ANNUAL VARIATION OF PRIMARY MOLT WITH AGE AND SEX IN CASSIN'S AUKLET

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ABSTRACT.—In Cassin's Auklet (*Ptychoramphus aleuticus*) on Southeast Farallon Island, California, 1979–1984, we found significant annual and seasonal variation in timing and rate of primary molt in adult males, adult females, and subadults (1–2 years old). Except in 1979, adult males began to molt at least 10 days before adult females, and males molted at a slower rate. Subadult birds initiated molt later and molted faster, but showed less annual variation than adults. Timing of breeding and breeding success varied annually but were not correlated directly with molt. In years of extended breeding, molt rates were slower apparently in response to the energetic demands caused by the overlap of breeding and molt. *Received 17 October 1989, accepted 12 April 1990.*

ANNUAL and seasonal variation in molt, as well as its overlap with other phenological events (e.g. breeding, migration), is rarely studied in wild birds. Only the broadest patterns of molt are known for most pelagic seabirds because they molt at sea, away from breeding colonies where they are most accessible. Minimal data are available for alcids because wing molt for most species is synchronous, which renders them flightless at sea. Consequently, most of the information on molt in alcids is based on museum specimens (Salomonsen 1944, Storer 1952) or on captive birds (Birkhead and Taylor 1977, Swennen 1977, but see Harris and Wanless 1990). The auklets (*Aethia* spp., *Cyclorrhynchus, Ptychoramphus*), however, molt their primaries over an extended period that overlaps with breeding (Payne 1965, Bédard and Sealy 1984).

Cassin's Auklet (*Ptychoramphus aleuticus*) lays a single egg and has an average 38-day incubation and 41-day nestling period. It is the only auklet with a subarctic distribution in the eastern Pacific (Manuwal 1974a, Ainley and Boekelheide 1990). A large breeding colony on Southeast Farallon Island (SEFI), California, is attended by auklets nearly year-round. The accessibility of this colony has accommodated numerous studies on the natural history and breeding biology of Cassin's Auklets (for a summary, see Ainley and Boekelheide 1990).

The Cassin's Auklet also is the only alcid known to double brood, though most Cassin's Auklets do so unsuccessfully (Ainley and Boekelheide 1990). In birds that double brood, molt may overlap extensively with breeding. In addition, this species undergoes significant annual variation in the timing of breeding and the amount of double brooding relative to oceanographic conditions (Manuwal 1974a, Ainley and Boekelheide 1990).

Payne (1965) showed that the progress and rate of molt are slower in Cassin's Auklets that have expended the most energy for breeding, although he was unaware that these birds can double brood. From 1979–1984, we studied the primary molt of Cassin's Auklets on SEFI to investigate further the effects of breeding on molt in consideration of the potentially confounding variables of individual age, sex, and body weight.

STUDY AREA AND METHODS

Southeast Farallon Island is located 42 km west of San Francisco and supports the largest breeding colony of seabirds in the continental United States (Ainley and Boekelheide 1990). Manuwal (1974a, b, 1979) described the breeding colony and habitats used by Cassin's Auklets on SEFI.

We used a 20 × 5 m fish net (1.27-cm^2 mesh) to capture and band birds as described by Ralph and Sibley (1970). The net was opened 2 to 3 times per month ca. 1 h before dawn when birds began to leave the colony for the day. Sampling dates varied each month until approximately 100 birds were captured. We recorded the following information on each captured or recaptured bird:

1. Weight—Measured to nearest gram.
2. Eye color—To estimate age we modified the methods of Manuwal (1978) to include nine (instead of four) pigmentation categories: from 1.0 (white eye) to 5.0 (dark eye) in scoring increments of 0.5. Birds

with dark eyes (≥3.5) were considered subadults (assumed nonbreeders, 1-2 yr old), and those with light eyes (≤3.0) were considered adult (assumed breeders). Accuracy of these criteria was tested by examination of known-age breeders on SEFI in 1988 and 1989.

