

## BREEDING BIOLOGY OF THE RHINOCEROS AUKLET IN WASHINGTON<sup>1</sup>

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**Abstract.** During 1974 through 1983, we investigated the breeding biology of the Rhinoceros Auklet (*Cerorhinca monocerata*) at three main colony sites on the coast of Washington: Destruction Island (offshore) and Protection and Smith islands (inland islands of the Strait of Juan de Fuca).

Average burrow densities were higher offshore, where the auklets nested on shrub-covered slopes; inland auklets nested on grassy slopes and level areas. Egg-laying patterns varied among years and populations, although initiation dates on all islands were similar. The incubation periods averaged 45 days and ranged from 39 to 52 days. Chicks were brooded, on average, for 3.9 days (range zero to 9 days). On Protection Island, early-hatched young grew more rapidly than chicks hatched at a later date. Chicks on offshore islands were fed a variety of fish, whereas those on inland islands were fed primarily two species. The inland chicks were fed heavier fish loads, reached heavier peak body weights, and were heavier when they fledged than were offshore chicks. Breeding success was higher on the inland colony sites.

**Key words:** *Rhinoceros Auklet*; *Cerorhinca monocerata*; *Washington (state)*; *breeding biology*; *puffins*.

### INTRODUCTION

Among the Pacific alcids, the puffins show strong structural (Storer 1945) and ecological similarities that provide an opportunity to examine the species' responses to their environment. Most published accounts of these birds reflect studies at single colony sites. We report here a comparative study of the breeding biology of one of these puffins, the Rhinoceros Auklet (*Cerorhinca monocerata*), at three different major colony sites in Washington State.

Marine birds that nest on islands differing in physiography and marine environment can be expected to differ among colonies in aspects of their biology. The breeding distribution of the Rhinoceros Auklet in Washington is ideally suited for comparisons of colonies because approximately half of the state's auklets nest off the outer coast of the Olympic Peninsula, while the remainder nest in the inshore waters of the eastern Strait of Juan de Fuca. The two populations may thus experience different environmental influences that are not masked by latitudinal effects.

Our specific objectives were (1) to gain new information on the major aspects of the breeding biology of the Rhinoceros Auklet, (2) to document the responses of individual colonies to terrestrial and marine components of their environment, and (3) to compare the breeding biology of the Rhinoceros Auklet with that of the other two Pacific puffins.

### DESCRIPTION OF STUDY SITES

Destruction Island (47°40'N, 124°24'W) is located 4.8 km west of the Olympic Peninsula and 29 km south-southeast of La Push, Washington (Fig. 1). The 0.15-km<sup>2</sup> island, part of an extensive sandstone reef, forms a nearly level terrace approximately 30 m high, with abrupt cliffs and steep slopes on all sides. Extensive rocky outcroppings entirely surround the island. The vegetation on the top of the island consists mostly of salmonberry (*Rubus spectabilis*) and salal (*Gaultheria shallon*), and is devoid of much understory. The surrounding slopes and cliffs have interspersed patches of salal and salmonberry, coast willow (*Salix hookeriana*), dune wildrye (*Elymus mollis*) and grass associations dominated by common velvetgrass (*Holcus lanatus*), orchardgrass (*Dactylis glomerata*), and red fescue (*Festuca rubra*). Mean annual precipitation for the area is 267 cm. Destruction Island is jointly administered by the U.S. Coast Guard, which maintains a lighthouse and other navigational aids on the island, and the U.S. Fish and Wildlife Service.

Protection Island (48°08'N, 122°55'W) lies 3.2 km off the mouth of Discovery Bay at the southeastern end of the Strait of Juan de Fuca (Fig. 1). About 80% of the island's 1.59 km<sup>2</sup> area consists of a plateau bounded by precipitous cliffs 35 to 76 m high. At the southeastern and southwestern ends, extensive grassy slopes terminate in sand and gravel spits. The vegetation of this plateau area consists of mixed coniferous woods and thickets of flowering shrubs, grassy areas, alfalfa fields, and sand

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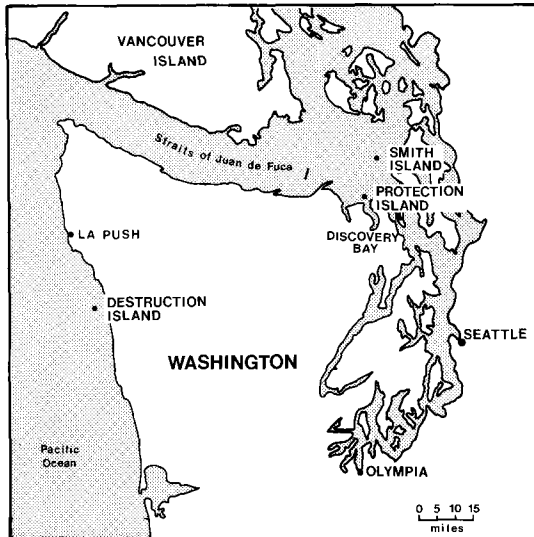


FIGURE 1. Locations of Rhinoceros Auklet study sites in Washington.

dunes. The vegetation of the grassy slopes and the more level, adjacent, peripheral areas consists primarily of annual grasses, with *Bromus rigidus* dominating other *Bromus* and *Aspris* grasses (Richardson 1961). Protection Island lies in the rain shadow of the Olympic Mountains and, consequently, has an annual precipitation of only about 41 cm. Approximately 85% of the island was privately owned at the time of our study. In recent years, numerous recreational homes have been built on the private portion of the island. Under recent legislation, the private portion of the island will be acquired by the U.S. Fish and Wildlife Service and will become part of the refuge system. The remaining 15% comprises the Zella Schultz Seabird Sanctuary, administered by the Washington Department of Game.

Smith Island (48°19'N, 122°51'W) is situated 16.5 km northeast of Protection Island, in the Strait of Juan de Fuca (Fig. 1). With the exception of several dense shrub thickets, most of the approximately 0.25-km<sup>2</sup> island is covered by beachgrass and various exotic grasses. The island has a somewhat triangular shape with a rapidly eroding cliff about 15 m in height on the western and southern sides. The top slopes gradually toward the east and terminates in a sandy point. Annual precipitation is approximately the same as at Protection Island. Smith Island is also administered by both the U.S. Coast Guard and the U.S. Fish and Wildlife Service.

