Growth Comparison of a Plankton- and a Fish-Feeding Alcid

KEES VERMEER and L. CULLEN

ABSTRACT.—Growth of the chicks of two nocturnal alcids, the plankton-feeding Cassin's Auklet (*Ptychoramphus aleuticus*) and the fish-feeding Rhinoceros Auklet (*Cerorhinca monocerata*) were compared on Triangle Island, British Columbia, in 1978.

Cassin's Auklet grew faster, attained adult weight earlier and lost less weight on a relative basis than did the Rhinoceros Auklet. The faster growth of the Cassin's Auklet apparently related to the relative large meals with high-energy plankton which the parent stores in a gular pouch for feeding its young. Differences in relative weight loss may indicate greater energy expenditure in smaller birds. Chicks of both species that hatched late were lighter at fledging than those that hatched earlier, perhaps resulting from an inadequate supply of high-quality food toward the end of the breeding season.

Cassin's Auklets (*Ptychoramphus aleuticus*) bring copepods, euphausiids, amphipods, and small fishes in a gular pouch to their chicks (Speich and Manuwal 1974, Vermeer 1981). Their plankton prey ranges from 6 to 30 mm in length while fish prey ranges from 15 to 45 mm long (Vermeer 1981). Rhinoceros Auklets (*Cerorhinca monocerata*) carry 4 to 24 cm long fishes crosswise in their bills to their chicks (Leschner 1976, Wilson 1977, Vermeer 1980). Both alcids are burrow nesters, breed at similar latitudes, lay one-egg clutches, and raise semi-precocial young, and each parent feeds the chick once at night (Richardson 1961, Thoresen 1969, Manuwal 1974, 1979, Vermeer 1979, 1980).

The purpose of this study was to compare the growth of two alcids with similar nesting strategies but different diets to determine how those different food regimes affect nestling growth. The study was conducted from 15 May to 1 September 1978 on Triangle Island, British Columbia (50° 52'N, 129° 05'W), where Cassin's and Rhinoceros Auklets nest in large numbers.

METHODS

Fifty-five Cassin's Auklet chicks and 35 Rhinoceros Auklet chicks were weighed daily with Pesola scales to the nearest 0.1 g from the time they hatched until they fledged. Of those chicks, 44 Cassin's Auklets and 20 Rhinoceros Auklets were weighed at approximately 0800 hr and 2000 hr PST daily to determine 12 hr weight losses. Not all chicks were weighed each time because some died and others could not always be located in the nest burrows. Many newly hatched chicks were not weighed because the adults readily deserted eggs and newly hatched chicks. Chick growth was analyzed by fitting standarized growth curves to weight data using Ricklef's (1967) graphical method as well as by plotting mean weights, standard deviations, and 95% confidence intervals of chicks of known age.

The acquisition and measurement of Cassin's and Rhinoceros Auklet meals has been previously described by Vermeer (1979, 1981). Caloric values of the birds' principal prey were determined by microbomb calorimetry.

RESULTS AND DISCUSSION

Growth as Related to Meal Size, Caloric Food Values, and Body Size

Cassin's Auklet and Rhinoceros Auklet chicks spent, on the average, 43.5 days and

51 days, respectively, in their burrows in 1978. Cassin's Auklets brought more food to their young relative to adult and fledging weights than did Rhinoceros Auklets (Table 1). Caloric values of the Cassin's Auklet food items, in particular *Calanus cristatus*, also averaged higher than those of Rhinoceros Auklets (Table 2). It is not surprising that Cassin's Auklet chicks reached adult weight a week prior to fledging and departed from the colony at 90% of the adult weight compared with 69% for Rhinoceros Auklet chicks. Cassin's Auklets have a logistic growth form (Sealy 1973, Vermeer and Cullen 1979) whereas the Rhinoceros Auklet has a Gompertz and slow-growth form (Table 3). Slow growth apparently reduces energy requirements of the nestlings and may also be an adaptation for early precocity of development of locomotion and temperature regu-

TABLE 1. Comparison of some parameters of Cassin's Auklets and Rhinoceros Auklets, Triangle Island, 1978.