3. Bill dimensions—Width and depth (in mm) were greatest at anterior edge of nares (Nelson 1981). Birds with a bill depth (or average bill depth from multiple captures) of >10.3 mm were classified as males, and those with a depth of <9.5 mm, females. Although Nelson (1981) found most females to have a bill depth of <10.3 mm, we used a stricter definition to account for multiple-observer and measurement error. Subadult birds were not sexed.
4. Primary molt—Molting feathers were scored as either old (score 0), missing, or growing. Growing feathers were classified into one of six stages of growth: pin or $\frac{1}{10}$, $\frac{3}{10}$, $\frac{5}{10}$, $\frac{7}{10}$, or $\frac{9}{10}$ grown, or new. These categories were recoded with standardized methods (e.g. Newton 1966, Ginn and Melville 1983). Accordingly, primaries (P1 to P10) in pin were scored as 1, $\frac{1}{10}$ to $\frac{3}{10}$ grown were scored 2, $\frac{5}{10}$ was scored 3, $\frac{7}{10}$ to $\frac{9}{10}$ were scored 4, and new primaries were scored 5. Summation of scores for all 10 primaries provided the *molt score* for each captured bird. We did not collect data on body or secondary molt, and hereafter *molt* refers to primary molt.

We used molt score rather than feather mass (see Summers et al. 1983) in our analysis. In Cassin's Auklet, P10 is only 25-29% longer than P1, and P7-P10 are nearly equal in length (within 2 mm; $n = 9$). Thus, we assume that a change in the amount of feather mass replaced during molt in Cassin's Auklet probably does not affect molt rate as it does in other Charadriiformes (Summers et al. 1983, Underhill and Zucchini 1988, Underhill et al. 1990).

We measured birds that were captured before, during, and after the molt period. Birds recaptured within the same month were excluded. These "Type II" data provided estimates of molt parameters with the smallest bias (see Underhill and Zucchini 1988). We did not use Underhill and Zucchini's (1988) numerical algorithm to estimate molt parameters because it relies on a linear relationship of molt rate with time. This relationship is not always linear in Cassin's Auklet (Payne 1965, and data here).

We used linear regression of Julian date on molt score (Pimm 1976) for all birds captured from April through October to estimate molt parameters for each year. The slopes of regression lines produced by this method do not give molt rate, but an inversion of molt rate (rate^{-1}). Although our statistical comparisons are based on the regression values, for clarity in discussing relationships of molt with age and sex, we refer to actual molt rates. All regression analyses were completed with SPSS/PC+ (Nurusis 1986).

Annual variation in molt among sex and age classes was assessed with an analysis of covariance (ANCOVA) on SPSS/PC+. The relationships of molt with body weight, timing of breeding, and breeding success were compared using Spearman's rank correlation (r_s, $P < 0.05$). We determined annual mean (±SD) laying dates (MLD) and breeding success (BS) of Cassin's Auklets from a sample of monitored nest sites (Ainley and Boekelheide 1990). Although MLD implies a normal distribution in laying dates, in Cassin's Auklets this distribution is often skewed towards the earlier part of the laying period (Ainley and Boekelheide 1990). The use of median laying dates resulted in a ranking of years similar to that by mean laying dates. We used data from first clutches only (excluding relays) to calculate MLD. *Breeding success* is the average number of chicks fledged per pair laying.

RESULTS

We confirmed our age classification of Cassin's Auklets by examining eye color of 53 known-age breeders on SEFI in 1988, and 89 in 1989. No breeders in either year had an eye color score of >3.0 (the maximum value used to identify adults captured in the net). The sample included 4 two-year-old birds (the earliest age of first breeding in this species) in 1988 and 10 in 1989. Thus, most birds with an eye color of >3.0 are probably one-year-old subadults.