## METHODS

Rhinoceros Auklets were studied by Manuwal and Wilson on Smith Island in 1974, by Lesch-

ner (1976) on Destruction Island in 1974 and 1975, and by Wilson on Protection Island in 1975 and 1976. Food habits, growth of chicks, and habitat preferences were further investigated by Wilson during short visits to Destruction and Protection islands during 1979 through 1981 and in 1983.

The distributions and densities of auklet burrows were determined either by counting all burrows or by obtaining average burrow densities for specific habitat types using randomly spaced quadrats that varied in size from 3 × 3 m to 10 × 10 m. On Protection Island, the slope was measured by placing an Abney level on the top of a two-by-four that was laid across the center of each quadrat; burrow occupancy patterns were determined by placing toothpicks on the entrances of auklet burrows. Because we saw no evidence that small mammals inhabited the nesting areas, we assumed that a pushed-over toothpick indicated that an auklet had entered the burrow. There is some evidence, however, that sub-adults may visit colony sites, although they do so generally after the main breeding is over (pers. observ.; Vermeer, in litt.).

We investigated activity patterns by recording the daily arrival time of the first auklet that we observed flying to the colony site. Furthermore, we attempted to quantify arrival and departure flights throughout the 1976 breeding season by erecting a blind in a major flight path below approximately 500 burrows that were located on a gradual slope at the southern end of Protection Island. Since Rhinoceros Auklets make a characteristic whistling sound with their wings when they fly, we could count the number of arrivals and departures every 15 min throughout the night at approximately two-week intervals. Because high winds, rain, and pounding surf drown out the sounds of flying auklets, this part of the study was limited to relatively calm nights.

We determined egg-laying dates, incubation periods, and dates of hatching and fledging in the following manner: a sample of burrows was staked, numbered, and excavated before the onset of egg laying. Excavation was done in the manner described by Manuwal (1974). During the spring, the sample burrows were checked daily for the presence of auklets and eggs. When an incubating bird was found, the egg date was recorded and the burrow was left undisturbed for 45 days, after which time the burrow was searched for the presence of a chick. If incubation was still in progress, the burrow was not checked again for another five days. Observations of chick developmental patterns were made daily throughout the nestling period during 1974 to 1976. Chicks were con-

TABLE 1. Use of nesting habitat by Rhinoceros Auklets on Destruction, Protection, and Smith islands, Washington.

Habitat type	Mean burrow density (burrows/m <sup>2</sup> )	Number of burrows on island	Percent of total	Sampled area (m <sup>2</sup> )
Destruction Island (23,621 burrows)				
Cliffs/steep slopes	0.13	1,167	4.9	1,200
Grass-covered slopes	0.47	3,938	16.7	768
Shrub-covered slopes	0.99	10,290	43.6	167
Willow-covered slopes	0.59	2,395	10.1	167
Dunegrass-covered slopes	0.74	5,023	21.3	180
Shrub-covered level edge	0.06	808	3.4	177
Protection Island (27,549 burrows)				
Cliffs/steep slopes	0.04	1,076	3.9	direct count
Grass-covered slopes	0.50	23,356	84.8	540
Grass-covered level edge	0.15	3,117	11.3	direct count
Smith Island (1,194 burrows)				
Cliffs/steep slopes	0.04	320	26.8	direct count
Grass-covered level edge	0.12	874	73.2	direct count

sidered to have fledged when they disappeared from their burrows.

We collected food samples at night from adult auklets returning to feed their chicks by scaring the birds as they approached the burrows, causing them to drop their fish. After each load was collected, the surrounding vegetation was carefully searched to ensure that no fish were overlooked. The prey species composition and total load weight, as well as the lengths and weights of individual prey items, were recorded for each food load. Food samples were collected throughout the nestling periods on Destruction Island in 1974 (Leschner 1976), on Protection Island in 1975 and 1976, and on Smith Island in 1974, but only for portions of the nestling period. In 1979 to 1981, food loads were collected during two nights just after hatching and again just before the onset of fledging on Destruction and Protection islands. The *El Niño* phenomenon of 1982 to 1983 prompted us to collect food loads on Destruction Island on 12 and 13 July, and on Protection Island on 21 and 22 July, of 1983. Names of fishes follow Hart (1973).

Chicks were obtained from burrows that were excavated before egg laying, as previously described. In 1974 to 1976, daily measurements were taken of the weight, flattened wing, tarsus, and culmen. Chicks were weighed with a 200-g or 500-g Pesola scale, depending on their size. Culmen and tarsus lengths were measured with metric calipers, and a metric ruler was used to obtain wing measurements. Growth was analyzed by fitting weight data to the Gompertz curve according to Ricklefs' (1967) graphical method of fitting equations to growth curves. Chick growth was further investigated on Destruction Island and Protection Island in 1979 to 1981 by weighing a sample of chicks (approximately 20 per year per island) after hatch-

ing and again 12 to 14 days later. From these data, composite growth curves were constructed according to Ricklefs and White (1975), and  $k$  values were computed following Ricklefs' (1967) method.

We studied breeding success by following the fates of eggs and chicks in marked burrows. The proportion of burrows that contained eggs was determined from a sample of burrows excavated before egg laying and checked daily until an egg was found. Because disturbance during incubation often causes desertion in alcids (Manuwal 1974), hatching success, as indicated by these burrows, was not indicative of natural conditions. To eliminate the disturbance factor introduced by burrow checks during egg laying, we checked a sample of previously undisturbed burrows for chicks after the hatching period. To make sure that excavated burrows did not deter breeding auklets, a sample of burrows was excavated before egg laying and was not checked again until after hatching. The percentage of pairs that produced chicks from these burrows did not differ markedly from those percentages in undisturbed burrows, indicating that breeders did not discriminate between excavated and non-excavated nest sites.