Parameters	Cassin's Auklet	Rhinoceros Auklet
No. feeding visits to young over 24 hr period	2[a]	2[b]
Mean meal size (g)	17.6(112)[c]	29.6(115)
Food per 24 hr. period (g) (Fo)	35.2	59.2
Mean adult weight (g) (Wa)	188 (25)	520 (48)
Mean fledging weight (g) (Wf)	169 (41)	361 (27)
Wf/Wa (%)	89.8	69.4
Fo/Wa (%)	18.7	11.4
Fo/Wf (%)	20.8	16.4

[a]Thoresen, 1969.

[b]Richardson, 1961.

[c]Sample size in parentheses.

TABLE 2. Caloric values in cal/g dry weight of typical prey of Cassin's and Rhinoceros Auklets, Triangle Island, 1978. (Values based on averages of 3 samples for each species.)

Cassin's Auklet		Rhinoceros Auklet	
Prey	Cal/g	Prey	Cal/g
Calanus cristatus	6236	*Nansenia candida*	5893
Thysanoessa spinifera	5354	*Ammodyte hexapterus*	5383
		Sebastes entomelas	5200
		Cololabis saira	4813

TABLE 3. Comparison of growth parameters of Cassin's and Rhinoceros Auklets on Triangle Island, 1978.

Growth parameters	Cassin's Auklet N	Cassin's Auklet $\bar{x}$ and SD	Rhinoceros Auklet N	Rhinoceros Auklet $\bar{x}$ and SD
Peak weight at 0800 PST (g)	41	188.1±14.5	27	377.4±34.4
Peak weight at 2000 PST (g)	41	172.6±16.3	18	347.6±36.0
Fledging weight at 0800 PST (g)	41	168.8±12.5	27	361.3±36.8
Fledging weight at 2000 PST (g)	41	159.2±11.7	18	342.9±35.2
Adult weight (g)	25	187.8±16.0	48	519.8±36.7[a]
Age at peak weight (d)	41	36.4± 3.7	27	47.0± 3.2
Age at fledging (d)	41	43.5± 4.4	27	51.2± 3.3
Growth curve type	Logistic		Gompertz	
K value	0.153		0.071	
t 10-90 value	28.7		43.7	

[a]From the years 1975 and 1976 combined.

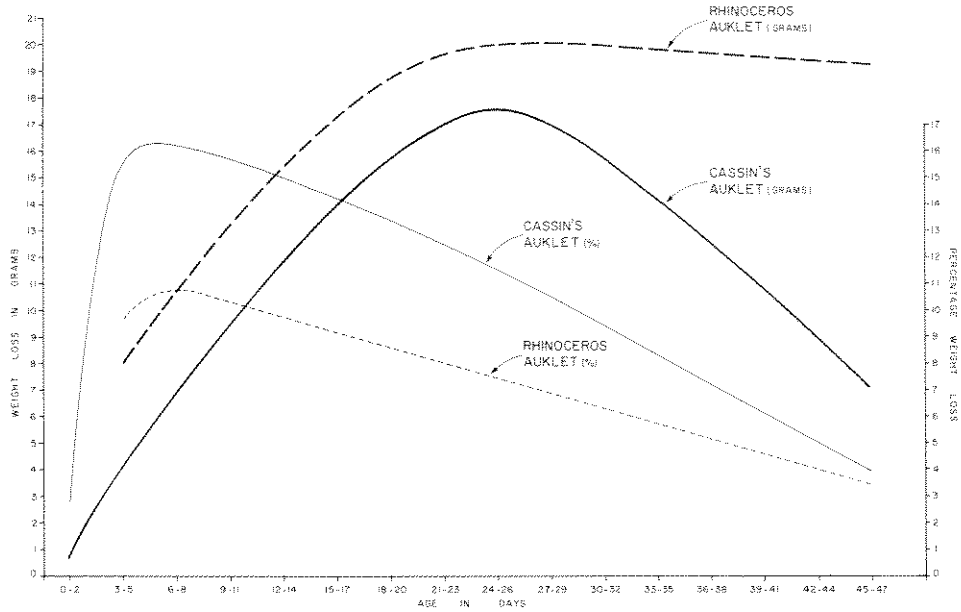

FIGURE 1. Absolute (g) and relative (% body weight) daily weight losses (between 0800 and 2000 PST) of Cassin's Auklet and Rhinoceros Auklet chicks on Triangle Island in 1978. Curves are drawn by eye to indicate trends.