We used the percentage of birds that initiated molt (P1 missing or growing) each month, from April through December, to assess annual variation in molt timing and duration. Monthly percentages of adult males, adult females, and subadults in molt for breeding seasons 1979-1984 indicate that, in all years except 1983, most birds (>50%) were molting by June (Fig. 1). All captured birds were in molt by July in each year. Any annual variation in these percentages occurred in May and June. Relatively more birds were in molt during May in 1980 and 1984, and fewer during June in 1979 and 1983, than in all other years.

Molt parameters.—The use of linear regression of Julian date on molt score has been criticized because most data are heteroscedastic (lacking homogeneity of variance), sampling dates are not random, and the results often underestimate the timing and rate of molt (Underhill and Zucchini 1988). We evaluated the effects of these problems on our data with an examination of scatterplots of regression variables. Plots for each year of data on adult and subadult auklets (see

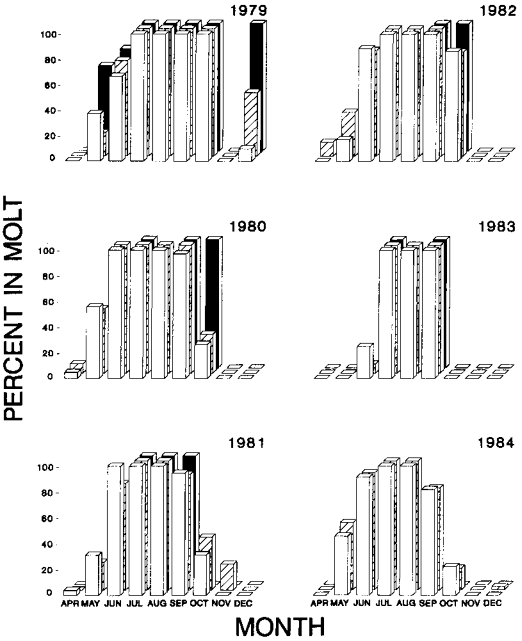

Fig. 1. The monthly percentage of adult males (open bars), females (hatched bars), and subadults (solid bars) in molt (missing or growing at least one primary) captured on Southeast Farallon Island, April through December, 1979-1984. A decrease in percentages after August each year denotes birds that have completed molt. Missing bars indicate absence of data, or when no captured birds were in molt (see Appendix 1 for sample sizes).

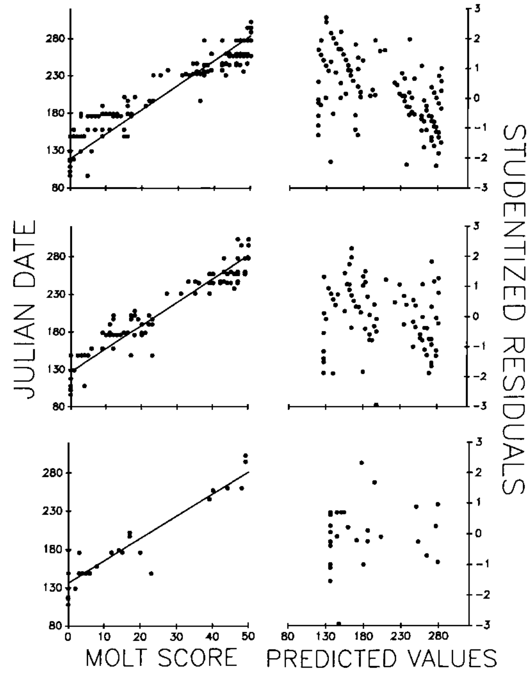

Fig. 2. SPSS/PC+ scatterplots of Julian date with molt score (left) and Studentized residuals with predicted values (right) for adult male (top), female (middle), and subadult (bottom) Cassin's Auklets captured on Southeast Farallon Island, April-October 1980 (see Table 1 for sample sizes and regression equations).