## RESULTS

### NESTING HABITAT

Destruction Island offered a much wider variety of nesting habitats than did either Protection Island or Smith Island (Table 1). On Destruction Island, the highest percentage of birds nested on salmonberry- and salal-covered slopes, where burrow densities averaged 0.99 burrows/m<sup>2</sup>. Dunegrass-, willow-, and grass-covered slopes were also used extensively, with average burrow densities of 0.74,

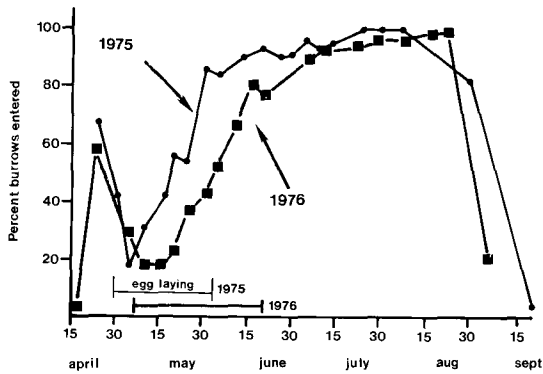


FIGURE 2. Seasonal burrow occupancy of Rhinoceros Auklets on Protection Island.

0.59 and 0.47 burrows/m<sup>2</sup>, respectively. Cliffs and steep slopes, as well as the dense salal- and salmonberry-covered upper level edge of the island, were used by only a small number of birds.

On Protection Island, the largest of the three colonies, 85% of the auklet population nested on the grass-covered southeastern and southwestern slopes. Burrow densities on these slopes averaged 0.50 burrows/m<sup>2</sup>, compared to 0.47 for this habitat type on Destruction Island. The rest of Protection Island auklets nested within the less-preferred level or cliff habitats. Burrow density was significantly correlated with angle of slope ( $P < 0.001$ ,  $r = 0.633$ , 80 df) on Protection Island.

The areas that were used by nesting auklets on Smith and Protection islands were similar in vegetation coverage and burrow density. Most of Smith Island's small auklet population nested along the flat, grass-covered upper edge of the island. This colony has little potential for expansion because it lacks moderate slopes.

#### SEASONAL COLONY ATTENDANCE

Seasonal colony attendance, as indicated by burrow occupancy, was investigated only on Protection Island. The overall burrow occupancy, in terms of the percentage of burrows that were entered at night, increased rapidly during the early part of April until it first peaked at approximately 60 to 65% (Fig. 2). In 1975 the first peak apparently occurred on 24 April, and in 1976 on 23 April. In 1976, 94% of the eggs were laid in burrows that were occupied during the "assembly period," which strongly suggests that the breeding population arrived on the island at that time. During both 1975 and 1976, overall colony attendance rapidly declined after the first peak of activity and reached its lowest level (about 20%) at the onset of egg laying in early May.

Occupancy records of individual burrows showed that most burrows active during the "assembly period" were initially occupied for

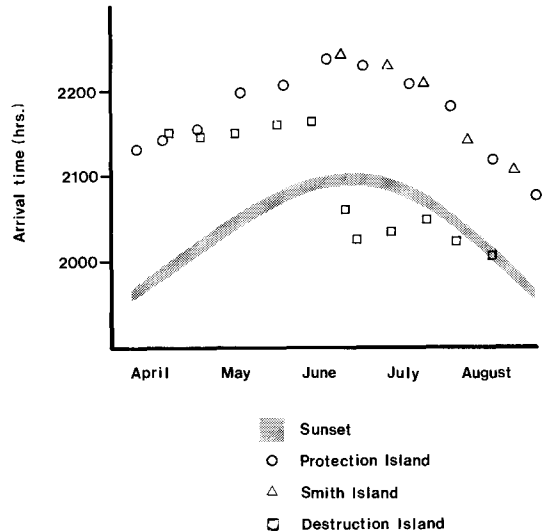


FIGURE 3. Nightly arrival times of first Rhinoceros Auklets landing on colony, Destruction Island, Smith Island, and Protection Island (Destruction Island data from Leschner 1976).

several days between 20 and 26 April. This initial occupancy, which may have been sporadic, was followed by a period of general absence that was usually terminated when an egg was laid in the burrow. The duration of this absence varied between 6 and 35 days. A few burrows, however, did not follow this pattern. Some were occupied almost continuously, whereas others were occupied sporadically between the time of first occupation and the day when the egg was laid.

These findings indicate that Rhinoceros Auklets arrived at the colony site at about the same date each year, when they spent a brief period cleaning out the old burrows or digging new ones. Most of the breeding pairs then departed the area of the colony and spent some time at sea before returning for egg laying. The duration of this period of absence varied among pairs and was strongly correlated with the date that the egg was laid.

#### NOCTURNAL ACTIVITY

Patterns of circadian activity varied considerably among populations. On Protection and Smith islands, the first auklets landed on the nesting areas approximately 1 to 1.5 hr after sunset; while on Destruction Island, breeding auklets began arriving after sunset before their eggs hatched and before sunset after the eggs hatched (Fig. 3).

A few hours before each evening arrival, Rhinoceros Auklets assembled in rafts close to the island. At Protection and Destruction islands they then left the rafts either singly or in small groups, circled in front of the colony site several times, and then landed close to their burrows. At Smith Island, however, there was

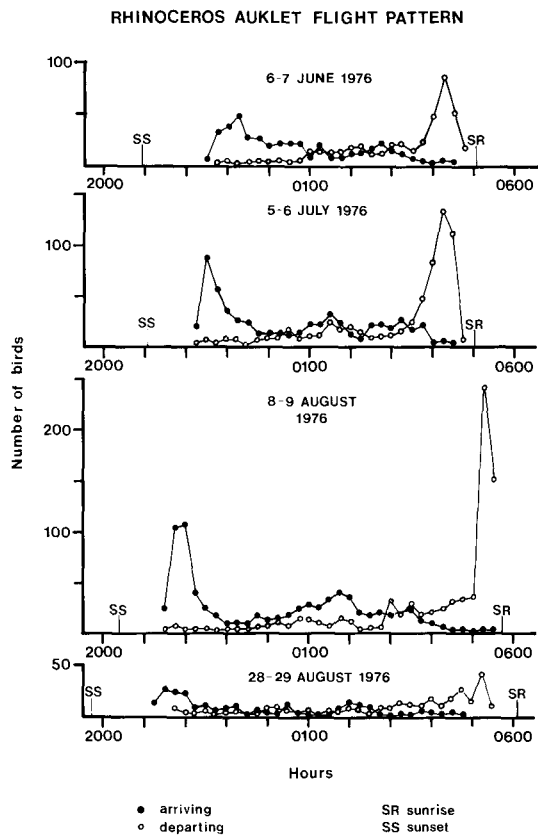


FIGURE 4. Rhinoceros Auklet arrival and departure flight schedules, Protection Island.

no staging and circling before the birds' arrival on the colony.