lation (Ricklefs and White 1981). However, the level of precocity may have ultimately been determined by the level of available nutrients. Differences in levels of precocity between Cassin's and Rhinoceros Auklets have not been investigated here.

Detailed growth comparisons between Cassin's and Rhinoceros Auklets chicks are made in Figure 1. Both species lose weight each day following a night-time feeding reflecting energy expenditure on growth and metabolic rate. Cassin's and Rhinoceros Auklet chicks are not active in their burrows until several days before fledging when they start to exercise their wings at the burrow entrance. On an absolute basis Cassin's Auklets decline less in daily body weight between feedings than do Rhinoceros Auklets. However, on a relative basis (weight loss expressed as a percentage of body weight) the Cassin's Auklet loses, on average, more weight during a 12 hr day than does the Rhinoceros Auklet (Fig. 1). This is to be expected as relative energy expenditure is probably greater in the smaller Cassin's Auklet because of its greater surface volume ratio (Kendeigh 1970). Relative weight loss is greatest when the chicks are about one week old (Fig. 1). The sudden and great relative loss may reflect increased energy expenditure on maintenance and temperature regulation as the parents stop brooding their chicks after their first week of life (Manuwal 1974). This period is the chick's most critical period of adjustment. Thereafter weight loss relative to body weight declines. A major adjustment of metabolic rate in the growing Cassin's Auklet is reached prior to fledging when feather growth is sufficiently advanced to reduce heat radiation and insulate the young bird for life outside the burrow. At that point the Cassin's Auklet chicks' daily weight loss on a relative basis is the same as that of the Rhinoceros Auklet (Fig. 1). The weight loss between feedings of both species increases up to three weeks of age, after which that of the Rhinoceros Auklet reaches a plateau while that of the Cassin's Auklet commences to decline (Fig. 1). The greater decline of the Cassin's Auklet chicks' absolute weight loss is to be expected because they spend less energy on growth and

maintenance at that time, having grown more quickly at an earlier age than Rhinoceros Auklet chicks. The greater relative food intake of the Cassin's Auklet chick allows it to grow faster and attain adult weight earlier than do Rhinoceros Auklet chicks.

Growth Related to Time of Hatching and Food

Early-hatched Cassin's Auklet chicks were significantly heavier than those hatched later (Vermeer 1981). Late-hatched chicks were also prone to abandonment, while parents of early-hatched chicks were on two occasions caught with food in burrows the day after the chicks fledged. Manuwal (1974) made similar observations on Cassin's Auklets on southeast Farallon Island.

Chick growth of Rhinoceros Auklets was similarly slower in later hatchings (Fig. 2). During two weeks prior to fledging, the late-hatching Rhinoceros Auklet chicks weighed less than those from preceding periods. Young and less experienced birds frequently breed later, produce smaller eggs, and have chicks with a lower growth rate than do older and more experienced birds (e.g., see review by Hedgren and Linnman 1979). However, it is unlikely that the results were due to inexperienced parents because a comparison of growth rates of early- to late-hatched auklet chicks showed little difference in the first three and four weeks of life, respectively (see Vermeer 1981, Fig. 2).