Fig. 2 for 1980) indicated that not all regressions are homoscedastic, which resulted in an underestimate of molt parameters. In most years, fewer than 50% of the birds were in molt by the initiation date estimated from regression (Fig. 1, Table 1). In 1980 and 1984, >50% of the adults were molting by the estimated date, a pattern that supports the regression model. Although most of the molt parameters were slightly underestimated, they provided relative differences in timing and rate of molt for adult males, adult females, and subadults.

Except in 1979, adult males began molt at least 9-10 days earlier than females (Table 1). In 1979, females began 9 days earlier than males. Molt duration was at least 11 days longer in males except in 1979.

Subadults began molt later than adults, and molted more rapidly, in 1979-1982. The 1983 and 1984 samples were too small for statistical comparison (Table 1). Significant variation in molt rate (all years combined) was apparent in adult males and adult females (ANCOVA, $P < 0.01$), but not in subadults ($P = 0.06$). Seasonal variation of molt rates between the sexes was significant in 1981-1984 (ANCOVA, $P < 0.05$, $F \geq 4.52$), but differences between adult females and subadults in 1979-1982, and between adult males and subadults in 1979, were not ($P > 0.05$, $F \leq 3.54$).

Body weight, molt, and breeding.—Mean bimonthly weights of adult male and adult female auklets vary significantly in all years (ANOVA, $P < 0.01$). Auklets of both sexes obtain their peak annual weight in winter, before breeding, and their lowest in summer, during and after breeding (see Fig. 3 for 1979 and 1982). A significant interaction between bimonthly period and sex occurred only in 1982 ($F = 3.31$, $P = 0.011$). In that year, males lost relatively less weight during breeding (May-June) than females, and gained weight at a higher rate after breeding (July-October) (Fig. 3).

Mean weights of adults in February is cor-

TABLE 1. Estimated molt parameters using linear regression of Julian date of capture on molt score for adult males, females, and subadult Cassin's Auklets on Southeast Farallon Island, 1979–1984. For each sample period, the top row is the regression equation (sample sizes in parentheses); the middle row is the standard error of the y-intercept and slope, respectively; and the bottom row is the estimated timing and duration (number of days in parentheses) of molt using molt score (x) values of 0 (no molt) and 50 (molt completed) in the regression equation. The y-intercept is mean Julian date of molt initiation, and the slope is the inverse of the mean molt rate (higher numbers indicate slower rates). All regressions have $r^2 > 0.83$.

Year	Males	Females	Subadults
All	$y = 129.7 + 3.21x$ (887)	$y = 140.6 + 2.92x$ (1,000)	$y = 143.9 + 2.92x$ (87)
	0.89, 0.032	0.86, 0.032	2.86, 0.132
	10 May–18 Oct (161)	21 May–14 Oct (146)	24 May–17 Oct (146)
1979	$y = 140.5 + 3.19x$ (178)	$y = 132.3 + 3.47x$ (52)	$y = 139.2 + 3.35x$ (24)
	2.05, 0.075	3.89, 0.159	7.23, 0.278
	21 May–27 Oct (159)	12 May–2 Nov (174)	19 May–3 Nov (168)
1980	$y = 118.7 + 3.32x$ (237)	$y = 126.9 + 3.10x$ (131)	$y = 136.1 + 2.91x$ (34)
	1.77, 0.057	2.45, 0.077	4.03, 0.196
	30 Apr–12 Oct (166)	8 May–10 Oct (155)	17 May–10 Oct (146)
1981	$y = 132.5 + 2.98x$ (143)	$y = 141.2 + 2.74x$ (184)	$y = 155.7 + 2.38x$ (14)
	1.81, 0.068	1.91, 0.067	6.57, 0.296
	13 May–9 Oct (149)	21 May–5 Oct (137)	5 Jun–2 Oct (119)
1982	$y = 128.8 + 3.35x$ (151)	$y = 148.5 + 2.91x$ (213)	$y = 152.3 + 2.75x$ (15)
	2.09, 0.064	1.89, 0.059	3.99, 0.238
	9 May–23 Oct (168)	29 May–21 Oct (146)	1 Jun–17 Oct (138)
1983	$y = 134.3 + 3.13x$ (73)	$y = 147.3 + 2.77x$ (179)	—
	2.67, 0.117	2.11, 0.089	—
	14 May–18 Oct (157)	27 May–13 Oct (139)	—
1984	$y = 129.0 + 3.17x$ (110)	$y = 138.4 + 2.89x$ (254)	—
	2.10, 0.091	1.48, 0.068	—
	10 May–16 Oct (159)	19 May–11 Oct (145)	—