Plotting the numbers of flights against time revealed peaks in both initial arrivals and final departures (Fig. 4). Since both weather and location of island may influence auklet activity cycles, these flight patterns were only representative of calm nights on Protection Island. Mass arrivals characteristically began 1 to 1.5 hr after sunset and lasted for approximately one hr. Although birds arrived and departed all night long, they tended to accumulate on the nesting areas during the night. Starting about 2 hr before sunrise, auklets began leaving the island in increasing numbers, reaching a peak between 60 and 30 min before sunrise. The last birds usually departed the island between 30 and 15 min before sunrise.

Flight activity to and from the colony sites was greatly reduced on moonlit nights (Fig. 5). Not only were there fewer flights on the moonlit night of 8 to 9 July than on the overcast night of 5 to 6 July, but also the arrival pattern was markedly different. Instead of the usual early peak, birds arrived throughout most of the night, and a much less pronounced peak was reached about midnight.

Activity, as indicated by the total number of nightly flights, fluctuated seasonally in the

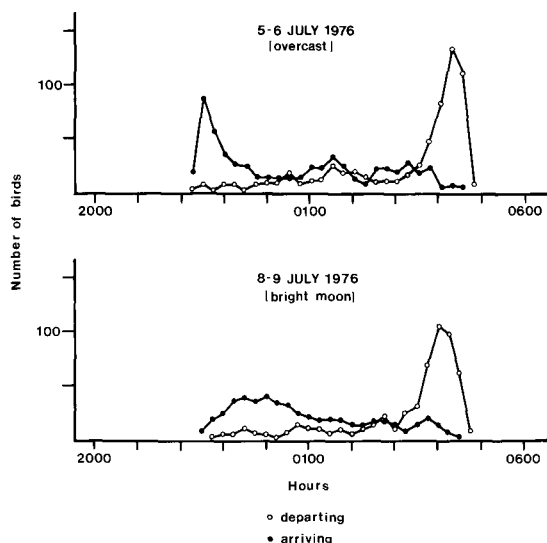


FIGURE 5. Effect of bright moonlight on Rhinoceros Auklet flight schedules, Protection Island.

same way as burrow occupancy rates (Fig. 2). It increased throughout the egg-laying and hatching periods, and peaked in early August, at the beginning of fledging. During July and early August, there was also a corresponding increase in vocalization during the early morning hours. This became most pronounced at the onset of fledging, when both adults and chicks called frequently between midnight and sunrise.

#### EGG-LAYING DATES

Egg laying on Protection and Destruction islands began between 30 April and 7 May during each year from 1974 through 1976 (Fig. 6). On Smith Island, where the population was less than one tenth that on the two larger islands, egg laying was later. The egg-laying schedules of the different populations differed most notably in synchrony and frequency distribution of laying. Frequency distributions in egg laying were significantly different not only among populations during the same breeding season, but also within populations between breeding seasons (Table 2). Synchrony and frequency of egg laying on Protection Island in 1976 were not significantly different from those on Destruction Island in 1974. Consequently, egg laying was not always more synchronized in the Destruction Island population, as data from 1975 suggest.

#### INCUBATION

Rhinoceros Auklets incubate their single egg by placing it next to one of the two lateral brood patches that are located beneath their wings. Incubation usually begins on the day the egg is laid, but sometimes eggs were not being incubated during the daytime for up to

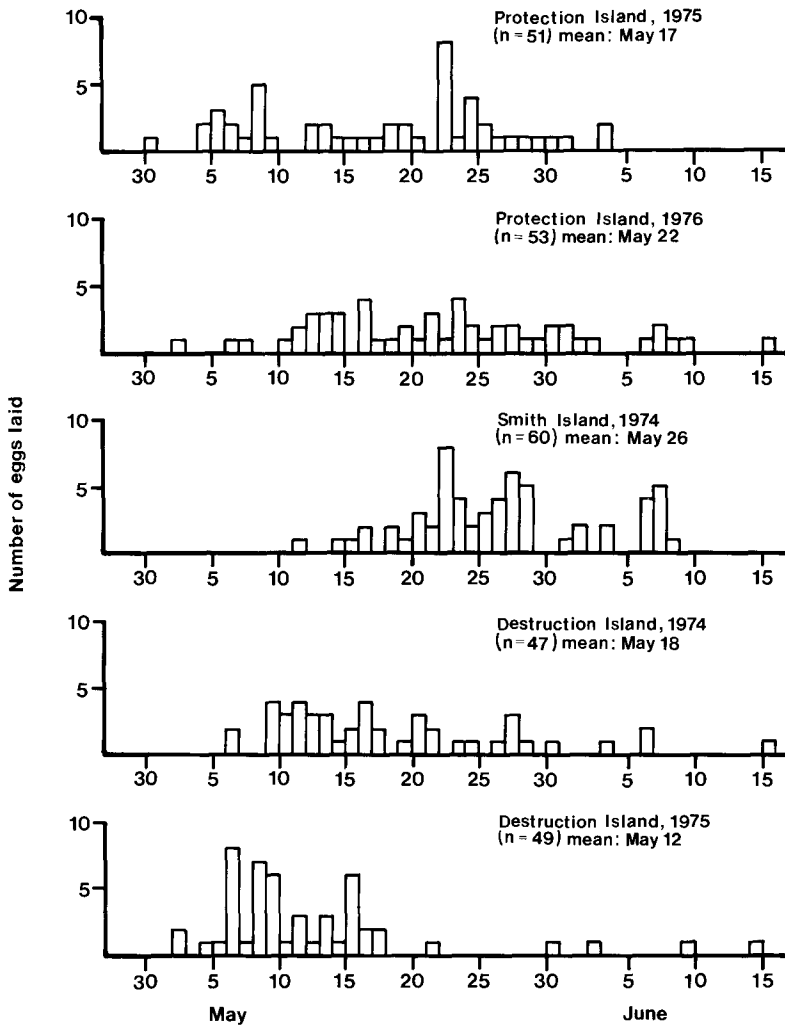


FIGURE 6. Rhinoceros Auklet egg-laying dates on Destruction Island, Smith Island, and Protection Island (Destruction Island data from Leschner 1976).

eight days. We do not know, however, if these eggs were incubated during the night. This seeming delay in beginning incubation did not seem to affect egg viability. We believe that both sexes incubated, but we did not ascertain the rhythm between them. Burrows with incubating birds were usually entered nightly, suggesting 24-hr incubation shifts. On several occasions, however, incubating birds were not relieved for up to four days during the early part of the incubation period. We also found that a pair of auklets frequently deserted their egg for periods lasting from 1 to 3 days. Incubation periods averaged 44.9 days (range 39 to 52 days) on Protection Island, and 45.1 days (range 41 to 49 days) on Destruction Island (Leschner 1976).

