while molting the inner ones. The inner primaries are fully grown before the outer ones are dropped. Storer notes that if the wings of the small auklets lost the remiges all at one time, the wing area

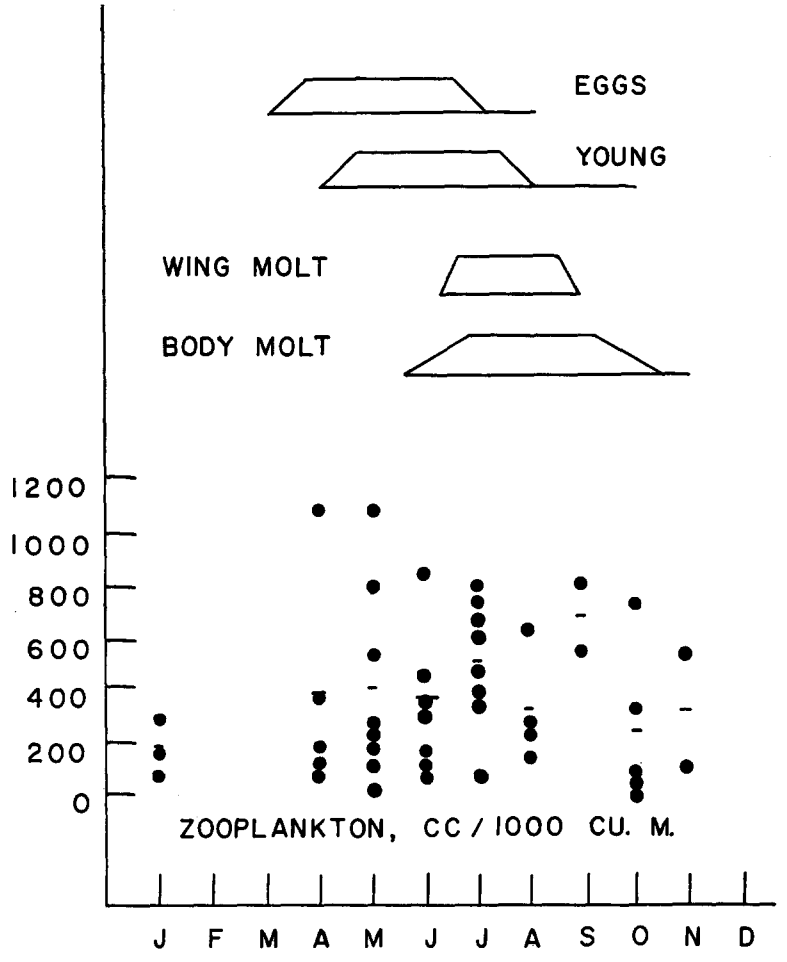

Fig. 2. Seasons of breeding and molt of Cassin Auklets on South Farallon Island. Data for abundance of small organisms is based on trawl net samples taken to 140 meters. Points show plankton volumes in different years, and lines show monthly averages.

would probably be too small for swimming and feeding during the molt. Although they may be slightly below their maximum flying and swimming efficiency, the molting Cassin Auklets are able to feed themselves and their young successfully.

The occurrence of molt during the period of breeding appears to be an adaptation which prolongs the breeding season. Some museum skins of Cassin Auklets taken on the breeding grounds in spring and summer have plumages which are extremely worn from months of life in the burrows. Retention of the extremely worn flight feathers and long retardation of molt in early summer would likely result in a period of flightnessness. Flightless adults would be unable to feed their young. On the Farallon Islands the molt of the primaries extends from July through August, and some young are fed in July and August throughout the period of the postnuptial molt. Parts of the worn plumage are replaced in time for the wings of the adults to be repaired while young are still in the burrows. The overlap of breeding and molt

in summer is associated with a longer successful breeding season for the population and probably on the average more young per year per adult.

Although the seasons of breeding and molt of Cassin Auklets do overlap, Lack's concepts of the increased energy demands of breeding and molt and of the timing of these events to the availability of food are appropriate. First, both breeding and molt of the auklets are drawn out in time and require relatively little extra energy each day. Second, probably many individuals have completed breeding before they begin the molt. Observations indicate that most young fledge in May and June, and by the beginning of the wing molt in early July many of the burrows are deserted. Third, the rate of molt is slowed when more energy has been expended on breeding. Finally, the period of overlap of breeding and molt occurs during the period of the greatest probability of abundant food.

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SUMMARY

Cassin Auklets (*Ptychoramphus aleutica*) on the Farallon Islands, California, molt in summer during the second half of the breeding season. Primaries are molted progressively a few at a time rather than synchronously. The birds fly during the period of molt. Adults begin the postnuptial body molt and the wing molt while courting, incubating, or feeding young. The progress of the molt is less and the rate of the molt is slower in the adults which have expended proportionally more energy in breeding. Individuals feeding young in July were farther behind in molt than the incubating auklets, and both were behind adults which had not yet laid eggs. On the average, birds feeding young were molting 40 per cent more slowly than were burrowing birds without eggs or young. Molt stops completely in some adults that are feeding young.

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