related with timing of breeding (mean laying date) (Table 2 and Fig. 3; $r_s = 0.83$, $P < 0.05$). Timing of breeding also is correlated with the percentage of double-brooded birds (Table 2). In years of early breeding, relatively more birds attempted a second brood ($r_s = 0.90$, $P < 0.01$). Timing of molt is not correlated with the percentage of birds with double broods ($r_s < 0.3$).

Timing and rate of molt are not correlated with timing of breeding for males or females, or with breeding success ($r_s < 0.6$). The seasonal percentage of birds that molted only one primary versus those that molted two or more primaries simultaneously correlated significantly with the percentage of birds each year that double brood (Table 2; $r_s = 0.83$). Fewer birds molted more than one primary at one time in years of high incidence of double brooding. Annual timing of molt in males ($r_s = 0.94$), but not in females ($r_s = 0.09$), is correlated with timing and rate of weight gain after breeding (Fig. 3). Males initiated molt later in years when weight gain was delayed relative to other years.

Individual molt parameters.—In birds captured at least twice during molt, the mean (±SD) molt rates of recaptured birds ($\bar{x} = 3.06 \pm 1.14$, $n = 128$, all years) are comparable to those estimated by linear regression (Table 1). An exception is 1983 when recaptured birds show a faster mean molt rate ($\bar{x} = 2.32 \pm 0.75$, $n = 30$) than the estimate. In addition, 5 of 13 birds captured three times during molt showed little or no change in molt rate between captures (<1.0 unit difference). Of the remaining 8, 6 slowed their rate by as much as 1.5 to 29.6 units. The bird with the greatest decrease apparently arrested molt in its late stages, between 16 October and 20 December 1979.

Arrested molt in Cassin's Auklets is not unusual. Payne (1965) observed one such bird in July 1965. In June 1989 we captured two birds that had 3–4 new (and all remaining old) primaries. Both birds were incubating a second clutch.

DISCUSSION

We did not collect data on body or secondary molt. Subadult Cassin's Auklets molt body feathers in spring, before adults begin (Manuwal 1978). Adult body feathers are molted in relation to breeding status. Payne (1965) found that adults without eggs or young were more advanced in body molt than those with eggs or young. Secondary feather molt begins after primary molt and may overlap slightly. For the entire molt, subadults begin earlier, and complete molt sooner, than adults. Adults overlap body and primary molt with breeding, and may continue molt throughout the autumn.

Our results agree with Payne (1965). Cassin's Auklets can alter timing and rate of molt in relation to breeding effort, apparently as a means to balance the energetic demands of both. Unfortunately, during Payne's study, which occurred for 1 week in July 1964, it was not known that Cassin's Auklets often attempt a second brood (see Manuwal 1974a, b). He was unaware of the true breeding status of birds captured in burrows. Auklets without eggs may have been nonbreeders or individuals that had completed a first clutch, and those on fresh eggs may have been attempting a second brood.

We confirm Payne's conclusion that there is less energy available for molt in auklet breeders than in nonbreeders and postbreeders. The energetic costs of breeding depress molt rates in adults, and the lack thereof for subadults may account for the lower variation in their molt cycle. In two other auklets (*Aethia pusilla* and *A. cristatella*), failed breeders and nonbreeders (and presumably subadults) molted body feathers earlier and faster than breeders (Bédard and Sealy 1984).