#### HATCHING AND BROODING

Auklet eggs on Protection Island hatched between 17 June and 17 July in 1975, and be-

tween 16 June and 27 July 1976. On Smith Island in 1974, hatching occurred between 20 June and 15 July; eggs on Destruction Island hatched that year between 15 June and 19 July, and between 15 June and 7 July 1975 (Leschner 1976).

In order not to disturb the birds, we did not attempt to observe the precise sequence of events during hatching. On several occasions, however, eggs that had pip holes about one cm in diameter were found during burrow checks. In all cases, there was much vocalization from the adult and the chick inside the egg during that time, and hatching was completed within 24 hr ( $n = 4$ ). On Protection Island, the mean period that chicks were brooded was 3.9 days ( $n = 23$ ,  $R = 0$  to 9,  $SD = 2.6$ ).

#### CHICK DIET

Rhinoceros Auklets feed fish to their chicks. During our study, the relative importance of

TABLE 2. Chi square analysis of egg-laying patterns of Rhinoceros Auklets on Protection Island (PI), Destruction Island (DI) and Smith Island (SI).

Comparison	$\chi^2$	df	Probability
PI (75) : PI (76)	17.88	8	$P < 0.025$
DI (74) : DI (75)	23.86	8	$P < 0.005$
PI (75) : DI (75)	25.17	8	$P < 0.005$
DI (74) : SI (74)	31.28	8	$P < 0.0005$
PI (76) : DI (74)	7.50	8	$P > 0.40$

major prey species consistently differed between the offshore Destruction Island and the inshore Protection and Smith islands' populations (Table 3). On the inshore islands, the two most important prey species were Pacific sandlance and Pacific herring, which comprised 89.4 to 96.6% of the total weight of fish that was delivered to chicks during the period 1974 to 1983. Pacific sandlance was always the predominant prey item, its relative frequency varying from 63.8 to 90.7%. Auklets on Protection Island infrequently delivered northern anchovy and immature salmonids to their chicks.

In contrast, on the offshore island the single most important prey species was the northern anchovy, which varied in relative frequency from 26.8% in 1975 to 73% in 1981. Rockfish,

sandlance, herring, night smelt, and Pacific saury were also major prey species, although their relative importance varied among years. Whereas Pacific herring was important in 1974, sandlance and night smelt were the predominant species in 1975, and rockfish were the most important prey in 1979 to 1981. During 1983, *El Niño* conditions persisted off the Washington coast, and water temperatures were 2 to 3°C higher than normal. At that time, Pacific saury became the major component of the chick diet on Destruction Island. The diverse diet of those nestlings also frequently included kelp greenling, popeye blacksmelt, and immature salmon.

During our study, Protection Island auklets consistently delivered heavier food loads to their chicks than did auklets from Destruction Island ( $P < 0.01$ ). The six-year average on Protection Island exceeded the average on Destruction Island by 12.4% (Table 4).

#### NESTLING GROWTH

Of the four growth parameters we measured (wing, culmen, tarsus lengths, and weight), weight was the most variable (Table 5). After hatching, the daily weight gain gradually increased and reached its highest average rate between 10 and 25 days after hatching. Fol-

TABLE 3. Relative frequency in weight (%) of prey species delivered to Rhinoceros Auklet nestlings in Washington, 1974-1983.

Colony site	Destruction Island						Protection Island						Smith Island	
	Year	1974 <sup>1</sup>	1974 <sup>1</sup>	1979	1980	1981	1983	1975	1976	1979	1980	1981	1983	1974
<i>n</i> (No. food loads)		25	94	105	73	57	43	32	180	89	72	30	46	32
Prey species:														
Rockfish sp. ( <i>Sebastes</i> sp.)		2.3	1.5	19.1	26.7	14.6								
Northern anchovy ( <i>Engraulis mordax</i> )		56.0	26.8	47.9	54.3	73.0	45.1	0.8	2.1	4.1		4.7	1.3	
Pacific sandlance ( <i>Ammodytes hexapterus</i> )		6.5	31.7	13.5	2.8	4.5		70.6	63.8	87.6	89.3	76.3	90.7	78.1
Herring ( <i>Clupea harengus</i> )		20.8	4.4	6.5	5.0	0.2	1.0	26.0	25.7	2.7	6.0	13.1	2.2	15.6
Salmon sp. ( <i>Oncorhynchus</i> sp.)				2.9	3.1	0.7		2.4	6.7	4.4	3.7	2.8	5.5	
Surf smelt ( <i>Hypomesus pretiosus</i> )		14.4	2.0						1.4			3.1	0.3	6.3
Night smelt ( <i>Spirinchus starksi</i> )			31.9	3.1	0.2	1.4								
Kelp greenling ( <i>Hexagrammos decagrammus</i> )				0.7	6.4	0.2								
Popeye blacksmelt ( <i>Bathylagus ochotensis</i> )				3.3		0.8								
Pacific saury ( <i>Colobis saira</i> )				2.1	0.8	3.7	51.9							
Miscellaneous		1.7	0.7	0.7	0.9	2.0	2.0	0.2	0.2	0.9		1.0		

<sup>1</sup> Data from Leschner (1976).