The average weight of meals carried by adult Cassin's Auklet remained the same (Vermeer 1981), while that of Rhinoceros Auklets increased slightly in the latter half of the 1978 nestling period (Vermeer 1980). Cassin's Auklets were observed to eat more fishes toward the termination of nesting perhaps because plankton prey declined (Vermeer 1981). Caloric values of these fishes were lower than that of the major plankton prey, *Calanus cristatus* (Table 2). Rhinoceros Auklet chicks were fed mostly widow rockfishes, *Sebastes entomelas*, and Pacific sandlance, *Ammodytes hexapterus*, in July and bluethroat argentines, *Nansenia candida*, and Pacific sauries, *Cololabis saira*, in August (Vermeer 1980). Pacific sauries had the lowest caloric values of all fishes

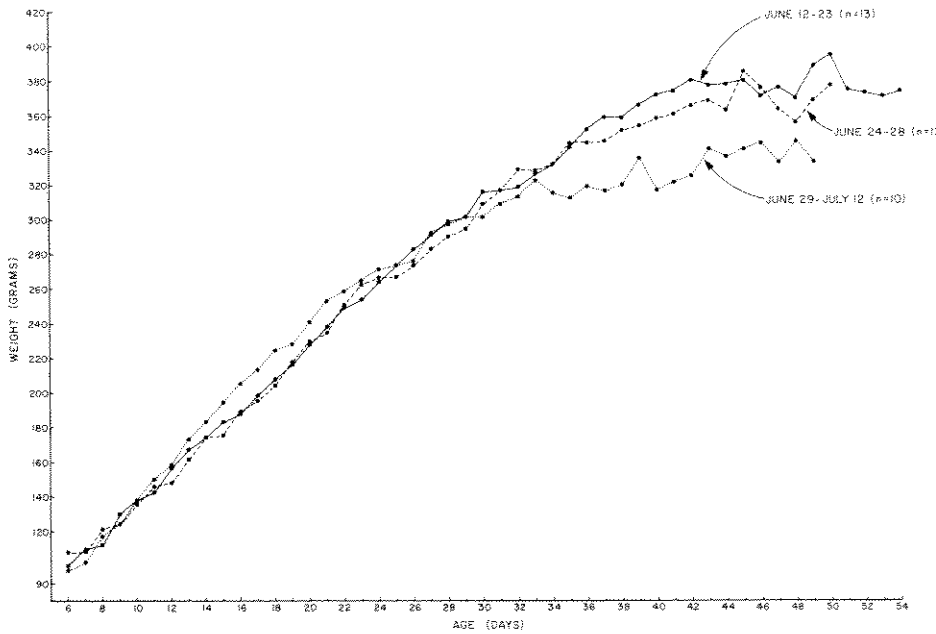

FIGURE 2. Comparison of growth of Rhinoceros Auklets, hatched at different periods, 1978.

(Table 2) and predominated towards the end of the nestling period. A shortage of plankton prey and lower caloric values of sauries may have been responsible for the lighter weights of late-hatched Cassin's Auklet and Rhinoceros Auklet chicks, respectively. Late-hatched Cassin's Auklet chicks in California (Manuwal 1979) and Rhinoceros Auklet chicks in Washington (Wilson 1977) were observed to fledge at lighter weight than did young hatched early. Those differences were also ascribed to a decrease in quality and availability of the bird's prey availability later in the season.

Growth Form Related to Fledging Success

Significantly fewer Cassin's Auklet chicks ($p < 0.05$) fledged from clutches that hatched after 7 June (38%) than from those that hatched earlier (75%). In contrast, the fledging success of Rhinoceros Auklets remained similar over the nestling period (83% before 28 June compared to 80% after). Perhaps the difference in fledging success between the late hatchers of the two species partly relates to their different growth forms. The slow-growth form of the Rhinoceros Auklet chick may allow for better survival when food is scarce than the logistic one of the Cassin's Auklet chick. Ricklefs and White (1981) also suggested that slower-growing Sooty Terns (*Sterna fuscata*) may be able to withstand longer periods of food deprivation than faster-growing Common Terns (*S. hirundo*), as the former accumulated larger lipid reserves at a faster rate than did the latter. No lipid measurements were made in this study, but in some years, Rhinoceros Auklet chicks were observed to fledge at approximately half of the adult's weight (Vermeer and Cullen 1979). The fact that they fledged at that weight indicates their adaptiveness to adverse conditions.

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Canadian Wildlife Service, P.O. Box 340, Delta, British Columbia, Canada V4K 3Y3.
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