Surprisingly, male Cassin's Auklets appeared to be more responsive than females to the energetic demands that render molt incompatible with breeding. In all years except 1979, males molted earlier and slower than females. This difference may be related to body size—mean (±SD) weight of males (176.0 g ± 11.1, n = 1,492) is significantly greater than that of females (165.7 g ± 11.3, n = 1402; t = 24.73, $P < 0.001$) and may affect energy demands for molt. These differences do not explain the pattern in 1979, when males molted later and faster than females.

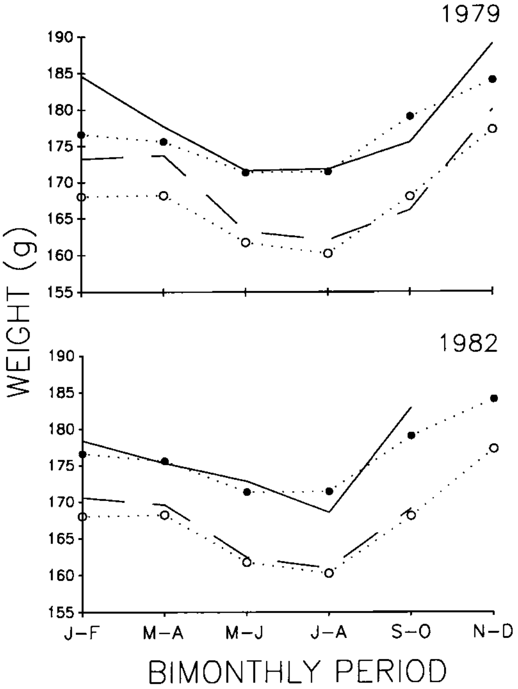

Fig. 3. Mean bimonthly weights (g) of adult male (——) and female (-----) Cassin's Auklets in 1979 and 1982 on Southeast Farallon Island (n > 10 for all points). Means (1979–1984) for males (·····●·····) and females (·····○·····) are plotted for comparison. Abbreviations: J-F (January-February), M-A (March-April), M-J (May-June), J-A (July-August), S-O (September-October), N-D (November-December).

TABLE 2. Annual mean egg-laying date and chicks per pair ($\bar{x}$ ± SD), percentage of adults captured that were molting one versus more than one primary at a time in June and July, and the percentage of birds each year with double broods, for Cassin's Auklets on Southeast Farallon Island, 1979–1984 (sample size is in parentheses; data on double broods from Ainley and Boekelheide 1990).

Year	Mean egg-laying date	Chicks per pair	% molting 1 P	% double brooding
1979	1 Apr ± 8.4 (76)	0.63 ± 0.35 (75)	40 (63)	41.3 (75)
1980	23 Apr ± 6.5 (78)	0.61 ± 0.49 (77)	27 (63)	0.0 (78)
1981	9 Apr ± 7.7 (80)	0.67 ± 0.44 (76)	9 (64)	8.5 (82)
1982	9 Apr ± 14.1 (82)	0.59 ± 0.43 (81)	32 (68)	12.2 (82)
1983	29 May ± 6.2 (39)	0.23 ± 0.42 (39)	1 (73)	0.0 (40)
1984	11 Apr ± 8.4 (77)	0.63 ± 0.44 (77)	28 (107)	5.8 (103)

Primary molt may affect energy requirements for foraging. During chick rearing, both adults spend the day at sea and return to the colony only at night to feed food stored in the gular pouch to the chick (Speich and Manuwal 1974). Foraging occurs primarily in deep waters off the continental shelf, at least 50 km north or south of the island (Ainley and Boekelheide 1990), but may shift closer to the colony (<25 km) in summer (Briggs et al. 1988). The absence of one or more primaries on each wing would increase wing loading, especially with the extra weight of food in the gular pouch ($\bar{x} \pm$ SD of each load = 27.78 ± 9.69 g, n = 22, Manuwal 1974a), and the energetic demands for flight.