TABLE 4. Mean weights (g) of food loads delivered to Rhinoceros Auklet chicks, Protection Island vs. Destruction Island.\*

Protection Island	Destruction Island
1975: 32.28 ( <i>n</i> = 32)	1974: 19.00 ( <i>n</i> = 25)
1976: 29.52 ( <i>n</i> = 180)	1975: 31.05 ( <i>n</i> = 94)
1979: 33.60 ( <i>n</i> = 89)	1979: 28.20 ( <i>n</i> = 105)
1980: 33.50 ( <i>n</i> = 72)	1980: 28.72 ( <i>n</i> = 73)
1981: 32.05 ( <i>n</i> = 30)	1981: 27.54 ( <i>n</i> = 57)
1983: 33.92 ( <i>n</i> = 46)	1983: 28.07 ( <i>n</i> = 43)
Pooled mean: 31.78 ( <i>n</i> = 449)	Pooled mean: 28.28 ( <i>n</i> = 397)

\*  $F = 8.73$ ,  $P < 0.01$ .

† Data from Leschner (1976).

lowing this, weight increase began to taper off, and chicks reached their maximum weight between the ages of 37 and 55 days. During our study, 85% of the chicks lost weight before fledging, up to nine days beforehand. Protection Island chicks fledged at approximately 75% of adult weight. The wing grew from approximately 25 mm at hatching to 140 to 160 mm (88% of adult length) at the time of fledging. Growth was fastest and variation greatest between 15 and 30 days of age. At fledging, the culmen was only 79% of adult length, but the tarsus was essentially fully grown at 40 days. In 20 chicks with known hatching dates, none had an egg tooth on the lower mandible. The mean time that an egg tooth persisted was 4.4 days ( $n = 20$ ,  $R = 2$  to 8,  $SD = 1.96$ ). Egg teeth appeared to be shed rather than worn off. Because these structures are so variable in their persistence, they have little value for estimating the age of young chicks. Growth parameters of chicks differed markedly between the coastal and inshore populations (Tables 6 and 7). During 1974 and 1975, chicks on the coastal island reached lower peak weights and fledged lighter than did chicks from the inshore colonies (Wilcoxon-Mann-Whitney rank-sum

test:  $P < 0.001$   $Z = -3.78$ ,  $P < 0.07$   $Z = -1.63$ ).

During 1974 Smith Island chicks reached 11% higher nestling weights and fledged 13% heavier than did birds from Destruction Island. Similarly, in 1975 Protection Island chicks attained 4% higher peak and fledging weights. Destruction Island chicks also remained in the burrow somewhat longer than those from the inshore colonies. During 1979 to 1981, Protection Island fledglings continued to be heavier than those on Destruction Island. We measured chicks from both colonies twice in July of each year and constructed growth curves following Ricklefs and White's (1975) method.  $K$  values for these curves were computed according to Ricklefs (1967). Comparative data were generated and analyzed for Destruction Island in 1974 and 1975 and for Protection Island in 1975 and 1976 (Table 7). Ricklefs and White (1975) pointed out that the composite growth curves obtained in this way are indicative of the environment of a population at a particular time and cannot be compared with curves obtained from a sample of nestlings that were measured throughout their development period, as we had done earlier (Table 6). The consistently higher asymptotes for the Protection Island birds compared to those on Destruction Island ( $F = 15.35$ ,  $P = 0.008$ ), however, indicate that the faster growth and heavier chicks from the inshore population were not isolated events in 1974 and 1975, but occur during other breeding seasons as well.

Auklets from inshore populations that hatched early in the nesting season tended to grow better than those hatched late in the season, but this was not found in the coastal population (Table 8). In 1976, early-hatched auklets from Protection Island attained significantly higher peak and fledging weights than did chicks hatched late. Similarly, during 1974 and 1975 early-hatched young from Smith and

TABLE 5. Development of Rhinoceros Auklet nestlings (Protection Island 1975,  $n = 31$ ), compared with measurements of breeding adults (Protection Island 1975,  $n = 12$ ).

Age (days)	Weight (g)		Wing length (mm)		Tarsus length (mm)		Culmen length (mm)		Nestling appearance
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	
1	55	(4)	24.8	(1.7)	24.6	(0.6)	15.5	(3.4)	Down almost black, egg-tooth present
5	79	(10)	28.1	(1.8)	27.2	(1.1)	16.4	(4.5)	Egg-tooth may or may not be present
10	121	(16)	33.4	(2.2)	29.3	(1.3)	18.1	(7.4)	Emergence of primary remiges
15	171	(26)	45.5	(3.3)	32.1	(1.5)	19.8	(8.2)	
20	215	(37)	63.8	(7.6)	34.1	(1.6)	21.2	(7.9)	Down becomes paler
25	263	(42)	84.0	(8.5)	35.7	(1.6)	22.3	(8.9)	
30	301	(45)	104.0	(8.3)	36.7	(1.6)	23.2	(9.0)	Loss of down around face
35	329	(50)	114.0	(7.3)	37.4	(1.4)	24.2	(9.6)	Loss of down on wings and back
40	346	(49)	131.1	(6.7)	37.7	(1.4)	25.2	(11.7)	Loss of down on breast and belly
45	360	(47)	142.8	(4.2)	37.9	(1.3)	26.0	(11.0)	Small down patches may remain on rump and neck
Adult	545	(38)	189.2	(5.5)	38.2	(1.1)	33.3	(2.8)	



TABLE 6. Comparisons of complete growth parameters of Rhinoceros Auklet chicks weighed daily from Destruction, Protection, and Smith islands, Washington.

Location and year	No. chicks measured	Mean hatching weight (g)	Mean peak chick weight (g)	Mean fledging weight (g)	Mean nestling period (days)	Mean daily weight gain (g/day)	$k^2$	$a^3$
Destruction Island <sup>1</sup>								
1974	19	51	331	308	54.3	4.73	0.064	338
1975	37	52	357	343	51.0	5.71	0.067	385
Smith Island								
1974	17	54	372	356	48.3	6.25	0.056	390
Protection Island								
1975	31	55	371	358	49.3	6.15	0.065	400
1976	40	53	369	353	50.6	5.93	0.071	398

<sup>1</sup> Data from Leschner (1976).<sup>2</sup>  $k$  = growth constant (Ricklefs 1967).<sup>3</sup>  $a$  = asymptote.

Protection islands, respectively, reached significantly higher peak weights than did late-hatched chicks, but their fledging weights did not differ significantly ( $P > 0.10$ ). On Destruction Island, we found no evidence of such relationships.

#### BREEDING SUCCESS

The reproductive success of Rhinoceros Auklets in Washington varied between populations and years (Table 9). In 1975 hatching success and fledging success were higher on Protection Island than on Destruction Island. Auklets from Destruction Island also reproduced better in 1975 than they did in 1974, and Protection Island birds had better success in 1976 than in 1975. During the three years for which we have detailed data, overall success was apparently higher on Protection Island than on Destruction Island (Table 9).

Causes of chick mortality are not entirely known, but the adult auklets may have been a major factor. Leschner (1976) found that several of the dead chicks on Destruction Island died from peck wounds to the head; some of these chicks may have wandered from their own burrows and entered another burrow where they were killed by the adults. Predation appeared to be unimportant during the time of our study. A few auklets on Protection Island were killed by Great Horned Owls (*Bubo virginianus*), and a few others died by flying into man-made objects.

#### DISCUSSION

As with Tufted Puffins, *Fratercula cirrhata* (Amaral 1977, Wehle 1983), Rhinoceros Auklets nest primarily on sea-facing slopes or on level areas adjacent to the edge of islands. The sloped areas, in particular, allow the birds easy access to burrows; by flying upslope during their approach, the birds can reduce air speed and make a softer, coordinated landing. Such

maneuverability may be important in avoiding large obstacles, and the occasional attempt by Glaucous-winged (*Larus glaucescens*) or Western (*L. occidentalis*) gulls to steal fish that are being taken to auklet chicks. Although kleptoparasitism occurs at Rhinoceros Auklet colonies, it does not appear to be as significant to the breeding success as it is with the Atlantic Puffin (*F. arctica*) in eastern Canada (Nettle-ship 1972). Very little kleptoparasitism of Tufted and Horned (*F. corniculata*) puffins was noted in the Barren Islands, Alaska (Manuwal and Boersma 1977), and none was mentioned by Wehle (1983) for other Alaskan colonies.

The colony attendance pattern of auklets appears to be typical for a seasonally breeding sea bird at northern latitudes. The pre-laying exodus which we found has been well documented for procellariiforms (Harris 1969) but not in alcids. Data that suggest a pre-laying exodus have been reported for Tufted Puffins (Amaral 1977, Wehle 1983) and for Ancient Murrelets (*Synthliboramphus antiquus*; Sealy 1975). This absence period appears to be necessary for females to store sufficient energy reserves for egg formation (Ashmole 1963, 1971; Lack 1966, 1967; Harris 1969; Perrins 1970). This would allow them to exploit distant fish-

TABLE 7. Comparisons of composite growth parameters of Rhinoceros Auklet chicks, Destruction Island vs. Protection Island, 1974 to 1981.

Year	Destruction Island			Protection Island		
	$k$	$a$	$n$	$k$	$a$	$n$
1981	0.049	412	18	0.061	440	18
1980	0.049	394	17	0.078	430	22
1979	0.058	400	18	0.076	432	19
1976				0.071	432	20
1975	0.068	395	19	0.076	412	20
1974	0.074	335	19			

All values computed from composite growth curves constructed according to Ricklefs and White (1975). Chicks were weighed twice in July.

TABLE 8. Growth comparisons between early- and late-hatched Rhinoceros Auklet chicks in Washington.

	Destruction Island <sup>1</sup>				Smith Island		Protection Island			
	1974		1975		1974		1975		1976	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
<b>Peak weight</b>										
Early hatch	337	(18.3)	366	(24.5)	415	(27.4)*	380	(27.0)**	380	(26.7)*
Late hatch	301	(55.5)	362	(24.6)	370	(17.9)*	341	(57.6)**	359	(22.6)*
<b>Fledging weight</b>										
Early hatch	319	(15.8)	362	(22.9)	380	(19.7)	368	(28.9)	368	(26.9)*
Late hatch	283	(56.3)	347	(27.0)	364	(17.4)	334	(60.5)	343	(28.5)*
<b>Nestling period</b>										
Early hatch	50.0	(3.0)	51.3	(5.1)	48.8	(5.1)	50.3	(3.9)	50.3	(3.1)
Late hatch	50.5	(2.1)	51.6	(2.7)	49.0	(4.8)	48.6	(3.4)	49.5	(2.1)
<b>Sample size</b>										
Early hatch		6		10		5		9		12
Late hatch		6		10		6		10		13

Comparisons are based on sub-samples of samples in Table 6 (first hatched third vs. last hatched third).

\*  $P < 0.05$  Wilcoxon-Mann-Whitney rank sum test.

\*\*  $P < 0.10$  Wilcoxon-Mann-Whitney rank sum test.

<sup>1</sup> Data from Leschner (1976).

ing areas that may be more productive than waters near the colony site.

Colony visitation patterns among the puffins show some interesting variability. The Tufted and Horned puffins are typically diurnal, whereas the Rhinoceros Auklet is usually nocturnal. Visitation patterns of auklets vary, however, among colonies: nocturnal or crepuscular—Protection and Smith islands (this study), British Columbia (Summers and Drent 1979, Vermeer 1979), and Alaska (Manuwal and Boersma 1977); both nocturnal and crepuscular, depending on the stage of the reproductive cycle—Destruction Island (Leschner 1976); and diurnal—Williamson Rocks, Washington (Thoresen 1980), Oregon (Scott et al. 1974), California (Ainley and Lewis 1974), and Japan (Thoresen 1983). One explanation for nocturnality is that it evolved as a way to avoid predation and kleptoparasitism (Lack 1966, Cody 1973). A thorough analysis of actual and potential predators around various Rhinoceros Auklet colony sites might clarify this interpretation. Alternatively, the nocturnal habit may be a partly learned behavior that persists where it is traditional. Evidence to support this view is that three of the four diurnal populations are small, new, or recently recolonized. A third possible explanation is that visitation times are related to food availability (Ashmole 1971, Vermeer 1979). Since diurnal, vertical migration habits differ among species of marine organisms, Rhinoceros Auklet populations that exploit different prey species may capture food for their chicks at different times. The time of prey availability, as well as the distance from colonies to the birds' fishing grounds, may also influence the auklets' initial arrival time.