It is possible that males expend more energy for breeding. Burrows are reoccupied or excavated by Cassin's Auklets in December and January each year, when most birds return to the colony to begin breeding activities (Manuwal 1974a). Presumably males are responsible for territory defense, and perhaps for burrow construction (Ainley and Boekelheide 1990). Moreover, Thoresen (1964) observed that fighting and chasing behavior at the colony is common in this species, though the sex of the birds was not known. The importance of winter site defense for future breeding is elevated on Southeast Farallon Island by the presence of a "floater" population (Manuwal 1974b). Thus, males may have to defend their nest burrows during the postbreeding season each year. Perhaps as a consequence of extended energy demands for breeding, especially in years of double brooding, body weight of males—but not females—correlates with timing of molt.

That males molted after females only in 1979 may be explained by higher mean body weights in January and February than in any of the next five years (Fig. 3). Breeding also began very early that year, which led to a higher incidence of birds attempting to double brood. Male Cassin's Auklets may delay molt more than females in years of early breeding because they are still expending energy for territory defense when the first clutch has fledged relatively early in the breeding season.

Our results and those of Bédard and Sealy (1984) indicate that extended overlap of molt with breeding in auklets causes considerable energetic stress. In Cassin's Auklet, the energetic demands of breeding and molt are independently unknown, but they are great enough to cause a slowing or suspension of molt. Although Cassin's Auklets apparently vary their timing of breeding and molt in relation to body weight, their ability to delay, slow, or arrest molt with breeding effort may explain why timing and rate of molt do not correlate with timing of breeding. We assume that body weight reflects food availability, which in the Gulf of the Farallons is influenced by sea temperature (Ainley and Boekelheide 1990). Annual variation in timing of body molt in the Black Guillemot (*Cepphus grylle*), a species that does not overlap breeding with molt, also appears to be correlated to sea temperature (Salomonsen 1944, Ewins 1988). Additional study is needed on the physiology of molt in Cassin's Auklets with known breeding status, and on the cost of reproduction for males and females, to understand fully the variation in timing and rate of molt.

Finally, the model proposed by Foster (1974) for birds that overlap breeding and molt is applicable to the molt cycle in Cassin's Auklet. In that model, birds will not overlap these two cycles unless there is a selective advantage to do so. In the Gulf of the Farallones, where annual food availability is often high but unpredictable, it appears that auklets have evolved a compromise of a single egg, an ability to raise a second brood when possible, and a prolonged primary molt overlapping breeding effort to reduce the rate of energy consumption.

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LITERATURE CITED

AINLEY, D. G., & R. J. BOEKELHEIDE. 1990. Seabirds of the Farallon Islands: ecology, structure and dynamics of an upwelling-system community. Stanford, Stanford Univ. Press.

BÉDARD, J., & S. G. SEALY. 1984. Moults and feather generations in the Least, Crested and Parakeet auklets. J. Zool. 202: 461-488.

BIRKHEAD, T. R., & A. M. TAYLOR. 1977. Moult of the Guillemot *Uria aalge*. Ibis 119: 80-85.

BRIGGS, K. T., D. G. AINLEY, L. B. SPEAR, P. B. ADAMS, & S. E. SMITH. 1988. Distribution and diet of Cassin's Auklet and Common Murre in relation to central California upwellings. Pp. 982-990 *in* Acta XIX congressus internationalis ornithologici (H. Ouellet, Ed.). Ottawa, Univ. of Ottawa Press.

EWINS, P. J. 1988. The timing of moult in Black Guillemots *Cepphus grylle* in Shetland. Ringing & Migr. 9: 5-10.

FOSTER, M. S. 1974. A model to explain molt-breeding overlap and clutch size in some tropical birds. Evolution 28: 182-190.

GINN, H. B., & D. S. MELVILLE. 1983. Moult in birds. Hertfordshire, United Kingdom, Br. Trust Ornithol. Guide No. 19.