Differences in egg-laying synchrony found among populations and years have been attributed in other species to differences in food availability (Lack 1966, Veen 1977, Manuwal 1979), to social factors (Darling 1938, Burger 1979, Gochfeld 1979), or to age composition (Coulson and White 1958; see Gochfeld 1980 for a review). Our information suggests that food availability is the most plausible explanation for the local and yearly variations we found in egg laying in auklets. This view is reinforced by the substantial differences in dietary composition between the coastal and inshore colonies.

Our data, as well as those of others (Manuwal and Boersma 1977; Vermeer 1979, 1980; Hatch 1984), indicate that prey species brought to nestling Rhinoceros Auklets may show substantial intercolonial, annual, and latitudinal variation. The striking difference between the diets of coastal and inshore populations may well reflect differences in the physical and biological marine environments of the two areas. Waters of Puget Sound and the Strait of Juan de Fuca are characterized by much tidal mixing (Long 1983). This effect is so strong that primary producers do not remain in the euphotic zone long enough for extensive, dense plankton blooms to occur. Off the coast, by contrast, coastal upwelling injects nutrient-rich waters into the euphotic zone, which is much more stratified during the summer. Extensive, dense plankton blooms are possible in this nutrient-limited system. This probably explains why the filter-feeding northern anchovies were more common in the diets of chicks on Destruction Island than of chicks on Protection Island. Coastal upwelling, however, is a result of prevailing winds. Since winds are as variable

TABLE 9. Reproductive success of Rhinoceros Auklets on Destruction Island, 1974–1975, and Protection Island, 1975–1976.

Attribute (all in percent)	Destruction Island <sup>1</sup>		Protection Island	
	1974	1975	1975	1976
Excavated burrows that had eggs laid in them	70 ( <i>n</i> = 99)	79 ( <i>n</i> = 107)	65 ( <i>n</i> = 82)	62 ( <i>n</i> = 80)
Excavated burrows with hatched eggs	20 ( <i>n</i> = 99)	26 ( <i>n</i> = 107)	34 ( <i>n</i> = 82)	39 ( <i>n</i> = 80)
Undisturbed burrows with chicks	53 ( <i>n</i> = 64)	59 ( <i>n</i> = 121)	53 ( <i>n</i> = 150)	57 ( <i>n</i> = 137)
Egg desertion owing to nest checks during incubation	33	33	19	18
Hatching success	76	75	82	92
Nestling mortality	26 ( <i>n</i> = 19)	16 ( <i>n</i> = 37)	7 ( <i>n</i> = 31)	3 ( <i>n</i> = 46)
Fledging success per chick hatched	74	84	93	97
Fledging success per egg laid	56	63	76	89

Calculations:  $D = C - B$ ,  $E = C/A$ ,  $G = 100 - F$ ,  $H = G \times E/100$ .

<sup>1</sup> Data from Leschner (1976).

as prevailing weather conditions, considerable fluctuations in the coastal system can be expected. The inshore water system, less influenced by weather and major offshore shifts in currents, is more stable, as shown by the 1983 breeding season. *El Niño* conditions in 1983 apparently forced Destruction Island auklets to switch their diet to Pacific saury, whereas those on Protection Island maintained their normal diet of sandlance. Differences in the nature and stability of the marine environment of these two auklet populations appear to explain differences in their diets. Unfortunately, Rhinoceros Auklet prey species have not been adequately sampled in either the Strait of Juan de Fuca or on the outer coast, so data on prey availability cannot be compared directly.

Presumably, changes in oceanographic conditions also account for annual differences in prey-species composition and abundance. When normal prey become scarce, sea birds switch to other prey. In our study, auklets responded to the *El Niño* effect in 1983 depending on their location as indicated above. Vermeer (1978, 1980) found that changes in oceanographic conditions apparently resulted in a reproductive failure in northern British Columbia in 1976. Rhinoceros Auklets there switched to an alternate prey, Pacific saury, compared with the normal sandlance and rockfish.

The three species of puffins in Alaska all rely heavily on capelin as the primary prey, and on sandlance as the secondary prey species (Wehle 1983). Capelin has not been found in auklet diets south of southeastern Alaska. Overall, the sandlance is the predominant species in nestling diets of all three puffins from Alaska to Washington.

Chick growth rates are sensitive to the types and quantities of prey that are brought by par-

ents (Hedgren and Linnman 1979, Vermeer and Cullen 1982). Furthermore, differential growth between early- and late-hatched young has been attributed to age and breeding experience of adults (Coulson 1966, Coulson and White 1958) and to social factors (Hedgren and Linnman 1979). We found differential growth in the inshore population on Protection Island but not on the coastal island. Intuitively, it would seem to make more sense to see differences in growth between early and late hatchers on Destruction Island, where auklets feed their chicks on a much less predictable food supply and deliver smaller feeds to their chicks, and where young peak and fledge lighter than auklets nesting in the Strait of Juan de Fuca. Again, the interactions between the birds and their prey probably are somehow involved in these observed differences in growth patterns.

Breeding success of Washington auklets falls within the ranges of puffin populations in British Columbia (Vermeer 1979, 1980) and in Alaska (Wehle 1983; Manuwal, unpubl.). Rates of hatching and fledging success were lower in the coastal colony than in the inshore colonies. Bad weather (e.g., precipitation or strong winds) can affect birds at the colony and at sea (Nettleship 1972, Dunn 1973, Birkhead 1976). This probably occurred at our study sites. Leschner (1976) found that burrows on Destruction Island were frequently flooded by heavy rains, but those on Protection and Smith islands never became flooded during our study. Flooding of burrows may well disrupt or even terminate incubation and may also force chicks to leave the safety of their nests. Nettleship (1972) found that breeding success of Atlantic Puffins during an extremely wet summer was approximately 50% lower than during a normal year. The fact that Protection and Smith islands lie in the rain shadow of the Olympic Mountains may

contribute to the higher breeding success of their auklet populations. Rough seas may also interfere with the ability of sea birds to capture prey. The more sheltered inland waters may afford better fishing conditions for the auklets during periods of heavy weather.

## CONCLUSIONS

With the exception of its nocturnality at most colonies, the breeding biology of the Rhinoceros Auklet is nearly identical to that reported for the Tufted and Horned puffins, with which it is sympatric in a few locations in northern British Columbia and Alaska. A more complete understanding of the biology of these puffins is possible with future detailed studies on behavior and on availability, distribution, and natural history of major prey species.

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