HARRIS, M. P., & S. WANLESS. 1990. Moult and autumn colony attendance of auks. Br. Birds 83: 55-66.

MANUWAL, D. A. 1974a. The natural history of Cassin's Auklet (*Ptychoramphus aleuticus*). Condor 76: 421-431.

———. 1974b. Effects of territoriality on breeding in a population of Cassin's Auklet. Ecology 55: 1399-1406.

———. 1978. Criteria for aging Cassin's Auklet. Bird-Banding 49(2): 157-161.

———. 1979. Reproductive commitment and success of Cassin's Auklet. Condor 81: 111-121.

NELSON, D. A. 1981. Sexual differences in measurements of Cassin's Auklet. J. Field Ornithol. 52(3): 233-234.

NEWTON, I. 1966. The moult of the bullfinch, *Pyrrhula pyrrhula*. Ibis 108: 41-67.

NURUSIS, M. J. 1986. SPSS/PC+ for the IBM PC/XT/AT. Chicago, Illinois, SPSS Inc.

PAYNE, R. B. 1965. The molt of breeding Cassin Auklets. Condor 67: 220-228.

PIMM, S. 1976. Estimation of the duration of bird molt. Condor 78: 550.

RALPH, C. J., & F. C. SIBLEY. 1970. A new method of capturing nocturnal alcids. Bird-Banding 41: 124-127.

SALOMONSEN, F. 1944. The Atlantic Alcidae. Medd. Göteborgs K. Vetensk.-o Vitter Samh. Handl., Sjatte Földer., ser. B Band 3, No. 5.

SPEICH, S., & D. A. MANUWAL. 1974. Gular pouch development and population structure of Cassin's Auklet. Auk 91: 291-306.

STORER, R. W. 1952. A comparison of variation, behaviour and evolution in the sea bird genera *Uria* and *Cepphus*. Univ. California Publ. Zool. 52: 121-222.

SUMMERS, R. W., R. L. SWANN, & M. NICOLL. 1983. The effects of methods on estimates of primary moult duration in the Redshank *Tringa totanus*. Bird Study 30: 149-156.

SWENNEN, C. 1977. Report on a practical investigation into the possibility of keeping sea-birds for research purposes. Texel, Netherlands Inst. Sea Res.

THORESEN, A. C. 1964. The breeding behavior of the Cassin Auklet. Condor 66: 456-476.

UNDERHILL, L. G., & W. ZUCCHINI. 1988. A model for avian primary moult. Ibis 130: 358-372.

———, ———, & R. W. SUMMERS. 1990. A model for avian primary moult-data types based on migration strategies and an example using the Redshank *Tringa totanus*. Ibis 132: 118-123.

APPENDIX 1. Sample sizes by month of the number of adult male (M), female (F), and subadult (S) Cassin's Auklets captured on Southeast Farallon Island, April through December, 1979-1984.

Year		Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1979	M	13	35	18	30	13	42	27	0	10
	F	10	11	4	7	4	10	6	0	4
	S	3	3	5	3	1	6	5	0	1
1980	M	64	27	28	9	20	34	22	44	21
	F	14	22	20	14	5	31	23	12	10
	S	4	27	7	3	0	5	2	3	2
1981	M	26	29	23	20	9	19	16	15	6
	F	21	28	40	21	22	29	22	10	1
	S	1	0	9	2	1	2	3	0	0
1982	M	24	29	18	2	4	13	60	0	0
	F	9	32	42	9	24	30	67	0	0
	S	0	6	7	0	0	2	1	0	0
1983	M	10	21	8	7	12	13	2	0	12
	F	8	39	14	36	42	28	4	0	5
	S	0	1	0	4	0	11	0	0	0
1984	M	31	35	12	4	7	11	9	0	24
	F	52	50	61	27	12	38	6	0	41
	S	1	1	0	0	0	0	0	0	0